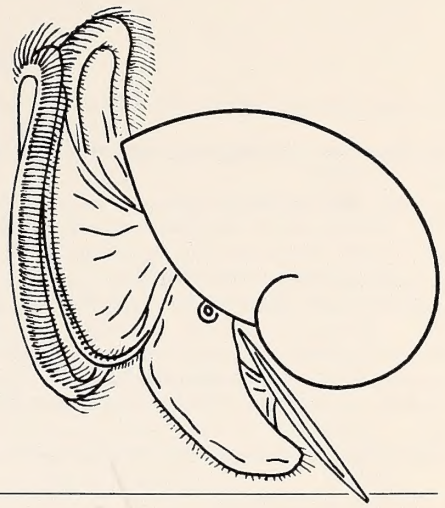

SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES


SMITHSONIAN INSTITUTION LIBRARIES

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 30

July 1, 1987 to April 1, 1988

TABLE OF CONTENTS

Number 1 (July 1, 1987)

Number 2 (October 1, 1987)

Number 3 (January 4, 1988)

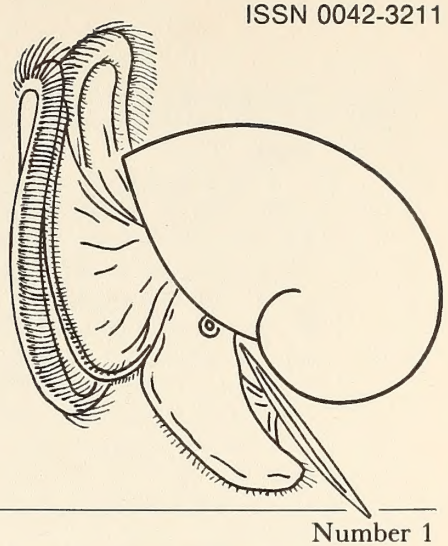
Number 4 (April 1, 1988)

AUTHOR INDEX

Page numbers for book reviews are indicated by parentheses.

ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 30 July 1, 1987 Number 1

Contents

Contents — *Continued*

The Veliger (ISSN 0042-3211) is published quarterly on the first day of July, October, January and April. Rates for Volume 29 are $25.00 for affiliate members (*including* domestic mailing charges) and $50.00 for libraries and nonmembers (*including* domestic mailing charges). An additional $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Department of Zoology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Scope of the journal

The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

Membership and Subscription

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. As an affiliate member, a person may subscribe to The Veliger for US $25.00, which now *includes* mailing charges to domestic addresses. There is a one-time membership fee of US $2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription; a reinstatement fee of US $3.00 will be required if membership renewals do not reach the Society on or before April 1 preceding the start of the new Volume. If a receipt is required, a self-addressed, stamped envelope (or in the case of foreign members, the envelope and two International Postal Reply coupons) should be included with the membership or subscription request.

The annual subscription rate to The Veliger for libraries and nonmembers is US $50.00, which now *includes* mailing charges to domestic addresses.

An additional US $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Memberships and subscriptions are by Volume only (July 1 to April 1) and are payable in advance to California Malacozoological Society, Inc. Single copies of an issue are US $25.00 plus postage.

Send all business correspondence, including subscription orders, membership applications, payments for them, changes of address, to: C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709, USA.

Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616, USA.

The Veliger 30(1):1–4 (July 1, 1987)

THE VELIGER

In Memoriam: Sir Maurice Yonge,

F.R.S. 1946; C.B.E. 1954; Kt. 1967

An era of great achievement and distinguished contributions by English naturalists to the study of the seas came to a close with the passing of C. M. Yonge (as he was known for most of his long career) on 17 March 1986. He was the last of the generation that included F. S. Russell, Alister Hardy and George Deacon, and the best known of all of them abroad. Our knowledge of the sea would be less were it not for the work of these "Old Men of the Sea," and their students, and our library shelves would be barren without their books and the symposia and serials they edited.

Among Yonge's most important contributions was his work on mollusks, especially the functional morphology of the bivalves. He began publishing on this subject with a paper on feeding and digestion in *Mya* in 1923 and by 1974 he had published at least 170 papers, including 12 on Pacific coast mollusks; one of these appeared in *The Veliger* (1962); most of the others were published in a series of papers in the *University of California Publications in Zoology* and three in the *Proceedings of the California Academy of Sciences.*

C. M. Yonge was born on 9 December 1899, about 14 months before the end of Queen Victoria's reign. He was named Charles Maurice (pronounced "Morris"), but he never used the Charles. His father was Headmaster of Silcoates School at Wakefield in Yorkshire, which he attended, receiving a good basic education. While in school he thought of becoming a journalist, but enlisted in the army in 1917, too late, fortunately, to be sent to the trenches. When released from service after the war he went up to Oxford with the intention of studying history, but after a term decided on forestry and went to Edinburgh. There he was exposed to zoology; entranced by his first dissection (of a frog) he fell under the influence of J. H. Ashworth (remembered for his studies of polychaetes) and from him developed a life long fascination with marine invertebrates. He was awarded the Baxter Natural History Scholarship and began a study of digestion in Crustacea for his Ph.D. An interlude at the Millport marine laboratory was his introduction to marine biology. After completing his Ph.D. he was employed as a physiologist at the Marine Biological Station at Plymouth, where he studied digestion in oysters. The pay was meager in those days and Maurice took to writing popular articles for the newspapers to augment his modest salary. In 1927 he teamed up with another young staff member, F. S. Russell, to write a popular book: *The Seas* (Russell & Yonge, 1928). This book was an immediate success, and was completely revised (essentially a new book) by the authors in 1975. It is a monument to the fine English tradition of scientific popularization, and to a lifelong friendship as well. It may well be the only book by two authors to survive almost 50 years and to be rewritten by them. Many of us were confirmed in our interest in the sea by reading this book in our youth and in my own career it stands second only to *Twenty Thousand Leagues under the Sea.* It was an honor and privilege for me to review the last edition of "Russell & Yonge" (Bio•Science, 1977). The book had an unexpected influence on Yonge's career, for on the strength of his chapter on coral reefs he was selected to be the director, at 28, of an expedition to the Great Barrier Reef, sponsored at the request of the Australian government by the British Association for the Advancement of Science while a Balfour student at Cambridge. He had written the chapter more or less by chance as it was one of several topics neither author knew much about at the time. The decision was not made on the toss of a coin, as rumor had it, however. As it turned out, Maurice was an excellent choice as expedition head, managing even to return with a bit of change left over from a very modest budget, although he remembered that he made "every possible mistake."

The Barrier Reef Expedition lasted over a year (from the spring of 1928 to July of 1929), and was the first expedition that investigated the general ecological aspects of a coral reef and, thanks to Maurice's skill as a writer, resulted in his book *A Year on the Great Barrier Reef* (1930), a classic of the literature of coral reefs. There was also a splendid series of monographs. Most of the members of the expedition had distinguished careers in the marine sciences after the expedition. For Yonge it established his reputation as an authority on coral reefs, his second speciality after the functional morphology of mollusks.

Maurice returned to Plymouth after the expedition, but was soon called to Bristol as the first professor of zoology there. During the war years he was the admirable Crichton, living in the basement, meeting the needs of Kings College, London, which had been evacuated from London, serving as Dean of Science and firewatcher, among other assignments. He was also awarded the George Medal. Somehow he managed to keep up with his research, and after the war (1944) was appointed Regius Professor at Glasgow, where he spent the rest of his academic career.

Figure 1

Sir Maurice Yonge giving an impromptu lecture at the University of Arizona's field station at Puerto Peñasco, Sonora, 19 March 1972. Photographs on left, by John Hendrickson; photographs on right, by J. W. Hedgpeth.

He presided over the largest zoology department in Great Britain, became F.R.S. in 1946, and was much in demand to serve on boards and commissions. For all of this he was honored with the knighthood. He became a world traveller, circling the globe so often for committee meetings in various parts of the world, that he lost track of how many times he had been around the world. Almost everywhere he went he found some mollusk to study, and wrote it up. He nevertheless accumulated quite a backlog and in his last retirement years before his final illness, completed about 30 papers. Somehow, in all this he found the time to write the great modern classic of seashore biology for the Collins New Naturalist series (*The Sea Shore,* 1949) and to accumulate a splendid private library of books on the seashore and mollusks. He also wrote a book on oysters for the same series, and with T. E. Thompson, a book on *Living Marine Molluscs* (reviewed by R. I. Smith in *The Veliger* 20(2):187). His library included, among other rarities, an obscure American item, a small work on conchology by Edgar Allan Poe. Fortunately this library has been kept intact and is now at the university in Townsville, appropriately near the Great Barrier Reef. It was my great triumph to find under his nose in an Edinburgh bookstore a small book he had never heard of, but reluctantly deferred to his seniority and let him buy it.

In 1949 C. M. Yonge came to Berkeley as visiting professor in the Department of Zoology for the spring term, and for the summer course, held at Hopkins Marine Station by arrangement with Stanford University. He was being earnestly courted by the department at Berkeley to replace S. F. Light, who had died in 1947. All sorts of inducements and propositions were tried; he had fallen in love with Pacific Grove and expressed the hope that an arrangement might be made to work there, and President Sproul was seriously considering arranging a joint professorship with Stanford University. Maurice, however, decided against leaving England, in part for his childrens' sake. However, he returned to California several times, and was a visiting professor at Friday Harbor and Seattle for several occasions, and continued his observations of mollusks on these trips; the Pacific Ocean appealed to him more than the Atlantic and he found our mollusks "infinitely fascinating."

Yonge found his first experience with our educational system a bit of a strain. Our custom of frequent in-session examinations was something he had difficulty adjusting to, and it is rumored that he threw one set of papers out of the car window on the way to Berkeley. Ralph Smith, who characterized himself as a "dour New Englander" was also a new experience. In a letter to me during the session at Pacific Grove, Maurice wrote that he had been working very hard to live up to the expectations of that "austere New England intellect."

As a student of mollusks Yonge was a facile and accurate observer of the living animals, and concentrated his attention on the action in the mantle cavity, as pointed out by Ralph Smith in the review cited above. The discovery of *Neopilina* was to him an irrelevancy that really didn't have much to do with what interested him, as implied in his commentary on the creature in *Nature.** He was a good lecturer, in spite of, or perhaps because of, his tendency to stammer at times, and his treatment of that irrelevant animal in an impromptu lecture at the University of Arizona's field station at Peñasco, Sonora, in the spring of 1972 was probably typical. After drawing a sketch of *Neopilina* on the blackboard, he contemplated it with some disdain and got on to the bivalves as soon as possible, and became more enthusiastic as he got more deeply into his talk. The series of photographs, taken by myself and John Hendrickson during this lecture, is a rare record of a master at work (Figure 1).

At home Maurice was a popular professor, responsible for many students who now hold significant posts in universities. Three students from California earned their Ph.D. from him at Glasgow: Joseph H. Connell, Peter Fankboner, and Edmund H. Smith. Maurice was an affable, easily approachable person (our friendship began with correspondence about our libraries) whose first words to me when I met him in the otherwise empty office once inhabited by C. A. Kofoid was an apology for the racket: "They've put me up here next to the doggery." He listened well and attentively, and if he had to disagree with you, he did it pleasantly. He carried his many honors lightly and lacked the well known tendency of some Britons (he was born a Yorkshireman, but of a Dorset family) to be a stuffed shirt. After his retirement from Glasgow he moved to Edinburgh, the city of his student days, and became an honorary member of the department there. Of the honors ceremony for the knighthood in Edinburgh Castle he said: "Too bad you weren't here to see it. I was a sight to behold!" I have Maurice to thank for many kindnesses, not the least, perhaps, our expedition to find the grave of Edward Forbes in a small cemetery in Edinburgh. We almost missed it because the stone was covered with moss. He assured me it would be cleaned up, and I am sure it was. I need no stone to remember Maurice by.

Maurice considered that the seventies were the best years of his life. On 18 October 1973 he was honored (with N.B. Eales) for 50 years of publication by the Malacological Society of London. He completed 30 papers during his retirement, and characterized himself as "a straight zoologist more and more fascinated by what evolution has done with the bivalve form in the molluscs" (letter to J.W.H., 17 Aug. 1976). He was active until his 83rd year, when he developed Parkinson's disease. His last years were saddened by the steady attrition of life-long friends, and at the last, by the death of his first son Robin from a fatal heart attack in the Lagos airport. He is survived by his second wife Phyllis (Lady Yonge), his daughter Elspeth, his second son Christopher, and five grandchildren.

Joel W. Hedgpeth

C. M. Yonge's Papers on Pacific Coast Mollusks

1951. Studies on Pacific coast mollusks. I. On the structure and adaptations of *Cryptomya californica* (Conrad). Univ. Calif., Publ. Zool. 55:395–400.
1951. Studies on Pacific coast mollusks. II. Structure and adaptations for rock boring in *Platyodon cancellatus* (Conrad). Univ. Calif., Publ. Zool. 55:401–407.
1951. Studies on Pacific coast mollusks. III. Observations on *Hinnites multirugosus* (Gale). Univ. Calif., Publ. Zool. 55: 409–420.
1952. Studies on Pacific coast mollusks. IV. Observations on *Siliqua patula* Dixon and on evolution within the Solenidae. Univ. Calif., Publ. Zool. 55:421–438.
1952. Studies on Pacific coast mollusks. V. Structure and adaptation in *Entodesma saxicola* (Baird) and *Mytilimeria nuttallii* Conrad, with a discussion on evolution within the family Lyonsiidae (Eulamellibranchia). Univ. Calif., Publ. Zool. 55:439–450.
1952. Studies on Pacific coast mollusks. VI. A note on *Kellia laperousii* (Deshayes). Univ. Calif., Publ. Zool. 55:451–454.
1953. Observations on *Hipponix antiquatus* (Linnaeus). Proc. Calif. Acad. Sci. 28:1–24.
1958. Observations in life on the pulmonate limpet *Trimusculus* (*Gadinia*) *reticulatus* (Sowerby). Proc. Malacol. Soc. Lond. 33:31–37.
1960. Mantle cavity, habits, and habitat in the blind limpet, *Lepeta concentrica* Middendorff. Proc. Calif. Acad. Sci. 31: 103–110.
1960. Further observations on *Hipponix antiquatus* with notes on North Pacific pulmonate limpets. Proc. Calif. Acad. Sci. 31:111–119.
1962. On the biology of the mesogastropod *Trichotropis cancellata* Hinds, a benthic indicator species. Biol. Bull. 122:160–181.
1962. Ciliary currents in the mantle cavity of species of *Acmaea*. Veliger 4:119–123.
*[1957. Reflexions on the monoplacophoran, *Neopilina galatheae* Lemche. Nature 179:672–673.]

Crest of the Yonges of Dorset.

"I am impressed by [your] coat of arms—but really not quite up to mine. . . . it is surmounted by a *marine unicorn*!!!!!!" (C.M.Y. to J.W.H. 17 Aug. 1976).

The Veliger 30(1):5–10 (July 1, 1987)

THE VELIGER

The Maintenance of Polymorphism and Cryptic Mimesis in the Limpet *Scurria variabilis* by Two Species of *Cinclodes* (Aves: Furnariinae) in Central Chile

by

PHILIP A. R. HOCKEY, ALISON L. BOSMAN, AND PETER G. RYAN

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa 7700

Abstract. On the central Chilean coast, the intertidal limpet *Scurria variabilis* is clinally polymorphic, ranging from essentially non-cryptic individuals to individuals that are highly cryptically mimetic with a barnacle model. Many species prey on *S. variabilis,* but birds, notably waders, such as oystercatchers, and two species of *Cinclodes* are the only visual, selective predators present. The influence of *Cinclodes* on limpet polymorphism is evidenced by the predominance of cryptic morphs in habitats accessible to *Cinclodes.* Such differences in morph ratios between accessible and inaccessible habitats were not present in areas without avian predators or where shorebirds, but not *Cinclodes,* were present. There is no evidence of genetic influence by avian predators on local *Scurria* populations, although survival of individual *Scurria* limpets is favored by polymorphism and particularly by cryptic mimesis. Selective predation is considered to be the mechanism maintaining the polymorphism, but under present conditions of predation, polymorphism is not considered necessary for survival of the *Scurria* population as a whole.

INTRODUCTION

Eucrypsis by virtue of homochromy and, to some extent, active selection of specific substrata have been demonstrated to increase survival of *Collisella* limpets (Mollusca: Patellidae) in Pacific North America (GIESEL, 1970; MERCURIO *et al.,* 1985). Until recently the distribution of the genus *Collisella* was thought to extend to Chile in Pacific South America, with the limpet community of the mid-littoral of the Chilean coast being dominated by one species, *C. araucana* (d'Orbigny, 1839) (MARINCOVICH, 1973; CASTILLA, 1976). The taxonomy of South American patellaceans is poorly understood. Examination of specimens of "*C. araucana*" collected in central Chile in November 1985 shows that, on the basis of shell-structure characters and plumbing of the heart vessels, these specimens belong to the genus *Scurria* and are probably *S. variabilis* (Sowerby, 1839) (D. R. Lindberg, *in litt.*). The mid-littoral of central Chile is characterized by extensive beds of small barnacles, principally *Chthamalus cirratus* Darwin (CASTILLA, 1981), and *S. variabilis* occurs both on bare rock surfaces and among these barnacle beds. *Scurria variabilis* is clinally polymorphic, ranging from individuals that are essentially non-cryptic to individuals exhibiting extraordinary cryptic mimesis (*sensu* PASTEUR, 1982) due to homomorphy and homochromy with the model *C. cirratus* (Figure 1). BOEHME (1974) erroneously described the barnacle-like morph of *S. variabilis* as a new species, *Collisella boehmita.*

Polymorphism in certain marine species has been shown to be adaptive in reducing predator hunting success (*e.g.,* HOAGLAND, 1977; REIMCHEN, 1979; PALMER, 1985). In such instances it is reasonable to conclude that predation pressure is a prime selective force in the evolution of polymorphism or mimicry in the prey species, although the process by which a relative advantage accrues to divergent phenotypes in the early stages of divergence has been demonstrated on few occasions (BROWER *et al.,* 1971). Mimicry in *Scurria variabilis* is visual and for any selective advantage to accrue to mimetic individuals the predator(s) of *S. variabilis* must be assumed to forage both visually and selectively. Intertidal predators in central Chile are numerous and diverse, and many species have been studied in detail (PAINE & PALMER, 1978; CASTILLA, 1981; BAHAMONDES & CASTILLA, in press). The only predators present that forage selectively using visual cues and prey on *S. variabilis* are certain shorebirds (Aves: Charadriiformes) and two species of *Cinclodes* (Aves: Furnariinae) (CASTILLA, 1981;

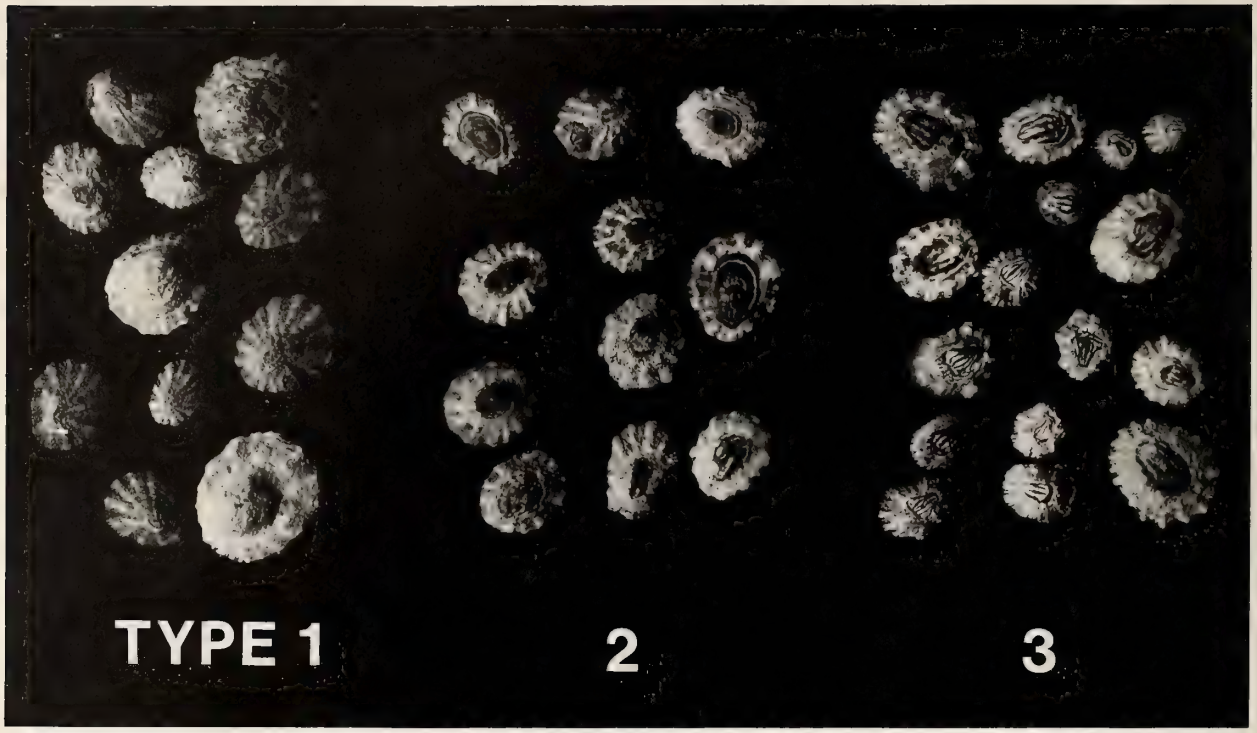


Figure 1

The three recognized morphs of *Scurria variabilis*. Type 1 = non-cryptic; Type 2 = intermediate; Type 3 = cryptically mimetic.

Bahamondes & Castilla, in press, and personal observations). This study quantifies the occurrence of polymorphism and mimicry in *S. variabilis* and identifies the predators most likely to be responsible for maintaining that polymorphism, based on predator occurrence and foraging behavior and on variations in morph ratios of *S. variabilis*.

MATERIALS AND METHODS

Three morphs of *Scurria variabilis* were recognized: Type 1 exhibited no cryptic coloration or modification of shape; Type 2 had a well-defined darker area apically, corresponding approximately to the area occupied by the tergal and scutal plates of a sessile barnacle; and, Type 3 was cryptically mimetic, being in all respects, including the outline of the tergum and scutum, an excellent mimic of *Chthamalus* (Figure 1). The mimicry of Type 3 limpets was so precise that on occasions it was necessary to remove the animal from the rocks to determine whether it was a limpet or a barnacle.

Absolute and relative frequencies of occurrence of the three morphs were recorded at 17 sites in central Chile between 30°S and 42°S during October and November 1985 (Figure 2). At each site, frequencies of occurrence of the three *Scurria* morphs were recorded in the midlittoral using randomly positioned 10 × 10 cm quadrats in two habitat types: (1) rocky slopes or flat areas accessible to avian predators and (2) vertical or steep rock faces inaccessible to avian predators. Between 8 and 76 quadrats (0.08–0.76 m^2) were sampled, dependent on limpet density. Limpet densities per m^2 were calculated by simple extrapolation from the area sampled at each site. Hence, confidence limits are not presented.

The number of intertidal avian predators present per 100 m of shore at each site was assessed, and on this basis three types of site were recognized: sites without avian predators, sites with *Cinclodes* but with no (or very few) shorebirds, and sites with many shorebirds but no *Cinclodes*.

RESULTS

At 13 of the 17 sites, less than 1% of all *Scurria variabilis* were >12 mm in length (12 mm corresponding to the size of a large specimen of *Chthamalus cirratus*). At sites Algarrobo 2 and 3, and at Ancud 1 and 2, up to 85% of all *S. variabilis* were >12 mm in length.

At sites without avian predators there were (with one exception) no significant within-site differences in the ratios of the three *Scurria* morphs on rock faces accessible and inaccessible to birds, but there was no consistency in morph ratios among sites (Table 1). In addition, there were no significant differences in the proportions of crypti-

cally mimetic (Type 3) morphs in the four habitats where birds had no direct predatory impact *viz.*: accessible and inaccessible habitats at sites without avian predators, and inaccessible habitats at sites where either waders or *Cinclodes* were present (Kruskal-Wallis one-way ANOVA, $N_1 = 4$, $N_2 = 4$, $N_3 = 4$, $N_4 = 9$, $H = 5.51$, $P = 0.138$).

At eight of the nine sites with *Cinclodes* present, there was a significant difference in morph ratios between accessible and inaccessible rock faces. Non-cryptic (Type 1) morphs formed a higher proportion of the *Scurria* population on inaccessible than on accessible rock faces (mean = 35.2 ± SD of 21.7% vs. 17.3 ± 16.2%) (Wilcoxon matched-pairs signed-rank test, $n = 9$, $T = 0.00$, $P = 0.008$) and the reverse was true of Type 3 morphs (38.1 ± 16.9% vs. 52.9 ± 19.4%; $n = 9$, $T = 1.00$, $P = 0.011$). Type 2 morphs were slightly better represented in accessible ($\bar{x} = 29.8 \pm 14.3\%$) than in inaccessible ($\bar{x} = 26.7 \pm 12.5\%$) habitats, but the difference was not significant ($n = 9$, $T = 9.00$, $P = 0.110$). In addition, the site with the highest density of *Cinclodes* (*viz.* Los Molles 1) showed the greatest difference between morph ratios in accessible and inaccessible sites, with the limpet population on accessible rocks being strongly biased towards mimetic individuals (Table 1, Figure 3).

Densities of foraging shorebirds were much higher than those of *Cinclodes* (up to 200 birds per 100 m of shore) but, at sites where shorebirds were present, the proportions of non-cryptic (Type 1) and mimetic (Type 3) *Scurria* in accessible and inaccessible habitats were not significantly different (Wilcoxon matched-pairs signed-rank test: Type 1, $n = 4$, $T = 0.00$, $P = 0.068$; Type 3, $n = 4$, $T = 3.00$, $P = 0.465$).

DISCUSSION

True mimicry in limpets is rare. There is a morph of the Pacific *Collisella stanfordiana* that resembles the toxic onchidiid *Hoffmanola hansi* (YENSEN, 1973), an example of Batesian mimicry. There is a barnacle-imitating morph of the Australian *Patelloida latistrigata* (G. M. Branch, personal communication) and in the Gulf of California, *Collisella acutapex* resembles the barnacle *Balanus amphitrite* (YENSEN, 1973). The adaptive advantage of these mimics has not been investigated. *Scurria variabilis* exhibits clinal polymorphism, with an extreme morph showing cryptic mimicry of *Chthamalus* barnacles.

On the central Chilean coast there are several vertebrate and invertebrate predators of limpets (reviewed by CASTILLA, 1981), but most of these have been shown to remove both limpets and barnacles using tactile stimuli in a non-selective manner. Examples of such predators are the seastar *Heliaster helianthus* (Lamarck, 1816), the muricid *Concholepas concholepas* (Bruguière, 1789) (CASTILLA *et al.*, 1979; CASTILLA, 1981) and the suckerfish *Sicyaces sanguineus* Muller & Troschel (PAINE & PALMER, 1978; CASTILLA, 1981). Small numbers of *Scurria variabilis* have been found in the gut of the surfbird *Aphriza virgata* (Gmelin, 1789), possibly ingested coincidentally when feeding on its preferred prey, the mussel *Semimytilus algosus* (R. Navarro, personal communication). The Kelp Gull *Larus dominicanus* preys on intertidal limpets, but *Scurria variabilis* is not an important prey species, the larger eulittoral

Figure 2

Map of the study area.

Table 1

Morph ratios and densities of *Scurria variabilis,* and densities of *Cinclodes* spp. at 17 sites in central Chile, October–November 1985.

Site type / Study site	*Scurria* density/m² Acc.	*Scurria* density/m² Inacc.*	*Cinclodes* density/100 m	Sp.†	Accessible habitat Morph type (%) 1	2	3	*N*	Inaccessible habitat Morph type (%) 1	2	3	*N*	χ^2	*P*
No avian predators														
Totoralillo 1	183	263	0.0		31	15	54	139	40	11	49	137	2.72	n.s.
Los Molles 3	684	804	0.0		69	15	16	171	57	17	26	201	−7.84‡	<0.05‡
Los Molles 4	1141	1100	0.0		19	21	60	194	16	13	71	176	4.98	n.s.
Los Molles 5	950	3725	0.0		19	32	49	190	16	41	43	298	3.03	n.s.
+*Cinclodes*														
Totoralillo 2	635	460	1.0	ni	1	40	59	165	15	30	55	138	18.85	<0.001
Los Molles 1	2770	418	6.0	ni	2	19	79	277	33	18	49	117	85.21	<0.001
Los Molles 2	low	low	1.3	ni	43	7	50	129	76	3	21	90	23.58	<0.001
Algarrobo 1	628	757	0.2	ni	38	21	41	113	62	16	22	106	12.36	<0.01
Punta El Lacho	2153	1205	1.0	ni	28	52	20	323	37	42	21	241	8.01	<0.05
Mehuin 1	464	374	1.0	pa	6	28	66	116	19	31	50	131	8.77	<0.05
Mehuin 2	760	527	0.6	pa	1	22	77	152	9	26	65	158	11.53	<0.01
Ancud 1	244	179	1.0	pa	19	33	48	122	31	34	35	125	5.93	n.s.
Ancud 2	543	271	1.0	pa	18	46	36	190	35	40	25	95	9.47	<0.01
+Shorebirds														
Algarrobo 2	318	79	0.0		45	33	22	159	69	17	14	35	6.99	<0.01
Algarrobo 3	952	low	0.0		45	41	14	238	64	17	19	47	9.70	<0.01
Las Salinas 1	703	610	0.0		40	29	31	207	45	34	21	183	4.35	n.s.
Las Salinas 2	1133	893	0.0		35	43	22	345	46	26	28	268	18.28	<0.001

* Acc. = Accessible, Inacc. = Inaccessible.

† ni = *Cinclodes nigrofumosus,* pa = *Cinclodes patagonicus.*

‡ At this site there were more cryptic limpets on inaccessible slopes, an opposite trend to that found elsewhere. This is indicated by a negative χ^2 value.

Collisella zebrina being taken preferentially (Bahamondes & Castilla, in press). The marine otter *Lutra felina* (Molina, 1782) occurs commonly on exposed coasts in central Chile, but its intertidal feeding activity is confined to the eulittoral zone and *Scurria variabilis* is not recorded as a prey item (Castilla & Bahamondes, 1979). The extent of predation by fish other than *Sicyaces sanguineus* during the high tide period is unknown, but few, if any, species other than *Sicyaces sanguineus* are likely to possess the morphological adaptations necessary to remove limpets from rock faces.

Based on the above, we hypothesized that the predators most likely to be morph-specific in their predation of *Scurria variabilis* were the Blackish Oystercatcher, *Haematopus ater* Vieillot & Ondart, 1825, which is recorded as preying on *S. variabilis* (Castilla, 1981), and two species of *Cinclodes,* an avian genus endemic to South America (Howard & Moore, 1980). The Seaside Cinclodes *C. nigrofumosus* (d'Orbigny & Lafresnaye, 1838) and the Duskybellied Cinclodes *C. patagonicus* (Lesson, 1828) both occur on the coast of central Chile, although the former does not occur south of about 39°S (Johnson & Goodall, 1967). *Cinclodes nigrofumosus* is exclusively coastal, whereas *C. patagonicus* occupies a range of habitats: both species include mid-intertidal barnacle beds within their range of foraging habitats and prey on *S. variabilis* (personal observations). *Haematopus ater* was observed at Algarrobo and Los Molles 2, but not at other sites. Effects of predation on *S. variabilis* by this species are likely to be inseparable from the effects of *Cinclodes.*

In areas where *Cinclodes* spp. are present, differences in morph ratios between accessible and inaccessible habitats provide clear evidence for the selection of non-cryptic morphs by *Cinclodes.* At high *Cinclodes* densities, the bias towards mimetic morphs in the limpet population is more pronounced (Table 1, Figure 3). Shorebirds, even though they occur at much higher densities than *Cinclodes* in some areas, have a negligible impact on *Scurria* morph ratios as evidenced by insignificant differences in morph ratios between accessible and inaccessible microhabitats (Table 1). This may be due to the concentration of their feeding activity in the low- rather than mid-shore region (personal observations). Some wader species may not prey on *Scurria* at all, and the nocturnal feeding habits of some species (movement rather than coloration of the prey probably being the prime visual cue to predators at night) would not result in morph-specific predation.

The impact exerted by visual, selective predators, chiefly

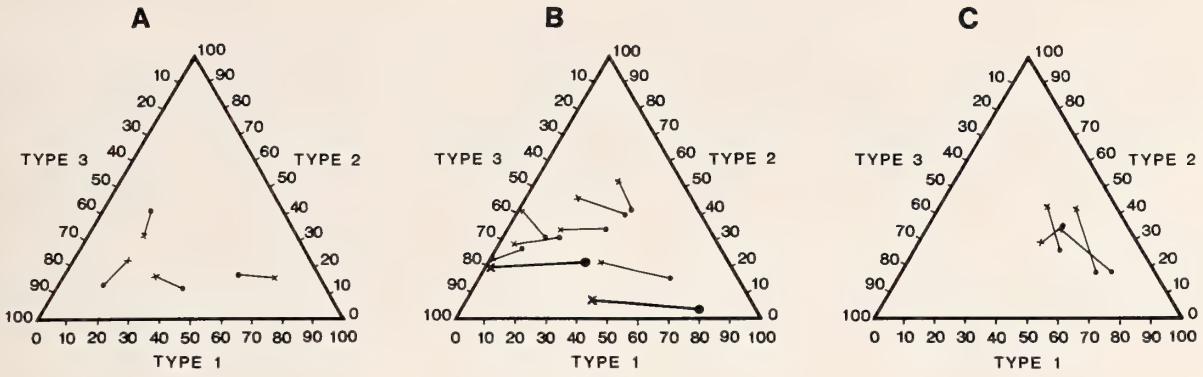


Figure 3

Ternary diagrams illustrating the relationship between morph ratios of *Scurria* and predation. A, no avian predators; B, with *Cinclodes*; C, with waders. Lines join crosses (accessible microhabitats) to solid circles (inaccessible microhabitats) at the same site. The larger crosses and dots in Figure 3B refer to sites at which the density of *Cinclodes* was >1 bird per 100 m of shore.

Cinclodes, on the survival of different morphs of *Collisella* is striking, but localized to the extent that morph ratios on inaccessible slopes within *Cinclodes* territories and in wader feeding areas do not differ from one another or from the morph ratios in areas where there are neither *Cinclodes* nor waders present. These observations suggest that, although *Cinclodes* may have a local influence on the occurrence of phenotypes, these birds are not exerting a detectable local genetic influence on the population, nor is limpet density correlated with predator abundance (Table 1). The presumed pelagic larval stage of *Scurria* limpets would tend to confound anything other than major local genetic influences. A situation exists on the central Chilean coast in which the predator apparently exerting the major influence on *Scurria* phenotypes in central Chile occurs patchily and at low density and appears to have no influence on *Scurria* density. At the same time, *S. variabilis* shows an effective and highly elaborate polymorphism that has arisen in the apparent absence of any strong selective force that is still evident today. However, despite the fact that predatory pressure is low, the selectivity of the predator provides the mechanism for the maintenance of polymorphism in the prey, inasmuch as the incipient mimic (*sensu* Brower *et al.*, 1971), the Type 2 *Scurria*, enjoys a selective advantage over the non-cryptic Type 1 individuals. The absolute abundance of Type 1 morphs suggests that, under present predation pressures, polymorphism is not essential for the survival of the *S. variabilis* population as a whole but strongly favors the survival of cryptically mimetic individuals in the presence of predatory *Cinclodes*.

ACKNOWLEDGMENTS

We are grateful to Professor Juan Carlos Castilla of the Pontificia Universidad Católica de Chile and to Professor Carlos Moreno of the Universidad Austral de Chile for the use of field station facilities on the Chilean coast and for logistical help. Professor George Branch, Dr. Fabián Jaksić and an anonymous referee are thanked for helpful comments on an earlier draft. We thank Dr. David Lindberg for identifying the Chilean limpet specimens. This paper forms part of the FitzPatrick Institute's 25th anniversary expedition to Chile. This work was supported financially by the South African CSIR and the University of Cape Town.

LITERATURE CITED

Bahamondes, I. & J. C. Castilla. In press. Predation of marine invertebrates by the Kelp Gull *Larus dominicanus* in an undisturbed intertidal rocky shore of southern Chile. Revista Chilena de Historia Natural.

Boehme, J. R. 1974. Nuevas especies chilenas de *Lucabina, Fissurella* y *Collisella* (Mollusca, Archaeogastropoda). Bol. Mus. Hist. Natur. Chile 33:15–34.

Brower, L. P., J. Alcock & J. V. Z. Brower. 1971. Avian feeding behaviour and the selective advantage of incipient mimicry. Pp. 261–274. *In:* R. Creed (ed.), Ecological genetics and evolution. Oxford: Blackwell.

Castilla, J. C. 1976. Guia para la observación del litoral. Santiago: Editora Nacional Gabriela Mistral.

Castilla, J. C. 1981. Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II. Depredadores de alto nivel trófico. Medio Ambiente 5:190–215.

Castilla, J. C. & I. Bahamondes. 1979. Observaciones conductuales y ecológicas sobre *Lutra felina* (Molina) 1782 (Carnivora: Mustelidae) en las zonas Central y Centro-Norte de Chile. Arch. Biol. Med. Exper. 12:119–132.

Castilla, J. C., C. Guisado & J. Cancino. 1979. Aspectos ecológicos y conductuales relacionados con la alimentación de *Concholepas concholepas* (Mollusca: Gastropoda: Muricidae). Biología Pesquera Chile 12:99–144.

Giesel, J. T. 1970. On the maintenance of a shell pattern and behaviour polymorphism in *Acmaea digitalis*, a limpet. Evolution 24:98–119.

Hoagland, K. E. 1977. A gastropod colour polymorphism:

one adaptive strategy of phenotypic variation. Biol. Bull. 152:360–372.

Howard, R. & A. Moore. 1980. A complete checklist of the birds of the world. Oxford: Oxford University Press.

Johnson, A. W. & J. D. Goodall. 1967. The birds of Chile, Vol. II. Buenos Aires: Platt Establecimientos Gráficos S.A.

Marincovich, L., Jr. 1973. Intertidal mollusks of Iquique, Chile. Bull. Natur. Hist. Mus. Los Angeles County 16:1–49.

Mercurio, K. S., A. R. Palmer & R. B. Lowell. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology 66:1417–1425.

Paine, R. T. & A. R. Palmer. 1978. *Sicyases sanguineus*: a unique trophic generalist from the Chilean intertidal zone. Copeia 1978(1):75–81.

Palmer, A. R. 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. Veliger 27:349–356.

Pasteur, G. 1982. A classificatory review of mimicry systems. Ann. Rev. Ecol. Syst. 13:169–199.

Reimchen, T. E. 1979. Substratum heterogeneity, crypsis and colour polymorphism in an intertidal snail (*Littorina mariae*). Can. Jour. Zool. 57:1070–1085.

Yensen, N. P. 1973. The limpets of the Gulf of California (Patellidae, Acmaeidae). M.S. Thesis, University of Arizona, Tucson. 146 pp.

The Veliger 30(1):11–23 (July 1, 1987)

THE VELIGER

Seasonal Growth Patterns in the Tropical Littorinid Snails *Littorina angulifera* and *Tectarius muricatus*

by

JEFF M. BURGETT,[1] JOHN D. CUBIT,[2] AND RICARDO C. THOMPSON

Smithsonian Tropical Research Institute, Apartado 2072,
Balboa, Republic of Panamá

Abstract. The seasonality of growth rates in the supralittoral snails *Littorina angulifera* and *Tectarius muricatus* was investigated from 1978 to 1983 at Punta Galeta, on the Caribbean coast of Panamá. Growth rates were determined from individually marked animals that were measured at monthly intervals. Meteorological and hydrographic conditions were monitored concurrently. Although the climate at this site was strongly seasonal, the growth rates of *L. angulifera* between 7 and 15 mm in length showed no seasonal pattern. Growth rates of *L. angulifera* larger than 15 mm peaked during the local dry season. Individuals of *Tectarius muricatus* less than 15 mm in length were too rare in the study area for examination of seasonal growth rates, but the growth of larger individuals was highest in the wet season. For both species, growth rates of individuals less than 15 mm in length decreased linearly with increasing size. Growth in larger individuals of both species occurred in discrete episodes separated by variable periods without growth. Maximum growth rates of both species were about five times faster than those previously reported.

INTRODUCTION

Galeta Reef, Panamá, is in the southernmost region of the Caribbean Sea, less than 10° north of the equator. Despite the low latitude, however, growth rates, abundances, and reproductive patterns of organisms in the subtidal and lower intertidal habitats of this reef vary seasonally, apparently in response to annual fluctuations in atmospheric and sea conditions (HENDLER, 1977; HAY & NORRIS, 1984; CUBIT *et al.,* 1986; Connor, Cubit, Hay, Kilar, Norris, unpublished data). Terrestrial organisms in nearby habitats also show strong patterns of seasonality in various aspects of their biology (references in LEIGH *et al.,* 1982). Here we describe seasonality in the growth rates of two species of littorinid snails that occupy the ecotone between the marine and the terrestrial environments on the Caribbean coast of Panamá.

Herbivorous gastropods are the predominant animals at the highest levels of many shores throughout the world (UNDERWOOD, 1979). Most studies of their growth have been in temperate and subtropical areas, where fluctuations in growth rates are associated with the winter–summer seasonality of higher latitudes (FRANK, 1965a; SUTHERLAND, 1970; NICOTRI, 1974; BORKOWSKI, 1974; MCQUAID, 1981; PHILLIPS, 1981). Relatively few gastropods have been examined for seasonal patterns of growth in the tropics, where seasonality involves a much different combination of weather factors (FRANK, 1969; LEWIS *et al.,* 1969; YAMAGUCHI, 1977). Only a few of these tropical studies involved snails of the upper intertidal zones (LEWIS *et al.,* 1969).

The littorinid snails monitored for growth in this study were found in the supralittoral zones of two adjacent, but much different, habitats: mangrove trees and rocky shore. Concurrent monitoring of several physical variables defined some aspects of local seasonality, and our analysis was designed to assess the degree to which snail growth reflected these environmental changes. This study was initiated by J. Cubit and R. Thompson and the data were analyzed by J. Burgett.

Study Species

Littorina angulifera Lamarck, 1822, is found on both sides of the tropical Atlantic, and may be synonymous with *L. scabra* (Linnaeus, 1758) of the Indo-Pacific (ROSEWATER, 1970). Although in protected waters it may occur on smooth artificial surfaces, *L. angulifera* is most commonly

[1] Present address: Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, U.S.A.

[2] Please send reprint requests to this author.

found on the red mangrove *Rhizophora mangle* Lamarck, 1753 (Plaziat, 1984). Individuals less than 10 mm in shell length are restricted to within a few centimetres of the waterline, but larger snails range to all levels of the mangrove trees (Lenderking, 1954). The snails can be observed apparently feeding on the surfaces of leaves and stems, but most grazing probably occurs during nocturnal migrations to the lower levels of the prop roots (P. Gutierrez, unpublished data). Fragments of diatoms and cyanobacteria can be found in the fecal pellets (J. Burgett, personal observations). *Littorina angulifera* cements itself to the undersides of stems and leaves and remains retracted during most daylight hours (J. Burgett & R. Thompson, personal observations).

Tectarius muricatus (Linnaeus, 1758) occurs higher on the rocky shores of the Caribbean than other gastropods (Bandel, 1974). It can remain immobile and retracted into the shell for long periods, adhering to the surface with a spot of mucus. *Tectarius muricatus* grazes at night or during heavily overcast days (J. Burgett, personal observations). Fragments of cyanobacteria and siliceous and carbonate rock can be found in the fecal pellets (J. Burgett, personal observations), suggesting a diet of epilithic and endolithic algae and cyanobacteria similar to that of *T. grandinatus* (Gmelin, 1791) in Polynesia (Salvat & Denizot, 1982).

MATERIALS AND METHODS

Study Areas

Study areas were on the fringing reef at Punta Galeta, on the Caribbean coast of Panamá (9°24′18″N, 79°51′48.5″W), adjacent to the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute. The topography and development (Macintyre & Glynn, 1976) and invertebrate fauna (Cubit & Williams, 1983) of this reef have been described elsewhere.

Littorina angulifera was studied on two adjacent clumps of *Rhizophora mangle* rooted in a sandy area at the back of the reef flat. No other gastropods were observed above water level on these trees. The two clumps lacked proproot connections to the neighboring forest and were chosen for this study to minimize dispersal of marked snails from the study area. Growth of the clumps during the study was estimated using aerial photographs taken in 1973, 1980, and 1984. By interpolation, the roots covered 8.5 m^2 in 1978 and grew to cover 16 m^2 by the end of the study in 1983. The tree crowns in 1984 were 2.8 and 3.7 m above the elevation of the sand bottom, which was between −2 and +6 cm relative to Mean Low Water (MLW, see Environmental Monitoring below).

The study area for *Tectarius muricatus* was a wall made of coral blocks and concrete mortar bordering the backreef, approximately 5 m from the *Littorina angulifera* study area. The wall, approximately 30 years old, was 0.7 m high and 16.5 m long, with a base in sand and coral rubble 27 to 35 cm above MLW. Two smaller species, *Nodilittorina* (*Littorina*) *interrupta* (Mörch, 1876) and *N.* (*L.*) *angustior* (C. B. Adams *in* Philippi, 1847) (nomenclature after Bandel & Kadolsky, 1982), occurred on the lower parts of the wall.

Sampling and Marking

All *Littorina angulifera* found on the trees were collected and marked between 19 September 1978 and 5 March 1982. After the latter date no new snails were collected, and the *L. angulifera* study was ended in March 1983.

The cryptic habit of the snails and the structural complexity of the trees made total collections difficult; therefore, estimates of recruitment were inexact. Because of the ability of *Littorina angulifera* to disperse by floating (J. Cubit & R. Thompson, personal observations) and the reappearance of individuals missing for up to eleven months, disappearance of snails could not be regarded as mortality.

Only a subset of the *Tectarius muricatus* on the wall was monitored during the study, which ran from July 1978 to April 1983. Small individuals of *T. muricatus* were rare in the study area, a situation also found at other sites (Lewis *et al.*, 1969; Borkowski, 1974). All marked snails visible on the wall were collected for each sample. If fewer than 50 marked animals were recovered, unmarked individuals were added to the study to make up this number. Recruitment, density, and mortality were not estimated.

Snails were kept for less than 24 h in wet containers in the laboratory while being measured and marked. The length of each shell (*i.e.*, height or longest dimension) was measured with vernier calipers to the nearest 0.1 mm. Growth was determined from extension of the shell margin or lip, which was a more sensitive measure than increase in overall length (Largen, 1967). A line of quick-drying enamel (Nissen Metal Marker) was applied to the outer surface of the shell margin after length measurement. At the next collection, the maximum growth past this line was measured to the nearest 0.05 mm using a dissecting microscope fitted with an ocular micrometer. The previous lip marking was then removed and a new line applied. Individuals were identified by numbered plastic bee tags (Bertness, 1982) attached with cyanoacrylate glue (*Littorina angulifera*) or by hand-painted numerals (*Tectarius muricatus*). After processing, the snails were taken to the study areas and allowed to adhere to the substratum before release.

Growth Analysis

Analyses of growth measurements from each sample were limited to snails also collected in the immediately preceding sample, so that the growth rates from each sample were based on a constant interval. Growth was converted to daily rates by dividing the measured lip extension of each snail by the number of days in the sample interval, which ranged from 28 to 50 days. This growth rate was

assigned to the arithmetic average of the snail's lengths at the beginning and end of the interval (GULLAND & HOLT, 1959; VAN DEVENDER, 1978).

A regression-based model of growth could not be applied to the entire length range of *Littorina angulifera* because of differences in the length-growth rate relationships of small and large snails. Growth rate variances could not be normalized owing to the predominance of zero values at some lengths (SOKAL & ROHLF, 1981:460). Moreover, the discontinuous growth patterns of the larger snails were not consistent with a continuous function (LOCKWOOD, 1974). Regression techniques were appropriate for smaller, continuously growing animals. Because virtually all snails smaller than 14 mm grew between samples, we divided the data sets at this length and analyzed data from the two size classes separately. The larger size class (>14 mm) unavoidably contained both snails that had not stopped growing and those that had resumed growth.

We restricted our regression analyses of the smaller size class (≤14 mm) to the 26 samples that contained at least 10 small animals. In all of these samples, preliminary tests showed significant ($P < 0.05$) product-moment correlations between length and growth rate. The functional relationships between length and growth rate were determined for each sample using the geometric mean (GM) method for Model II linear regressions (RICKER, 1973). To facilitate the corrections detailed below, these regressions were done using the rates of length increase rather than lip extension.

Because growth was a decreasing function of length, and the data were length differences over finite intervals rather than instantaneous rates, the true growth rates of the snails were underestimated (KAUFMANN, 1981; SUNDBERG, 1984). Use of average length rather than initial length on the abscissa reduced this error (LOCKWOOD, 1974), which was a function of the growth rate and the length of the sample interval (YAMAGUCHI, 1975; SUNDBERG, 1984). The error was negligible at low growth rates and zero at the x-intercept.

The slopes obtained by GM regression were corrected for this error by the following procedure. For each sample an arbitrary regression of growth rate on length was constructed with the same x-intercept as the GM regression. Starting from several initial lengths, daily growth increments were calculated from this slope for the number of days in the sample interval. The slope was adjusted until the growth rates and average lengths obtained at the end of the simulation fell on the GM regression line calculated from the observed data. The absolute values of these corrected slopes yielded the von Bertalanffy growth coefficient, K, with higher values of K representing faster growth rates at all sizes smaller than the x-intercept. The 95% confidence intervals of the original GM regressions (RICKER, 1973) were used with the corrected slopes.

The frequency distributions of growth rates for the larger *Littorina angulifera* were not consistently fit by normal, log-normal, or delta distributions (PENNINGTON, 1983). The growth rates of this size class and of *Tectarius muricatus* were therefore summarized by the sample medians.

Environmental Monitoring

As part of a continuing monitoring program, water level, air temperature, salinity, rainfall, wind speed, and wind direction were measured for the duration of the study.

Water level over the central reef flat was recorded on a continuous chart by a Stevens Type-A water-level recorder mounted in a stilling well. Water levels were read from the charts using a digitizer. CUBIT *et al.* (1986) present details of this method and a discussion of the water-level regime at Galeta. Water levels and elevations of the study areas are expressed with reference to the 10-yr MLW described in that paper. The average daily tidal range was 24.5 cm (CUBIT *et al.*, 1986).

Rain from a rooftop collector was recorded by another Stevens recorder. Data were digitized from the charts and combined into weekly totals.

Daily maximum and minimum air temperatures were read five mornings per week from a recording thermometer originally suspended beneath the laboratory dock. In January 1981 the thermometer was moved to a shaded, ventilated enclosure of polystyrene foam. Sea surface salinity was measured five mornings per week using a hand-held refractometer.

Wind speed and direction were recorded on a continuous chart by a mechanical weather station (Meteorology Research, Inc., model 1072) and converted to numeric values by hand. The daily mean speed of winds from the northern quadrant was cubed to yield a value proportional to northerly wind energy. This measure was assumed to be correlated with the intensity of wind-driven waves as well as with other effects of wind, such as transport of salt spray. Waves driven by northerly winds are suspected to raise water levels on the Galeta reef flat (CUBIT *et al.*, 1986), and can reach the back-reef areas when water levels are high. Swells from distant sources could not be estimated from local data.

Daily values of total radiant exposure, or insolation (wavelengths 280–2800 nm), were recorded from an Eppley pyranometer at the U.S. Army Tropic Test Center's open sunfield at Fort Sherman, a coastal site 11 km from Galeta.

Instrument failures resulted in incomplete data sets for all variables except rainfall. Only weeks containing four or more days of data were used to calculate weekly means for the other variables. Four-week running averages were computed from the weekly values using a minimum of three weeks of data per four week period.

The unbroken time series for rainfall was used as the representative seasonal variable in tests for correlation with snail growth rates. Growth rates were also tested for correlation with maximum water level because of its less

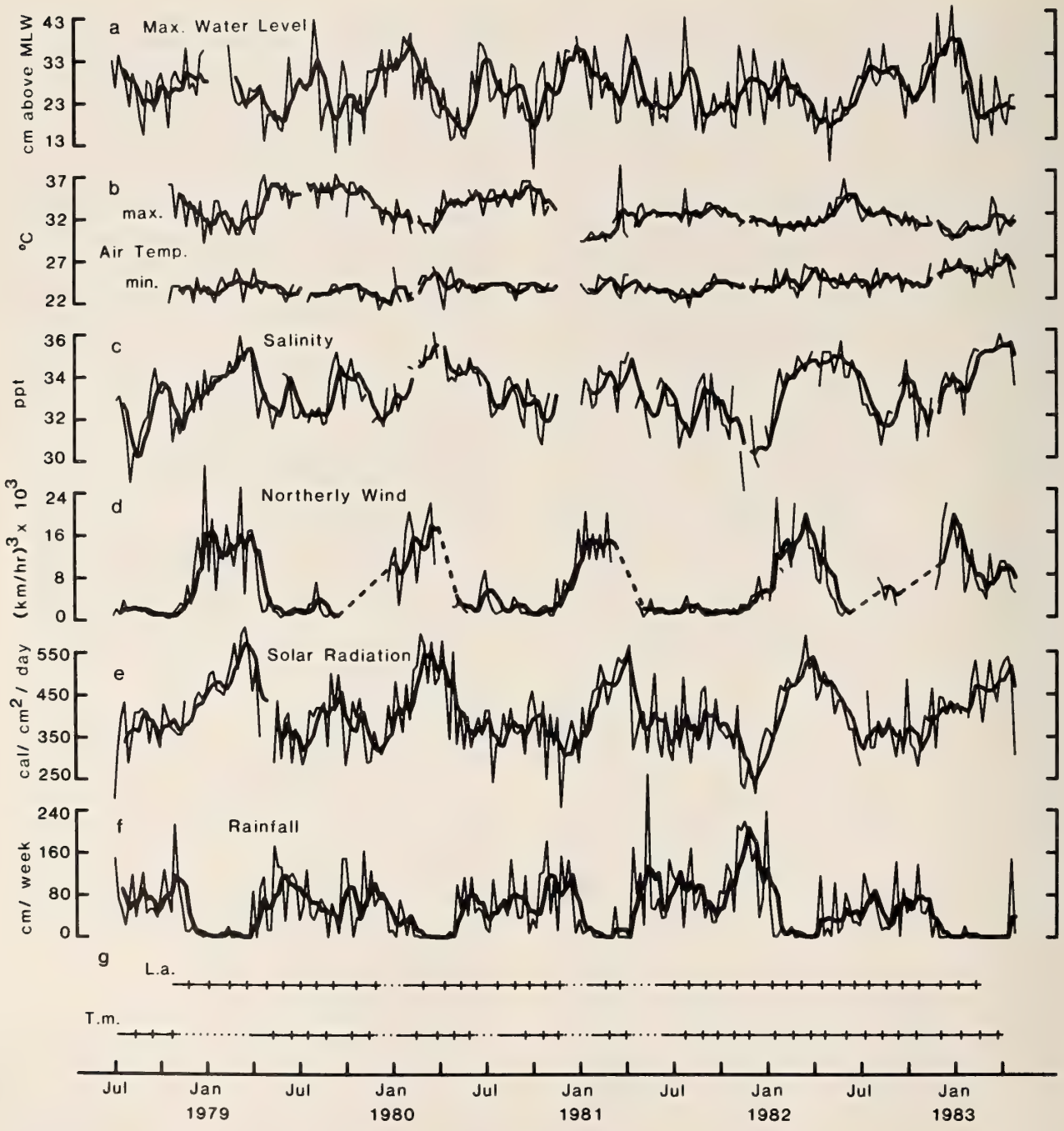


Figure 1

Environmental variation and sampling periods during the study. Light lines are weekly totals (rainfall) or weekly means of daily values (all others); heavy lines are running means of weekly values for previous four weeks. Variables: a, maximum water level above Mean Low Water; b, maximum and minimum air temperature; c, surface salinity; d, wind from northern quadrant (NE–NW); e, total radiant exposure (280–2800 nm); f, rainfall; g, sampling schedule for *L. angulifera* (L.a.) and *T. muricatus* (T.m.). Samples used in analysis of growth (vertical marks) are separated by solid lines showing length of sample intervals. Measurements after sample intervals longer than 50 days (dotted lines) were not used.

seasonal character and its potential importance to these supralittoral snails. In these correlations, median growth rates were paired with the running means of the physical variables from the previous four weeks.

RESULTS

Environmental Seasonality

The dry season at Galeta usually began in December and ended in May or late April, and was characterized by strong northerly trade winds, high maximum water levels, high insolation, little rain, and salinity over 33‰ (Figure 1). The wet season made up the remainder of each year, with more rainfall, lighter winds, less insolation, and lower salinity. A short period of dry season weather usually interrupted the wet season between August and October. Although the maximum air temperatures were generally higher from May to September, minimum temperatures were relatively stable. Rainfall was anomalously low in 1982, possibly owing to the strong El Niño phenomenon of that year. The consistent nature of the annual cycle was reflected in the high correlations between most of the physical variables (Table 1). Gaps in the sampling schedule of the snails (Figure 1g) occurred principally near the transitions between dry and wet seasons.

Water levels on the Galeta reef flat are affected by the combined action of waves, tidal patterns, and fluctuations in mean sea level (Cubit *et al.*, 1986). Maximum water level had lower correlation with the other factors (Table 1) because its period was approximately double that of the main seasonal cycle. Peaks in this variable (Figure 1a) occurred in both the dry and wet seasons, with a low point after the dry-to-wet season transition. The maximum water levels were rarely below the bases of the mangrove roots (−2 to +6 cm relative to MLW), but the base of the *Tectarius muricatus* study area (+27 cm) was above the high water line for several weeks at a time, usually between April and July.

Growth of *Littorina angulifera*

Selected scatterplots of growth rate versus length (Figures 2a–c) illustrate several features of growth in *Littorina angulifera* examined in more detail below. Growth rates were fastest in the smallest animals, and showed a roughly linear decline with length up to about 15 mm. At lengths over 14 mm, a variable proportion of snails showed no growth during the sample intervals. The maximum growth rate and the rate at which growth decreased with size varied over time.

As explained above, data from *Littorina angulifera* 14 mm long and smaller were analyzed separately from the data for larger snails. The growth coefficient of the smaller size class was computed by regression analysis of change in length, rather than the lip extension used to measure growth in larger *L. angulifera*. The close, linear relationship between these two measures of growth is shown in Figure 3.

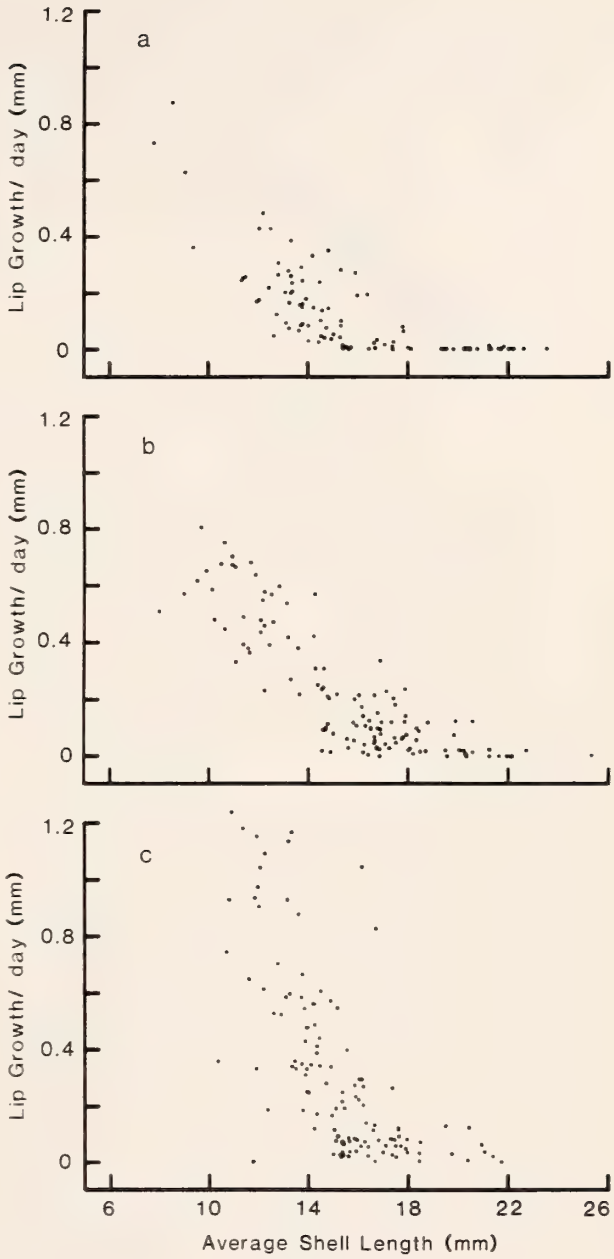


Figure 2

Littorina angulifera. Growth rate versus average of shell length at start and end of sample interval: a, 4 September 1979; b, 27 February 1980; c, 17 March 1981.

The x-intercepts of the regressions, where a linear projection would predict no growth, were consistently near 14 mm ($\bar{x}$ = 14.62 mm, SD = 0.52). At lengths over 14 mm, many *Littorina angulifera* grew in discrete episodes separated by periods of no growth. Despite generally sporadic recovery of individuals, the growth of some snails

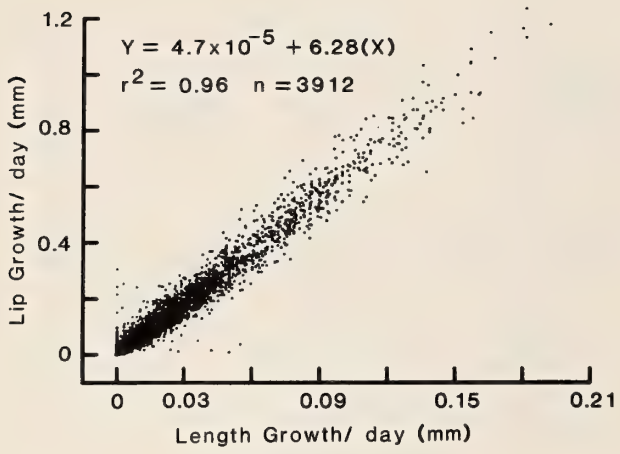


Figure 3

Littorina angulifera. Relationship between growth rates of shell lip (Y) and length (X) using pooled data from all samples.

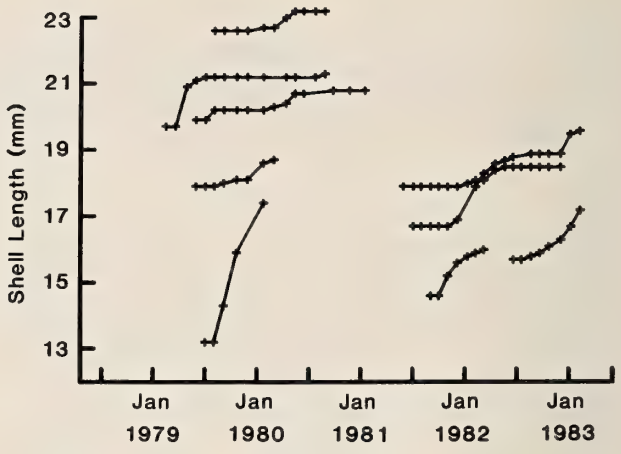


Figure 4

Littorina angulifera. Shell length at successive recaptures (+) for nine snails initially marked at length <14 mm; each trace begins at the first interval with no lip growth.

could be traced continuously up to and beyond the first halt in lip growth. Examples (Figure 4), chosen to indicate the variety of growth histories observed, show that the initial cessation of growth could occur at a wide range of lengths. The period of time over which individuals showed no growth was variable, as were the duration and rate of subsequent growth.

The growth coefficients of the small *Littorina angulifera* varied over time but showed little seasonality (Figure 5a), and were not correlated with rainfall ($r = 0.06$) or maximum water level ($r = 0.04$, both $n = 26$, $P > 0.05$).

Snails larger than 14 mm had a clearly seasonal pattern of growth, with faster median growth rates (Figure 5b) and greater proportions of growing individuals (Figure 5c) between September and June, a period that includes all of the dry season and much of the wet season. The growth rates of the larger snails showed a negative correlation with rainfall ($r = -0.41$, $n = 42$, $P < 0.01$) but were independent of maximum water level ($r = -0.06$, $n = 41$, $P > 0.05$).

The median growth rates of the larger *Littorina angulifera* were correlated with the growth coefficients of the smaller snails ($r = 0.42$, $n = 26$, $P < 0.05$). This was not due to influxes of small, fast-growing snails into the larger size class, because median lengths and growth rates in samples of larger animals were not correlated ($r = 0.02$, $n = 42$, $P > 0.05$).

The range of observed growth rates declined in 1982 (Figure 5b) owing to the termination of the marking program. The proportions of growing snails also declined at that time as the smaller individuals eventually stopped growing, but as dry season approached most snails resumed growth (Figure 5c).

Unmarked snails were found on the trees during each collection. The rate of recruitment (Figure 5d) showed a rising trend which paralleled the growth of the study trees. Peaks in recruitment occurred twice each year, in late dry season and in mid-wet season.

Growth of *Tectarius muricatus*

The relationship between length and growth rate in *Tectarius muricatus* is most easily seen by combining all

Table 1

Product-moment correlations of four-week running means of the following weekly values: total rainfall (Rain), mean daily insolation (Solar), mean daily salinity (Salin.), mean daily northerly wind energy (Wind), mean daily maximum water level (Water), and mean daily maximum air temperature (Temp.). Number of data pairs used: Rain vs. Water, 229; Wind vs. Salin., 166; all others 211. Significance levels: **, $P < 0.01$; ns, $P > 0.05$.

	Rain	Solar	Temp.	Water	Wind	Salin.
Rain	—					
Solar	−0.77**	—				
Temp.	0.39**	−0.36**	—			
Water	−0.10 ns	−0.12 ns	−0.32**	—		
Wind	−0.72**	0.71**	−0.72**	0.42**	—	
Salin.	−0.71**	0.80**	−0.25**	−0.26**	0.50**	—

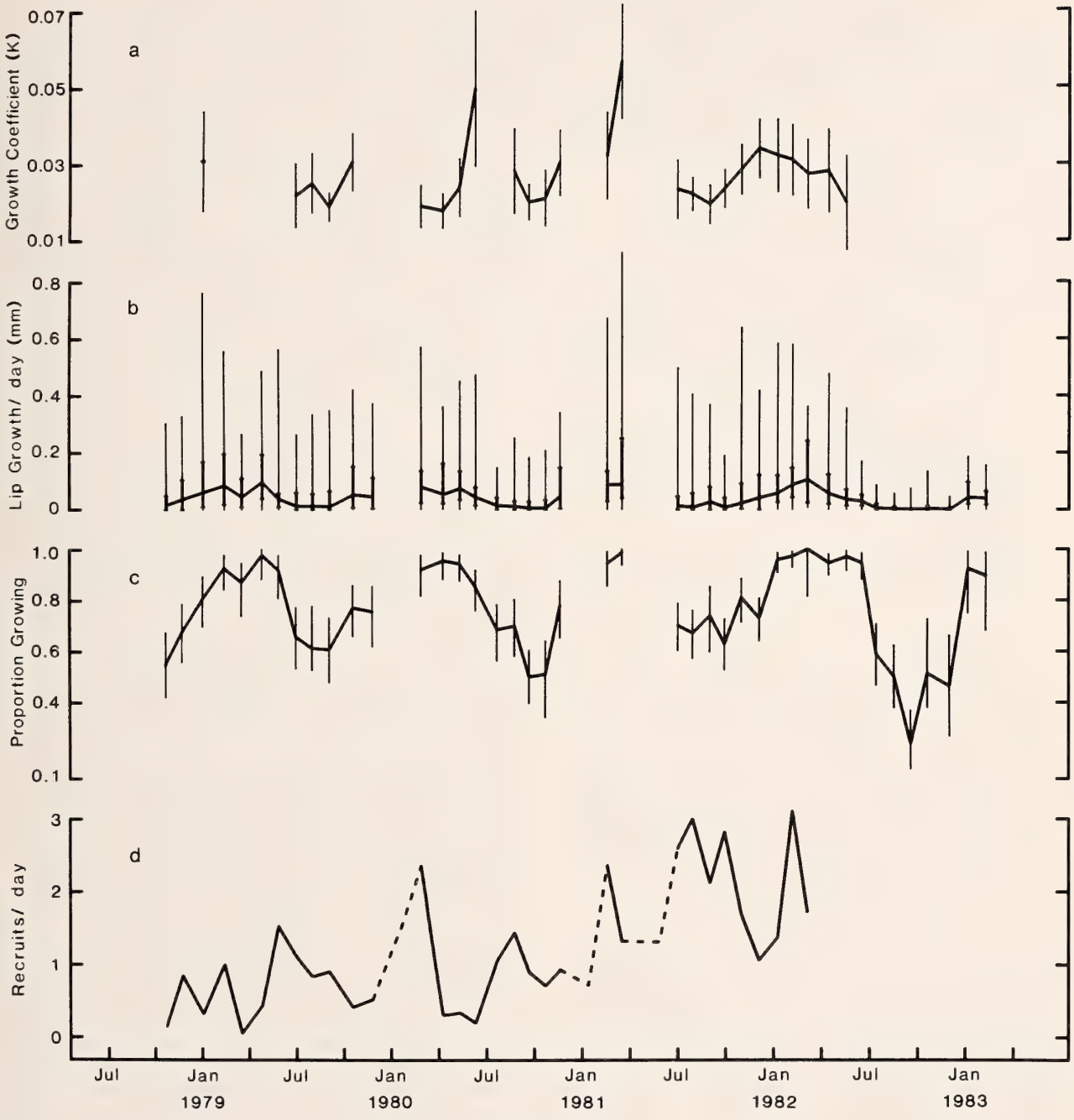


Figure 5

Littorina angulifera. a. Growth coefficients (±95% confidence intervals) for snails ≤14 mm average shell length. b. Growth rates of snails >14 mm average shell length: medians (points connected by line), quartiles (thick bars), and ranges (thin bars). See Appendix 1 for sample sizes. c. Proportions (±95% confidence intervals) of snails >14 mm average shell length with growth since previous sample. d. Number of new (unmarked) snails in sample per day of sample interval.

samples into a single scatterplot (Figure 6), because few snails grew in each sample interval. Periods of no growth were common at nearly all lengths, although snails smaller than 14 mm were poorly represented. Most growth was slow, and the maximum rates observed decreased with increasing length. Growth rates of the smallest *T. muricatus* were comparable to those of *Littorina angulifera* at similar lengths. As in that species, lip extension rates of *T. murica-*

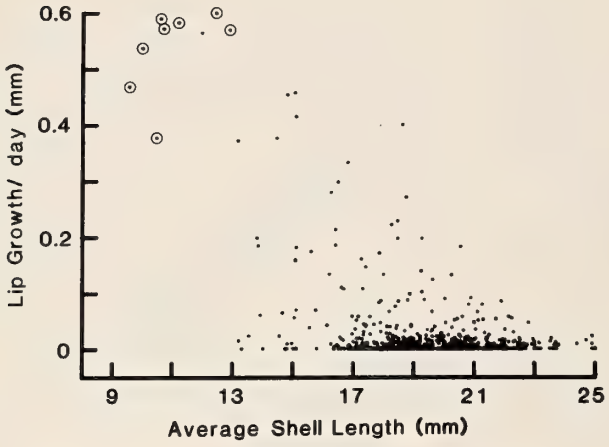


Figure 6

Tectarius muricatus. Growth rate versus average of shell length at start and end of interval, all samples combined. Rates recorded from 4 June to 24 July 1985 (circles) to illustrate growth of small snails were not used in analyses.

tus were linearly related to rates of length increase (r^2 = 0.92, n = 1549). The Model II regression formula was:

$$\text{Lip extension} = 1.2 \times 10^{-5} + 8.45(\text{Length increase})$$

Growth histories of *Tectarius muricatus* (examples in Figure 7) showed an episodic pattern similar to that of the larger *Littorina angulifera* (Figure 3). Growth could resume more than two years after cessation. Small increments in length were not cumulative effects of slow growth, because lip extension was rarely observed between episodes of measurable increase in length. As in *L. angulifera,* the timing and duration of growth episodes and the amount of growth during an episode were variable, and not obviously related to the length of the snail.

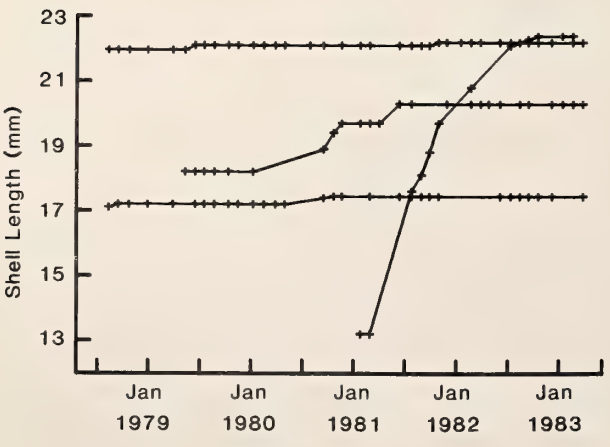


Figure 7

Tectarius muricatus. Shell length at successive recaptures (+) for four snails.

The median growth rates of the marked *Tectarius muricatus* were zero on all but two occasions (Figure 8a) owing to the large proportion of non-growing animals in most samples. The maximum growth rates in each sample were positively correlated (r = 0.59, n = 34, $P < 0.01$) with the proportion of animals growing, which varied between zero and just over half of the animals sampled (Figure 8b).

Both maximum growth rates and the proportion growing peaked during wet seasons and appeared to reach minima during dry seasons, although these data were sparse. The proportion of snails growing showed a significant correlation with rainfall (r = 0.54, n = 34, $P < 0.01$) but maximum growth rates did not (r = 0.22, n = 34, $P > 0.05$). Maximum water level was not correlated with either maximum growth rates (r = 0.01) or with the proportion growing (r = −0.13, both n = 34, $P > 0.05$).

DISCUSSION

Seasonal Patterns of Growth and Possible Causes

Consistent, annual cycles were found in the growth rates of large *Littorina angulifera* and *Tectarius muricatus* at Galeta. Despite the proximity of the study areas, the timing of these cycles differed between the two species. The median growth rates of *L. angulifera* showed a broad peak centered on the dry season, while the growth rates of *T. muricatus* were slow at that time and fastest in the first half of the wet season. Growth rates of the smaller *L. angulifera* varied greatly, but with little evidence of a seasonal pattern.

Seasonal changes in growth rates have been reported for herbivorous gastropods both in temperate zones (*e.g.,* Orton, 1928; Frank, 1965a; Sutherland, 1970; Phillips, 1981) and in the tropics (*e.g.,* Frank, 1969; Yamaguchi, 1977). In most cases the causes of this variation are not known, but have been attributed to external factors such as temperature (Largen, 1967; Vermeij, 1978; Ekaratne & Crisp, 1984) or food supply (Cubit, 1984; Fletcher, 1984; Underwood, 1984a), or to internal factors such as costs of reproduction (Orton, 1928; Coe & Fox, 1942; Borkowski, 1974; Ekaratne & Crisp, 1984).

Although minimum temperatures did not fluctuate seasonally, peaks in maximum temperature coincided with more rapid growth in *Tectarius muricatus,* a pattern also observed in Florida by Borkowski (1974). Because several other physical factors had similar seasonal patterns (Figure 1, Table 1), no causal link can be inferred from this relationship.

Experimental manipulations of densities of herbivorous gastropods (Sutherland, 1970; Creese, 1980; Underwood, 1984a; Jernakoff, 1985) and correlations of algal abundance with their growth rates (Sutherland, 1970; Fletcher, 1984; Underwood, 1984a) suggest that primary production may control growth rates in these grazers. Because primary production depends upon the availability of moisture during daylight (Johnson *et al.,* 1974),

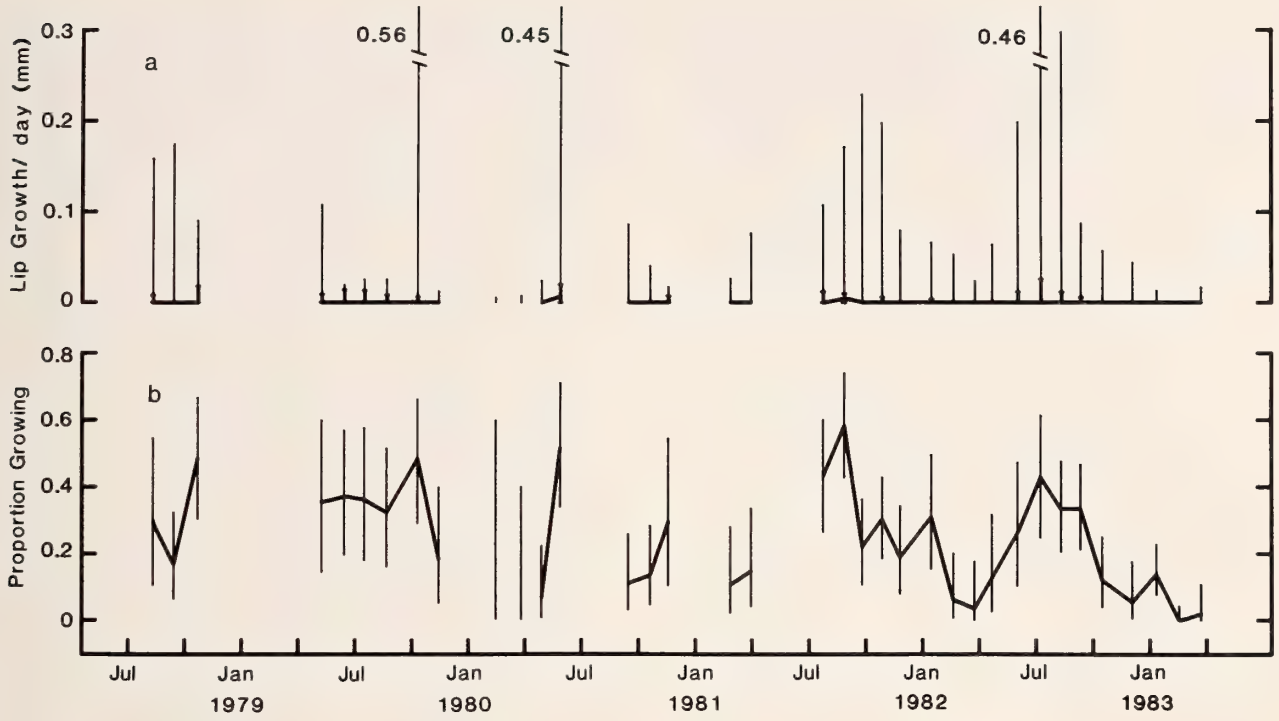


Figure 8

Tectarius muricatus. a. Growth rates: medians (points connected by line), quartiles (thick bars), and ranges (thin bars). Medians were not calculated for sample sizes <10 (February and March 1980; see Appendix 2 for all sample sizes). b. Proportions (±95% confidence intervals) of snails with growth since previous sample.

conspicuous blooms of algae high on shores are thought to be partly due to seasonal increases in wetness of the substratum (Lawson, 1957; Castenholz, 1961; Nicotri, 1974; Cubit, 1984). The temporal patterns of wetness in the two habitats studied here may have differed significantly. Moisture retained in the porous coral rock of the *Tectarius muricatus* study area may have increased the abundance of epilithic and endolithic microalgae, which colored the rock green during the wet season (J. Burgett, personal observations). In the dry season, the more intense wind and sun may have dried the surface layers of these rocks despite wetting by the tides, thus reducing the supply of food available to *T. muricatus*.

In contrast to the strictly supralittoral *Tectarius muricatus* (Borkowski, 1971; Bandel, 1974), *Littorina angulifera* grazes intertidal surfaces during nocturnal migrations to lower levels of the mangroves (Plaziat, 1984; P. Gutierrez, unpublished data). Although *L. angulifera* might eat mangrove exudates or epiphyllic fungi, mangrove tissue apparently is not ingested, as feeding behavior on clean stems and leaves does not produce scrape marks (J. Burgett, personal observations). Individuals on inert artificial surfaces at Galeta grew to lengths of more than 25 mm, apparently feeding on deposited material and (or) microalgae (J. Burgett & J. Cubit, personal observations). Algal production on the surfaces of the mangrove roots, which do not retain water, could follow a seasonal pattern distinct from that on the higher coral wall. The relatively non-seasonal pattern in the growth rates of the small *L. angulifera* may be related to their remaining closer to the water level than do the larger snails.

It is also possible that the availability of food for *Tectarius muricatus* or *Littorina angulifera* was influenced by other grazers, as competition has been shown to affect grazing gastropods high on other intertidal shores (Underwood, 1979, 1984b). Different sets of potential competitors occurred in the two habitats. Other herbivores in the rocky habitat of *T. muricatus* were isopods (*Ligia* sp.), crabs, terrestrial arthropods and the two species of *Nodilittorina*. Although *L. angulifera* was the only grazer we observed on supralittoral parts of *Rhizophora*, intertidal areas of the trees are exposed to herbivorous fish and invertebrates (Batista, 1980).

In some mollusks, the allocation of material and energy to reproduction is thought to depress the rate of growth (Orton, 1928; Coe & Fox, 1942; Borkowski, 1974; Ekaratne & Crisp, 1984), although these processes can occur simultaneously (Leighton & Boolootian, 1963; Phillips, 1981; Cubit, 1984). In southern Florida (25°30′N), Lenderking (1954) observed *Littorina angulifera* spawning through at least 10 months of the year (no samples were taken in January or February). At this site,

the wet season occurred between June and December. The proportion of animals spawning was greatest in the spring and autumn and least between December and March.

Our data show year-round recruitment, which would be consistent with a long spawning season. If the reproductive pattern of *Littorina angulifera* at Galeta is similar to that reported from Florida, then shell growth and spawning have broad, overlapping cycles, with alternating peaks in the dry and wet seasons, respectively.

BORKOWSKI (1971) studied the reproductive cycle of *Tectarius muricatus* in southern Florida, as LEWIS (1960) did to a lesser extent in Barbados (13°N), where the seasonal patterns of rainfall and temperature were comparable to those at Galeta (LEWIS *et al.,* 1969). *Tectarius muricatus* in Florida had ripe gonads from May to September, but spawning was observed only between July and September during extreme high tides, a pattern also shown by the presence of egg capsules in plankton tows at Barbados (LEWIS, 1960). The annual growth pattern of *T. muricatus* reported from Florida (BORKOWSKI, 1974) coincides with that observed at Galeta. If the pattern of reproduction in Panamá is similar to those at the other sites, then both shell growth and gonadal development occur between May and August, suggesting a large increase in available nutrients during the wet season.

Growth, Length, and Regional Comparisons

Littorina angulifera and *Tectarius muricatus* smaller than 14 mm grew faster than the larger snails that predominated in the study populations. Small *L. angulifera* could add more than 1 mm of lip per day (Figure 2c), while the maximum rate seen in *T. muricatus* was 0.6 mm per day (Figure 6), similar to rates of *L. angulifera* of the same length. These rates are about five times faster than those reported from previous studies. LENDERKING's (1954) data on growth of *L. angulifera* over six weeks yielded a rate of 0.028 mm of length per day for snails 7.6 mm long (initial length 7 mm), equal to 0.18 mm lip growth per day if the ratio of length growth to lip extension was the same in Florida as in Panamá (Figure 4). BORKOWSKI (1974) reported that *T. muricatus* initially 11 to 12 mm in length grew 0.017 mm per day over 60 days, equivalent to 0.13 mm of lip per day using his conversion ratio.

The processes causing latitudinal differences in growth rates in these species and other prosobranchs (*e.g., Tegula funebralis* Adams, 1855, by FRANK, 1975; *Littorina neritoides* Linnaeus, 1758, by HUGHES & ROBERTS, 1980) remain obscure. Temperatures at the sites in southern Florida were within the range of those at Galeta (BORKOWSKI, 1971), but many other biotic and abiotic environmental factors that could affect growth rates probably differed among sites. Genotypic clines have been proposed as explanations for these patterns (FRANK, 1975), and gene frequencies in *L. angulifera* are known to vary among neighboring populations (GAINES *et al.,* 1974).

The rate of decline in growth rates for the smaller *Littorina angulifera* was expressed by the parameter K of the von Bertalanffy growth function. However, this function was not an appropriate model for growth over the full length range of either species. In addition to assuming an asymptotic length where none may exist (KNIGHT, 1968), the model requires that very small animals grow according to the linear function. For *L. angulifera* (LENDERKING, 1954) and probably many other invertebrates, this assumption does not hold (YAMAGUCHI, 1975). We, therefore, have used K solely as a convenient descriptor of the linear rate of decline in growth rates of *L. angulifera* between 7 and 14 mm. Our plotting of growth rates against average length rather than the more common initial length gave closer estimates of growth rates at a given length (LOCKWOOD, 1974), although it would not have been appropriate for actual fitting of the model (YAMAGUCHI, 1975). The GULLAND & HOLT (1959) method used here recently has been found to underestimate K when Model I regression is used (SUNDBERG, 1984). By using a Model II regression technique and adjusting for variable sample intervals by simulation, we have partially corrected for this bias.

A linear decline in growth rate with length implies a length at which growth is zero. Although linearity past a length of 14 mm was not tested, the values obtained were consistent and close to the mean length (15 mm) at first spawning of *Littorina angulifera* in Florida (LENDERKING, 1954). If the attainment of reproductive maturity coincides with initial cessation of growth in *L. angulifera,* then this length may be essentially constant with latitude, despite the differences in growth rates of small animals. A similar pattern has been reported in the trochid *Tegula funebralis* (FRANK, 1975). The wide variation in the length at which individuals of *L. angulifera* first stop growing (Figure 3) may be related to gender. Females in Florida grew larger in one year than did males (LENDERKING, 1954), although in that paper it was unclear whether growth rates differed among immature snails.

In Florida, *Tectarius muricatus* matured at the same length as *Littorina angulifera* (BORKOWSKI, 1974). Thickening of the shell lip, associated with temporary halts of growth in other prosobranchs (LAXTON, 1970; FRANK, 1965b, 1969), was observed in *T. muricatus* in Florida at lengths of 13 to 16 mm (Singletary, in BORKOWSKI, 1974). Our data support this range as the length at initial cessation of growth in *T. muricatus* in Panamá. This species may thus resemble *L. angulifera* in having rapid growth when small, a temporary halt in growth at maturity, and subsequent episodic growth.

Individual differences in growth rates were large enough in both species to make length an unreliable indicator of age. The median growth rates of both species were affected by the varying proportions of growing animals in the samples. In *Littorina angulifera,* at least one-quarter, and often all, of the snails in a sample grew, while no more than one-half of the sampled *Tectarius muricatus* grew during

any interval. In both *L. angulifera* and *T. muricatus,* females have faster long-term rates of growth than do males (LENDERKING, 1954; BORKOWSKI, 1974), suggesting that some of the individual differences in episodic growth may be sex-specific. If female *L. angulifera* grew more during episodes, they would dominate the larger size classes, as reported by LENDERKING (1954). However, because all *L. angulifera* larger than 14 mm grew during some intervals, males of this species must also grow episodically.

Episodic growth has been found in both tropical (FRANK, 1969) and temperate gastropods (*e.g.,* ORTON, 1928; LAXTON, 1970; SUTHERLAND, 1970; FRANK, 1975; HUGHES & ROBERTS, 1980). This phenomenon may be common, but it cannot be detected with measurements separated by long intervals or by methods that average growth rates and thus lose information from individuals. Detailed investigation of growth patterns requires frequent measurements of large numbers of individually identified animals. With sufficient resolution, patterns of growth within and among populations can provide a base for more analytical observations and experimental studies of physiological adaptations, food supply, phenology, and interactions among species.

To our knowledge, Punta Galeta is at a lower latitude than other sites from which seasonal growth rates of snails have been reported. The asynchrony of the observed growth patterns implies that no single overriding factor of the environment controlled the growth of both *Littorina angulifera* and *Tectarius muricatus.* The correlations of growth rates with changes in the physical environment suggest several explanatory hypotheses. These could be tested by a combination of observational and experimental investigations of, for example, competitive interactions, foraging behavior, reproductive investment and timing, and abundance of microalgae.

ACKNOWLEDGMENTS

We thank D. Windsor for summarizing the environmental data, the Tropic Test Center of the United States Army for solar radiation data, S. Williams and F. Chang for marking and measuring snails, M. Fogarty for statistical advice, S. Churgin and R. Sarmiento for help with references, H. Caffey for figure preparation, and P. Gutierrez for unpublished data. The manuscript was improved by the comments of C. Brock, H. Caffey, P. Frank, K. McGuinness, and an anonymous reviewer. This study was supported by a grant to J. Cubit from the Environmental Sciences Program of the Smithsonian Institution.

LITERATURE CITED

BANDEL, K. 1974. Studies on Littorinidae from the Atlantic. Veliger 17:92–114.

BANDEL, K. & D. KADOLSKY. 1982. Western Atlantic species of *Nodilittorina* (Gastropoda: Prosobranchia): comparative morphology and its functional, ecological, phylogenetic and taxonomic implications. Veliger 25:1–42.

BATISTA, V. 1980. Estudio de las comunidades que habitan las raices del mangle rojo *Rhizophora mangle* L. de Punta Galeta, Costa Atlantica de Panamá. Dissertation, Fundacion Universidad de Bogotá Jorge Tadeo Lozano, Bogotá, Colombia.

BERTNESS, M. D. 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. Jour. Exp. Mar. Biol. Ecol. 64:159–187.

BORKOWSKI, T. V. 1971. Reproduction and reproductive periodicities of south Floridian Littorinidae (Gastropoda: Prosobranchia). Bull. Mar. Sci. 21:826–840.

BORKOWSKI, T. V. 1974. Growth, mortality and productivity of south Floridian Littorinidae (Gastropoda: Prosobranchia). Bull. Mar. Sci. 24:409–438.

CASTENHOLZ, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42:783–794.

COE, W. R. & D. L. FOX. 1942. Biology of the California sea mussel (*Mytilus californianus*). Jour. Exp. Zool. 90:1–30.

CREESE, R. G. 1980. An analysis of distribution and abundance of populations of the high-shore limpet, *Notoacmea petterdi* (Tenison-Woods). Oecologia 45:252–260.

CUBIT, J. C. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. Ecology 65:1904–1917.

CUBIT, J. C. & S. WILLIAMS. 1983. The invertebrates of Galeta Reef: a species list and bibliography. Atoll Res. Bull. 269: 1–45.

CUBIT, J. D., D. M. WINDSOR, R. C. THOMPSON & J. M. BURGETT. 1986. Water level fluctuations, emersion regimes, and variations of echinoid populations on a Caribbean reef flat. Estuar. Coast. Shelf Science 22:719–737.

EKARATNE, S. U. K. & D. J. CRISP. 1984. Seasonal growth studies of intertidal gastropods from shell micro-growth band measurements, including a comparison with alternative methods. Jour. Mar. Biol. Assoc. U.K. 64:183–210.

FLETCHER, W. J. 1984. Intraspecific variation in the population dynamics and growth of the limpet, *Cellana tramoserica.* Oecologia 63:110–121.

FRANK, P. W. 1965a. The biodemography of an intertidal snail population. Ecology 46:831–844.

FRANK, P. W. 1965b. Shell growth in a natural population of the turban snail, *Tegula funebralis.* Growth 29:395–403.

FRANK, P. W. 1969. Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia 2:232–250.

FRANK, P. W. 1975. Latitudinal variation in the life history features of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae). Mar. Biol. 31:181–192.

GAINES, M. S., J. CALDWELL & A. M. VIVAS. 1974. Genetic variation in the mangrove periwinkle *Littorina angulifera.* Mar. Biol. 27:327–332.

GULLAND, J. A. & S. J. HOLT. 1959. Estimation of growth parameters for data at unequal time intervals. Jour. Cons. Perm. Int. Explor. Mer 24:47–49.

HAY, M. E. & J. N. NORRIS. 1984. Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sand plain. Hydrobiologia 116/117:63–94.

HENDLER, G. L. 1977. The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. Pp. 217–223. *In:* Proceedings, Third International Coral Reef Symposium. University of Miami: Miami, Florida.

Hughes, R. N. & D. J. Roberts. 1980. Growth and reproductive rates of *Littorina neritoides* (L.) in North Wales. Jour. Mar. Biol. Assoc. U.K. 60:591–599.

Jernakoff, P. 1985. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. Jour. Exp. Mar. Biol. Ecol. 88:287–302.

Johnson, W. S., A. Gigon, S. L. Gulmon & H. A. Mooney. 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology 55: 450–453.

Kaufmann, K. W. 1981. Fitting and using growth curves. Oecologia 49:293–299.

Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. Jour. Fish. Res. Board Can. 25: 1303–1307.

Largen, M. J. 1967. The influence of water temperature upon the life of the dog-whelk *Thais lapillus* (Gastropoda: Prosobranchia). Jour. Anim. Ecol. 36:207–214.

Lawson, G. W. 1957. Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. Jour. Ecol. 45:831–860.

Laxton, J. H. 1970. Shell growth in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). Jour. Exp. Mar. Biol. Ecol. 4:250–260.

Leigh, E. G., Jr., A. S. Rand & D. M. Windsor (eds.). 1982. The ecology of a tropical forest: seasonal rhythms and long-term changes. 468 pp. Smithsonian Institution Press: Washington, D.C.

Leighton, D. & R. A. Boolootian. 1963. Diet and growth in the black abalone, *Haliotis cracherodii*. Ecology 44:227–238.

Lenderking, R. E. 1954. Some recent observations on the biology of *Littorina angulifera* Lam. of Biscayne and Virginia Keys, Florida. Bull. Mar. Sci. Gulf Caribbean 3:273–296.

Lewis, J. B. 1960. The fauna of rocky shores of Barbados, West Indies. Can. Jour. Zool. 38:391–435.

Lewis, J. B., F. Axelsen, I. Goodbody, C. Page, G. Chislett & M. Choudhoury. 1969. Latitudinal differences in growth rates of some intertidal marine molluscs in the Caribbean. Marine Sciences Manuscript Rept. No. 12. 89 pp. McGill University, Montreal.

Lockwood, S. J. 1974. The use of the von Bertalanffy growth equation to describe the seasonal growth of fish. Jour. Cons. Int. Explor. Mer 35:175–179.

Macintyre, I. G. & P. W. Glynn. 1976. Evolution of modern Caribbean fringing reef, Galeta Point, Panama. Amer. Assoc. Petrol. Geol. Bull. 60:1054–1072.

McQuaid, C. D. 1981. Population dynamics of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. Jour. Exp. Mar. Biol. Ecol. 54:65–76.

Nicotri, M. E. 1974. Resource partitioning, grazing activities, and influence on the microflora by intertidal limpets. Doctoral Thesis, University of Washington, Seattle, Washington.

Orton, J. H. 1928. Observation on *Patella vulgata,* Part II. Rate of growth of shell. Jour. Mar. Biol. Assoc. U.K. 15: 863–874.

Pennington, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. Biometrics 39:281–286.

Phillips, D. W. 1981. Life-history features of the marine intertidal limpet *Notoacmea scutum* (Gastropoda) in central California. Mar. Biol. 64:95–103.

Plaziat, J. C. 1984. Mollusk distribution in the mangal. Pp. 111–143. *In:* F. D. Por & I. Dor (eds.), Hydrobiology of the mangal. Dr. W. Junk Publishers: The Hague.

Ricker, W. E. 1973. Linear regressions in fishery research. Jour. Fish. Res. Board Can. 30:409–434.

Rosewater, J. 1970. The family Littorinidae in the Indo-Pacific. Part I. The subfamily Littorininae. Indo-Pacif. Mollusca 2:417–506.

Salvat, B. & M. Denizot. 1982. La distribution des mollusques supralittoraux sur substrats carbonates tropicaux (Polynésie Française) et leur régime alimentaire. Malacologia 22:541–544.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. W. H. Freeman & Co.: San Francisco. 776 pp.

Sundberg, P. 1984. A Monte Carlo study of three methods for estimating the parameters in the von Bertalanffy growth equation. Jour. Cons. Int. Explor. Mer 41:248–258.

Sutherland, J. 1970. Dynamics of high and low populations of the limpet, *Acmaea scabra* (Gould). Ecol. Monogr. 40: 169–188.

Underwood, A. J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16:111–210.

Underwood, A. J. 1984a. Microalgal food and the growth of the intertidal gastropods *Nerita atramentosa* Reeve and *Bembicium nanum* (Lamarck) at four heights on a shore. Jour. Exp. Mar. Biol. Ecol. 79:277–291.

Underwood, A. J. 1984b. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. Oecologia 64:211–222.

van Devender, R. W. 1978. Growth ecology of a tropical lizard, *Basiliscus basiliscus*. Ecology 59:1031–1038.

Vermeij, G. J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press: Cambridge. 332 pp.

Yamaguchi, M. 1975. Estimating growth parameters from growth rate data: problems with marine sedentary invertebrates. Oecologia 20:321–332.

Yamaguchi, M. 1977. Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Mariana Islands. Mar. Biol. 44:249–263.

Appendix 1

Littorina angulifera. Sample dates (day/month/year), number of snails used in analysis of each size class (n), and number of days since previous sample (Interval). Data following intervals >50 days (*) were not used in analyses.

Date	n (≤14 mm)	n (>14 mm)	Interval
23/10/78	8	62	33
24/11/78	5	68	32
3/1/79	20	67	40
13/2/79	7	68	41
19/3/79	3	54	34
27/4/79	1	44	39
29/5/79	9	48	32
1/7/79	20	64	34
2/8/79	38	59	31
4/9/79	38	61	33
19/10/79	19	74	45
26/11/79	9	57	38
21/1/80	9*	61*	56
27/2/80	35	88	37
9/4/80	46	87	42
11/5/80	23	102	32
10/6/80	16	88	30
21/7/80	7	73	41
24/8/80	19	70	34
21/9/80	36	96	28
22/10/80	27	47	31
19/11/80	25	59	28
12/1/81	11*	57*	53
17/2/81	20	55	36
17/3/81	39	81	28
27/5/81	8*	92*	71
1/7/81	29	103	35
29/7/81	42	103	28
31/8/81	45	50	33
28/9/81	47	97	28
30/10/81	50	90	32
3/12/81	44	115	34
7/1/82	19	125	35
4/2/82	33	148	28
5/3/82	30	14	29
14/4/82	23	129	40
18/5/82	10	103	34
16/6/82	5	91	29
14/7/82	1	68	28
17/8/82	1	68	34
17/9/82	1	59	31
19/10/82	0	43	32
30/11/82	0	26	42
4/1/83	0	26	35
7/2/83	0	19	34

Appendix 2

Tectarius muricatus. Sample dates (day/month/year), number of snails used in analysis (n), and number of days since previous sample (Interval). Data following intervals >50 days (*) were not used in analyses.

Date	n	Interval
6/7/78	17*	181
11/8/78	17	36
14/9/78	36	34
23/10/78	31	39
28/12/78	27*	66
28/3/79	19*	90
5/10/79	17	43
6/15/79	27	36
17/7/79	25	32
22/8/79	28	36
11/10/79	30	50
14/11/79	22	34
7/1/80	9*	54
14/2/80	6	38
26/3/80	9	41
28/4/80	30	33
28/5/80	36	30
27/7/80	32*	60
14/9/80	36	49
19/10/80	37	35
17/11/80	17	29
22/1/81	15*	65
25/2/81	29	34
30/3/81	28	33
10/6/81	31*	72
23/7/81	37	43
26/8/81	36	34
24/9/81	41	29
26/10/81	46	32
24/11/81	37	29
13/1/82	29	50
18/2/82	33	36
24/3/82	29	34
21/4/82	24	28
1/6/82	23	41
8/7/82	28	37
10/8/82	51	33
10/9/82	57	31
15/10/82	43	35
2/12/82	38	48
10/1/83	94	39
16/2/83	68	37
23/3/83	50	35

The Veliger 30(1):24–39 (July 1, 1987)

THE VELIGER

Courtship and Dart Shooting Behavior of the Land Snail *Helix aspersa*

by

DANIEL J. D. CHUNG[1]

Division of Biological Sciences and Museum of Zoology,
University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

Abstract. The dart apparatus, found in a number of pulmonate and opisthobranch gastropods, contains a dart that is used to pierce the flesh of a partner during courtship and mating. It has usually been assumed that dart receipt somehow "stimulates" co-operative courtship behavior, but previous studies have been unable to confirm this hypothesis. In this study, the courtship and dart shooting behavior of the stylommatophoran *Helix aspersa* Müller was studied in order to document in detail the courtship of this snail and to determine whether dart receipt stimulates courtship or has another function. As in *H. pomatia,* there are two basic courtship sequences in *H. aspersa*: one in which dart shooting behavior occurs and one in which it is omitted. The courtship sequence is determined solely by the internal condition of the snail. Young snails have courtship behavior that differs slightly from that of older snails. Quantitative tests show that dart receipt has no effect on the fraction of time spent out of genital contact or the mean rate of biting, but dart receipt appears to decrease the rate of attempted copulation. Dart shooting, by contrast, appears to stimulate the shooter into attempting copulation and into decreasing its rate of biting. It is theorized that the dart may have evolved as a result of sexual selection in hermaphrodites to coerce a mate into acting more as a "female" or to prevent a mate from "cheating" as a "male."

INTRODUCTION

The dart apparatus is a set of organs found in the terminal genitalia of a number of hermaphroditic pulmonate and opisthobranch gastropods. The dart apparatus consists of one or more dart sacs containing a dart—a chitinous or calcareous spear that is thrust into the flesh of a courting partner during "dart shooting"—and associated glands. In general, there are two basic types of dart apparatuses: those with hollow darts perforated at the tip and with a gland at its base, which may be used as hypodermic devices, and those with darts not perforated at the tip and with glands ("mucous glands") near the base. Helicids have the latter type of dart apparatus. Helicids also have deciduous darts; that is, they are cast off during dart shooting and replaced shortly after courtship. It is possible that all non-helicid dart-bearing snails possess non-deciduous darts. Darts may have evolved independently in the helicaceans, ariophantaceans, zonitaceans, philomycids, soleoliferans, nudibranchs, and possibly cephalaspideans and cavoliniids (see Tompa, 1980; Pruvot-Fol, 1960). It has usually been assumed that the dart somehow "stimulates" the courting partner (see Tompa, 1980, for review), although courtship observations have not been able to demonstrate any function for the dart.

Observations on courtship behavior, with descriptions of dart shooting or use of the dark apparatus, in dart-bearing land snails have been given for a number of species, including: the helicids *Helix pomatia* Linnaeus (Meisenheimer, 1912; Lind, 1976; Jeppesen, 1976), *H. aspersa* Müller (Herzberg & Herzberg, 1962); Giusti & Lepri, 1980), *Eobania vermiculata* (Müller), *Tacheocampylaea tacheoides* (Pollonera), *H. lucorum* (Linnaeus) (Giusti & Lepri, 1980); the bradybaenid *Eulota fruticum* Müller (Künkel, 1928); the vitrinids *Vitrina elongata* Draparnard (Künkel, 1933), *V. brevis* Férussac (Künkel, 1929, 1933), *V. major* Férussac (Gerhardt, 1935; see also Forcart, 1949); the parmacellid *Parmacella deshayesi* Moquin-Tandon (Gerhardt, 1935); the zonitid *Ventridens* Binney (Webb, 1948, 1968b); the helminthoglyptids *Helminthoglypta* Ancey (Webb, 1942, 1951, 1952b), *Monadenia* Pilsbry (Webb, 1952a), *Cepolis* Denys de Montfort (Webb, 1952b), *Humboldtiana ultima* Pilsbry (Webb, 1980); the

[1] Mailing address: 3324 Wiliama Place, Honolulu, Hawaii 96816, U.S.A.

philomycid *Philomycus carolinianus* (Bosc) (Webb, 1968a); and the ariophantids *Ariophanta ligulata* (Férussac) (Dasen, 1933), *Macrochlamys pedina* (Benson) (Rensch, 1955), and *M. indica* Godwin-Austen (Raut & Ghose, 1984). With the exception of the studies of Lind (1976) and Jeppesen (1976), these reports are primarily brief descriptive accounts of courtship.

Lind (1976) provided a detailed ethological analysis of courtship and mating behavior in *Helix pomatia* and attempted to determine the role of dart shooting in the overall courtship sequence through a quantitative analysis of behaviors (1) before and after receipt of a dart and (2) between snails that received versus snails that did not receive a dart. Lind found that dart receipt was not a prerequisite for completion of courtship and copulation and that dart receipt at best appeared to have a slightly negative effect on courtship activity. He found some evidence that dart receipt harmed snails and caused cessation of courtship. Jeppesen (1976) obtained similar results from observations of courtship in *H. pomatia* that had the dart sac or mucous glands surgically removed.

The more descriptive reports of courtship and dart shooting in land snails provide little evidence for any specific function of dart shooting. Webb (1952b) suggested that the dart was used by a snail to force its partner to cooperate in courtship by inducing sexual excitement and also to prevent the partner from biting or harming the dart shooter's everted genitals. Künkel (1929, 1933) believed that the dart apparatus in *Vitrina major* was a holdfast organ operating by suction, although Gerhardt (1935) could not verify this hypothesis.

The study reported here is an attempt to understand the function of the dart apparatus through behavioral observations of dart shooting during the courtship of *Helix aspersa*. This study describes in detail the courtship of *H. aspersa*, which had previously been reported in only cursory fashion by Giusti & Lepri (1980) and Herzberg & Herzberg (1962), and tests the hypothesis that dart receipt has a stimulatory effect on courtship behavior.

MATERIALS AND METHODS

Specimens of *Helix aspersa* were obtained from College Biological Supply (Escondido, California). The snails were individually isolated in small plastic containers lined with soil and were provided with egg shells and carrot slices. Snails were kept at 21–26°C under a 12 h light : 12 h dark photoperiod for at least two months before being used in courtship observations. This period of isolation appeared to increase the likelihood of snails courting when put together again. Only fully adult snails with a reflected lip and deflected body whorl were used for descriptions of courtship and quantitative analysis of courtship behavior. Courtship in young snails (defined as "subadults" on the basis of conchological characters—large snails without a reflected lip) was observed for qualitative comparison with courtship in older snails. The subadult snails were all virgins, having been raised from an early juvenile stage in isolation. The field-collected adult snails had an unknown history.

Detailed quantitative observations of courtship were made on 60 pairs of snails, and qualitative observations were made on the courtship and mating of more than 40 other pairs. Of these more than 100 pairs, 10 were pairings of subadults. Of the 60 pairs observed in detail, the data for 36 pairs were detailed enough for quantitative analysis of behaviors presumably related to dart shooting.

Observations on courtship behavior of isolated pairs were taken at night in a lighted room. For each observation session about 12 snails were removed from isolation, washed in water, and placed in an "introductory arena" (a transparent plastic box) where the crawling snails could be observed to identify which snails would court. Snails that exhibited slight eversion of the genitals were noted, and pairs of these snails were transferred to an "observation arena" (a smooth plastic lid, 18 × 13 cm, with upturned sides 2 cm high). Recording of courtship behavior was begun as soon as the pair was placed in the center of the arena and was terminated after the snails attained intromission, one (or both) of the snails withdrew from courtship by crawling out of the arena, or courtship was terminated by the observer. Behavioral records were made on a 20-channel recorder or on a pocket card printer with numerical codes for defined acts. Terminations by the observer were confined to cases where snails had difficulty attaining intromission after 30 min of attempted copulation.

Observations were made on snails courting upright on a horizontal surface. Although snails often mate upside down on the ceilings of laboratory containers, courtship does not appear to be affected by physical orientation to their substrate.

Statistical tests were performed on behavioral data (see below) as described in Conover (1980) and Sokal & Rohlf (1969).

LIST OF BEHAVIORS RECORDED IN COURTSHIP

Labial-head contact (LH) (Figure 1A) occurs when a snail probes the head and labial region of another snail with its mouth and labial palps. The head of the snail is raised off of the substrate, and its tentacles are fully extended. The snail moves its jaws and radula actively, and intermittently bites its partner or nuzzles it. Reciprocation appears to be necessary for prolonged LH behavior. The genital pore shows some swelling, or the genitals may be partially everted.

Labial probing of the region of the genitals (LG) (Figure 1C) occurs when a snail presses its mouth and labial palps on the genitals or on the skin next to the genitals of the partner. The oral probing is focused primarily in a region just posterior to the genital pore of the partner. This behavior can occur with or without genital eversion of either

Figure 1

Courtship behavior in *Helix aspersa*. A. Labial-head contact. B. Interruption of courtship. C. Labial-genital contact. This pair is in LG-1. D. IDS behavior is shown by the snail on the left; the snail on the right shows LG behavior.

the actor or recipient, although full genital eversion usually begins at this time. A full genital eversion occurs when the atrium is evaginated and swollen, and the female (vaginal, anterior) and male (penial, posterior) openings are visible. When the behavior occurs simultaneously and reciprocally in both snails, the everted genitals will be appressed and apposed. Genital apposition was not regarded as a separate behavior and was regarded as a result of the simultaneous orientation of the two partners in LG contact, because orientation of the snails towards each other did not appear to depend on genital apposition. LG behavior occurred before and after dart shooting, although with different consequences. LG behavior before dart shooting (LG-1) could not be distinguished from LG behavior after dart shooting (LG-2) except that each led to different behavioral acts in the courtship sequence.

Intention of dart shooting (IDS) (Figure 1D, snail on the left) is a behavior that is seen immediately before dart shooting; the term is borrowed from LIND (1976). A snail showing well-developed IDS behavior has shortened (but not invaginated) tentacles, a swollen and distended anterior head foot, very swollen and turgid genital eversion with a distension of the anterior (vaginal) region (where the dart sac is located), and a sole that is contracted and reduced in size. The snail in IDS pushes its everted genitals against its partner in a constant pushing motion. There appears to be no oral probing by the snail in IDS of its partner. The everted genitals and anterior headfoot are more swollen at this time than at any other time in courtship; this may be due to increased hydrostatic pressure caused by tensing of the body musculature of the foot and posterior headfoot. IDS persists only as long as the genitals are maintained in contact with the partner's body. The eversion may be pressed against any area of the partner, including the shell, and the pushing may result in the partner even being swept off the substrate and onto the snail in IDS. IDS is terminated by dart shooting. Occasionally, a snail may show very little or essentially no IDS behavior

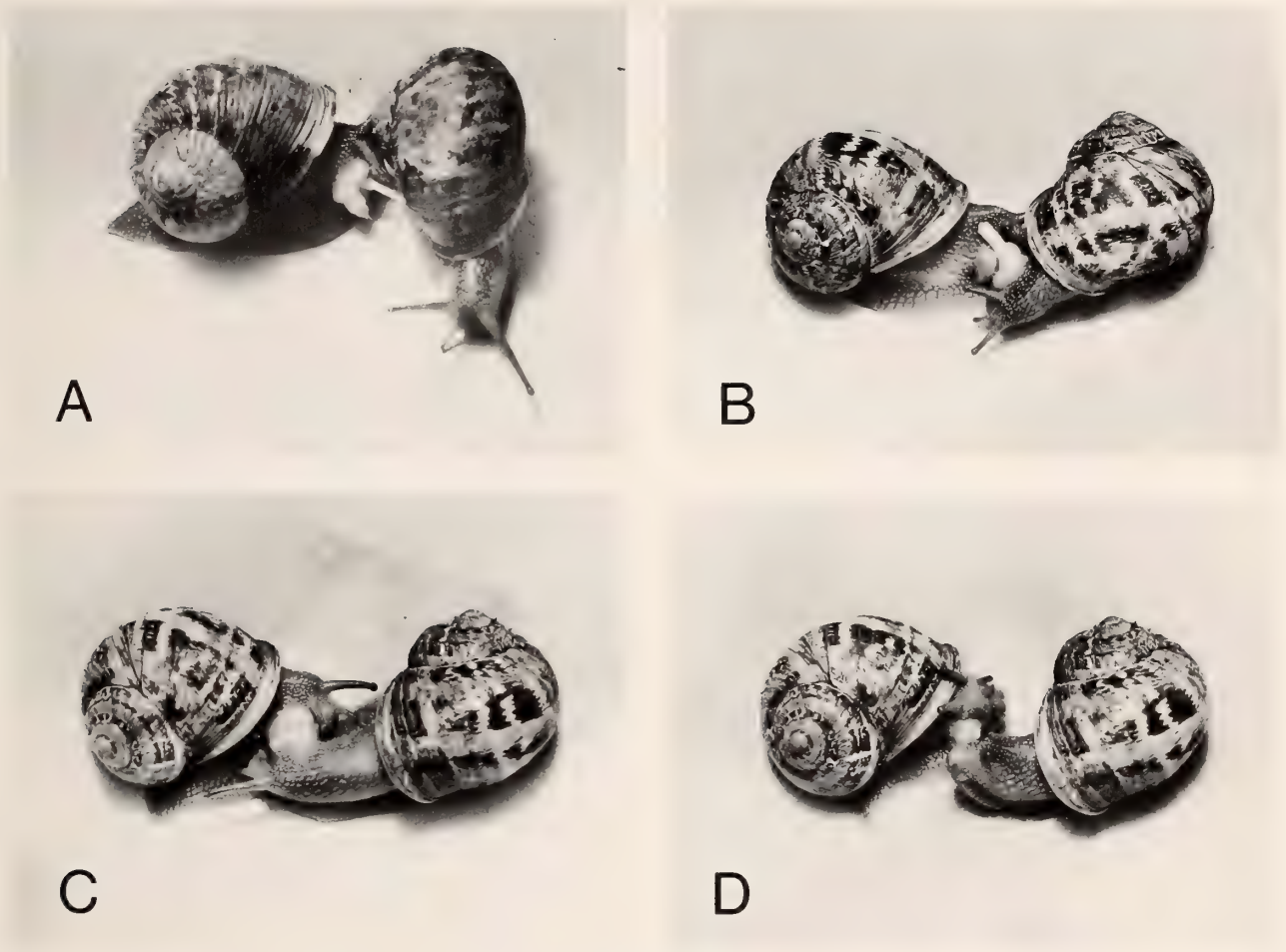


Figure 2

Courtship behavior in *Helix aspersa*. A. Dart shooting behavior shown by snail on the left. The dart of the snail did not penetrate well the partner and was withdrawn back into the dart sac. B. Penial eversion (AC) shown by snail on the right. C. Both snails going through AC. Note the swollen genitals. D. Copulating snails. Both snails have taken the "mating posture."

before dart shooting. Young snails have poorly developed IDS behavior (see below).

Dart shooting (DS) (Figure 2A) occurs when a snail quickly everts the basal tubercle of the dart sac out of its everted genitals. The dart, which is attached by its base to the tubercle in the base of the dart sac, is rapidly pushed from the dart sac and usually pierces the flesh of the partner. Virgin snails possess no dart (see Discussion), and DS behavior leads only to the rapid eversion of the fleshy tubercle in these snails. The eversion of the tubercle takes a fraction of a second, and withdrawal of the tubercle takes 3–10 sec. The dart is never propelled through the air, because it is firmly attached by its base to the tubercle until it is lodged in the partner's tissues. Once lodged in the partner, the dart is detached from the tubercle and is left in the partner. Occasionally, the dart either does not hit the partner or it does not lodge in the flesh and is withdrawn partially or entirely back into the dart sac. Once DS behavior has occurred, the dart is never used again. Dissections of snails that had withdrawn their darts back into the dart sacs showed that these darts are discarded into the bursal diverticulum shortly before reception of a spermatophore from the partner during copulation. A new dart starts to grow within 6 h after expulsion of a dart and is fully grown within 5 to 7 days after DS (see Dillaman, 1981; Tompa, 1982). During the expulsion of the dart, a globule of whitish mucus, probably from the mucous glands, is usually seen adhering to the dart. Immediately after DS, a snail may evert its penis once.

Penial eversion and attempted copulation (AC) (Figure 2B). Penial eversion occurs repeatedly until a snail either achieves intromission or courtship is broken off. In the normal development of AC behavior, the snail, while oriented with its everted atrium pressed against the body of

the partner, exhibits a momentary tensing of the body wall of the anterior headfoot. This is followed immediately by increased turgescence of the everted atrium and then by penial eversion. The everted penis (about 5–10 mm long) invaginates immediately if the snail does not achieve successful intromission; the total act takes less than 10 sec. After the act is over, the snail pauses before attempting copulation again. Normally, the everted atrium of a snail is pressed against the everted atrium of its partner (*i.e.*, the genitals are apposed) when AC occurs. However, a snail can also evert its penis when the everted atrium is pressed against the tail, shell, or any other part of its partner. Thus, tactile stimulation of the genitals appears to be necessary for AC behavior to be triggered.

Copulation (C) (Figure 2D) was defined by the externally observable behavior of obtaining successful intromission and adoption of the "mating posture." The deposition of sperm in the partner could usually not be verified without dissecting the partner after copulation. In successful intromission, the everted penis of a snail is allowed to penetrate the vagina of a partner and to lodge in the vaginal canal. The snail attaining intromission takes on the mating posture, where the head is lifted off the substrate, the tentacles are shortened and held vertically, and the snail remains immobilized until it deposits its spermatophore into the partner's bursal diverticulum.

In dissected specimens, the intromitted penis (about 2 cm long) is found to lie in the vagina of the partner; the swollen, bulbous head of the penis is lodged at the base of the bursal (spermathecal) stalk and free oviduct. Thirty minutes after achieving successful intromission, the penis is anchored in the vaginal canal to the extent that the snails cannot be pulled apart without physical injury. In this study, if a snail had intromitted and maintained the mating posture for at least half an hour, it was assumed to have gone on to complete copulation.

Tail following (TF). A snail showing tail following behavior follows the tail of its partner, either touching the tail with its oral region or closely following the tail. It is possible that a snail showing TF behavior is following the mucous trail of the partner, but this could not be determined with certainty. Usually, TF behavior is non-reciprocal, but occasionally two snails will follow one another's tail in a circle which eventually tightens up and leads to the snails meeting head to head.

Pauses (P). During a pause, a snail stops courtship activity, does not crawl around, and does not have its head oriented towards its partner. The snail may move its mouth or rasp at the mucus on the substrate. If it has an eversion, the eversion may decline. The muscles of the body are not tensed and the anterior headfoot is not swollen.

Biting (B). Biting was recorded as a separate act during any part of courtship outside of LH contact. The biting snail makes rasping movements against the skin of the partner, and the partner reacts by retracting slightly after each bite.

Interruptions (I) (Figure 1B). During an interruption, a snail crawls away from the partner. The snail may make a tight circling pivot and return within a few seconds, or the snail may crawl far away from the courtship spot. A long interruption may lead to withdrawal from courtship. If a snail has an eversion, the eversion declines.

Withdrawal from courtship (W) occurs when a snail ceases all courtship behavior, persistently avoids all contact with its partner, and crawls away from the courtship site and out of the observation arena.

COURTSHIP SEQUENCE

Two types of courtship sequences are observable in fully mature *Helix aspersa*: primary courtship and secondary courtship (Figure 3; terms from LIND, 1976). In addition, the courtship behavior in young snails just mature enough to court is qualitatively slightly different from that of fully mature snails.

A primary courtship sequence (Figure 3A) includes dart shooting behavior and is seen in courting snails with a fully formed dart and in virgin snails (which possess no dart) courting for the first time. A secondary courtship sequence (Figure 3B) does not include IDS or DS behavior and is seen in snails that have not yet fully grown a replacement for a dart shot in a previous courtship attempt. Whether or not a snail goes through a primary or a secondary courtship sequence appears to depend solely on the internal state of the animal and is not altered by the behavior of the partner it is courting. Thus, one snail of a courting pair may go through a primary courtship sequence while its partner may go through a secondary courtship sequence.

Orientation towards the partner in courtship occurs principally by physical contact with the tentacles and oral region, although some orientation towards mucous trails or the thick patch of mucus that develops at the courtship site may also occur. Orientation towards the partner and a certain amount of synchrony in behavior is necessary for courtship to continue.

Primary Courtship Sequence

The behavior sequences of 34 pairs of snails are summarized in a simplified diagram (Figure 3A). These snails were part of a group of 36 pairs used for quantitative analysis in this study. The number of pairs in which the acting snail made a transition from one behavior to another in the sequence is given next to each arrow. The diagram says nothing about the synchrony or lack of synchrony between the partners. However, because the snails are simultaneous hermaphrodites, and both snails go through the same basic sequence, the numbers given are those for pairs and not individuals.

The diagram does not show pauses, and it does not show two atypical pairs: (1) one pair in which a snail in LG-1 withdrew from courtship after its partner (which had no

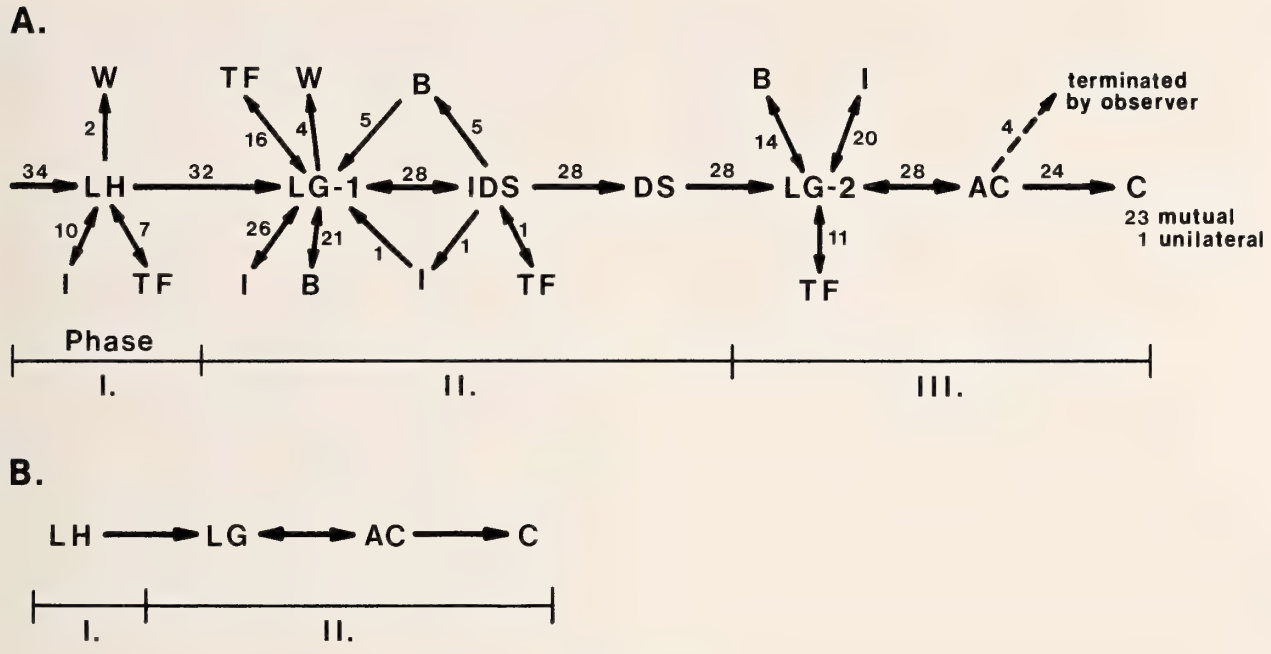


Figure 3

Diagram of courtship behavior in *Helix aspersa*. The number of courting pairs making the transition from one behavior to another is shown next to the arrow. Behaviors of actors (not recipients) are shown. Pauses are not shown. Complicated interactions between B, I, and TF are for the most part not shown. 3A. Primary courtship sequence. 3B. Simplified diagram for secondary courtship sequence. Biting, interruptions, withdrawals, and tail following not shown. LH, labial-head contact; LG-1, labial-genital contact before dart shooting; IDS, intention of dart shooting; DS, dart shooting behavior; LG-2, labial-genital contact after DS; AC, attempted copulation (penial eversion); C, copulation; B, biting; I, interruption; TF, tail following; W, withdrawal from courtship.

dart) went through DS, and (2) a pair in which one snail ejaculated alone without copulating (ignoring its partner) after going through DS. Observations on 4 of the 28 pairs reaching AC were terminated when it was noticed that they had great difficulty achieving mutual intromission. Although these four pairs probably would have eventually attained intromission, the terminations are indicative of the number of snails having difficulty in synchronizing their behavior to effect copulation.

The courtship sequence is basically linear (Figure 3A). There are three phases in primary courtship: (1) an introductory phase (Phase I) which consists of LH behavior, (2) a dart shooting phase (Phase II) which consists of LG behavior (LG-1) leading to DS, and (3) a copulation phase (Phase III) which consists of repeated AC during LG behavior (LG-2) leading to successful intromission.

The diagram of courtship behavior for 34 pairs shown in Figure 3A accurately reflects the variation in courtship behavior of this species. The behavior sequence and certain aspects of courtship related to DS behavior are fairly rigid. Observations of more than 150 courting snails indicate that DS is not a conditional behavior and always occurs in snails with a fully formed dart and in virgin snails courting for the first time. The timing of AC in the courtship sequence also appears to be rigid; AC occurs only after the actor has gone through DS and does not depend on receipt of a dart from its partner. The timing of withdrawals may also be constrained; it is noticeable in Figure 3A that no snail withdrew from courtship after it had gone through DS; withdrawals late in courtship may be relatively rare.

Variation in courtship behavior in *Helix aspersa* is seen chiefly in (1) the number of bites (B), interruptions (I), and TF episodes, (2) the degree of development of IDS behavior, (3) the type of dart wound, (4) the number of AC occurring before copulation, and (5) the success of mutual, reciprocal intromission during copulation.

IDS behavior can be virtually absent, partially developed (in young snails), or be fully developed. Omission of IDS behavior was found to be significantly associated with known and presumed virgin snails (snails without darts going through DS): only 5 of 14 snails (36%) showing no IDS possessed darts, while 38 of 44 snails (86%) showing IDS possessed darts ($P < 0.01$, two-tailed Fisher's exact test).

In snails showing normal IDS behavior, maintenance of IDS appears to depend, in part, on the partner's movements. A snail in IDS pushes indiscriminately against the

partner's body and does not orient itself well towards its partner. If the partner does not orient itself towards the snail in IDS, physical contact with the genitals of the snail in IDS will be lost and IDS will cease. Thus, the partner's movements, in large measure, determine where in its body it receives a dart.

Whereas DS behavior always occurs in a primary courtship sequence, the degree and location of dart penetration into the partner varies. In a group of 42 darted snails, penetration varied as follows: the dart was completely lost in the hemocoel of 6 snails (14%), pushed partly into the body and left there in 26 snails (62%), or pushed partly into the body but then withdrawn back into the dart sac of the shooter in 10 snails (24%).

In a group of 57 darted snails, the location of dart penetration varied as follows: 2 snails were darted on the left side of the headfoot (3%); 8 snails were darted on the right side of the headfoot, anterior to the genitals (*i.e.*, in the head) (14%); 19 snails were darted on the right side of the headfoot, posterior to the genitals (33%); 4 snails were darted in the sole close to the mouth or on the mouth (7%); 16 snails were darted in the sole away from the mouth (28%); 1 snail had the dart pierce its everted penis (2%); 1 snail was darted in the penial lobe (2%); 5 snails were darted in the vaginal lobe (9%); and 1 snail was not hit by the dart at all (2%). None of the five darts that hit the vaginal lobe penetrated well; the darts penetrated less that 2 mm and fell out. This may have been due to the fact that the vaginal lobe includes the collar of the dart sac, which is hardened with numerous, tiny calcium carbonate crystals (see TOMPA, 1982). In contrast, in only 3 of the 16 snails darted in the sole and in only 1 of the 19 snails darted in the headfoot posterior to the genitals did the dart penetrate poorly and fall out.

Snails that go through DS behavior but have no dart are virgins and do not inflict a wound on their partners; these snails will begin to grow a dart after this first attempt at DS (see CHUNG, 1986b).

The timing of DS—both the time from the start of courtship to DS and the relative synchrony of DS behavior between partners—is also variable (see quantitative analysis below).

Spermatophore release and reception almost always occur in the context of reciprocal and simultaneous intromission. However, a few pairs intromit non-reciprocally—"unilateral copulation," with one male- and one female-acting snail (3 of 71 pairs, or 4%)—and a few snails were observed to take on the mating posture without intromitting and to ejaculate without a partner, after an otherwise normal courtship (2 of 88 snails, or 2% of individuals). Self-copulation was never observed.

The behavior of snails in AC indicates that copulation is not attained until a snail allows intromission by its partner, and it appears that a snail will normally not allow intromission unless it too achieves intromission at the same time. Copulation cannot apparently be forced on an unwilling partner in these snails, because the entrance to the vagina is normally closed by a sphincter muscle, which is relaxed only when the snail is also everting its own penis, and the closed sphincter cannot be penetrated by the soft penis. Simultaneous intromission is complicated by the fact that snails of a courting pair rarely shoot darts simultaneously (see below), and thus AC behavior following DS is not synchronized between the snails until after both have gone through DS behavior. To attain copulation, two snails must have their genitals perfectly apposed, go through AC simultaneously, and allow intromission of the partner. The momentary turgescence of the everted genitals immediately preceding AC may be a tactile cue or a stimulus to trigger AC in the partner. However, in spite of this possible cue, AC frequently fails. Transient unilateral intromission is frequent but is almost always terminated. When a snail gains unilateral intromission, it assumes the mating posture, but the partner does not go into the mating posture and immediately pulls away from the first snail or bites at its penis until it is dislodged, or it "ejects" the penis, with the penis appearing to be shoved out of the vagina.

Snails ejaculating without a partner and those allowing unilateral copulation (female-acting snails) behaved similarly to each other in that both acted as though they had attained intromission, although they had failed to penetrate their partners during AC. These snails attempted copulation with their partners, failed to intromit successfully, and then went into the mating posture with their penes everted slightly (3 mm long) and projected anteroventrally. The snails that mated non-reciprocally either remained in the mating posture until they expelled their spermatophores from their penes onto the ground or they eventually came out of the mating posture after 30 min and quietly coupled with their male-acting partners. Because it takes about 30 min for the penis to be anchored and effectively locked in the vaginal canal, it was assumed that these female-acting snails had no alternative but to remain united with their partners after 30 min had passed. The few snails taking on the mating posture without obtaining intromission were considered to be behaving abnormally; snails that did this did not appear to be morphologically abnormal.

The duration of primary courtship varies considerably. The time from start of courtship to DS averages 35 ± 19 min ($\bar{x}$ ± SD; n = 63 snails, range: 1–75 min). The time from DS to C usually takes 15–45 min, although a few pairs take more that 4 h to attain copulation after both have gone through DS.

Copulation was not studied in detail and was marked by little external behavior. The duration of copulation was not recorded for most snails but was observed to last from 4 to over 12 h. In a sample of 20 pairs, spermatophores were found forming in the penial flagellum and penis between 1 and 6 h after start of copulation. Transfer of the spermatophore from the penis to the bursal diverticulum of the partner occurs slowly over the last half of the

copulatory period and is usually not strictly simultaneous for both snails. Once a snail transfers its spermatophore, it comes out of the mating posture, retracts its penis, and waits for its partner to finish.

Secondary Courtship

Secondary courtship is seen only in snails that have gone through DS within the previous 5–7 days and have not yet grown a fully formed dart in the dart sac. These are snails that either have recently mated or recently gone through an unsuccessful courtship (through DS). Secondary courtship was not analyzed quantitatively. It is essentially like a primary courtship sequence without a dart shooting phase (Figure 3B) and is of much shorter duration than primary courtship. The first phase is an introductory phase that is qualitatively like the introductory phase of primary courtship. The second phase is a copulation phase that is also qualitatively like the copulation phase in primary courtship. *Helix aspersa* has the ability to mate twice within a 24-h period (one primary and one secondary courtship) and pass two full spermatophores to its partners. This does not occur frequently, as the majority of snails appear to become refractory to mating for at least two days after a primary courtship.

Courtship in Young Snails

Young *Helix aspersa* that have not yet grown a deflected lip on the shell show courtship behavior like that of fully adult snails, except that IDS behavior is not well developed, and snails in IDS tend to slide rather than press their genitals against the body of the partner (10 of 12 snails, or 83%). These snails have mature ovotestes (*i.e.*, they have sperm and mature oocytes), and they have pallial gonoducts that appear to be mature in shape and nearly of adult size. Some of these snails laid fertile eggs after mating. This type of precocious mating has been observed before in *H. aspersa* (Cowie, 1980) and in other stylommatophorans (Baur, 1984).

Quantitative Analysis of Courtship Behavior Related to Dart Shooting

Of the 34 pairs of snails in Figure 3A that went through a primary courtship sequence, enough data were available on 30 pairs to analyze (1) the timing of DS in courtship, and (2) the effect of dart receipt on courtship behavior. Seventeen of the 30 snails (28%) possessed no darts but showed DS behavior. The histories of these snails were unknown, and the possession of a dart by a snail before DS was unknown to the observer. This natural difference between snails allowed comparisons of courtship behavior to be made between snails receiving darts and those not receiving darts, in addition to the comparisons that could be made between behaviors before and after DS in those snails that received darts.

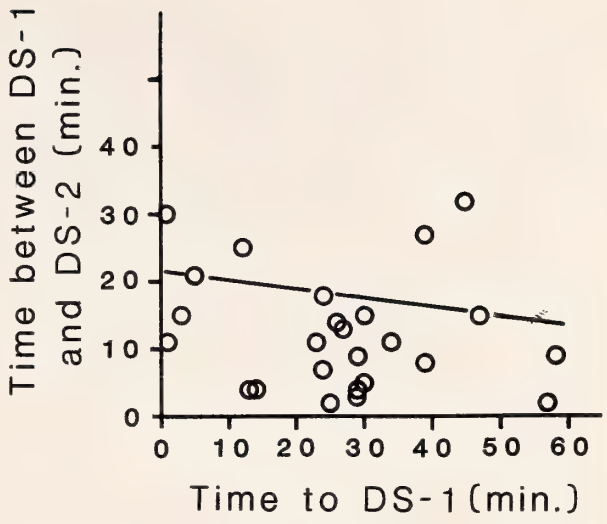


Figure 4

Time between dart shootings (DS-1 and DS-2) vs. time from start of courtship to the first dart shooting. Two groups were pooled—pairs in which both partners possessed darts and pairs in which only the second shooter possessed a dart—because the regression lines for each of the two groups had slopes and y-intercepts not significantly different from one another ($P > 0.10$, two-tailed t-tests). Both shooters with darts: $Y = -0.036X + 13.575$, $r = -0.056$ ($n = 15$). Only second shooter with dart: $Y = -0.285X + 18.222$, $r = -0.300$ ($n = 10$). Pooled data: $Y = -0.13X + 21.29$, $r = -0.186$ ($n = 25$). In all three lines r is not significantly different from zero ($P > 0.10$, two-tailed t-tests).

Data from the 30 pairs could be grouped according to the relative order in which they went through DS and whether or not they possessed a dart (see Table 1). The data indicate that snails probably do not choose their partners assortatively by possession of a dart, because there is no significant difference between the observed and expected numbers of pairs in which both snails possess darts (observed, 15 pairs in which both snails possessed darts, vs. expected, 16 pairs; $P > 0.10$, two-tailed binomial test).

Table 1 shows that the timing of DS during courtship appears to vary greatly and appears to be affected by the condition or age of the snail. The average time from the beginning of courtship to DS in the first shooter varies from 1 to 58 min, with a mean of 26 min. Table 1 shows that in pairs formed of one partner without a dart and one partner with a dart, snails lacking a dart are likely to go through DS first (10 vs. 3 pairs; $P < 0.05$, one-tailed binomial test; assuming *a priori* $p = q = 0.5$). A pair-wise comparison of the row marginals for the time to first DS gives a similar result. There is a significant difference in the time to first DS between snails without darts (16.8 min) and snails with darts (32.4 min) ($P < 0.01$, one-tailed Wilcoxon two-sample test). A comparison of the time to first DS between snails lacking darts and snails possessing darts, both mated to partners with darts (the first column on the left in Table 1), also shows that snails

Table 1

Helix aspersa. Time to DS-1 from start of courtship. $\bar{x} \pm$ SD; sample size in parentheses.

	Second shooter		
First shooter	With dart	Without dart	Totals
With dart	34.4 ± 13.7 (15)	22.7 ± 5.1 (3)	32.4 ± 13.4 (18)
Without dart	14.8 ± 10.8 (10)	26.5 ± 30.4 (2)	16.8 ± 14.2 (12)
Totals	26.6 ± 15.8 (25)	24.2 ± 15.8 (5)	26.2 ± 15.5 (30)

Table 2

Helix aspersa. Time between DS-1 and DS-2. $\bar{x} \pm$ SD; sample size in parentheses.

	Second shooter		
First shooter	With dart	Without dart	Totals
With dart	16.5 ± 10.7 (15)	27.3 ± 12.3 (3)	18.3 ± 11.4 (18)
Without dart	19.9 ± 11.8 (10)	16.0 ± 11.3 (2)	19.2 ± 11.0 (12)
Totals	17.4 ± 11.4 (25)	22.8 ± 12.1 (5)	18.7 ± 11.2 (30)

lacking darts go through DS sooner (14.8 min) than snails possessing darts (34.4 min); ($P < 0.01$, one-tailed Wilcoxon two-sample test). This last result is essentially equivalent to the test on the row marginals, because the condition of the second shooter appears to make no difference on the time to DS in the first shooter ($P > 0.05$, two-tailed Wilcoxon two-sample tests on the upper row—34.4 vs. 22.7 min—and column marginals—26.6 vs. 24.2 min). Comparisons involving the data on the two pairs where both partners lacked darts cannot be made, owing to the small sample size of this group.

The time that the second shooter took to go through DS after its partner went through DS is shown in Table 2. A comparison of the column marginals (17.4 vs. 22.8 min) in Table 2 shows that the condition of the second shooter (possession or non-possession of a dart) does not appear to affect the timing of DS in the second shooter ($P > 0.05$, two-tailed Wilcoxon two-sample test). However, comparison of the two cells of the upper row of Table 2 indicates that snails without darts are significantly slower to go through DS (27.3 min) than snails with darts (16.5 min) ($P < 0.025$, one-tailed Wilcoxon two-sample test). These results indicate that snails without darts are perhaps more easily injured or slowed down by dart receipt than snails with darts.

As shown in Table 2, there is no synchrony in DS between the two partners; second shooters take an average of 19 min (range: 4–41 min) to go through DS after the partner has gone through DS. Also, a plot of the time between the first and second DS versus the time to the first DS for the 25 pairs in which the second shooter possessed a dart (Figure 4) shows no correlation between the two variables ($P > 0.05$, two-tailed t-test of H_0: slope = 0). These results indicate that courting snails tend to space their DS behavior apart, although the data do not indicate what cues the snails use to achieve this. Receipt of a dart does not appear to be the cause of the spacing of DS, because the regression line for the group in which the second shooter received a dart (first shooter possessed a dart) appears to be coincident with the regression line for pairs in which the second shooter received no dart (first shooter lacked a dart) (two-tailed t-tests for equal slopes and Y-intercepts, $P > 0.05$).

The data in Table 2 can also be used to test the effect that dart receipt has on subsequent courtship behavior, because the time between the first and second DS can be used as a measure of how quickly the second shooter makes the transition to the copulation phase after the partner has gone through DS. A comparison of the row marginals in Table 2 shows that snails receiving a dart do not take a significantly shorter time to make the transition to the copulation phase than snails not receiving a dart (18.3 min vs. 19.2 min, respectively; $P > 0.05$, two-tailed Wilcoxon two-sample test). The same result is obtained when comparing the cells on the left in Table 2 (second shooter with a dart, first shooter with or without a dart) (16.5 min vs. 19.9 min; $P > 0.05$, two-tailed Wilcoxon two-sample test).

The effect of dart receipt was examined on three other measures of courtship behavior: (1) rate of biting, (2) fraction of time spent away from genital contact (FTC), and (3) rate of AC. Data were most complete for pairs in which the second shooter possessed a dart, and tests for the effect of dart receipt on courtship were performed only on this group (equivalent to the two cells of the column on the left in Table 1). Two types of tests were performed. The first type of test was a comparison of the behavior of snails receiving a dart versus snails not receiving a dart—*i.e.,* the behavior in the group where the first shooter had a dart versus the group where the first shooter lacked a dart. The second type of test, performed on the same variables, was a comparison between the behavior of snails before and after receiving a dart, in the group where both snails possessed darts.

In addition to these tests on dart receipt, the effect of dart *shooting* on a snail's behavior was examined. The rate of biting and the fraction of time spent out of genital contact (FTC) were each compared for the first shooter before and after it went through DS, in the group where both snails possessed darts.

The variables were defined as follows.

(1) *Biting rate:*

$$\text{(a) before partner went through DS} = \frac{\text{\# bites initiated by snail from beginning of LG-1 to DS-1}}{T_{\text{before receipt}} - TC_{\text{before receipt}}}$$

$$\text{(b) after partner went through DS} = \frac{\text{\# bites initiated by snail between DS-1 and DS-2}}{T_{\text{after receipt}} - TC_{\text{after receipt}}}$$

Both (a) and (b) calculated for the second shooter.

$$\text{(c) before going through DS} = \frac{\text{\# bites initiated by snail from beginning of LG-1 to DS-1}}{T_{\text{before shooting}} - TC_{\text{before shooting}}}$$

$$\text{(d) after going through DS} = \frac{\text{\# bites initiated by snail between DS-1 and DS-2}}{T_{\text{after shooting}} - TC_{\text{after shooting}}}$$

Both (c) and (d) calculated only for the first shooter.

(2) *Fraction of time spent out of genital contact* (FTC):

$$\text{(a) before partner went through DS} = \frac{TC_{\text{before receipt}}}{T_{\text{before receipt}}}$$

$$\text{(b) after partner went through DS} = \frac{TC_{\text{after receipt}}}{T_{\text{after receipt}}}$$

Both (a) and (b) calculated for the second shooter.

$$\text{(c) before going through DS} = \frac{TC_{\text{before shooting}}}{T_{\text{before shooting}}}$$

$$\text{(d) after going through DS} = \frac{TC_{\text{after shooting}}}{T_{\text{after shooting}}}$$

Both (c) and (d) calculated only for the first shooter.

(3) *Rate of AC:*

$$\text{(a) before partner went through DS} = \frac{\text{\# of AC from DS-1 to DS-2}}{\text{time from DS-1 to DS-2 (min)}}$$

$$\text{(b) after partner went through DS} = \frac{\text{\# of AC from DS-2 to C}}{\text{time from DS-2 to C (min)}}$$

Both (a) and (b) calculated for the first shooter, and (b) also calculated for the second shooter.

$T_{\text{before receipt}}$ = total time the second shooter spent in dart shooting phase before partner went through DS (time from beginning of LG-1 to DS-1, in min)

$T_{\text{after receipt}}$ = total time the second shooter spent in dart shooting phase after partner went through DS (time from DS-1 to DS-2, in min)

$T_{\text{before shooting}}$ = total time the first shooter spent in dart shooting phase before it went through DS (time from beginning of LG-1 to DS-1, in min)

$T_{\text{after shooting}}$ = total time the first shooter spent in copulation phase after going through DS and before being darted by its partner (time from DS-1 to DS-2, in min)

$T_{\text{before receipt}} = T_{\text{before shooting}}$; $T_{\text{after receipt}} = T_{\text{after shooting}}$

$TC_{\text{before receipt}}$ = time from LG-1 to DS-1 spent in I + TF + P that the second shooter initiated (min)

$TC_{\text{after receipt}}$ = time from DS-1 to DS-2 spent in I + TF + P that the second shooter initiated (min)

$TC_{\text{before shooting}}$ = time from beginning of LG-1 to DS-1 spent in I + TF + P that the first shooter initiated (min)

$TC_{\text{after shooting}}$ = time from DS-1 to DS-2 spent in I + TF + P that the first shooter initiated (min)

DS-1 = first DS, DS-2 = second DS. LG-1 begins for both partners at the same time.

A comparison of snails that received a dart with snails that received no dart shows that there are no significant differences in the means for biting rate and FTC between these two groups (Table 3A). Similar tests for the effect of dart receipt (Table 3B) shows that there are no significant differences in the mean biting rate and mean FTC before and after dart receipt. However, a signed ranks test for equal variances shows that the variance in biting rate is greater in snails that received a dart than in snails that received no dart (Table 3A). There is no statistically significant difference in the variances of snails receiving and snails not receiving a dart in FTC (Table 3A). These results suggest that dart receipt has no influence on FTC but that dart receipt (or a behavioral change associated with DS in one or both of the partners) has an effect on the biting rate. Dart receipt appears to cause a heterogeneous change in the rate of biting—an increase in biting rate in a few snails and a decrease in others, so that the variance in the biting rate increases.

Tests of the effect of dart receipt on the rate of AC (Table 4) yielded results that appear contradictory. Snails receiving a dart have a significantly lower rate of AC than those not receiving a dart (Table 4A; for second shooters). However, the rate of AC after dart receipt is significantly higher after than before dart receipt in first shooters (Table 4B). The differences in the results may possibly be explained by the differences in the two types of tests. Probably the best intepretation of the results is that dart receipt causes a decrease in the rate of AC and that the IDS

Table 3

Helix aspersa. Effect of dart receipt on biting rate and FTC. $\bar{x} \pm$ SD; n = sample size.

A. Snails receiving a dart (the first snail to receive a dart in pairs in which both snails have darts) vs. snails not receiving a dart (partner did not possess a dart).

	Received dart	Received no dart
Biting rate[1]	0.24 ± 0.52 n = 15	0.02 ± 0.04 n = 10
FTC[2]	0.30 ± 0.25 n = 15	0.14 ± 0.19 n = 10

B. Before vs. after dart receipt in pairs where both partners possessed darts.

	Before receipt	After receipt
Biting rate[3]	0.08 ± 0.06 n = 11	0.33 ± 0.60 n = 11
FTC[4]	0.17 ± 0.12 n = 15	0.30 ± 0.25 n = 15

[1] Variances, but not means, significantly different. $P > 0.10$, one-tailed Wilcoxon two-sample test for means; $P < 0.001$, one-tailed squared ranks test for equal variances.

[2] Variances and means not significantly different. $P > 0.10$, two-tailed Wilcoxon two-sample test for means; $P > 0.05$, one-tailed squared ranks test for equal variances.

[3] Difference between means not significantly different. $P > 0.10$, two-tailed Wilcoxon test for paired observations.

[4] Difference between means not significantly different. $P > 0.10$, two-tailed Wilcoxon test for paired observations.

Table 4

Helix aspersa. Effect of dart receipt on rate of AC. Rate: $\bar{x} \pm$ SD; n = sample size.

A. Snails receiving a dart vs. snails not receiving a dart.[1]

Received dart	Received no dart
0.53 ± 0.17 n = 13	0.83 ± 0.23 n = 8

B. Before vs. after receiving a dart.[2]

Before receipt	After receipt
0.47 ± 0.63 n = 13	0.56 ± 0.21 n = 13

[1] Means, but not variances, significantly different. $P < 0.05$, two-tailed Wilcoxon two-sample test for equal means; $P > 0.10$, two-tailed squared ranks test for equal variances.

[2] Differences between means significantly different. $P < 0.05$, two-tailed Wilcoxon test for paired observations.

behavior of the partner depresses the rate of AC in a snail to a possibly greater degree than that caused by dart receipt. The snails in Table 4A interacted with a partner that had already passed into the copulation phase and was also attempting copulation. In contrast, the snails in Table 4B that had not yet received a dart were interacting with partners in IDS; and it was observed in this study that IDS behavior in a snail frequently made it difficult for a partner to court. If IDS in a snail suppresses the rate of AC in a partner, then the rate of AC in the partner may increase after the snail has gone through DS, in spite of the partner's receipt of a dart wound.

By comparison to the mostly negative effects of dart receipt on the courtship behavior of the receiver, dart shooting has a pronounced effect on the shooter. It has already been noted that penial eversion and attempted copulation never occurs before dart shooting in snails going through primary courtship. Another behavioral change appears to be a decrease in the rate of biting after dart shooting (Table 5). FTC appears to be unaffected by dart shooting (Table 5).

DISCUSSION

Major differences in courtship behavior between *Helix aspersa* and *H. pomatia* are seen in the courtship positions used to maintain physical contact and in the method of spermatophore transfer. To maintain physical contact, courting individuals of *H. pomatia* lift the anterior region of the soles off the substrate and press them together, while courting *H. aspersa* remain with their soles on the substrate and press their genitals together. Copulation in *H. pomatia* is of brief duration (spermatophores expelled in 4.5 min; intromission lasting 5.6 min), and part of the spermatophore is deposited external to the genital opening (LIND, 1973, 1976), whereas in *H. aspersa* virtually the entire spermatophore is transferred directly into the partner's genitals over a period of an hour or more towards the end of an intromission that lasts 6 h or longer.

A comparison of the overall courtship sequences of *Helix aspersa* and *H. pomatia* shows that major aspects of dart shooting behavior are similar in both species. The integration of DS behavior in the courtship sequence of *H. aspersa* is like that of *H. pomatia* in that (1) the possession of an immature dart is always accompanied by a secondary courtship sequence, (2) DS behavior is never omitted (*i.e.*, is not a conditional behavior) in a primary courtship sequence, and (3) AC never takes place in primary courtship until after a snail has gone through DS. In both species the courtship sequence is fairly rigid, and the type of courtship sequence that a snail goes through is strictly associated with the contents of its dart sac and not with the condition of the partner.

In addition to the association of the type of courtship sequence with the contents of the dart sac, there is an association between the absence of a dart in a snail going through DS and the prior sexual history of the snail. CHUNG (1986b) found that virgin *Helix aspersa* lack darts (an hypothesis proposed in the last century by BOUCHARD-CHANTEREAUX, 1839) and that at least 95% of the virgin snails start growing darts after going through an initial DS. (All fully adult, non-virgin *H. aspersa* possess

Table 5

Helix aspersa. Effect of dart shooting on rate of biting and FTC on snails that shot their dart first. $\bar{x} \pm$ SD; n = sample size.

	Before shooting	After shooting	n
Biting rate[1]	0.11 ± 0.08	0.05 ± 0.07	11
FTC[2]	0.18 ± 0.10	0.19 ± 0.23	15

[1] Means significantly different. $P < 0.05$, two-tailed Wilcoxon test for paired observations.

[2] Means not significantly different. $P > 0.10$, two-tailed Wilcoxon test for paired observations.

darts.) Thus, a snail going through DS but not possessing a dart is likely to be a young snail.

Because the presence or absence of DS and the possession or lack of a dart during DS behavior reflect the reproductive condition of the shooter, a snail might be able to assess the physical condition of a partner by the presence or absence of DS behavior or a dart in the partner. For instance, receipt or non-receipt of a dart might be used by a snail to decide on whether or not to continue with courtship and copulation. However, there is little evidence from either the courtship sequences (Figure 3) or the quantitative tests that this occurs. In only one of 34 pairs going through a primary courtship sequence did a snail withdraw from courtship after its partner went through DS (its partner had no dart); and snails receiving darts appear to be more likely to reduce their rate of attempted copulation rather than increase it (Table 4). The decrease in the rate of AC in snails receiving darts indicate that snails are physically hurt by dart receipt.

DS is unlikely to be used by a shooter to test the vigor or readiness of a partner, because (1) snails appear to be harmed by dart receipt and (2) none of the snails that withdrew from courtship withdrew after receiving a dart. It is unlikely on theoretical grounds that DS is used by a shooter to test the vigor of a partner, because there is a prolonged period of courtship that takes place before dart shooting in which snails can assess one another. Dart shooting is also unlike a final act in an escalated aggressive display, because dart shooting is not a conditional behavior in the courtship of snails that possess a fully formed dart.

The results of the quantitative tests on dart shooting in *Helix aspersa* are similar to the resutls of tests on *H. pomatia* (Lind, 1976; Jeppesen, 1976) in that they show that dart receipt apparently has no obvious stimulatory effect on snails of either species. Lind (1976) tested the following hypotheses on the effect of dart receipt: (1) receipt was a prerequisite for carrying through copulation, (2) receipt caused an immediate increase in the intensity of mating activity, (3) receipt caused a decrease in the latency of mating activity after dart receipt, and (4) receipt sped subsequent pre-copulatory behavior. Lind could not prove any of the hypotheses. The first hypothesis was rejected by both Lind and Jeppesen and is also rejected in this paper, because both *H. pomatia* and *H. aspersa* that have shot darts will attempt copulation whether or not they receive darts. Thus, dart receipt in these two species does not act to trigger copulatory behavior and does not appear to signal a snail's vigor to its partner. The tests of the effect of dart receipt on the rate of AC and on FTC reported here are essentially tests of Lind's second hypothesis, and the results of the tests (Tables 3, 4) do not support this hypothesis.

Goddard (1962) believed that the injury to the body caused by dart receipt in *Helix aspersa* stimulated an "injury discharge" from the nervous system that subsequently induced penial activity at the time of copulation. His hypothesis appears to be incorrect, as this study and Lind's (1976) study show that dart receipt does not cause penial eversion.

The test of the effect of dart receipt on the biting rate reported here is, in part, a test of Webb's (1952b) hypothesis that darts are used to stimulate courtship and also prevent a partner from biting the shooter's genitals. Webb's hypothesis could not be verified. The test on biting rate (Table 3) appears to indicate that dart receipt causes some snails to decrease their rate of biting and others to increase their biting rate, although the average rate does not change significantly. The cause of this heterogeneity in response is unknown but may be due to an underlying heterogeneity in the vigor or reproductive condition of darted snails.

The effect of dart receipt may possibly be delayed until after courtship, or the dart may influence the physiology of the snail. Tompa (1980, 1984) suggested that the effect of dart receipt may be to stimulate maturation and release of ova in a recipient snail, and thereby increase the chances of fertilization of eggs by the dart-shooting snail. This hypothesis has not been tested directly. Dorello's (1925) and Bornchen's (1967) hypothesis that darts are used to convey stimulatory substances from the mucous gland secretions into the circulation of a darted snail suggests that the primary effect of dart receipt may be a physiological change that may not greatly affect specific courtship behaviors.

The hypothesis that darts are used to inoculate a snail with bioactive mucous gland secretions was tested by Chung (1986a). Injection of mucous gland extract into non-courting snails caused genital eversions similar to those seen in courting snails; topical application of the extract had no effect on the behavior of assayed snails. The results of the study suggested that the bioactive substance in the mucous glands (possibly a peptide) stimulates the simultaneous relaxation of the muscles of the terminal genitals and contraction of the body wall musculature to cause genital eversion. No great changes in genital eversion were seen in courting *Helix aspersa* that received a dart in this study and none were noted in the studies of Lind (1976) and Jeppesen (1976) on *H. pomatia*. This might be explained by the fact that courting snails almost always have a full

genital eversion at the time of dart receipt, and any further change in the condition of the genitals after dart receipt cannot be detected easily in behavioral observations.

The courtship observations made on *Helix aspersa* and observations made on other dart-bearing land snails suggest two possible effects of dart receipt that are inconsistent with the physical stimulation hypothesis (as defined by GODDARD, 1962, and by LIND, 1976) but are not inconsistent with the chemical stimulation hypothesis (as developed by CHUNG, 1986a). Dart receipt may (1) cause a snail to slow its movements and remain quiescent during the copulation phase of courtship, or (2) affect the functioning of the penis.

The *Helix aspersa* observed in this study appeared to crawl more slowly after receiving a dart, although the average crawling speed could not be quantified. The slowing of movement may be due to the physical injury of dart receipt; however, mucous gland secretions might possibly affect the muscles used for crawling. WEBB (1952b) suggested from courtship observations that dart receipt in helminthoglyptids prevent premature withdrawal during transmission of the spermatophore. However, this hypothesis has never been tested.

Darting of the penis has been observed in a few species and may be a function of the dart in some species. The fusion of the male and female tracts near the genital aperture in stylommatophorans would appear to allow the dart to be shot into the everted genitals of mating partners; and the anatomical placement of the dart sac on the vagina in many species of dart-bearing snails would appear to allow the darting of the penis during copulation. The penis is almost never darted in *Helix aspersa,* and darts are always shot before intromission in this species, but darting of the penis might occur regularly in *Philomycus carolinianus* and species of *Ventridens.* WEBB (1968a) reported that the dart in *Philomycus* injures the partner's penis during copulation. The dart is also reported to pierce the everted penis, along with other organs, during courtship and copulation in *Ventridens* (WEBB, 1968b). Whether the non-deciduous dart in *Philomycus* and *Ventridens* is used to impair the functioning of the male organs or is used as a kind of holdfast was not determined by Webb. In this study, only one *H. aspersa* (about 1% of more than 100 snails observed) received a dart in its everted penis; this snail could not achieve intromission and copulated as a "female" (allowing intromission and accepting a spermatophore but not secreting a spermatophore). This unusual case cannot be regarded as normal, but the suppression of male functioning by the dart in this case is interesting. The dart in *H. aspersa* and other helicids cannot be used as a holdfast, because it is deciduous.

The morphology and anatomical placement of the dart indicate that the darts in most dart-bearing species with non-deciduous darts do not function as purely physical holdfasts, in the way that penial hooks function. None of the published observations of dart shooting behavior clearly shows a dart being used as a holdfast, although the thin, curved dart of *Ventridens* might theoretically be able physically to restrain a partner. KÜNKEL's (1929, 1933) hypothesis that the hollow, perforated dart of *Vitrina elongata* is used as a suction cup for holding onto the shell of the partner seems unlikely. Künkel did not demonstrate how effective suction could be applied from a dart tip that has a diameter of 0.078 to 0.094 mm, on a partner about 1 cm long; and no one has demonstrated a suction mechanism in the dart apparatus of *Vitrina elongata* or in any other dart-bearing species.

Adaptive Significance of the Dart Apparatus

Observations on the courtship behavior of *Helix aspersa* and other dart-bearing snails have not been able to determine the adaptive significance and evolution of dart-shooting behavior, but the data from this and other studies indicate that the dart apparatus may have arisen in the context of sexual selection in simultaneous hermaphrodites. There are three general evolutionary models that could account for the evolution of the dart apparatus: (1) the reproductive isolation model, (2) the courtship co-ordination model, and (3) the sexual selection model. The data on dart-shooting and reproductive behavior in dart-bearing snails are most consistent with the sexual selection model, least consistent with the courtship co-ordination model, and do not provide any support for the reproductive isolation model.

Both DIVER (1940) and WEBB (1952b) assumed that the dart was used in species recognition during courtship and evolved in this context. However, this hypothesis has never been tested, and appears unlikely on theoretical grounds. *Helix aspersa, H. pomatia,* and other dart-bearing snails go through a fairly prolonged period of introductory courtship behavior (with physical contact) before they show dart-shooting behavior. This would argue against the use of the dart as a species recognition device, because both physical cues (*e.g.,* the differences in courtship postures between *H. aspersa* and *H. pomatia*) and probable chemical cues are capable of being passed during the introductory phase before dart shooting. The physical stimulus of dart penetration may not be an ideal signal in species recognition, because the degree and location of dart penetration vary greatly (LIND, 1976; this study). The transfer of a chemical signal used in species recognition by the dart may be an evolutionarily suboptimal strategy, because (1) dart receipt harms a potential mating partner and (2) sexual pheromones, including contact pheromones used in courtship, are usually among the first signals transferred in courtship.

WEBB (1951) noted a single instance of heterospecific courtship between two species of dart-bearing *Helminthoglypta,* where one of the snails died four days after receiving a dart wound during courtship. This is the only observation suggesting that the dart might be used in species

recognition; however, no evidence obtained since Webb's observation has supported his contention that the dart evolved as a species-recognition device.

In the courtship co-ordination model, the behavior of a courting partner is assumed to be an adaptation for promoting co-operative exchange and use of gametes. It is in the context of this model that LIND (1976) implicitly defined the "stimulatory" action of the dart of *Helix pomatia,* and it was in this context that the "stimulation" hypothesis was defined in this paper. The lack of evidence for the stimulation hypothesis, as defined by the courtship co-ordination model, for both *H. pomatia* and *H. aspersa* indicates that the dart is not used to aid co-ordination in courtship. Dart receipt, in fact, appears to cause physical harm: *H. pomatia* is less likely to complete courtship when darted (LIND, 1976), and *H. aspersa* appears to reduce the rate of penial eversion when darted. Dart *shooting,* by contrast, appears to facilitate the completion of courtship by the shooter: *H. pomatia* and *H. aspersa* attempt copulation only after going through DS in primary courtship, and *H. aspersa* reduces the rate of biting after shooting its dart. Thus, it is the shooter and not the receiver of the dart that appears to be "stimulated" by DS behavior.

Evidence for the evolution of species-specific genital structures through sexual selection is growing (see reviews by WEST-EBERHARD, 1983; EBERHARD, 1985), and species-specific dart morphologies likely reflect sexual selection rather than selection for prezygotic reproductive isolating mechanisms. The data showing that the shooter and not the receiver is stimulated by DS behavior and that the receiver is hurt by dart receipt suggests that there is an evolutionary conflict of interest between the mating partners, similar to that between the males and females of gonochoristic species. Because the variance in male reproductive success is usually greater than variance in female reproductive success (see BLUM & BLUM, 1979; WILLSON & BURLEY, 1983), under certain conditions simultaneous hermaphrodites that act as "males" (those transferring sperm but not using received sperm) may be favored over those acting as pure hermaphrodites. The form of sexual selection occurring in these simultaneous hermaphroditic snails might be of two forms: (1) "cheating" by male-acting hermaphrodites and the use of anti-cheating devices by pure hermaphrodites, and (2) the use of coercion by male-acting hermaphrodites to force partners to behave as a "female." Cheating (acting as a "male," by transferring sperm but not accepting or using received sperm) and the use of anti-cheating strategies have been hypothesized to occur in the hamlet *Hypoplectrus* (FISCHER, 1981, 1984). In this fish, cheating may have given rise to a counter strategy, or anti-cheating strategy, known as egg trading, in which mating partners alternate male and female roles several times in a single spawning bout. Sperm trading in the opisthobranch *Navanax* (LEONARD & LUKOWIAK, 1984) may have evolved under similar sexual selection pressures. In the other form of sexual selection in hermaphrodites, coercive tactics in courtship and mating (*e.g.,* incapacitating a partner's male organs, or forcefully stimulating the female organs to receptivity) can be simultaneously used offensively and defensively. These two forms of sexual selection are theoretically similar, although cheating does not necessarily involve any type of coercion of the mates. The dart may have arisen either as an anti-cheating mechanism or as a device used in coercion. The dart may have evolved from smaller penial stylets or genital hooks in a kind of evolutionary arms escalation that allowed the evolution of increasingly larger or more effective darts to force the partner to act as a "female." Any destabilizing effect of strong sexual selection on the hermaphroditic condition (see CHARNOV, 1979, 1982) might be reduced by energy recouped from allosperm digested in the gametolytic organs found in pulmonates and many opisthobranchs.

Because dart receipt appears to be harmful to a snail, it does not seem likely that darts evolved through runaway sexual selection by female choice on stimulatory male genital structures (as suggested by EBERHARD, 1985, for darts and other elaborate genitalia). The commonly made assumption that darts (and other spicular genital structures in animals) act to stimulate co-operative mating behavior by mating partners may have to be re-examined.

By comparison with work done on the male accessory gland secretions in insects (see GILLOT & FRIEDEL, 1977; CHEN, 1984), mucous gland pheromones of *Helix* might affect: (1) potentiation of sperm, (2) induction of egg maturation or oviposition (TOMPA, 1980), and (3) the reduction of subsequent receptivity in mating partners (reduction of subsequent "female" receptivity). The possession of separate sperm-digestion and allosperm-storing organs in pulmonates and many opisthobranchs suggest several other theoretical functions of dart receipt, including (1) suppression of allosperm digestion, (2) displacement of previously stored allosperm, or (3) prevention of subsequent allosperm storage. Of these possible effects, a reduction of subsequent mating seems to be unlikely in *H. aspersa,* because snails will mate repeatedly with different partners in a single breeding season in the laboratory (personal observations). The other hypotheses have not been tested directly. The consideration of these and other evolutionary hypotheses may prove to be as profitable to the study of molluscan reproductive biology as they have been to studies on other groups of animals (*e.g.,* see BLUM & BLUM, 1979).

ACKNOWLEDGMENTS

I am deeply indebted to Alex Tompa for sharing with me his considerable expertise on malacology and darts. I thank James Cather, Norman Kemp, and Brian Hazlett for offering important and useful suggestions on this study. Richard Alexander and Joel Weichsel were helpful in discussing with me various hypotheses on the evolution of the dart apparatus. Finally, I must thank William Ham-

ilton for pointing out the cheating/anti-cheating hypothesis and providing early encouragement to me. This study was financed in part by grants from the University of Michigan and the Hawaiian Malacological Society.

LITERATURE CITED

Baur, B. 1984. Early maturity and breeding in *Arianta arbustorum* (L.) (Pulmonata: Helicidae). Jour. Moll. Stud. 50: 241–242.

Blum, M. S. & N. A. Blum. 1979. Sexual selection and reproductive competition in insects. Academic Press: New York. 463 pp.

Bornchen, M. 1967. Untersuchungen zur Sekretion der fingerformigen Drusen von *Helix pomatia*. Z. Zellforsch. Mikrosk. Anat. 78:402–426.

Bouchard-Chantereaux, N. R. 1839. Observations sur les moeurs de divers Mollusques terrestres et fluviatiles observés dans le département du Pas-de-Calais. Ann. Sci. Natur. (Zool.) 11:295–307.

Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. Proc. Natl. Acad. Sci. 76:2480–2484.

Charnov, E. L. 1982. The theory of sex allocation. Monogr. Pop. Biol. 18:1–355.

Chen, P. S. 1984. The functional morphology and biochemistry of insect male accessory glands and their secretions. Ann. Rev. Entomol. 29:233–255.

Chung, D. 1986a. Stimulation of genital eversion in the land snail *Helix aspersa* by extracts of the glands of the dart apparatus. Jour. Exp. Zool. 238:129–139.

Chung, D. 1986b. Initiation of growth of the first dart in *Helix aspersa* Müller. Jour. Moll. Stud. 52:253–255.

Conover, W. J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley & Sons: New York. 493 pp.

Cowie, R. H. 1980. Precocious breeding of *Theba pisana* (Müller) (Pulmonata: Helicidae). Jour. Conch. 30:238.

Dasen, D. D. 1933. Structure and function of the reproductive system in *Ariophanta ligulata*. Proc. Zool. Soc. (1933):97–118.

Dillaman, R. M. 1981. Dart formation in *Helix aspersa*. Zoomorphology 97:247–261.

Diver, C. 1940. The problem of closely-related species living in the same area. Pp. 303–328. *In:* J. S. Huxley (ed.), The new systematics. Clarendon Press: Oxford.

Dorello, P. 1925. Sulla funzione della glandole digitate nel gen. *Helix*. Atti della reale academia nazionale dei lincei, Ser. 6, Rendiconti, Classe di scienze fisiche, matematiche e naturali 1:47–51.

Eberhard, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press: Cambridge, Mass. 244 pp.

Fischer, E. A. 1981. Sexual allocation in a simultaneously hermaphroditic coral reef fish. Amer. Natur. 117:64–82.

Fischer, E. A. 1984. Local mate competition and sex allocation in simultaneous hermaphrodites. Amer. Natur. 124:590–596.

Forcart, L. 1949. Die Erektion der Kopulationsorgane und der Kopulationsmodus von *Phenacolimax major* (Fér.). Arch. Moll. 77:115–119.

Gerhardt, U. 1935. Weitere Untersuchung zur Kopulation der Nacktschnecken. A. Morphol. Oekol. Tiere 30:297–332.

Gillott, C. & T. Friedel. 1977. Fecundity-enhancing and receptivity-inhibiting substances produced by male insects: a review. Adv. Invert. Reprod. 1:199–218.

Giusti, F. & A. Lepri. 1980. Aspetti morphologici ed etologici dell'accoppiamento in alcune specie della famiglia Helicidae (Gastropoda, Pulmonata). Atti Accademia Fisiocritici Siena (1980):11–71.

Goddard, C. K. 1962. Function of the penial apparatus of *Helix aspersa*. Australian Jour. Biol. Sci. 15:218–232.

Herzberg, F. & A. Herzberg. 1962. Observations on reproduction in *Helix aspersa*. Amer. Natur. 68:297–306.

Jeppesen, L. L. 1976. The control of mating behaviour in *Helix pomatia* L. (Gastropoda: Pulmonata). Anim. Behav. 24:275–290.

Künkel, K. 1928. Zur Biologie von *Eulota fruticum* Müller. Zool. Jahr. Jena (Abt. f. allg. Zool. u. Physiol.) 45:317–342.

Künkel, K. 1929. Experimentelle Studie über *Vitrina brevis* Férussac. Zool. Jahrb. Jena (Abt. f. allg. Zool. u. Physiol.) 45:575–626.

Künkel, K. 1933. Vergleichende experimentelle Studie über *Vitrina elongata* Draparnaud und *Vitrina brevis* Férussac. Zool. Jahr. Jena (Abt. f. allg. Zool. u. Physiol.) 52:399–432.

Leonard, J. L. & K. Lukowiak. 1984. Male-female conflict in a simultaneous hermaphrodite resolved by sperm trading. Amer. Natur. 124:282–286.

Lind, H. 1973. The functional significance of the spermatophore and the fate of spermatozoa in the genital tract of *Helix pomatia* (Gastropoda: Stylommatophora). Jour. Zool. (Lond.) 169:39–64.

Lind, H. 1976. Causal and functional organization of the mating behaviour sequence in *Helix pomatia* (Pulmonata, Gastropoda). Behaviour 59:162–202.

Meisenheimer, J. 1912. Die Weinbergschnecke *Helix pomatia*. Leipzig. 140 pp.

Pruvot-Fol, A. 1960. Les organes génitaux des opisthobranches. Arch. Zool. Exp. et Gen. 99:135–224.

Raut, S. K. & K. C. Ghose. 1984. Pestiferous land snails of India. Zool. Survey India, Tech. Monogr. No. 11.

Rensch, I. 1955. On some Indian land snails. Jour. Bombay Natur. Hist. Soc. 53:163–176.

Sokal, R. R. & F. J. Rohlf. 1969. Biometry. W. H. Freeman & Co.: San Francisco. 776 pp.

Tompa, A. 1980. The ultrastructure and mineralogy of the dart from *Philomycus carolinianus* with a brief survey of the occurrence of darts in land snails. Veliger 23:35–42.

Tompa, A. 1982. X-ray radiographic examination of dart formation in *Helix aspersa*. Netherlands Jour. Zool. 32:63–71.

Tompa, A. 1984. Land snails. Pp. 48–140. *In:* A. Tompa, N. H. Verdonk & J. A. M. van den Biggelaar (eds.), The Mollusca, Vol. 7, Reproduction. Academic Press: New York.

van Mol, J. J. 1970. Révision des Urocyclidae (Mollusca, Gastropoda, Pulmonata). Ann. Mus. Roy. de l'Afrique Centr., Tervuren, No. 180.

Webb, G. R. 1942. Comparative observations of the mating habits of three California land snails. Bull. So. Calif. Acad. Sci. 41:102–108.

Webb, G. R. 1948. Notes on the mating of some *Zonitoides* (*Ventridens*) species of land snails. Amer. Midl. Natur. 40: 435–461.

Webb, G. R. 1951. An instance of amixia between two species of landsnails. Amer. Natur. 85:137–139.

Webb, G. R. 1952a. Pulmonata, Xanthonycidae: comparative sexological studies of the North American land-snail, *Monadenia fidelis*—a seeming ally of Mexican helicoids. Gastropodia 1:1–3.

Webb, G. R. 1952b. Pulmonata: Helminthoglyptidae: sexological data on the landsnails *Cepolis maynardi* and *Hel-*

minthoglypta traski fieldi and their evolutionary significance. Gastropodia 1:4–5.

Webb, G. R. 1968a. Observations on the sexology of *Philomycus carolinianus* (Bosc.). Gastropodia 1:62.

Webb, G. R. 1968b. Sexological notes on *Ventridens elliotti, V. acerra, V. demissus brittsi,* and *V. ligera.* Gastropodia 1:67–70.

Webb, G. R. 1980. The sexology of a Texan *Humboldtiana.* Gastropodia 2:2–7.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. Quart. Rev. Biol. 58:155–183.

Willson, M. F. & N. Burley. 1983. Mate choice in plants: tactics, mechanisms, and consequences. Monogr. Pop. Biol. 19:1–251.

The Veliger 30(1):40–45 (July 1, 1987)

THE VELIGER

Ecology and Burrowing Behavior of *Ascobulla ulla* (Opisthobranchia: Ascoglossa)

by

DUANE E. De FREESE

Department of Biological Sciences, Florida Institute of Technology,
Melbourne, Florida 32901, U.S.A.

Abstract. A population of *Ascobulla ulla,* a tectibranch ascoglossan (=sacoglossan), was sampled on a high-energy jetty environment at Fort Pierce Inlet, Florida. The highest densities of *A. ulla* occurred during warm summer months when the surf was calm and the alga *Caulerpa racemosa* was more abundant. The habitat requirements for *A. ulla* appear to be narrow, resulting in seasonal fluctuations in population size. The ability to burrow in the more protected microhabitats where *C. racemosa* occurs is an important specialization that also adapts *A. ulla* for life in its high-energy habitat. The unusual burrowing behavior of *A. ulla,* involving the bilobed cephalic shield and a rotational twisting and periodic flexion of the thin shell, is described from field and laboratory observations.

INTRODUCTION

Ascobulla, Volvatella, and *Cylindrobulla* represent a phylogenetic link between the burrowing cephalaspidiform opisthobranchs and the more advanced epifaunal tectibranch Ascoglossa (Thompson, 1979; Clark, 1982). Information about *Ascobulla ulla* has been limited to taxonomic descriptions (Marcus & Marcus, 1956, 1970; Marcus, 1972) and some brief ecological observations (Clark & Jensen, 1981; Jensen & Clark, 1983). *Ascobulla ulla* has been reported from "muddy algae" at the Enseada of Guarujá, east of Santos, Brazil (Marcus & Marcus, 1956); in association with mangroves at Key Biscayne, Florida (Marcus, 1972); on the rhizoids of the alga *Caulerpa paspaloides* (Bory) Grev. at Key Largo, Florida (Jensen & Clark, 1983); in association with mangroves at Twin Cays, Belize, Central America (Clark and De Freese, unpublished data); and on the rhizoids of *C. racemosa* (Forsskål) J. Ag. at Crawl Key, Florida (personal observation) and at Fort Pierce Inlet, Florida (Jensen & Clark, 1983).

The inlet at Fort Pierce represents the northernmost record for *Ascobulla ulla* and is close to the northern limits of the tropical siphonalean algal community (Jensen & Clark, 1983). Although high-energy habitats are often overlooked as suitable collecting sites for ascoglossans, 13 ascoglossan species have been collected from this habitat type (Jensen & Clark, 1983). The aim of this paper is to describe aspects of the behavior and population biology of *A. ulla,* emphasizing the burrowing behavior, habitat selection, and effects of environmental stress on the population at Fort Pierce Inlet, Florida.

STATION DESCRIPTION

Fort Pierce Inlet (27°28′N, 80°18′W) connects the Indian River Lagoon system to Florida's Atlantic Coast (Figure 1). The inlet is defined by two man-made rock jetties that extend into the Atlantic Ocean. *Ascobulla ulla* predominantly inhabits the tidepools and the leeward side of boulders along the north face of the north jetty and is associated with algal mats of *Caulerpa racemosa.* These microenvironments are often subjected to severe wave disturbance, especially during late summer and fall (tropical disturbances) and during the winter (northern cold fronts). The inlet is also affected by upwelling events that occur each summer along the east coast of Florida (Green, 1944; Smith, 1982).

MATERIALS AND METHODS

The population of *Ascobulla ulla* at Fort Pierce Inlet was sampled monthly from May 1984 to September 1985. Initially, samples were taken along two transects parallel to the jetty. One transect was positioned along the northern edge of the jetty where the rocks outcrop on the sandy beach. This transect included *Caulerpa racemosa* patches. The other transect, established 2 m to the north, was located in an area of bare sand only. *Ascobulla ulla* occurred only in association with *C. racemosa.* This alga was re-

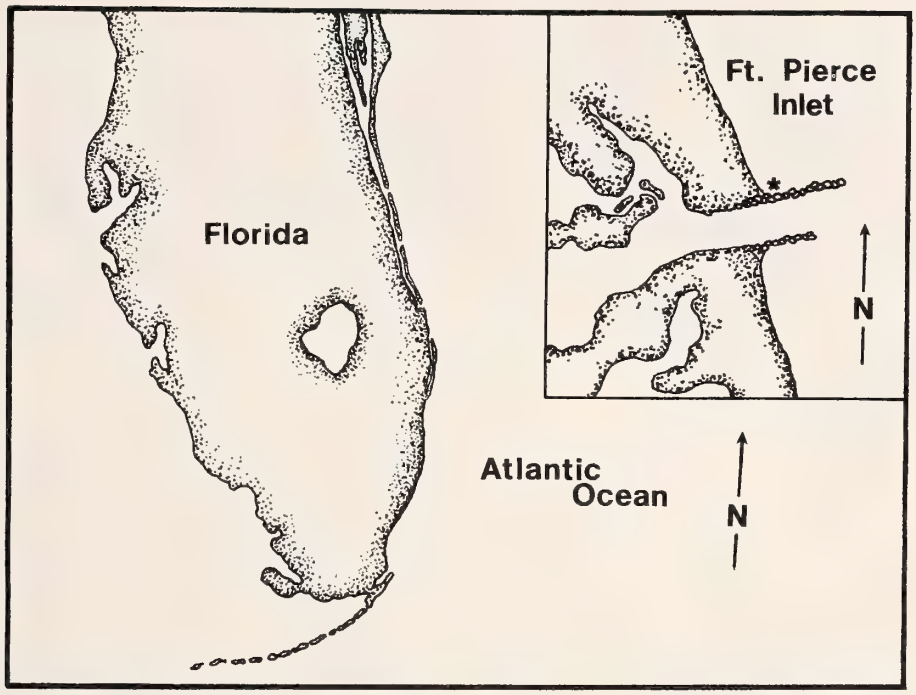


Figure 1

Location of the sampling site at Ft. Pierce Inlet, Florida. Site indicated by asterisk.

stricted to hard substrata and the areas of sand adjacent to boulders of the jetty. All subsequent samples were taken at sites having 100% algal cover. Because optimal habitats were chosen for sampling sites, the population density data are presented as "maximal density" (*i.e.,* the highest animal densities found for each monthly sampling date). Samples were taken using a 10-cm diameter PVC corer inserted to an approximate depth of 10 cm. Deeper cores (20 cm) were taken between December 1984 and March 1985, in an attempt to locate *A. ulla.* Sample sites were categorized as upper intertidal, midtidal, or subtidal habitats. Samples were washed through a 0.5-mm sieve and sorted in the field. Animals were transported live to the laboratory in 2-L plastic bottles containing seawater.

A midsummer (1985) sediment sample was collected from a site adjacent to the jetty where *Ascobulla ulla* was abundant. This sample was analyzed for particle size composition (median particle size = 0.22 mm, 2.2 ϕ) (Wentworth classification). Based upon graphical analysis (Buchanan & Kain, 1971) the sediment was poorly sorted (σ_ϕ = 1.23), coarse skewed (SK_ϕ = 0.11), and mesokurtic (K_ϕ = 1.10). For consistency, this sediment sample was used for all burrowing trials.

Burrowing time was measured at 10, 15, 20, 26, and 30°C. Animals were allowed to adjust at experimental temperatures for approximately 30 min in fingerbowls containing seawater. After 30 min the animals were transferred to a fingerbowl containing the midsummer (1985) sediment sample and seawater maintained at the experimental temperature. The "digging period," defined as the time elapsed between the first probing by the foot and the complete coverage of the shell by sand (Trueman & Ansell, 1969), was measured with a stopwatch.

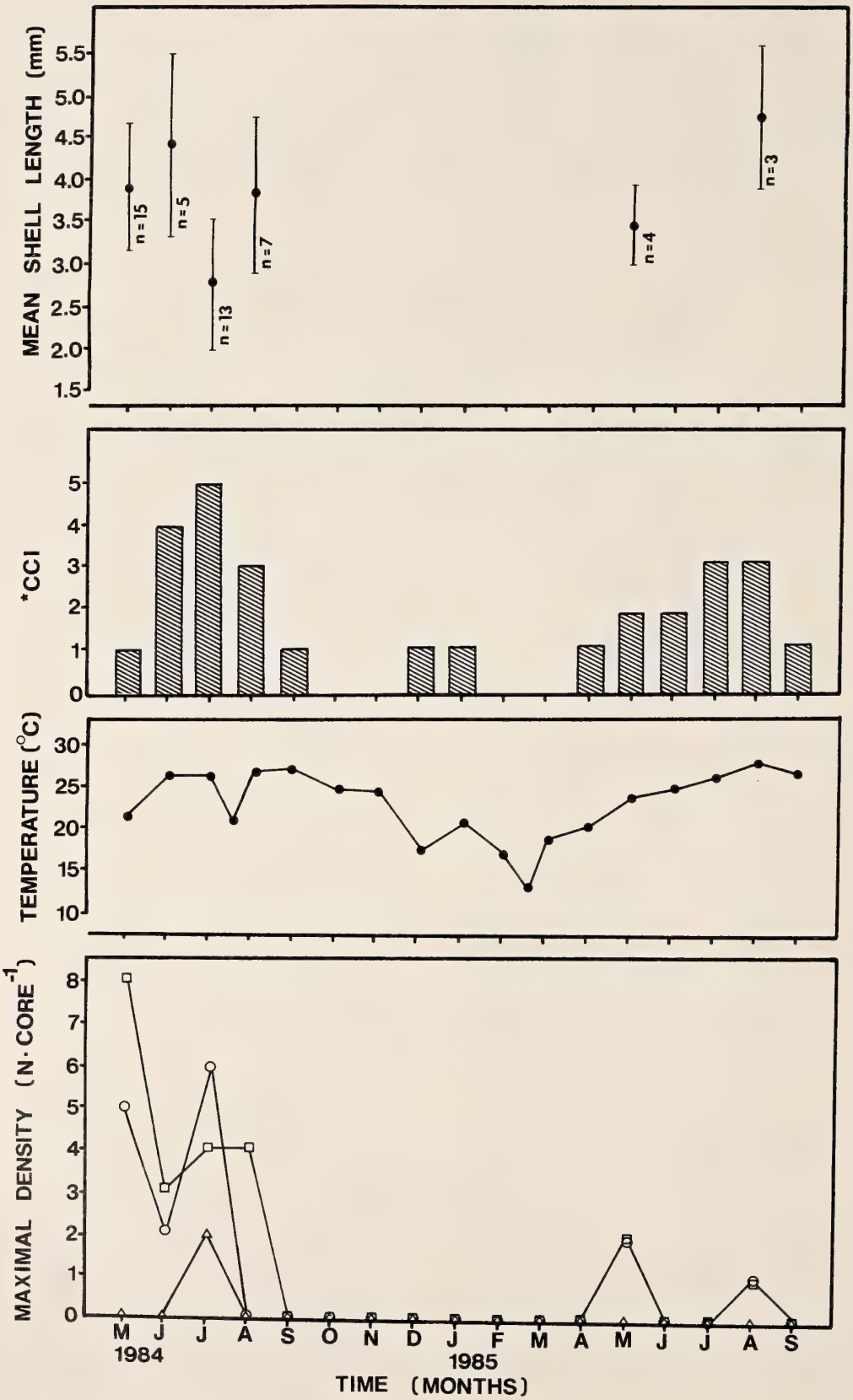
Burrowing behavior was observed in narrow, glass aquaria containing sediment and seawater. The mechanism of burrowing was recorded with a video camera and video cassette recorder (VCR). *Ascobulla ulla* was carefully placed on the substratum at the glass-sediment interface. Burrowing activity began immediately and often proceeded along this interface, enabling detailed observations of subsurface behavior.

RESULTS

Distribution and Abundance

Densities of *Ascobulla ulla* were generally low (Figure 2) except for population peaks during May (1984 and 1985), which coincided with the presence of stable stands of *Caulerpa racemosa.* Animal lengths and densities fluctuated during the summer months. In July 1984, the populations of both *A. ulla* and *C. racemosa* appeared to decline with lower temperatures accompanying an apparent upwelling event, and by August both populations were significantly reduced.

Most individuals of *Ascobulla ulla* were collected in the sediment layer associated with the algal mat. The sediment


MEAN SHELL LENGTH (mm)
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
n=15
n=5
n=13
n=7
n=4
n=3
*CCI
5
4
3
2
1
0
TEMPERATURE (°C)
30
25
20
15
10
MAXIMAL DENSITY (N·CORE⁻¹)
8
7
6
5
4
3
2
1
0
M J J A S O N D J F M A M J J A S
1984
1985
TIME (MONTHS)

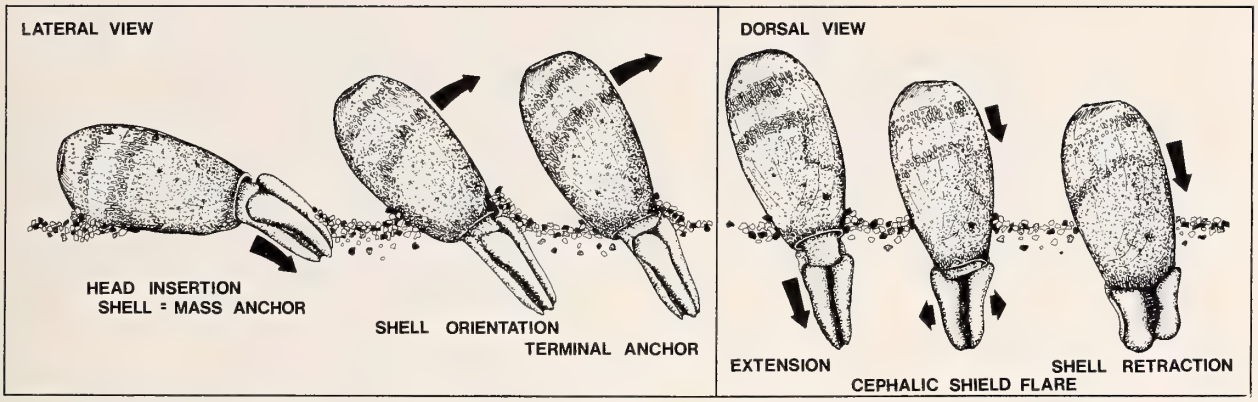


Figure 3

The mechanism of burrowing in *Ascobulla ulla*. Sequence from lateral and dorsal views.

that accumulated along the leeward rock faces rarely exceeded 1 cm in depth. *Ascobulla ulla* was usually in direct contact with the rhizoids of *Caulerpa racemosa* (0–3 cm depth). Animals were also collected in the sand surrounding anchored clumps of *C. racemosa* in protected tidepools. Under these protected conditions, *A. ulla* occasionally emerged from the sediment and crawled up the assimilators of the alga for egg deposition and feeding. This behavior has also been observed in the laboratory and at other field collection sites (Belize, Central America; Crawl Key, Florida Keys).

Maximal animal size and density occurred during the warm summer months, when surf conditions were generally calm. *Caulerpa racemosa* was most abundant along the shallow areas of the jetty. In deeper water (2–3 m), well-developed stands of another alga, *Halimeda discoidea* (Decaisne), predominated, and *C. racemosa* was uncommon at these depths. A decrease in the *C. racemosa* population was observed after upwelling events, coastal storms, and heavy rainfall. During the fall and winter months, no specimens of *Ascobulla ulla* were collected, and *C. racemosa* was observed only occasionally.

The Mechanism of Burrowing

The mechanism of burrowing in *Ascobulla ulla* is illustrated in Figure 3, and described using the burrowing terminology of Trueman & Ansell (1969).

When *Ascobulla ulla* is placed on the sandy substratum, the animal begins burrowing almost immediately and continues until it is completely buried. Burrowing is initiated by the insertion of the propodium and the anterior end of the bilobed cephalic shield into the substratum. At this stage, the shell functions as a mass anchor, enabling the anterior end to take on a vermiform shape, which probes and wedges into the substratum. This penetration phase is accompanied by slight side-to-side movement. After the head is inserted into the substratum, it functions as a terminal anchor, facilitating shell orientation and increasing the angle of penetration. During the shell-orientation phase, the head and propodium continue to extend deeper into the sediment. As the shell approaches a vertical position in relation to the substratum, the cephalic shield flares, laterally compresses the sediment, and thus firmly establishes the terminal anchor. The shell is then slowly pulled into the substratum until it contacts the median furrow at the posterior end of the cephalic shield. Shell insertion is accompanied by the rhythmic pumping and rotational twisting of the shell as it "augers in." The shell apex bears a spiral slit that physically separates the whorls (Marcus & Marcus, 1956), thus permitting the periodic contraction and expansion of the shell. This allows the shell to function as a penetration anchor during the expansion phase (when mantle musculature relaxes), and presents minimal cross-sectional area during retraction (terminal anchoring by head). When observed from the apical view, the shell appears as a spring that coils and uncoils. The rotational twisting of the shell has not been reported for other infaunal opisthobranchs and appears to facilitate shell retraction. The animal repeats this

←

Figure 2

Composite figure of seasonal data taken at Ft. Pierce Inlet. Mean Shell Length: ● = mean; vertical lines = standard deviation. *Caulerpa* Coverage Index (*CCI): 0 = no *Caulerpa*, 1 = sparse coverage, 2 = short growth + clumped distribution, 3 = well-developed growth + clumped distribution, 4 = well-developed growth + broad coverage, 5 = dense growth + broad coverage. Temperature: ● = water temperature in °C. Maximal Animal Density: △ = upper intertidal zone, ○ = midtidal zone, □ = subtidal zone.

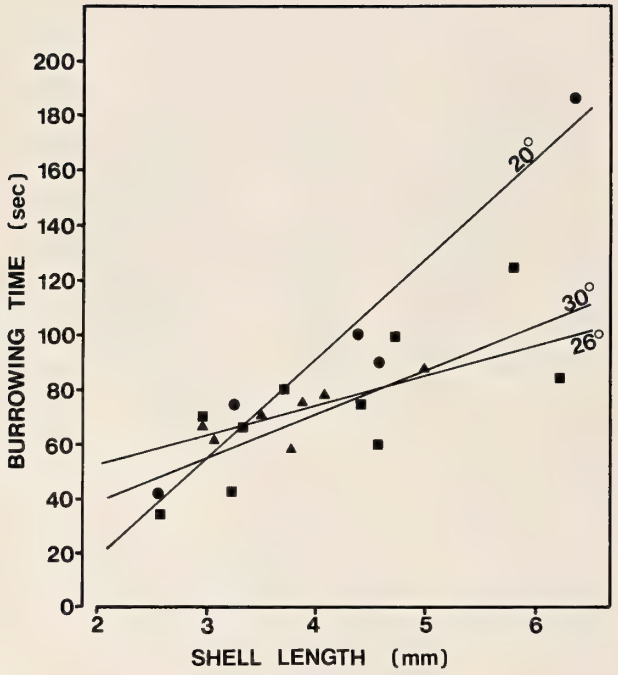


Figure 4

Rate of burrowing versus shell length of *Ascobulla ulla,* at three temperatures. ● = 20°C: (Y = 36.86X − 56.80, r = 0.9659, n = 5). ▲ = 26°C: (Y = 11.45X + 28.65, r = 0.7912, n = 7). ■ = 30°C: (Y = 16.43X + 5.25, r = 0.7462, n = 10).

sequence of penetration, shell orientation, head extension, cephalic shield flare, and shell retraction until burial is complete. Mucus secreted at the anterior end of the shell appears to prevent the movement of substratum particles into the mantle cavity. Slight disturbances such as water currents or rough handling resulted in a rapid, copious discharge of dilute, milky white mucus from the posterior region of the shell. Animals anchor to the algae or sediment by viscous mucous threads *in situ* if exposed during wave surge.

Burrowing Rate

Figure 4 shows the effects of animal size and water temperature on the burial rate of *Ascobulla ulla.* At 10°C, *A. ulla* was immobilized; no movements or attempts at burrowing were observed. At 15°C, the experimental animals slowly twisted their head and attempted to probe the substratum. After 10 minutes, several animals had achieved head penetration, although burial was clearly impaired. At 20, 26, and 30°C, burrowing time generally increased with increasing animal size.

DISCUSSION

Peak population densities of *Ascobulla ulla* coincide with the presence of well-developed mats of the alga *Caulerpa racemosa,* their specific food source. Reductions in the population of *A. ulla* appear to coincide with thermal stress, rainfall-induced salinity changes, and high-energy surf conditions. The great magnitude of these population reductions suggests that climatic variations in the high-energy intertidal zone heavily constrain populations of *A. ulla* and such high-energy areas appear to represent a marginal habitat.

In *Elysia tuca* Marcus, 1967, an epifaunal ascoglossan that feeds on *Halimeda* spp., seasonal climatic factors appear to affect several parameters, including the retention of functional plastids, egg deposition, feeding rate, and growth rate (Waugh & Clark, 1986). The biotic and abiotic constraints on ascoglossan populations are not fully understood, providing a fertile area for additional research.

A variety of environmental factors appear to have important effects on the stability of the *Caulerpa racemosa* population. Changes in the quality or quantity of the food alga may have a direct effect on the animal population owing to the stenophagous nature of *Ascobulla ulla.* The algal population appears to decline at lower temperatures associated with summer upwelling events. In addition, *C. racemosa* may be adversely affected by high summer temperatures, which often exceeded 30°C in the shallow intertidal pools. This was especially evident when low tides prevented an open exchange of seawater.

The apparent disappearance of *Ascobulla ulla* during the fall and winter months coincides with a seasonal transition to rougher surf conditions, increased turbidity, and decreasing water temperatures. The effects of these factors and others, such as photoperiod and irradiance, are not known. *Ascobulla ulla* appears to be capable of maintaining its position on the assimilators of the alga in a moving current or a light surge, but the animals are easily displaced from the alga by moderate shaking of the thallus, which indicates a vulnerability to high surf or heavy surge conditions during emergence. *Ascobulla ulla* may also emerge at high tide, when depth could provide some protection from surface waves. *Ascobulla ulla* may burrow more deeply into the sediment during fall and winter. Although deeper core samples were taken during the winter months when *A. ulla* was uncommon or absent, no evidence was found to confirm this hypothesis. *Ascobulla ulla* has direct development (Clark & Jensen, 1981); therefore, a winter burrowing response or undiscovered, subtidal, winter habitats could account for the rapid spring colonization observed at the sampling site. The disappearance of *A. ulla* from the jetty habitat during the winter suggests that vernal recolonization occurs from deep-water populations inhabiting reefs adjacent to the jetty. Direct development presents some advantages to the colonization of high-energy beaches because juveniles are presumably able to burrow immediately and faster if juvenile size approximates sediment grain size, and the efficient recruitment associated with direct development should enable a rapid increase in the population. The coincidence of low tides and freezing temperatures observed during the winter of 1985 might

also explain the slow rate of vegetative recolonization of *Caulerpa racemosa* in the intertidal areas.

The habitat requirements for *Ascobulla ulla* appear to be quite narrow, resulting in seasonal fluctuations in population stability. Data on population dynamics, zoogeographic distribution, and the effects of temperature on burrowing rates support a hypothesis that *A. ulla* is relatively stenothermal. Because Fort Pierce represents the distributional limit of several tropical and subtropical ascoglossan and siphonalean species (JENSEN & CLARK, 1983), minor climatological conditions may have important effects on floral and faunal distributions.

The bilobed cephalic shield characteristic of *Ascobulla ulla* enhances the burrowing capability of this primitive ascoglossan and may function as a more efficient terminal anchor than the single broad cephalic shield of most primitive infaunal cephalaspids. The distinctive apical spiral slit of the thin shell permits cross-sectional changes that may aid the flow of water through the mantle cavity as well as provide a more efficient penetration anchor during burrowing. Contraction and passive relaxation of the shell adductor muscle control the rhythmic pumping of the shell (MARCUS & MARCUS, 1956). A detailed analysis of muscular structure, similar to BRACE's (1977) anatomical study of some tectibranch opisthobranchs, would further clarify the burrowing mechanics of *A. ulla*.

The burrowing sequence in *Ascobulla ulla* diverges from the behavior of the cephalaspid *Haminea antillarum* (d'Orbigny, 1842). *Haminea antillarum* has a single broad cephalic shield, which is used to plow slowly into the sediment at a shallow angle of penetration (TRUEMAN & ANSELL, 1969; De Freese, personal observations).

Ascobulla ulla shares some similarities with the oxynoacean *Volvatella laguncula* (Sowerby, 1894), which also exhibits adduction movements of its flexible shell (THOMPSON, 1979). Because there was no obvious exclusion of particulate matter, THOMPSON (1979) suggested that *V. laguncula* pumped a suspension of fine sediment through its mantle cavity. An alternate hypothesis, by CLARK (1982), suggests that shell adduction in *V. laguncula* may assist burrowing in compacted sand, by loosening the sediment surrounding the shell, and coincidentally increasing the availability of interstitial water for respiratory needs.

Ascobulla ulla burrows at considerably slower rates than more typical, infaunal, high-energy beach organisms: *Mactra olorina* burrows in 1.5 sec (ANSELL & TREVALLION, 1969) and the burrowing rate of *Donax denticulatus* declines from 2.9 sec at 32°C to 8.15 sec at 24°C (TRUEMAN, 1983).

Data on burrowing rates, habitat preference, and seasonal population stability suggest that *Ascobulla ulla* should not be strictly viewed as a high-energy beach organism. However, burrowing is an important capability that allows *A. ulla* to exploit the high-energy habitat at Fort Pierce Inlet, Florida.

ACKNOWLEDGMENTS

Great appreciation is expressed to Kerry B. Clark for his guidance, suggestions, and criticisms. I would also like to thank R. L. Turner, W. G. Nelson, and two anonymous reviewers for critically reviewing the manuscript. The work was partly supported by the Lerner-Gray Fund for Marine Research of the American Museum of Natural History and by a Doctoral Dissertation Research Improvement Grant OCE-8501715 from the National Science Foundation.

LITERATURE CITED

ANSELL, A. D. & A. TREVALLION. 1969. Behavioral adaptations of intertidal molluscs from a tropical sandy beach. Jour. Exp. Mar. Biol. Ecol. 4:9–35.

BRACE, R. C. 1977. The functional anatomy of the mantle complex and columellar muscle of tectibranch molluscs (Gastropoda: Opisthobranchia), and its bearing on the evolution of opisthobranch organization. Phil. Trans. R. Soc. Lond. B, 277:1–56.

BUCHANAN, J. B. & J. M. KAIN. 1971. Measurement of the physical and chemical environment. Pp. 30–58. *In:* N. A. Holme and A. D. McIntyre (eds.), Methods for the study of marine benthos. IBP Handbook No. 16. Blackwell Scientific Publ.: Oxford.

CLARK, K. B. 1982. A new *Volvatella* (Mollusca: Ascoglossa) from Bermuda, with comments on the genus. Bull. Mar. Sci. 32(1):112–120.

CLARK, K. B. & K. R. JENSEN. 1981. A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). Int. Jour. Invert. Reprod. 3:57–64.

GREEN, C. 1944. Summer upwelling—northeast coast of Florida. Science 100:546–547.

JENSEN, K. & K. B. CLARK. 1983. Annotated checklist of Florida ascoglossan Opisthobranchia. Nautilus 94(1):1–13.

MARCUS, E. 1972. On some opisthobranchs from Florida. Bull. Mar. Sci. 22:284–308.

MARCUS, E. & E. MARCUS. 1956. On the tectibranch gastropod *Cylindrobulla*. Anais Acad. Brasil. Ciências 28:119–128.

MARCUS, E. & E. MARCUS. 1970. Opisthobranchs from Curaçao and faunistically related regions. Stud. Fauna Curaçao 33:1–129.

SMITH, N. P. 1982. Upwelling in Atlantic shelf waters of south Florida. Florida Sci. 45(2):125–138.

THOMPSON, T. E. 1979. Biology and relationships of the South African sacoglossan mollusc *Volvatella laguncula*. Jour. Zool. (Lond.) 189:339–347.

TRUEMAN, E. R. 1983. Observations of the responses of the tropical surf clam *Donax denticulatus* to changes of temperature and salinity. Jour. Moll. Stud. 49:242–243.

TRUEMAN, E. R. & A. D. ANSELL. 1969. The mechanisms of burrowing into soft substrata by marine animals. Oceanogr. Mar. Biol. Ann. Review 7:315–366.

WAUGH, G. R. & K. B. CLARK. 1986. Seasonal and geographic variation in chlorophyll content of *Elysia tuca* (Ascoglossa: Opisthobranchia). Mar. Biol. 92:483–487.

The Veliger 30(1):46-54 (July 1, 1987)

THE VELIGER

Cryptomya californica (Conrad, 1837): Observations on Its Habitat, Behavior, Anatomy, and Physiology

by

EDWIN V. LAWRY

29681 Dane Lane, Junction City, Oregon 97448, U.S.A.

Abstract. Descriptions and photographs of the estuarine habitat, external and internal structures, and gut contents of the lamellibranch clam *Cryptomya californica* (Myoida: Myidae) are presented. Also included are behavioral observations, and experimental information on the digestive tract and its associated bacteria.

INTRODUCTION

During my studies on spirochete bacteria of the genus *Cristispira* (LAWRY, 1981; LAWRY *et al.,* 1981), which are isolated most frequently from the crystalline styles of various pelecypods and gastropods, few literature references were found to my favorite source of spirochetes, the marine clam *Cryptomya californica* (Conrad, 1837). However, the importance of this small, burrowing lamellibranch in estuarine ecosystems must be considerable, as it is a predominant animal in vast areas of mudflats along the Pacific coast of America from Alaska to Peru (BROWN *et al.,* 1977; HERTLEIN & GRANT, 1972; KEEN, 1971; PETERSON, 1984; WEST *et al.,* 1976; WICKSTEN, 1978).

The majority of information available on *Cryptomya californica* comes from a limited portion of its range (*e.g.,* the central coast of California), and is contained in three articles (MACGINITIE, 1934, 1935; YONGE, 1951). These papers discuss the clam's Monterey Bay habitats, its shell morphology, anatomy, and particle filtering behavior, and its unusual utilization of the tunnels of other burrowing organisms. Curiously, almost nothing has been published concerning the habitats of *C. californica* throughout the rest of its range, its ecological niche, burrowing behavior, digestive physiology, or reproduction.

In this paper, I compare Oregon estuarine habitats of *Cryptomya californica* with those previously described in California. The clam's burrowing behavior is discussed, and pre-existing anatomical data are reviewed, photographically documented, and embellished with new observations about the digestive tract, wandering amebocytes, and gametes. The nature of the clam's food and its processing by the digestive system are investigated. Special problems related to digestion are addressed, such as the function of the crystalline style, how this organ is affected by tidal rhythms, whether it contains digestive enzymes, and, if so, whether they are of clam or bacterial origin. Also discussed are other possible roles played by the clam's gut-associated bacteria.

MATERIALS AND METHODS

Cryptomya californica was collected from sandy mudflats of Yaquina Bay and Coos Bay, Oregon. Photographic records were made of the habitat, substrate, arrangement of clams around the tunnels of the ghost shrimp *Callianassa californiensis* (Dana, 1854) (see MACGINITIE, 1934), and the burrowing behavior of the clam. In order to determine the nature of the diet, intestinal contents and fecal pellets were obtained from freshly collected clams.

To microscopically observe the internal anatomy of *Cryptomya californica,* de-shelled, whole clams were fixed and dehydrated using a freeze substitution technique. They were then embedded in paraffin and cut into 7-μm thick sections. These were stained with Harris' hematoxylin and eosin (H and E), and observed and photographed using a Zeiss Universal microscope equipped with a Nikon AFM automatic exposure meter and a 35 mm camera. Brightfield optics were used to make photomicrographs of the digestive organs. Phase contrast was used to demonstrate the presence of *Cristispira* within sections of the crystalline style. Intestinal contents were photographed *in situ* using Nomarski optics.

A clam submerged in seawater was vivisected and photographed through a Nikon SMZ-10 zoom-lens dissecting microscope in order to observe the digestive organs and the direction and periodicity of crystalline style rotation, which could be seen through the nearly transparent wall of the style sac.

To observe the structure of the crystalline style (NELSON, 1918; YONGE, 1932), styles were extracted by making a small incision into the stomach and forcing the style through the opening by exerting light pressure onto the side of the visceral mass. Each style was placed in a drop of seawater, and phase contrast and Nomarski optics were used respectively to photograph amebocytes on the outer surface of the style (MATHERS, 1972; YONGE, 1926) and *Cristispira* within the matrix. Sperm and eggs were collected during vivisections and photographed in seawater using Nomarski optics.

To determine whether populations of spirochetes in *Cryptomya californica* are self-perpetuating, or whether they dwindle after the clams are removed from their natural habitat, the following test was performed. Changes in populations of *Cristispira* within the styles of clams held in aquaria for several weeks were monitored by periodically dissolving a known number of styles in an isotonic saline solution (LAWRY *et al.*, 1981), measuring the total volume, and counting all the spirochetes in 5-μl portions, using darkfield microscopy. The average number of bacteria per style was then calculated.

To gain further clues as to the roles of the crystalline style in digestion, the possible presence of amylase, a starch-hydrolyzing enzyme common in molluscan styles, was investigated (IORDACHESCU & DUMITRU, 1978; MATHERS, 1973). Styles were analyzed for amylase activity by placing extracted styles, sterilized and washed with toluene, on 0.5% starch/marine nutrient agar culture medium (6 g Sigma no. S-2630 soluble starch, 66 g Difco 2216 marine nutrient agar, 1200 ml distilled water, autoclaved at 121°C for 15 min) for 24 h at 20°C. Hydrolysis of the starch in the medium was checked for by color-developing the plates with Gram's iodine.

To investigate whether gut-associated bacilli can produce amylase, possibly contributing to that stored in the crystalline style, the following experiment was performed. Colonies of Gram-negative, motile bacilli were isolated from the surfaces of extracted, unsterilized styles streaked on to the above-described medium. Their ability to hydrolyze starch was determined by subculturing the bacteria to the same medium, incubating for 24 h at 20°C, and color-developing the plates with Gram's iodine.

The following observations were made to determine whether the style is always present, or whether its presence is affected by fluctuations in tides or food supplies, as in some other intertidal mollusks (LANGTON, 1977; MATHERS, 1974). The presence of styles in freshly collected clams during low tides was noted. Clams removed from seawater for 24 h at 10°C were checked for the presence of styles. *Cryptomya californica* maintained (with food) in aerated seawater (27 to 30‰ salinity, 8°C) for extended periods of time were examined for styles. The effects of 6 weeks of starvation on style production were studied.

To observe the initial distribution of ingested particulate matter within the digestive organs, carmine dye particles (Allied Chemical Corp., National Aniline Div., Biological Stains Dept., cat. no. 475) were fed to clams. Other clams were given the flagellated unicellular green alga *Dunaliella salina*. The clams were dissected after 1 h, and the digestive organs examined for the location of the ingested carmine particles or algae.

RESULTS

Habitat

Cryptomya californica was easily found in sandy lower estuarine mudflats of Yaquina Bay and Coos Bay, Oregon, during tides lower than +0.3 m (Figure 1a). Individuals were especially prevalent in areas inhabited by the ghost shrimp *Callianassa californiensis* (Figures 1b, c). The clams were usually embedded in the walls of the tunnels of the shrimp (Figure 1d), with only their short siphons protruding into the tunnels. This was sometimes difficult to observe, as the tunnels tended to collapse during excavation. Some specimens, however, were interred with no obvious connection to a tunnel. Often hundreds of clams were found in a square meter of substrate.

Burrowing Behavior

Clams placed on their side on submerged sand began to burrow after a few minutes, if left undisturbed. Burrowing takes place as follows. First, the siphons and large, ciliated foot emerge (Figure 2a). The extended foot can assume shapes ranging from knife-shaped to spade-shaped (Figure 3a), and muscular contractions, along with ciliary action on the outer surface, enable the foot to dig rapidly into the sand. The foot digs directly down into the sand, and when it is firmly anchored, the animal pulls itself off its side onto the anteroventral portion of the shell (Figure 2b). As the foot continues to dig, the entire animal periodically rocks in a dorsoventral plane, and with each rocking cycle the animal works itself deeper into the substrate (Figure 2c). After about 5 min the entire clam, except for the siphons, is completely buried (Figure 2d). Eventually the organism burrows deeper into the sand. How far or fast the clam can dig through the substrate, or how long it can survive without reaching an adequate tunnel was not determined in this study.

Anatomy

Shell morphology: The yellow-white, oblong shells are fragile and small. Although specimens of *Cryptomya californica* greater than 30 mm in length have been reported, the majority of shells collected in this research were less than 20 mm long. The shells gape at the posterior end, and the right valve is slightly fuller than the left. Delicate concentric growth lines are present. A brown periostracum extends beyond the growing shell margin and protects the mantle when it protrudes. The prominent chondrophore (Figure 3b) protruding from the hinge of the left valve is held by an internal resilium in the right valve (ABBOTT,

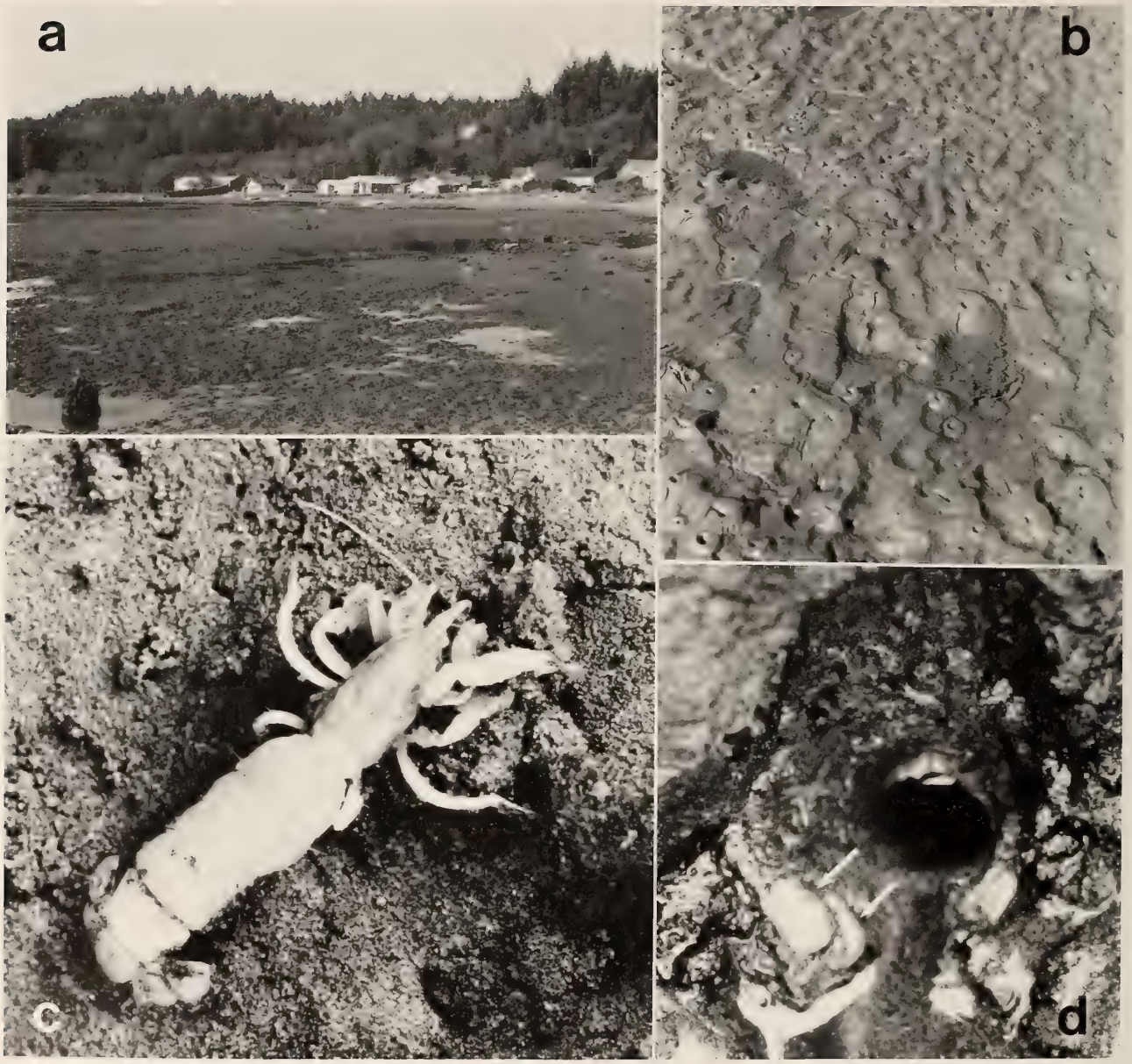


Figure 1

The habitat of *Cryptomya californica.* a. A typical sandy estuarine mudflat, representative of the normal habitat of *C. californica.* Coos Bay, Oregon. b. The usual appearance of the sandy substrate in which lives *Cryptomya californica,* often in proximity to the tunnels of *Callianassa californiensis.* As seen from a height of 1.5 m. c. *Callianassa californiensis* (female, 9 cm in length) burrowing into the sand. d. An excavation of a *Callianassa* burrow showing two *Cryptomya californica* (arrows) with their short siphons oriented toward the tunnel. Found down to depths of 50 cm beneath the surface of the sand, *Cryptomya californica* is usually 1 to 2 cm in length.

1974; HADERLIE & ABBOTT, 1980; QUAYLE, 1973; RUDY & RUDY, 1983).

Siphons: The siphons, as described by YONGE (1951), are extremely short (less than 1 mm in length). A membrane controls the opening of the excurrent siphon, and a row of tentacles protects the entrance of the incurrent siphon. Both siphons are surrounded by an outer ring of tentacles.

Gills and palps: The relatively large gills (two demibranchs on either side of the body) are covered with cilia, which rapidly pump water through the mantle cavity. The

Figure 2

The burrowing behavior of *Cryptomya californica*. a. A submerged *C. californica* lying on its right side, siphons and foot extended. The foot begins to penetrate the sand. b. When the foot is anchored, the clam rights itself. c. The clam rocks in a dorsoventral plane, and works itself into the substrate. In the gaping posterior portion of the shell are the excurrent siphon (membrane closed) and the incurrent siphon, with its surrounding tentacles. Both are encircled by an outer ring of tentacles. d. After about 5 min the clam is completely buried except for the siphons. The scale in all four photographs is the same. Bar = 1 cm.

cilia also filter food particles from the water and concentrate them into streams of mucus, which are carried to the mouth. Unusable particulate matter is sorted out by the labial palps and condensed into pseudofeces, which are transported by cilia posteriorly along the ventral portion of the mantle, and periodically expelled through the incurrent siphon (YONGE, 1951).

Stomach and intestine: The esophagus and stomach are surrounded by a large mass of digestive diverticula. The intestine emerges from the right side of the stomach, and I found its lumen to be connected for a short distance with the lumen of the style sac. The intestine then winds ventrally toward the posterior portion of the foot, where it loops dorsally to pass through the heart. The rectum runs dorsally of the posterior adductor muscle, leading to the anus just inside the excurrent siphon (YONGE, 1951).

Crystalline Style

A large style sac extends ventrally from the stomach (Figures 3c, d). The style sac is nearly transparent and has a seamlike structure, comprised of the major and minor typhlosoles, along the length of the right side. I discovered the ventral end of the style sac to be open to the body cavity. Therefore, the organ is actually a tube rather than a sac. The entire inner surface of the sac is lined with cilia, which cause the crystalline style to rotate and to press its

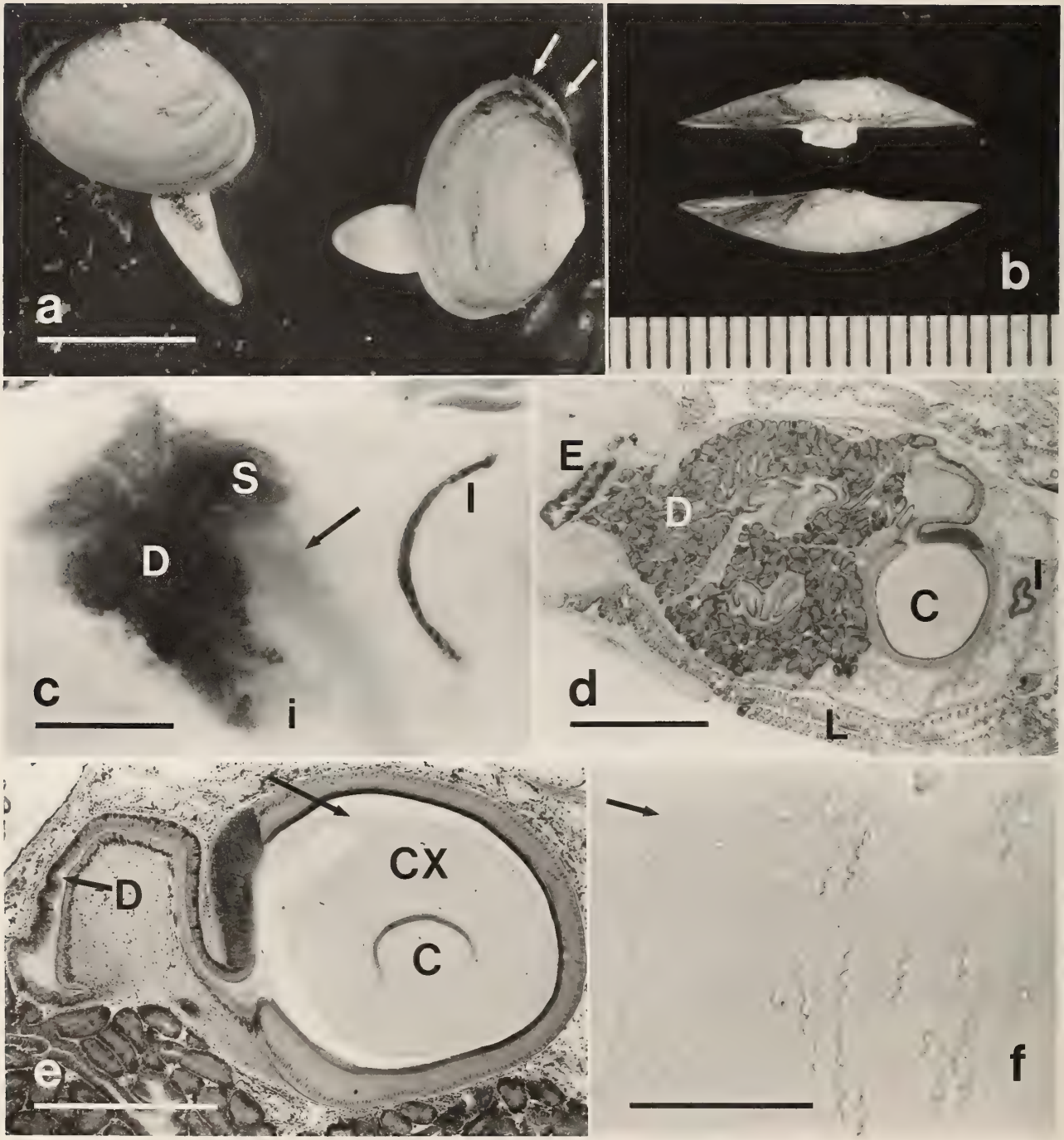


Figure 3

External and internal features of *Cryptomya californica.* a. Two specimens of *C. californica,* each with its muscular, ciliated foot extended. The short siphons (arrows) are indicated at the posterior end of one clam. Bar = 1 cm. b. Dorsal view of the valves of *C. californica,* with the chondrophore extending from the hinge of the left valve. The ruler is marked in 1 mm intervals. c. Dissection of the digestive organs of *C. californica,* as seen from the left side. The crystalline style, which is encased in a sac (arrow), protrudes into the stomach (S). Food is digested and absorbed primarily in the digestive diverticula (D). The intestine (i) loops twice as it descends from the right side of the stomach to an area near the ventral end of the style sac, where it curves dorsally (I) and carries waste materials to the anus. These organs are surrounded by gonad. Bar = 2 mm. d, Photomicrograph of a section of the

dorsal end against a prominent gastric shield in the stomach.

The style of a vivisected clam submerged in seawater was observed to rotate 7 to 30 rpm within its sac at water temperatures from 10 to 21°C respectively. The speed increased during several hours of observation, possibly owing to a rise in water temperature or a loss of ciliary control. The style rotated in a clockwise direction, the opposite direction noted by YONGE (1951), as seen from the dorsal end. I made these observations directly through the wall of the intact style sac, as a grain of black sand was fixed to the side of the style, and could be easily seen with each rotation. Even after the style was removed, style sac ciliary action continued for more than 5 h.

The crystalline style consists of a gelatinous, laminated cortex and a liquid core. Mucoid material, apparently being applied to or wound around the outer surface of the style (as seen in the section in Figure 3e), appears to originate from the intestine and, possibly, secretory cells along the right side of the sac.

A crystalline style was always present in freshly collected clams, those exposed to air for 24 h, those kept submerged for long periods, and in clams that had been starved for 6 weeks.

Spirochete bacteria of the genus *Cristispira* (Figure 4f) were invariably found actively moving within the cortex and core of the entire style (Figure 3f). They were also observed in the stomach fluid, but not in the intestine or rectum. Freshly collected clams contained thousands of *Cristispira*. Although these bacteria appeared healthy and active, and were observed to divide, their populations within fed clams decreased steadily at rates of 5 to 12% per day after clams were removed from their natural habitat.

Sterilized styles demonstrated amylase activity by hydrolyzing starch. Bacilli isolated from the surfaces of unsterilized styles also hydrolyzed starch.

Nutrition

The microscopic examination of intestinal contents (Figure 4a) and fecal pellets (Figure 4b) from freshly collected clams showed that the animals normally ingest detritus consisting mostly of diatoms and bacteria, but sometimes containing dinoflagellates, crustacean and annelid setae, sand, and even pollen grains. The digestive diverticula of fresh clams were usually green, presumably from chlorophyll of ingested algae (MATHERS, 1972). Carmine particles fed to clams passed quickly through the stomach into the intestine. No particles were observed in the digestive diverticula or the style. Clams that had been fed *Dunaliella salina* had algae (some still living) in the stomach 1 h after feeding. Chlorophyll had been incorporated into the core of the style in some cases.

Amebocytes

Rapidly moving amebocytes (Figure 4e) were often observed on the outside of the anterior end of the crystalline style. Such cells are elongate, measuring about 20 μm in length and 6 μm in width. The round nucleus, 2.3 μm in diameter, is centrally located. A large karyosome is in the middle of the nucleus. The cytoplasm contains numerous granules and vacuoles. These cells may be protozoan.

Gametes

The abundant gonads of *Cryptomya californica*, which fill most of the visceral cavity, contain either sperm (Figure 4c) or eggs (Figure 4d). The acrosomes of sperm are 5 μm long, tapered, and slightly curved. Including the flagellum, sperm measure 45 μm in length. The mature eggs are somewhat oblong, measuring 65 μm long and 53 μm at the widest point. There is a round, eccentric nucleus which is 30 μm in diameter and contains a large, round, eccentric nucleolus measuring 13 μm across. The abundant cytoplasm contains numerous inclusions (DOHMEN, 1983; LONGO, 1983; RAVEN, 1958).

DISCUSSION

Cryptomya californica occupies a nearly identical niche in the Oregon estuaries studied as it does in Monterey Bay, California. Dense populations of these clams are present in large areas of marine bays and lower estuarine sandy mudflats, especially in communities dominated by the ghost shrimp *Callianassa*. Because of its short siphons, deeply buried *Cryptomya californica* cannot have direct access to the surface of the sand. The animals are, therefore, usually embedded in the walls of tunnels of other burrowing or-

←

digestive organs lying immediately below the stomach (dorsal view). The crystalline style (C) is in a sac anterior to the ascending intestine (I) and posterior to the digestive diverticula (D) and the esophagus (E). At this level, the descending intestine is connected along its left portion to the style sac. They separate at about 1 mm below the stomach. The extensive lamellae (L) are also shown. H and E stain. Brightfield. Bar = 1 mm. e. Photomicrograph of a cross section of the crystalline style and style sac. The style has a liquid core (C) and a laminated cortex (CX). As seen from this dorsal view, the style rotates clockwise, propelled by the cilia of the columnar epithelial cells of the sac. Style cortex material (arrow) seems to originate from the typhlosoles of the style sac. In this section, the descending intestine (D) is connected to the style sac. H and E stain. Brightfield. Bar = 0.5 mm. f. Detail of the style cortex from Figure 3e, showing the orientation of its contained spirochete bacteria, *Cristispira*. The arrow indicates the outer edge of the style. Phase contrast. Bar = 0.1 mm.

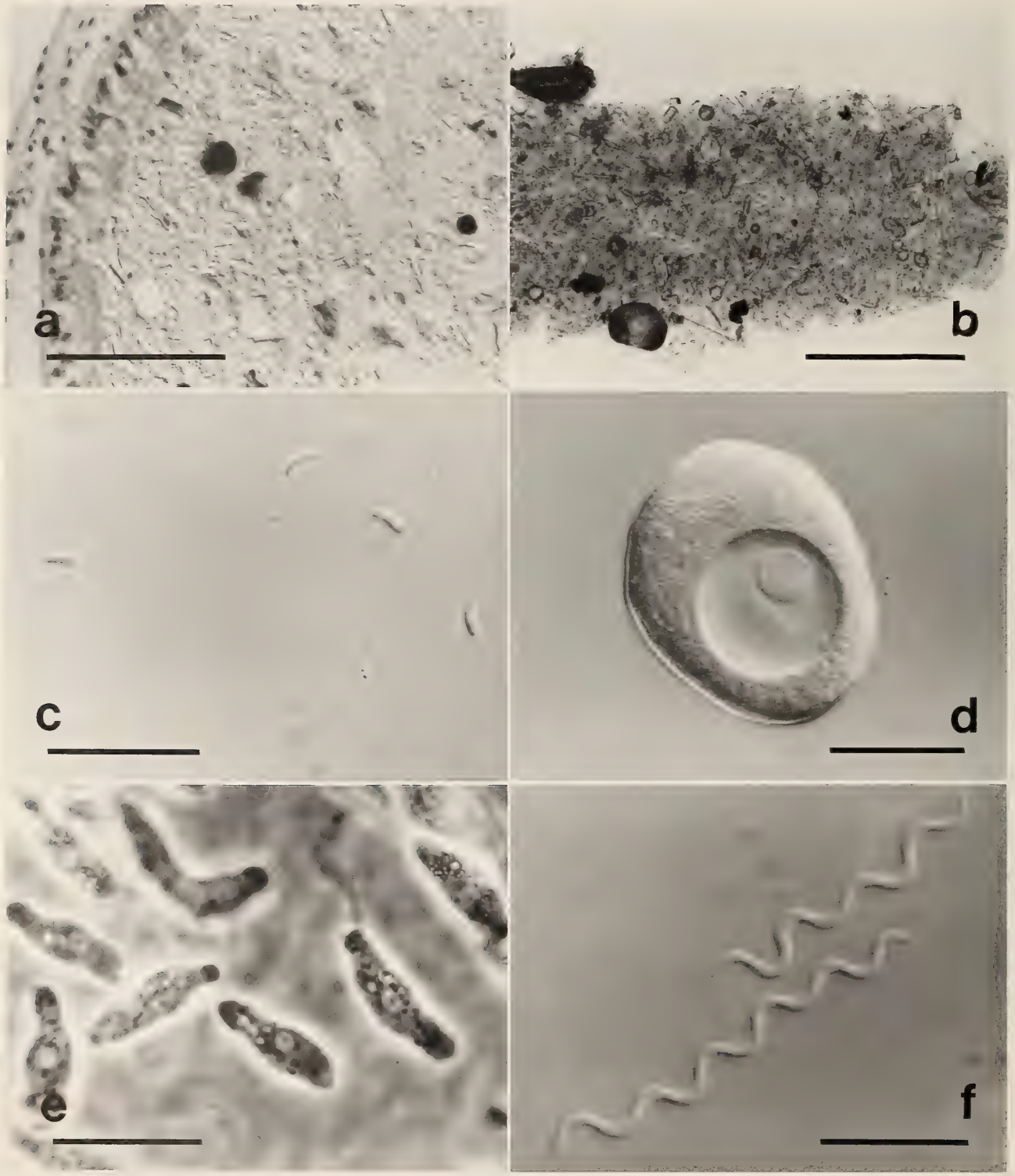


Figure 4

Cryptomya californica. a. A section through the descending intestine of a clam fixed immediately after collection, showing ingested detritus, especially diatom fragments. H and E stain. Nomarski optics. Bar = 70 μm. b. A portion of a fecal pellet from a freshly collected clam. It contains the valves of diatoms and dinoflagellates, crustacean and

ganisms such as the shrimps *Callianassa californiensis* and *Upogebia pugettensis,* and (in California) the echiuran worm *Urechis caupo.* The siphons protrude slightly into the tunnel, and the water therein is the source of oxygen and food, and the depository for waste products.

The clams avoid predation and desiccation by living at safe depths (down to 50 cm) within the sand, where they undoubtedly take up residence early in their larval lives. The collapsing of tunnels by tidal forces, the incessant burrowing activities of *Callianassa* (MacGinitie, 1934), or the searching of humans for edible clams and ghost shrimp for bait, may force *Cryptomya californica* to make frequent moves. The large cilia-covered foot, which can be extended through the pedal gape in the anteroventral portion of the mantle, the small slim shell, and the unencumbering siphons surely would facilitate movement through the sandy substrate.

The stomach clearly plays an essential role in the partial digestion and sorting of ingested substances (Yonge, 1923). As a result of ciliary activity, rotation of the crystalline style against the gastric shield, the release of enzymes from the style and digestive diverticula, and possibly some bacterial digestive action, several digestive processes are initiated in the stomach. First, large particles, such as diatoms, are shunted into the intestine, where degradation of contained organic material may be facilitated by the action of bacteria. Large numbers of motile bacilli were observed in fresh fecal pellets, and I noted that they actively congregated around masses of organic matter and diatoms contained in the pellets. Second, lysis of some plant cells takes place in the stomach. Third, much of the lysate and probably considerable amounts of bacteria are directed into the digestive diverticula to undergo further digestion and absorption. Lastly, some of the partially digested food is carried, along with quantities of mucus, into the style sac to form the liquid core of the style. The substance forming the laminated cortex of the style appears to be secreted by cells of the intestine and the typhlosoles along the right side of the style sac. While the core is continuously being replenished in the stomach, the anterior portion of the cortex is probably being dissolved there (Mathers, 1974). The significance of the opening in the ventral end of the style sac is not clear. Some nutrient material may conceivably pass directly from the style sac into the body cavity through this aperture.

The crystalline style of *Cryptomya californica* is always present regardless of prolonged periods of submergence or exposure, or the presence or absence of food. *Callianassa* beds are normally exposed only during tides below +0.3 m, and during most low tides the shrimps' tunnels probably contain enough water to permit *Cryptomya californica* to continue its respiratory and feeding activities (MacGinitie, 1934). The persistence of the style is likely an adaptation to a nearly continuous feeding behavior.

MacGinitie (1934) felt that competition for food between *Cryptomya californica* and *Upogebia* or *Urechis,* both of which are efficient plankton filterers, may explain why the clam seems to be more plentiful in burrows of *Callianassa.* The repiratory, burrowing, grooming, and sand-filtering activities of *Callianassa* not only circulate food-laden seawater through the burrow during high tides, but also stir up detritus (mostly diatoms and bacteria) during low tides. The alimentary canals of clams that I collected were always full of detritus.

Cryptomya californica normally has thousands of *Cristispira* in the stomach and matrix of the crystalline style. It seems that this population of spirochetes must be continuously replenished by ingestion of bacteria from the environment, as their numbers steadily decrease in clams removed from their natural habitat, even though the size of the styles does not decrease. The majority of the *Cristispira* are probably first incorporated into the core of the style as mucus is drawn from the stomach into the style sac. Afterwards, they make their way into the cortex, the substance of which they are able to partially liquify. They can be observed moving actively back and forth in liquid-filled channels apparently of their own making. I have observed these bacteria dividing *in situ,* but their growth rate within the style probably cannot keep up with attrition. Most are probably lost through the intestine, although none were identified there in this study. The invariable presence of a large, active population of spirochetes in the styles of freshly collected clams suggests that the bacteria may aid in the digestion of food materials ingested by the host. Upon degradation, however, they may also serve as a source of nutrition for the clam.

The crystalline style possesses the starch-hydrolyzing enzyme amylase. The release of this enzyme in the stomach assists in the digestion of plant materials normally consumed by *Cryptomya californica.* Gram negative bacilli, possibly *Vibrio* spp., which are always present in the stomach and style sac, also produce starch-hydrolyzing enzymes. Thus, at least part of the enzyme found in the style may be of bacterial origin. In my opinion, there is some validity to each of the following hypotheses: (a) that the crystalline style is an organ that stores digestive enzymes

←

annelid setae, plant material (including pollen grains), sand, and bacteria. Brightfield. Bar = 250 μm. c. Sperm of *C. californica.* Nomarski optics. Bar = 20 μm. d. An egg from *C. californica,* with its large round nucleus, prominent nucleolus, and extensive cytoplasm. Nomarski optics. Bar = 30 μm. e. Living, active amebocytes *in situ* on the outer surface of the crystalline style. Numerous cytoplasmic inclusions are visible. Phase contrast. Bar = 20 μm. f. Living *Cristispira* sp. *in situ* within the matrix of the crystalline style. Nomarski optics. Bar = 20 μm.

needed during feeding, (b) that it is itself a site where some digestion takes place, and (c) that some nutrients may be stored within its matrix for subsequent use during periods of food scarcity.

Amebocytes are often present on the outer surface of the anterior half of a style taken from a fresh clam. These cells are very active and contain numerous cytoplasmic inclusions. If they are indeed of clam origin, which remains to be shown, then presumably they act as scavengers maintaining the style and style sac. They may transport nutrients to other portions of the body.

The majority of the body cavity is filled with gonad, and immense numbers of sperm or eggs are produced. Although I observed fecund specimens in May, no seasonal data are available. Gametes are probably shed directly into the tunnels of *Callianassa* and other mud-dwelling organisms. The feeding activities of crustaceans, worms, mollusks, and gobies within the tunnels no doubt contribute greatly to the attrition of embryos and larvae (MacGinitie, 1934) of *Cryptomya californica.*

ACKNOWLEDGMENTS

I thank John Baross, James Carlton, Carol Cogswell, Daniel Gleason, Suzanne Hamilton, Harrison Howard, Tena Lawry, Bayard McConnaughey, James McLean, Norman McLean, Richard Morita, Sonja Rasmussen, Paul and Lynn Rudy, and Donald Wimber for their kind assistance during this research.

LITERATURE CITED

Abbott, R. T. 1974. American seashells: the marine Mollusca of the Atlantic and Pacific coasts of North America. Van Nostrand Reinhold Company: New York. 663 pp.

Brown, D. A., C. A. Bawden, K. W. Chatel & T. R. Parsons. 1977. The wildlife community of Iona Island jetty, Vancouver, B.C., and heavy-metal pollution effects. Environmental Conservation 4:213–216.

Dohmen, M. R. 1983. Gametogenesis. Pp. 1–48. *In:* K. M. Wilbur, N. H. Verdonk & J. A. M. van den Biggelaar (eds.), The Mollusca, Vol. 3: Development. Academic Press: New York. 352 pp.

Haderlie, E. C. & D. P. Abbott. 1980. Bivalvia: the clam and allies. Pp. 355–411. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford University Press: Stanford, California. 690 pp.

Hertlein, L. G. & U. S. Grant. 1972. The geology and paleontology of the marine Pliocene of San Diego, California. Paleontology: Pelecypoda. San Diego Society of Natural History, Memoir 2(Part 2B):135–409.

Iordachescu, D. & I. F. Dumitru. 1978. Some physiochemical properties of α-amylase purified from the marine mollusc *Mya arenaria.* Revue Roumaine de Biochimie 15:279–285.

Keen, A. M. 1971. Sea shells of tropical West America: marine molluscs form Baja California to Peru. Stanford University Press: Stanford, California. 1064 pp.

Langton, R. W. 1977. Digestive rhythms in the mussel *Mytilus edulis.* Mar. Biol. 41:53–58.

Lawry, E. V. 1981. The fine structure of *Cristispira* from the lamellibranch *Cryptomya californica* Conrad. M.S. Thesis, University of Oregon. 49 pp.

Lawry, E. V., H. M. Howard, J. A. Baross & R. Y. Morita. 1981. The fine structure of *Cristispira* from the lamellibranch *Cryptomya californica* Conrad. Cur. Microbiol. 6:355–360.

Longo, F. J. 1983. Meiotic maturation and fertilization. Pp. 49–89. *In:* K. M. Wilbur, N. H. Verdonk & J. A. M. van den Biggelaar (eds.). The Mollusca, Vol. 3: Development. Academic Press: New York. 352 pp.

MacGinitie, G. E. 1934. The natural history of *Callianassa californiensis* Dana. Amer. Midl. Natur. 15:166–177.

MacGinitie, G. E. 1935. Ecological aspects of a California marine estuary. Amer. Midl. Natur. 16:629–765.

Mathers, N. F. 1972. The tracing of a natural algal food labelled with a carbon 14 isotope through the digestive tract of *Ostrea edulis* L. Proc. Malacol. Soc. Lond. 40:115–124.

Mathers, N. F. 1973. A comparative histochemical survey of enzymes associated with the processes of digestion in *Ostrea edulis* and *Crassostrea angulata* (Mollusca: Bivalvia). Jour. Zool. (Lond.) 169:169–179.

Mathers, N. F. 1974. Digestion and pH variation in two species of oysters. Proc. Malacol. Soc. Lond. 41:37–40.

Nelson, T. C. 1918. On the origin, nature, and function of the crystalline style of lamellibranchs. Jour. Morphol. 31: 53–111.

Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? Amer. Natur. 124:127–133.

Quayle, D. B. 1973. The intertidal bivalves of British Columbia. British Columbia Provincial Museum: Victoria, B.C. Handbook No. 17:104 pp.

Raven, C. P. 1958. Morphogenesis: the analysis of molluscan development. Pergamon Press: New York. 311 pp.

Rudy, P. & L. H. Rudy. 1983. Oregon estuarine invertebrates: an illustrated guide to the common and important invertebrate animals. Fish & Wildl. Serv., U.S. Dept. Inter.: Washington, D.C. 225 pp.

West, R. R., P. C. Twiss, J. E. Mathewson & R. S. Swain. 1976. Some intertidal infauna and their substrate: Puerto Penasco, Sonora. Trans. Kansas Acad. Sci. 79:113.

Wicksten, M. K. 1978. Checklist of marine mollusks at Coyote Point Park, San Francisco Bay, California. Veliger 21:127–130.

Yonge, C. M. 1923. The mechanism of feeding, digestion, and assimilation in the lamellibranch *Mya.* Jour. Exper. Biol. 1: 15–63.

Yonge, C. M. 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis.* Jour. Mar. Biol. Assoc. U.K. 14:295–386.

Yonge, C. M. 1932. The crystalline style of the Mollusca. Science Progress 26:643–653.

Yonge, C. M. 1951. Studies on Pacific coast mollusks: I. On the structure and adaptations of *Cryptomya californica* Conrad. Univ. California Publ. Zool. 55:395–400.

The Veliger 30(1):55–68 (July 1, 1987)

THE VELIGER

Gametogenesis and Reproductive Cycle of the Surf Clam *Mesodesma donacium* (Lamarck, 1818) (Bivalvia: Mesodesmatidae) at Queule Beach, Southern Chile

by

SANTIAGO PEREDO, ESPERANZA PARADA, AND IVÁN VALDEBENITO

Department of Biology, Catholic University of Chile-Temuco,
Casilla 15-D, Temuco, Chile

Abstract. The gonadal organization, cytological characteristics of gametogenesis, and reproductive cycle in the surf clam *Mesodesma donacium,* from Queule Beach, southern Chile, were studied histologically using light microscopy. Monthly analysis of the proportion of sexes revealed a sex ratio of 1:1. In both sexes, gonads are ramified organs bearing numerous follicles closely packed among coils of the intestine. Gametogenesis follows the general plan described in most marine bivalves. Gametes at different stages of maturation can be recognized by their shape, size, and nuclear features in both sexes. The reproductive cycle is annual, with a maturation period from June through November (winter and spring). Spawning extends from December to April (summer and early autumn), peaking in December and January. Gonads undergo a short recovery period during May and then start a new cycle.

INTRODUCTION

The reproductive cycles of mollusks of commercial value inhabiting Chile's extensive coastline have been described from a variety of locations on the coast. Among the lamellibranch bivalves are *Aulacomya ater* (LOZADA, 1968; SOLÍS & LOZADA, 1971), *Choromytilus chorus* (LOZADA *et al.,* 1971; PEREZ-OLEA, 1981), *Ostrea chilensis* (WALNE, 1963; SOLÍS, 1967) and *Venus antiqua* (LOZADA & BUSTOS, 1984). These studies, in addition to furnishing reproductive data that have allowed an adequate management of these species, have also shown variations in the timing of gametogenesis and spawning in populations from different geographical areas. These latitudinal variations are ascribed to environmental factors that present local variations and exert exogenous control on reproduction. Among these factors, the most relevant are temperature and abundance of food (GIESE & PEARSE, 1977).

The reproductive cycle of the surf clam *Mesodesma donacium* has been studied by BROWN & GUERRA (1979) in Guanaqueros (30°15′S, 71°41′W) and TARIFEÑO (1980) at the Laguna Beach area of Valparaíso (32°30′S, 71°30′W). These studies have shown differences in the timing of gametogenesis and spawning period in the populations studied. The present study describes the sex ratio, gametogenesis, and seasonal gonadal changes of a surf clam population from Queule Beach (39°25′S, 73°13′W). This locality was selected as the study area because it has potential for commercial operations and the area appears to contain a large population of the surf clam.

MATERIALS AND METHODS

Monthly samples of surf clams were collected from a bed in the mid-littoral level of Queule Beach (39°25′S, 73°13′W) from August 1983 to November 1984. Each sample consisted of 230 clams. From these samples, 15 males and 15 females in the shell length range of 61 to 75 mm were selected for histological study. This size range was chosen to avoid inclusion of juvenile surf clams (sexually immature individuals). The viscera were fixed in aqueous Bouin's fixative. After embedding in paraffin, 7-μm serial sections were cut and stained with hematoxylin and eosin. Ten to 15 sections through different regions of the gonads of each specimen were examined under the light microscope to determine the gonadal organization, the cytological characteristics of gametogenesis, and the seasonal gametogenic cycle.

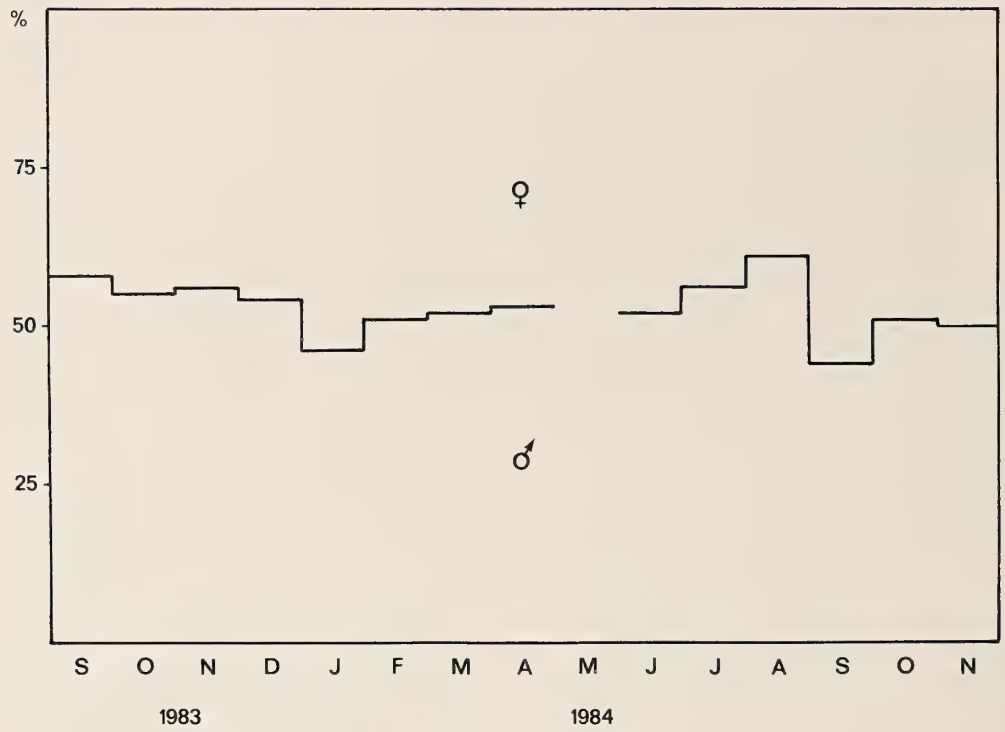


Figure 1

Proportions of females and males in the *Mesodesma donacium* population from Queule Beach.

The remaining specimens of the monthly samples were used to determine the sex ratio and the dry weight of the soft tissues. Chi-square analysis was used for sex-ratio determinations. To determine the dry weight, the body soft tissues were kept in an oven at 90°C until reaching constant weight.

Water temperature data during the study period were supplied by the Marine Station at Mehuín of the Zoological Institute, Universidad Austral de Chile.

RESULTS

Mesodesma donacium is a dioecious species as revealed by microscopic examinations. These results support former reports of studies on populations of this species occurring at different locations on the Chilean coast (Brown & Guerra, 1979; Tarifeño, 1980). Monthly analysis of the proportion of sexes in the mature population of *M. donacium* revealed a sex ratio of 1:1. Of the total number examined, 52% of the individuals were males, 46% females, and 2.1% indeterminate (Figure 1). Sexual dimorphism is absent.

Male Gonad and Germ Cells

The male gonad consists of numerous follicles located in the visceral mass surrounding the intestinal coils. The follicles vary in shape and size and are delimited by a thin, cellular, enveloping membrane (Ancel's layer) (Figure 2). Fibroblast-like cells with spindle-shaped nuclei are seen in the follicle walls (Figures 3, 4). The cytoplasm of these cells is difficult to visualize.

In the period of maximum gonadal activity, the follicles are crowded with cells at different stages of spermatogenesis. The cells of particular stages can be recognized by their nuclear features (shape, size, and staining properties) and by their location in the gonadal follicles (Figure 5).

→

Explanation of Figures 2 to 7

Figure 2. Topographical view of the male gonad of *Mesodesma donacium*. The well delimited follicles (F) show diversity in size and shape and occupy the visceral mass (mesosoma) surrounding the intestine (I). ×20.

Figure 3. Primary spermatogonia (spg1) and secondary spermatogonia (spg2) lying in the periphery of the follicle. Close to the spermatogonia, the nucleus of a supporting cell (sc) can be seen. The spindle-shaped nucleus (arrow) is from a cell of the follicle wall. ×500.

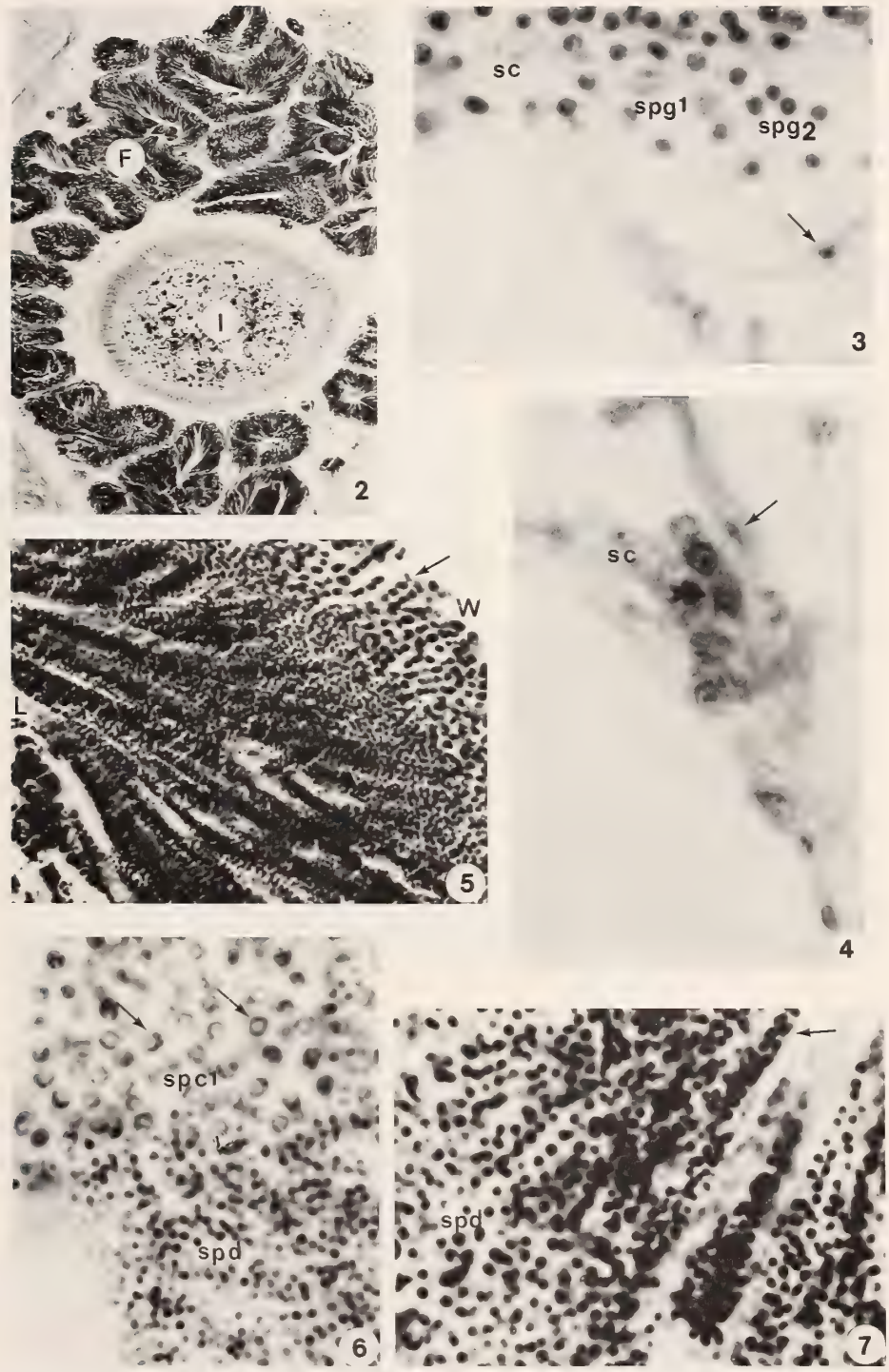
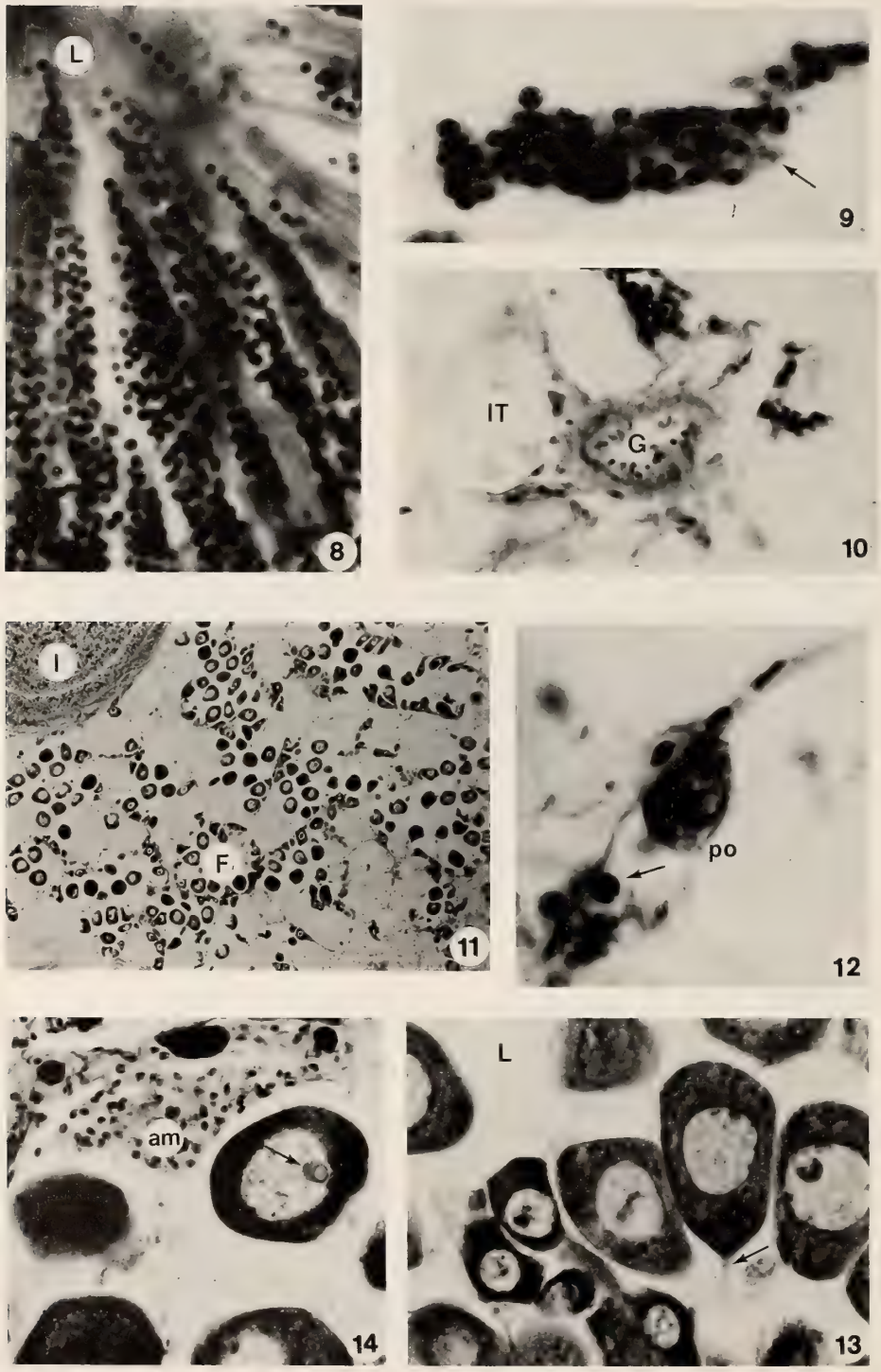


Figure 4. Primary spermatogonia showing some mitotic figures. A spindle-shaped nucleus from a cell of the follicle wall (arrow) is visible and a supporting cell nucleus (sc) is seen next to the germ cells. ×500.

Figure 5. Germ cells within a male gonadal follicle. Primary spermatocytes (arrows) are in single-cell columns oriented from the walls (W) toward the lumen of the follicle (L). ×200.

Figure 6. Primary spermatocytes (spc1) showing meiotic figures (arrows). Next to the primary spermatocytes, a cluster of secondary spermatocytes is interspersed with spermatids (spd). The nuclei of these two cell types are hardly distinguishable. ×500.

Figure 7. Clusters of spermatids (spd). Spermatids in more advanced stages of differentiation (arrow) form radially oriented columns with the flagella oriented toward the center of the follicles. ×500.



Explanation of Figures 8 to 14

Figure 8. Radially oriented columns of spermatozoa and advanced spermatids. Bundles of flagella occupy the lumen (L) of the gonadal follicle. ×500.

Figure 9. Dense mass of amoebocytes within a follicle. The nucleus of a supporting cell (arrow) can be seen. ×500.

Figure 10. A gonoduct (G) in the interstitial tissue (IT). ×200.

Figure 11. Topographical view of the female gonad of *Mesodesma donacium*. The follicles (F) in the visceral mass surround the intestine (I). ×20.

Primary spermatogonia: These spermatogonia have large (about 3 μm diameter) spherical or slightly oval nuclei with scanty and finely granular chromatin and one or more conspicuous nucleoli (Figure 3). Primary spermatogonia are less numerous than secondary spermatogonia and lie against the membrane enveloping the follicles. Occasionally, mitotic figures can be seen in this type of spermatogonia (Figure 4).

Secondary spermatogonia: Spermatogonia of this type have smaller nuclei (2.0–2.5 μm) and stain more heavily than the nuclei of primary spermatogonia. Secondary spermatogonia are more numerous than primary spermatogonia and lie close to them (Figure 3).

Primary spermatocytes: These cells form numerous, compact clusters. They have small nuclei (about 1.8 μm in diameter) that vary in appearance as the chromatin assumes different consistencies and locations within the nucleus. The chromosomes can be scattered in the nucleus or they may be polarized at the periphery, showing typical figures of meiotic prophase (Figure 6).

Secondary spermatocytes: Secondary spermatocytes are seen less commonly than primary spermatocytes. They occur in groups generally intermingled with spermatids, thus forming mixed cell groups. The nuclei of secondary spermatocytes are very similar to those of spermatids (Figure 6).

Spermatids: These cells have small, round nuclei with granular and heavily staining chromatin. They form compact clusters with secondary spermatocytes located toward the center of the follicles (Figure 6). Spermatids in more advanced stages of differentiation form radially oriented columns with the flagella oriented toward the center of the follicles (Figure 7).

Spermatozoa: Spermatozoa are formed in the center of the follicles where they accumulate. The mature spermatozoon has a small round head (1.0 μm in diameter). The chromatin is dense and stains homogeneously. Together with advanced spermatids, mature spermatozoa form columns oriented toward the center of the follicles with bundles of flagella occupying the lumina (Figure 8). Owing to the small size of the sperm head, it is not possible to visualize with the light microscope such structures as the acrosome and middle piece described in the sperm of other bivalves (Retzius, 1904, 1905; Franzén, 1955, 1969, 1983; Ockelmann, 1964; Thompson, 1973; Popham, 1974).

Somatic cells—Supporting cells: These cells have a pale and irregularly shaped nucleus with a prominent nucleolus. The cytoplasm is not visible. Supporting cells are seen next to the follicle walls and intermingled with spermatogonia (Figures 3, 4). Cells of this type are seen in the connective tissue within the follicles when the latter are empty or partially full of gametes.

Amoebocytes: These cells have a nucleus of a size similar to that of the primary spermatocytes, but amoebocyte nuclei are darkly and homogeneously stained and placed toward one edge of the cytoplasm. These cells are especially abundant in follicles that contain residual gametes (Figure 9).

The gonoducts are branched and smaller in diameter than follicles; the walls are lined with ciliated cells, which define a narrow lumen. Gonoducts are seen in the interstitial connective tissue that surrounds the gonadal follicles (Figure 10).

Female Gonad and Germ Cells

As in the male, the female gonad of *Mesodesma donacium* is a branched organ embedded in the visceral mass. Numerous follicles surround the intestinal coils. The follicles are irregular in size and shape, and are delimited by a connective tissue wall (Figure 11).

In the follicles, germ cells at different stages of development can be recognized by their size, shape, and staining properties.

Oogonia: Oogonia are embedded in the follicle walls, frequently in small groups or "nests." The nucleus of an oogonium is spherical, with reticulate and heavily stained chromatin; a nucleolus is not visible (Figure 12). The cytoplasm is scanty or not visible.

Previtellogenic oocytes: The shape of previtellogenic oocytes may be square, oval, triangular, or cylindrical. The scarce cytoplasm is basophilic and bulges from the follicle walls. The nucleus is large, stains lightly, and has disperse chromatin that is usually peripherally placed and prominent; there is a basophilic nucleolus (Figure 12).

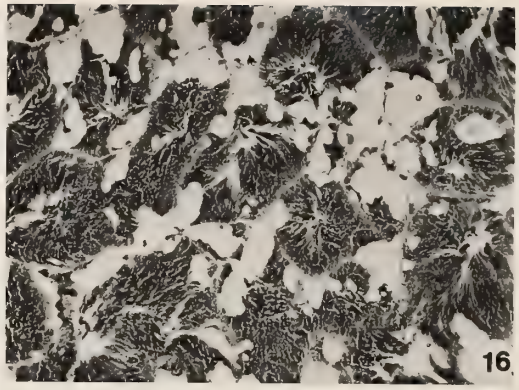
Vitellogenic oocytes: The size of vitellogenic oocytes varies with the amount of yolk accumulated. As the oocytes grow they elongate and protrude into the center of the follicles. The basal region of the cytoplasm is thinner than the distal end, forming a stalk that attaches oocytes to the follicle walls. The nucleus is prominent (Figure 13).

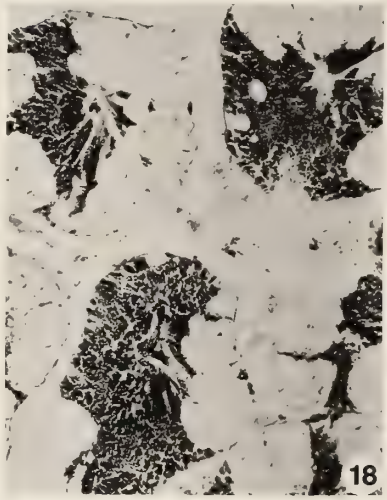
←

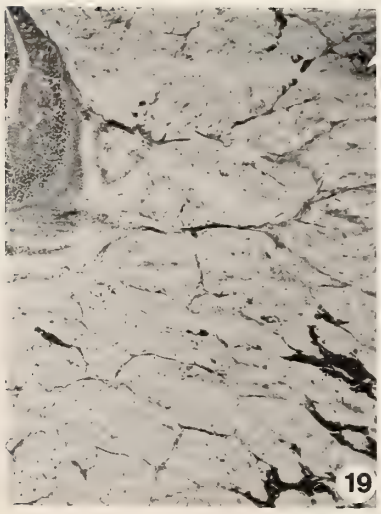
Figure 12. Oogonium (arrow) embedded in the follicle wall. Next to it a previtellogenic oocyte (po) is seen bulging from the follicle wall. ×500.

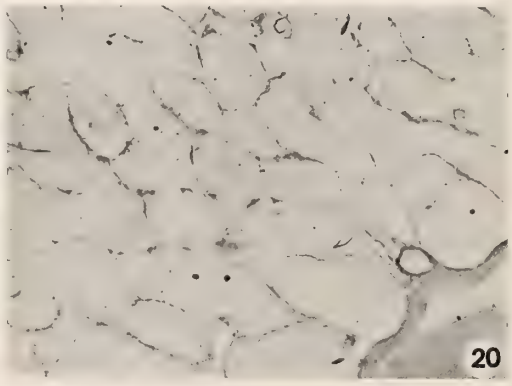
Figure 13. Vitellogenic oocytes of various sizes and shapes protruding into the lumen (L) of the follicle. An oocyte with a slender stalk (arrow) can be seen. ×200.

Figure 14. Vitelline (full-grown) oocytes in follicles. The amphinucleolus (arrow) can be seen in one of them. Amoebocytes (am) are seen as dense granular bodies, yellowish in sections. ×200.









Explanation of Figures 15 to 20

Figure 15. Section of gonad tissue from a male *Mesodesma donacium* in the early active stage. Gonadal follicles are small and well delimited. Germinal cells are beginning to invade the intrafollicular spaces.

Figure 16. Section of gonad tissue from a male *M. donacium* in the late active stage. Most of the follicles are almost full of gametes, with small portions of connective tissue remaining. ×20.

Figure 17. Section of gonad tissue from a male *M. donacium* in the ripe stage. Mature sperm form dense masses. Follicles are expanded with their limits poorly delimited. ×20.

Mature oocytes (morphologically mature): Vitelline oocytes are larger than early oocytes and are oval or round. These oocytes have become free of the follicle wall and have moved into the lumen. The germinal vesicle is intact with dispersed chromatin and stains lightly. One or more nucleoli can be seen with eosinophilic and basophilic areas (amphinucleoli). The cytoplasm is loaded with vitelline platelets. The size of mature oocytes ranges from 35 to 48 μm in diameter, with an average of 41 μm (Figure 14).

Somatic cells: Cells similar to the supporting cells of the male follicles can be seen in the female follicles, close to the follicle walls. In the interstitial tissue and in follicles containing residual gametes, one can see amoebocytes having the same features described for those of the male gonad. These cells are frequently seen as dense, yellowish, granular bodies in the female follicles.

Gonadal Cycle

Histological examination of the gonads in *Mesodesma donacium* allows recognition of the following stages of development: early active, late active, ripe, partially spawned, spent, and recovery.

Male gonad—Early active stage: This is a phase of intense gamete proliferation and development. Gonadal follicles are rather small and are clearly demarcated by relatively thick walls. The interstitial tissue is abundant and disseminated among the gonadal follicles. Germinal cells are beginning to invade the intrafollicular spaces (Figure 15). Primary and secondary spermatogonia are close to the thickened follicular walls. Primary spermatocytes proliferate toward the lumina. Occasional spermatids at an initial stage of differentiation can be seen close to primary spermatocytes toward the center of the follicles. Most of the intrafollicular spaces are filled with connective tissue in which supporting cells can be seen. Supporting cells can also be seen close to the follicular walls.

Late active stage: The remaining spermatogenic stages are seen in the late active stage. Primary spermatogonia are now scarce. In contrast, secondary spermatogonia, primary spermatocytes, and spermatids are numerous. Spermatozoa can also be visualized at this stage of gonadal development. The sperm form radially oriented columns with the tails toward the center of the follicles. Germinal cells do not completely fill the follicles; small portions of the follicles contain connective tissue (Figure 16).

Ripe stage: Gonadal follicles are expanded in the ripe phase with their limits poorly defined. Mature sperm form dense masses in the follicles of clams in the ripe stage (Figure 17). Cells in early stages of spermatogenesis are much less numerous at the periphery of follicles than are sperm.

Partially spawned stage: Partially spawned follicles still contain sperm but these are less numerous than in the ripe stage. Spermatids and primary spermatocytes can be seen located toward the periphery of the follicles (Figure 18).

Spent stage: Most of the follicles contain no spermatozoa or very few, and the lumina are empty (Figure 19).

Recovery stage: Gonadal follicles at this stage are empty, except for residual gametes. Close to the follicular walls lie supporting cells and numerous amoebocytes. The interstitial tissue has increased, branching from the intestine and surrounding the follicles (Figure 20).

Female gonad—Early active stage: In the early active stage there is an intense proliferation and growth of gametes. Gonadal follicles are small and well delimited by thickened walls. Interstitial tissue is abundant. Embedded in the follicular walls are oogonia and, bulging to the center of the follicles, previtellogenic oocytes can be seen. Vitellogenic oocytes of different size and shape lie at the periphery of the follicle walls and the cytoplasm extends into the lumen of the follicles (Figure 21).

Late active stage: In the late active phase, vitellogenic oocytes are more numerous than in the early active stage. In addition to vitellogenic oocytes of various sizes, some mature oocytes are free in the lumina of the follicles (Figure 22).

Ripe stage: Ripe gonads typically have a dense appearance because the follicles are crowded together and filled with mature (full-grown) oocytes (Figure 23).

Partially spawned: In partially spawned gonads a few vitelline (mature) oocytes are free in the lumen of the follicles and some vitellogenic oocytes are attached to the walls. Less often, follicles are devoid of ripe oocytes (Figure 24).

Spent stage: In spent gonads most of the follicles are devoid of ripe gametes, with few residual oocytes. Other follicles, less numerous, contain a few full-grown and even vitellogenic oocytes (Figure 25).

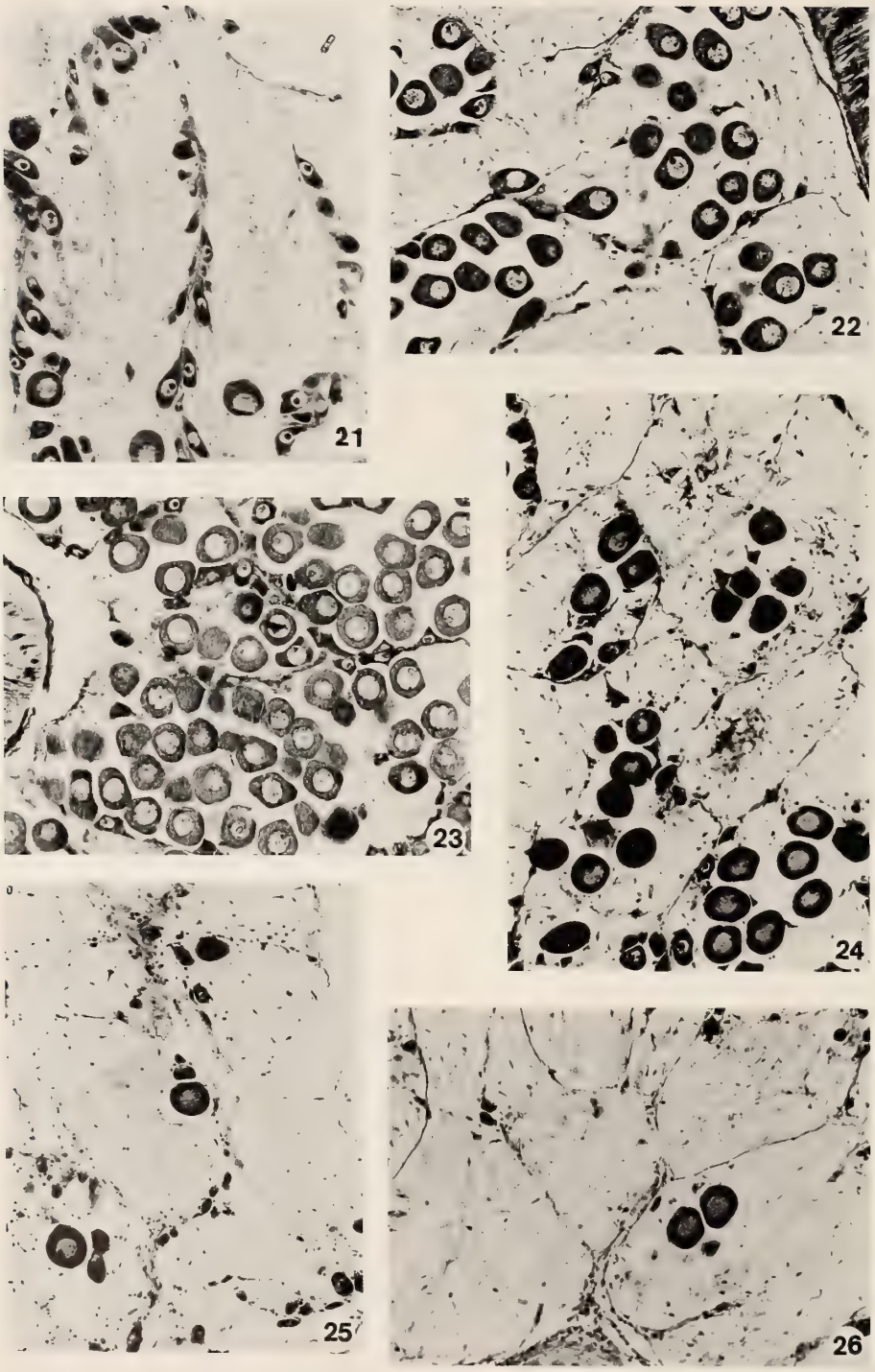
Recovery stage: In the recovery stage most of the follicles are completely devoid of gametes, although some follicles have a few residual oocytes. Amoebocytes are present within the follicles, close to the walls and in the center

←

Figure 18. Section of gonad tissue from a male *M. donacium* in the partially spawned stage. Follicles still contain sperm but these are less numerous than in the ripe stage. Spermatids and primary spermatocytes are located toward the periphery of the follicles. ×50.

Figure 19. Section of gonad tissue from a male *M. donacium* in the spent stage. Almost all of the follicles contain no spermatozoa, but a few others still have scarce gametes. ×20.

Figure 20. Section of gonad tissue from a male *M. donacium* in the recovery stage. Follicles are empty except for residual gametes. Interstitial tissue has increased, branching from the intestine and surrounding the follicles. ×20.



Explanation of Figures 21 to 26

Figure 21. Section of gonad tissue from a female *Mesodesma donacium* in the early active stage. Embedded in the follicular walls are oogonia, and vitellogenic oocytes can be seen bulging toward the center of the follicles. ×50.

Figure 22. Section of gonadal tissue from a female *M. donacium* in the late active stage. Vitellogenic oocytes are larger and more numerous than in the former stage of gonad development. Some vitelline oocytes can be seen free in the lumina of the follicles. ×50.

Figure 23. Section of gonad tissue from a female *M. donacium*

Table 1

Percentage frequency of the sampled population of *Mesodesma donacium* from Queule Beach in each reproductive phase during the study period.

	Early active				Late active				Ripe				Partly spawned				Spent			
	Males		Females		Males		Females		Males		Females		Males		Females		Males		Females	
Date	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Sept. 83	0	0	0	0	8	53	12	87	7	47	4	13	0	0	0	0	0	0	0	0
Oct. 83	0	0	0	0	1	8	7	70	12	92	3	30	0	0	0	0	0	0	0	0
Nov. 83	0	0	0	0	0	0	3	19	15	100	13	81	0	0	0	0	0	0	0	0
Dec. 83	0	0	0	0	0	0	0	0	3	24	0	0	10	76	11	100	0	0	0	0
Jan. 84	0	0	0	0	0	0	0	0	1	7	0	0	14	93	15	100	0	0	0	0
Feb. 84	0	0	0	0	0	0	0	0	2	13	0	0	2	13	11	100	11	73	0	0
Mar. 84	0	0	0	0	0	0	0	0	0	0	0	0	6	43	5	33	8	57	10	66
Apr. 84	0	0	0	0	0	0	0	0	0	0	0	0	2	12	3	25	14	88	9	75
May 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jun. 84	16	100	23	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul. 84	9	50	18	100	9	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug. 84	0	0	13	86.6	14	80	2	13.4	3	20	0	0	0	0	0	0	0	0	0	0

of the follicles. Interstitial tissue occurs in the spaces between the loosely arranged follicles (Figure 26).

Annual Reproductive Cycle

Histological examination of the gonadal sections revealed a seasonality of gonadal stages (Table 1, Figures 27, 28). During the study period (August 1983–November 1984) male clams in the late active stage were encountered from July to September and females from August through September. In September 1983, 53% of the males and 87% of the females were in this stage. During October, 92% of the males and 30% of the females were in the ripe stage. Ripe males (100%) and females (81%) were most abundant in November.

Clams in a spawning condition were first encountered in December and were last observed in the early April 1984 samples. Males in this stage were most abundant in January (93%) and then declined in the following months (February, March, and April) to 13%, 43%, and 12% respectively. Females in partially spawned stage were most abundant (100%) from December through February and then dropped to 33% and 25% in March and April respectively.

Spent clams were present from February to April, with the highest percentage of males (73%) occurring in February and the highest percentage of spent females (75%) in April. Histological examination of gonads during April revealed that clams in the spent stage had already initiated the resting or recovery stage.

Even though no samples were collected in May 1984, the observed histological features of the gonads in April and in June 1984 suggested that during May, clams were in the recovery stage, a condition observed in part of the population in April.

In June, 100% of the males and females were in the early active stage. During July, 50% of the males were in the early active phase and the other 50% were the first individuals encountered in the late active stage. In the same month (July), 100% of the females were still in the early active phase.

In August 1984, the last month in which samples were histologically examined, 80% of the males and 10% of the females were in the late active stage. This low percentage

←

in the ripe stage. The gonad has a dense appearance with follicles crowded together and filled with vitelline (full-grown) oocytes. ×50.

Figure 24. Section of gonad tissue from a female *M. donacium* in the partially spawned stage. Some follicles have a few vitelline and vitellogenic oocytes attached to the walls. Other, less numerous follicles are completely devoid of oocytes. ×50.

Figure 25. Section of gonad tissue from a female *M. donacium* in the spent condition. In this stage, most of the follicles are devoid of gametes, with a few residual oocytes. Other, less numerous follicles contain some full grown and even vitellogenic oocytes. ×50.

Figure 26. Section of gonad tissue from a female *M. donacium* in the recovery stage. Most of the follicles are completely devoid of gametes, but other, less numerous follicles contain residual gametes. Interstitial tissue extends from the intestine wall among the loosely arranged follicles.

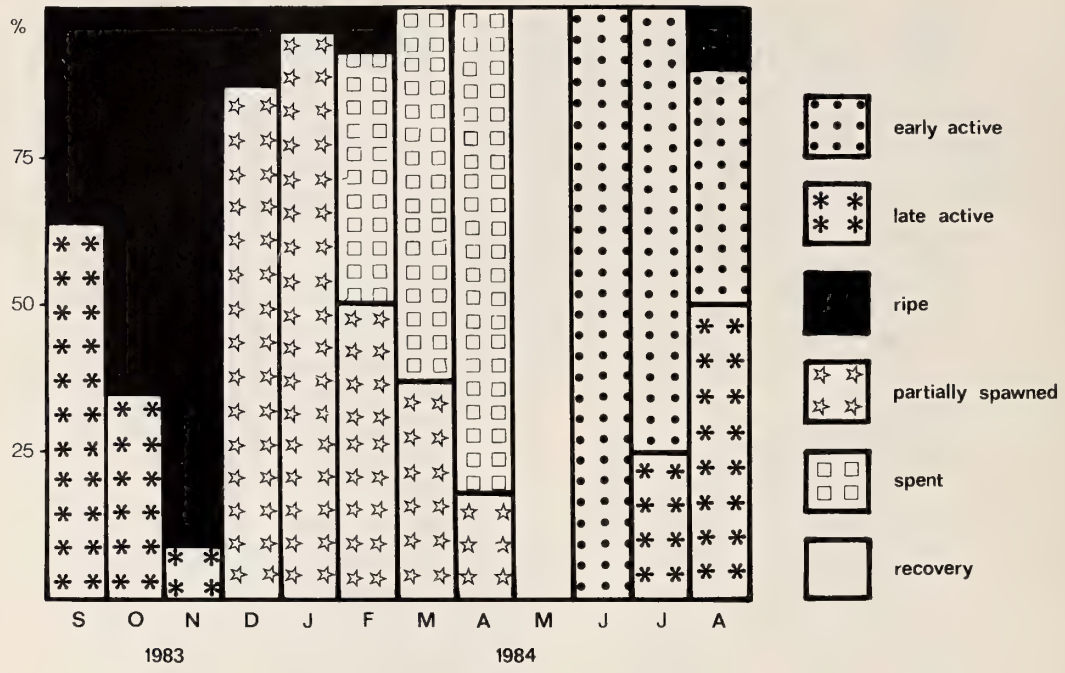


Figure 27

Reproductive cycle of *Mesodesma donacium* from Queule Beach during the study period. The length of each shaded area represents the percentage frequency of the population in each reproductive phase.

shows that August corresponds to the beginning of the late active phase in females. This stage extends through September and October as revealed by the histological examination of gonad sections at the beginning of the study period.

The dry weight of specimens changed throughout the year. A first increase in the dry weight was shown in November–December and then it decreased in January. A second increase in the dry weight of specimens was observed in March, followed by a progressive decrease from that month until the end of the study (Figure 29).

DISCUSSION

Male germ cells recognized in *Mesodesma donacium* correspond to the usual types observed in the spermatogenesis of various marine bivalves (Sastry, 1977), thus indicating that this process in *M. donacium* follows the same general plan described elsewhere in invertebrates as well as in vertebrates (Roosen-Runge, 1977).

Two types of spermatogonia can be recognized (Figure 3). Primary spermatogonia derived from primordial germ cells proliferate and give rise to secondary spermatogonia, which are definitive spermatogonia as these are the end products of spermatogonial mitosis (Figure 4). Secondary spermatogonia directly give rise to primary spermatocytes.

Secondary spermatocytes were difficult to identify. Apparently meiotic division is rapid at this stage; consequently, secondary spermatocytes would be very transient cells, giving rise to spermatids (Giese & Pearse, 1977; Roosen-Runge, 1977). Probably the nuclei of secondary spermatocytes are very similar to those of initial spermatids and thus they cannot be distinguished using light microscopy.

Neither cells of atypical spermatogenesis nor atypical sperm, described in several marine bivalves and gastropods (Loosanoff, 1937a, 1953; Coe & Turner, 1938; Ankel, 1958; Bulnheim, 1962; Nishiwaki, 1964; Ockelmann, 1965; Shaw, 1965), were observed in the spermatogenesis of *Mesodesma donacium,* thus indicating that in this species atypical spermatogenesis does not occur or occurs very rarely.

Somatic cells observed within gonadal follicles in *Mesodesma donacium* correspond to two different functional types of cells. The first and more abundant type corresponds to supporting and, possibly, nutritional cells. Somatic cells of the second type are phagocytic cells (amoebocytes) which are similar to those called cell Type C by Tranter (1958). Phagocytic cells have been described in the gametogenesis of several bivalves. Such cells also have been assigned a nutritional role (Loosanoff, 1937b; Tranter, 1958; Wilson & Hodgkin, 1967).

Oogenesis in *Mesodesma donacium* has the usual characteristics described for other marine bivalves. It was not possible to distinguish primary and secondary oogonia, as described in other mollusks (Tranter, 1958; Raven, 1961). Diffuse chromatin of the nucleus of previtellogenic oocytes indicates that these oocytes are in the vegetative phase

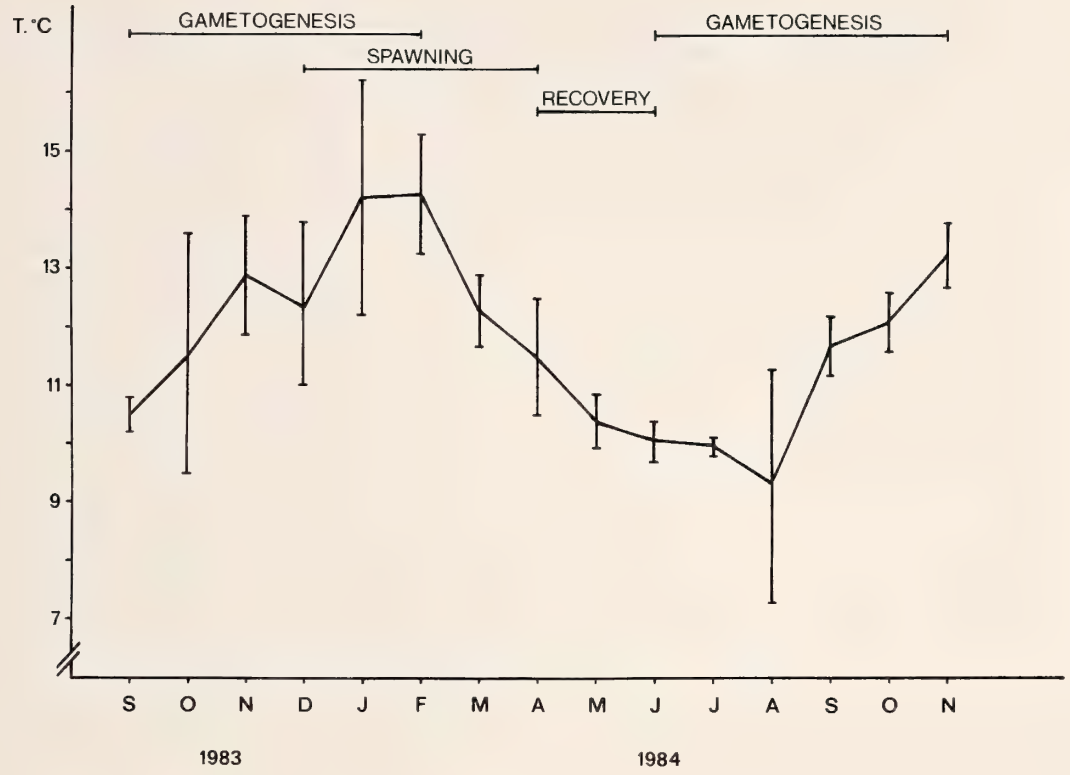


Figure 28

Monthly mean, and standard deviation, of water surface temperature at Mehuín (39°25'S, 73°13'W), located next to Queule Beach, during the study period. Corresponding periods of gametogenesis, spawning, and recovery are indicated for reference.

(Raven, 1966), that is, in meiosis arrested at early prophase.

Growing oocytes with a cytoplasmic stalk have also been described in several marine bivalves (Saleuddin, 1964; Ropes, 1968; Porter, 1974; De Villiers, 1975; Rae, 1978) including Chilean bivalves (Cifuentes, 1975; Lozada & Reyes, 1981; Lozada & Bustos, 1984) and also in freshwater bivalves (Beams & Sekhon, 1966; Zumoff, 1973; Peredo & Parada, 1984). Beams & Sekhon (1966) assign a mechanical and also a possible nutritional role to the cytoplasmic stalk. Mature (full-grown) oocytes show the germinal vesicle intact, thus indicating that meiosis is not completed within the gonadal follicles, a situation also described in other bivalves such as *Crassostrea virginica* (Galstoff, 1937), *Spisula solidissima* (Ropes, 1968) and *Donax serra* (De Villiers, 1975). This situation is turn differs from that in other bivalves such as *Cyprina islandica* and *Venus mercenaria* (Loosanoff, 1953), *V. striatula* (Ansell, 1961), *Mya arenaria* and *Mercenaria mercenaria* (Stickney, 1963), in which at the time of ovulation, the oocytes possess broken down germinal vesicles and the chromosomal spindle is formed. Possibly *Mesodesma donacium* oocytes, like *S. solidissima,* requires fertilization for germinal vesicle breakdown to occur and, consequently, meiosis to be re-initiated (Allen, 1953; Tumboh-Oeri & Koide, 1982). Therefore, in *Mesodesma donacium,* full-grown oocytes contained in gonadal follicles reach only morphological maturity; physiological maturity is achieved once they have left the gonad.

Reproductive Cycle

Histological examination of gonad sections during the study period allowed us to determine that the reproductive cycle of *Mesodesma donacium* is a biological event with annual periodicity. A maturation period occurs from June through November (winter and spring) and a spawning period extends from December to April (summer–early autumn), followed by a short recovery period during May, and then the start of a new cycle.

The percentage of individuals of the population in different stages of gonadal development during the study period (Table 1) indicates that males and females are in synchrony at the beginning of the maturation period (early active stage) because practically 100% of the males and females are in the early active stage during June. This synchrony disappears as the maturation period proceeds (late active and ripe stages), such that during October, 92%

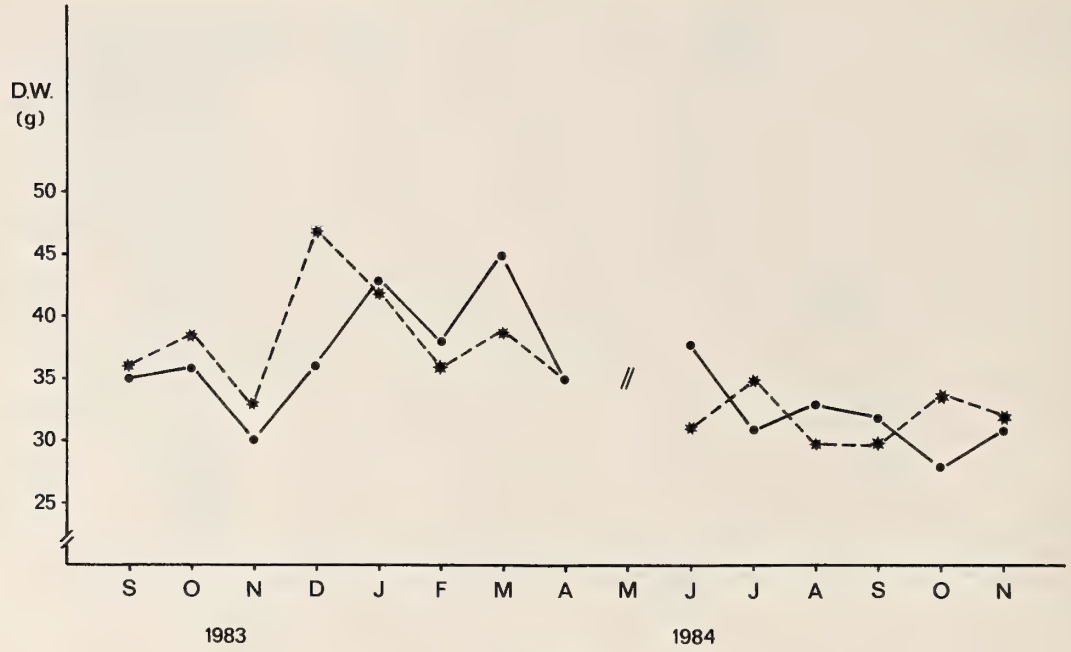


Figure 29

Seasonal changes in soft tissues in *Mesodesma donacium* from Queule Beach, calculated for a standard animal of 70-mm shell length (males —·— and females ---★---).

of the males are in the late active stage, whereas in that month only 30% of the females are in the same stage of gonadal development. In November, 100% of the males and 81% of the females have reached the ripe stage. The differences in the timing of the gonadal condition of the two sexes is attributable to the different rate at which spermatogenesis and oogenesis proceed, the latter being a slower process mainly owing to the accumulation of food reserves in the oocytes.

The spawning period starts in December in both sexes, as no specimens in that condition were registered before then. Spawning is partial and asynchronous. In December, 100% of the females were in the partial spawning stage. In males, the highest proportion of individuals in that condition was observed one month later (January). Even though in males the onset of spawning occurs gradually, this stage ends more abruptly than in females: by April, 88% of the males were in the spent stage whereas only 75% of the females were in that stage in the same month.

Although adverse climatic conditions hampered sampling in May, the histological characteristics of gonads in both sexes in the month immediately before (April, 1984) and immediately after (June, 1984) indicate that during May, gonads are in the recovery phase, a stage already present in a proportion of the individuals examined in April. This indicates an overlap between the spent and recovery stages, the majority of the population being found in the latter stage during May.

Although the percentages of clams in different stages of gonadal development show that the entire population of *Mesodesma donacium* does not reach ripeness at the same time, the majority of the population was ripe at the beginning of the spawning phase. This shows that the breeding period of *M. donacium* in the study area is limited to a certain period of the year (summer–early autumn) coincident in this respect with several bivalves that have an annual reproductive cycle with only one spawning period. A similar situation has been described in *Mercenaria mercenaria* and *Cyprina islandica* (Loosanoff, 1937b, 1953), *Mya arenaria* (Coe & Turner, 1938; Ropes & Stickney, 1965; Porter, 1974), *Venus striatula* (Ansell, 1961) and *Macoma balthica* (Lammens, 1967) among others. The congeneric species *Mesodesma mactroides* that inhabits the Atlantic coast of South America has two breeding periods: October–December and February–March (Olivier *et al.*, 1971).

The results of the present study differ from those reported on the reproductive cycle of populations of *Mesodesma donacium* occurring at other latitudes on the Chilean coastline. Brown & Guerra (1979) reported that the *M. donacium* population in Guanaqueros, northern Chile (30°15′S, 71°40′W) spawns in spring–summer, with the maximal intensity at the beginning of November, followed by a resting period. Tarifeño (1980) determined the maturation period of *M. donacium* at Laguna Beach in the Valparaíso area, central Chile (32°30′S, 71°30′W) to be during the fall–winter season (April through July). There, the maximal population ripeness was reached in mid-win-

ter and the spawning season extended from the end of the winter to the beginning of spring. The resting period of that population extended from spring to mid-autumn (October through May).

The observed differences in the timing of the different phases of the reproductive cycle in *Mesodesma donacium* in the different latitudes are probably ascribable to local variations of environmental factors, the major ones being water temperature and the availability of food. Several authors have reviewed the influence of temperature on the reproductive cycle of marine invertebrates. As an external factor, temperature can exert a selective pressure in the determination of the breeding season of a species (ultimate factor) and its fluctuations act as external clues that synchronize the reproductive cycle of a species (proximate factor) (Giese, 1959; Fretter & Graham, 1964; Giese & Pearse, 1977).

Tarifeño (1980) suggests that the increase in water temperature variation that occurs at the end of the winter could trigger spawning of surf clams at Valparaíso. In the area of the present study, the greatest monthly thermal changes occurred in November 1983 and 1984, with the difference between the monthly maximum and minimum temperature being 1.3°C and 1.1°C respectively. Although the maximal thermal oscillations coincided with the end of the maturation period and the beginning of the spawning season, this factor alone, with its meager change, probably does not trigger spawning of the *Mesodesma donacium* population at Queule Beach. The spawning season observed in the present study also coincides with the period of increasing surface water temperature in the area (Figure 28). Therefore, perhaps spawning of the surf clam population at Queule Beach is due to the combined effect of both variables of water temperature: the increase of water temperature and the increase in the monthly thermal oscillation that occurs from November on.

The increase in the phytoplankton biomass registered in the area from spring to mid-autumn (Toro, 1984) represents a greater food supply for planktotrophic organisms. In this way, the reproductive cycle of *Mesodesma donacium* is timed such that gamete emission, from December on, allows larvae to hatch during the season of the greatest abundance of phytoplankton in the area, a period that lasts from November to May (Toro, 1984).

Seasonal changes in the dry weight of specimens (Figure 29) show that the first increase reaches its maximum at the end of spring (November–December) and then dry weight decreases in January. This change is due to the increase in gonad weight at the end of the maturation period, which is followed by the spawning period. The second increase in the dry weight of specimens reaches its maximum in March, after which a progressive decline in dry weight is observed. These variations may be caused by the accumulation of food reserves during the period of food abundance (weight increase) and then by the depletion of these reserves in the maturation period during the winter–spring seasons.

From the above discussion it can be concluded that *Mesodesma donacium* has evolved a reproductive strategy in which gametes are produced during the winter–spring period, utilizing food reserves stored in the gonad itself or in other body tissues. Furthermore, this strategy increases larval survival through gamete emission during the summer and beginning of fall so that clam larvae find an adequate food supply at the time of hatching.

ACKNOWLEDGMENTS

This work was supported with funds from the Comision de Investigacion Catholic University of Chile-Temuco. The authors are indebted to the Zoological Institute, Universidad Austral de Chile for furnishing the unpublished water temperature records for 1983–84 from the Biological Marine Station in Mehuín. The authors thank Katherine Bragg for reading the manuscript.

LITERATURE CITED

Allen, R. D. 1953. Fertilization and artificial activation in the egg of the clam, *Spisula solidissima*. *Biol. Bull.* 105:213–239.

Ankel, W. E. 1958. Beobachtungen und uberlunger zur Morphogenese des atypischen Spermiens von *Scala clathrus* L. Zool. Anz. 160(11–12):261–276.

Ansell, A. D. 1961. Reproduction, growth and mortality of *Venus striatula* (Da Costa) in Kames Bay, Millport. Jour. Mar. Biol. Assoc. U.K. 41:191–215.

Beams, H. W. & S. S. Sekhon. 1966. Electron microscope studies on the oocyte of the fresh-water mussel (*Anodonta*) with special reference to the stalk and mechanism of yolk deposition. Jour. Morph. 119:477–501.

Brown, D. & R. Guerra. 1979. Estados en el ciclo estacional de la gónada de la macha *Mesodesma donacium* (Lamark, 1818) en la bahía de Guanaqueros. Arch. Biol. Med. Exp. 12(4):500.

Bulnheim, H. P. 1962. Untersuchumgen zum spermatozoen Dimorphismus von *Opalia crenimarginata* (Gastropoda Prosobranchuia). Z. Zellforsch. Microsk. Anat. 56:300–343.

Cifuentes, A. S. 1975. Estudio sobre la biología y cultivo de *Mytilus chilensis* Hupe, 1854 en Caleta Leandro. Tesis U. de Concepción-Chile. 124 pp.

Coe, W. R. & H. J. Turner. 1938. Development of the gonads and gametes in the soft-shell clam (*Mya arenaria*). Jour. Morph. 62:91–111.

De Villiers, G. 1975. Reproduction of the white sand mussel *Donax serra* Röding. Sea Fisheries Branch Investigational Rept., South Africa No. 102: 33 pp.

Franzén, A. 1955. Comparative morphological investigations into the spermiogenesis among Mollusca. Zool. Bidr. Uppsala 30:399–456.

Franzén, A. 1969. Comparative spermatology. *In:* Baccio Baccetí (ed.), Proc. 1st Inst. Symp. (Rome Siena) Accademia Nazionale Dei Lincei. No. 137:1–46.

Franzén, A. 1983. Ultrastructural studies of spermatozoa in three bivalves species with notes on evolution of elongated sperm nucleus in primitive spermatozoa. Gam. Res. 7:199–214.

Fretter, V. & A. Graham. 1964. Reproduction. Pp. 127–163. *In:* K. M. Wilbur & C. M. Yonge (eds.), *Physiology of Mollusca*. Academic Press: New York.

Galstoff, P. S. 1937. Spawning and fertilization of the oyster *Ostrea virginica*. Pp. 537–539. *In:* Galstoff *et al.* (eds.), Culture methods for invertebrate animals. Comstock: Ithaca, New York.

Giese, A. C. 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. Ann. Rev. Physiol. 21:547–576.

Giese, A. C. & J. S. Pearse. 1977. General principles. Pp. 1–49. *In:* A. C. Giese & J. S. Pearse (eds.), Reproduction of marine invertebrates. Academic Press: New York.

Lammens, J. J. 1967. Growth and reproduction in a flat population of *Macoma balthica* (L.). *Neth. Jour. Sea Reb.* 3:315–382.

Loosanoff, V. L. 1937a. Development of the primary gonad and sexual phases in *Venus mercenaria* Linnaeus. Biol. Bull. 72:387–405.

Loosanoff, V. L. 1937b. Seasonal gonadal changes in adult clams, *Venus mercenaria* (L.). Biol. Bull. 72:406–416.

Loosanoff, V. L. 1953. Reproductive cycle in *Cyprina islandica*. Biol. Bull. 104:146–155.

Lozada, E. 1968. Contribución al estudio de la cholga *Aulacomya ater* en Putemún (Mollusca, Bivalvia, Mytilidae). Biol. Pesq. Chile 3:3–39.

Lozada, E. & H. Bustos. 1984. Madurez sexual y fecundidad de *Venus antiqua* King y Broderip 1835 en la Bahía de Ancud (Mollusca: Bivalvia: Veneridae). Rev. Biol. Mar. Valparaíso. 20(2):91–112.

Lozada, E. & P. Reyes. 1981. Reproductive biology of a population of *Perumytilus purpuratus* at El Tabo, Chile. Veliger 24:147–154.

Lozada, E., J. Rolleri & R. Yañez. 1971. Consideraciones biológicas de *Choromytilus chorus* en dos sustratos diferentes. Biol. Pesq. Chile 5:61–108.

Nishiwaki, S. 1964. Phylogenetical study on the type of the dimorphic spermatozoa in Prosobranchia. Sci. Rept. Tokyo Kyoiku Daigaku (B) 11:237–275.

Ockelmann, K. W. 1964. *Turtonia minuta* (Fabricius), a neotaneous veneranacean bivalve. Ophelia 1:121–146.

Ockelmann, K. W. 1965. Redescription, distribution, biology and dimorphous sperm of *Montacuta tenella* Loven (Mollusca, Leptonacea). Ophelia 2:211–222.

Olivier, S. R., D. A. Capezzani, J. I. Carreto, H. E. Christiansen, V. J. Moreno, J. E. Aispun de Moreno & P. E. Penchazzadeh. 1971. Estructura de la comunidad, dinámica de la probleción y biología de la almeja amarilla (*Mesodesma mactroides* Desh 1854) en Mar Azul. Proyecto de Desarrollo Pesquero. Mar del Plata. Argentina. Publ. No. 27:90 pp.

Peredo, S. & E. Parada. 1984. Gonadal organization and gametogenesis in the fresh-water mussel *Diplodon chilensis chilensis* (Mollusca: Bivalvia). Veliger 27(2):126–133.

Perez-Olea, M. 1981. Biología reproductiva del choro zapato *Choromytilus chorus* (Molina 1872) en un estuario del sur de Chile (Queule, IX Región). Tesis Universidad Austral de Chile. 35 pp.

Popham, J. D. 1974. Comparative morphometrics of the acrosome of the sperm of externally and internally fertilizing sperms of the shipworms (Teredinidae, Bivalvia, Mollusca). Cell Tiss. Res. 150:291–297.

Porter, R. G. 1974. Reproductive cycle of the soft-shell clam, *Mya arenaria* at Skagit Bay, Washington. Fish. Bull. 72: 648–656.

Rae, J. G. 1978. Reproduction in two sympatric species of *Macoma* (Bivalvia). Biol. Bull. 155:207–219.

Raven, C. P. 1961. Oogenesis: the storage of developmental information. Pergamon Press: New York.

Raven, C. P. 1966. Morphogenesis: the analysis of molluscan development. 2nd ed. Pergamon Press: New York.

Retzius, G. 1904. Zur Kenntnis der Spermien der Evertebraten. Biol. Unters. 9:1–32.

Retzius, G. 1905. Zur Kenntnis der Spermien der Evertebraten II. Biol. Unters. 12:79–102.

Roosen-Runge, E. C. 1977. The process of spermatogenesis in animals. Cambridge University Press: London.

Ropes, J. W. 1968. Reproductive cycle of the surf clam *Spisula solidissima* in offshore New Jersey. Biol. Bull. 135(2):349–365.

Ropes, J. W. & A. P. Stickney. 1965. Reproductive cycle of *Mya arenaria* in New England. Biol. Bull. 128:315–327.

Saleuddin, A. S. M. 1964. The gonads and reproductive cycle of *Astarte sulcata* (Da Costa) and sexuality in *A. elliptica* (Brown). Proc. Malacol. Soc. Lond. 36:141–148.

Sastry, A. N. 1977. Reproduction of pelecypods and lesser classes. *In:* A. C. Giese & J. S. Pearse (eds.), Reproduction of marine invertebrates. Academic Press: New York.

Shaw, W. N. 1965. Seasonal gonadal cycle of the male soft shell clam *Mya arenaria* in Maryland. U.S. Fish. Wildl. Serv. Spec. Sci. Rept. Fish. 508:5.

Solís, I. 1967. Observaciones biologicas en ostras (*Ostrea chilensis*) Philippi de Pullinque. Biol. Pasq. Chile 2:51–82.

Solís, I. & E. Lozada. 1971. Algunos aspectos biológicos de la cholga de Magallanes *Aulacomya ater* Mol. Biol. Pesq. Chile 5:105–144.

Stickney, A. P. 1963. Histology of the reproductive system of the soft shell clam (*Mya arenaria*). Biol. Bull. 125:344–351.

Tarifeño, E. 1980. Studies on the biology of the surf-clam *Mesodesma donacium* (Lamarck 1818) (Bivalvia: Mesodesmatidae) from Chilean sandy beaches. Doctoral Thesis, University of California, Los Angeles. 229 pp.

Thompson, T. E. 1973. Euthineuran and other molluscan spermatozoa. Malacologia 14:167–206.

Toro, J. E. 1984. Determinacion de las fluctuaciones mensuales de la abundancia y de la biomasa fitoplanctónica en el estuario del Río Queule (Chile, IX Región). Rev. Biol. Mar. Valparaíso 20(1):23–37.

Tranter, D. T. 1958. Reproduction in Australian pear oysters (Lamellibranchia) II. *Pinctada albina* (Lamarck): gametogenesis. Austral. Jour. Mar. Freshwater Res. 9:144–158.

Tumboh-Oeri, A. G. & S. S. Koide. 1982. Mechanism of sperm-oocyte interaction during fertilization in the surf clam *Spisula solidissima*. Biol. Bull. 162:124–134.

Walne, P. 1963. Breeding of the Chilean oyster (*Ostrea chilensis* Phil.) in the laboratory. Nature 197(4868):676.

Wilson, B. R. & E. P. Hodgkin. 1967. A comparative account of the reproductive cycle of five species of marine mussels (Bivalvia: Mytilidae) in the vicinity of Fremantle, Western Australia. Austral. Jour. Mar. Freshwater Res. 18:175–203.

Zumoff, C. H. 1973. The reproductive cycle of *Sphaerium simile*. Biol. Bull. 144:212–228.

The Veliger 30(1):69–75 (July 1, 1987)

THE VELIGER

Oxygen Uptake and the Effect of Feeding in *Nautilus*

by

M. J. WELLS

Department of Zoology, University of Cambridge, Cambridge, U.K. CB2 3EJ,
Lizard Island Research Station, Queensland, Australia

Abstract. Specimens of *Nautilus pompilius* (Linnaeus, 1758) and *N. stenomphalus* (Sowerby, 1849) were caught off the Great Barrier Reef. The animals can regulate their oxygen uptake successfully down to ambient PO_2s of 60 mm Hg and beyond at 10–20°C; some individuals reduced the PO_2 in their respirometer to 15 mm Hg and lower before ventilation ceased; spontaneous recovery occurred when a well-oxygenated circulation was restored. The effect of feeding was investigated. There was no sign of a transient rise and fall in oxygen uptake following a meal, but some indication that, in the longer term, regular feeding or starvation could double or halve the metabolic rate. Oxygen uptake is very dependent on temperature, which would make the nightly vertical migrations into shallower, warmer water of considerable importance in terms of the animal's energy budget. A crude estimate of this budget suggests that a 500-g (flesh weight) *Nautilus* could maintain its normal activity pattern in the sea on about 2 g (wet weight) of fish per day; a good cropful would last it a month, or considerably longer, as metabolic rate falls in starvation.

INTRODUCTION

Nautilus is the sole living representative of the many shelled cephalopod mollusks found in the fossil record. Morphologically, the shells of the four surviving species (*N. belauensis* Saunders, 1981; *N. macromphalus* Sowerby, 1849; *N. pompilius* Linnaeus, 1758; *N. scrobiculatus* Lightfoot, 1786; SAUNDERS, 1981) differ rather little from those of their Palaeozoic ancestors. There is every reason for studying the physiology and behavior of the modern animal; it is the only model for the extinct species that we have, and it is arguably more likely to resemble them in its habits and ecology than are the coleoids.

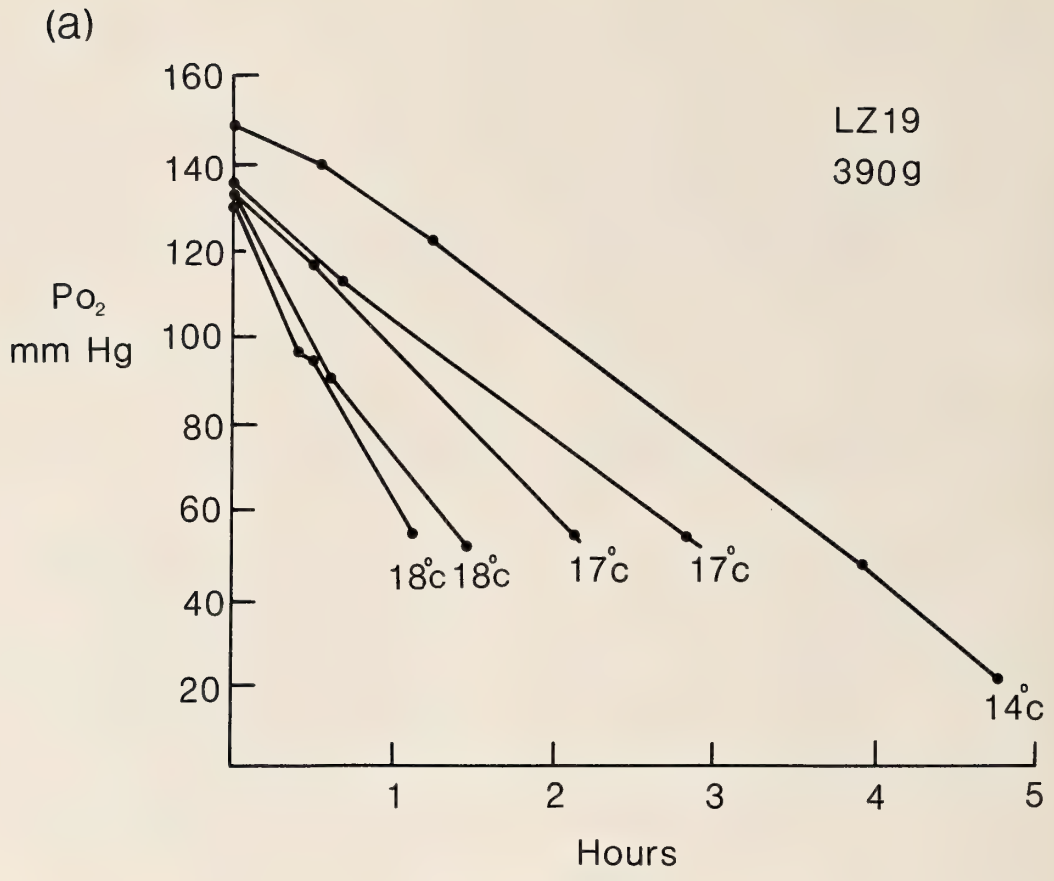
In 1985, *Nautilus pompilius* was trapped off the Great Barrier Reef near Lizard Island, Queensland, as part of a research program examining the distribution of *Nautilus* species (see SAUNDERS, 1981). As well as *N. pompilius,* specimens of *N. stenomphalus,* which may or may not be a valid species, were found. This was the first time that *N. stenomphalus* had been seen alive. As well as the known *N. stenomphalus* shell characteristics (open umbilicus and reduced shell pigmentation compared with *N. pompilius,* which it otherwise closely resembles), the animal has a distinct papillose hood. The data obtained gave no grounds for separating these two, but the availability of freshly caught *Nautilus* at a laboratory with some refrigeration facilities made possible the collection of fresh data on the capacity to regulate O_2 uptake and to survive acute hypoxia, as well as information on metabolic rate and feeding, which is presented here.

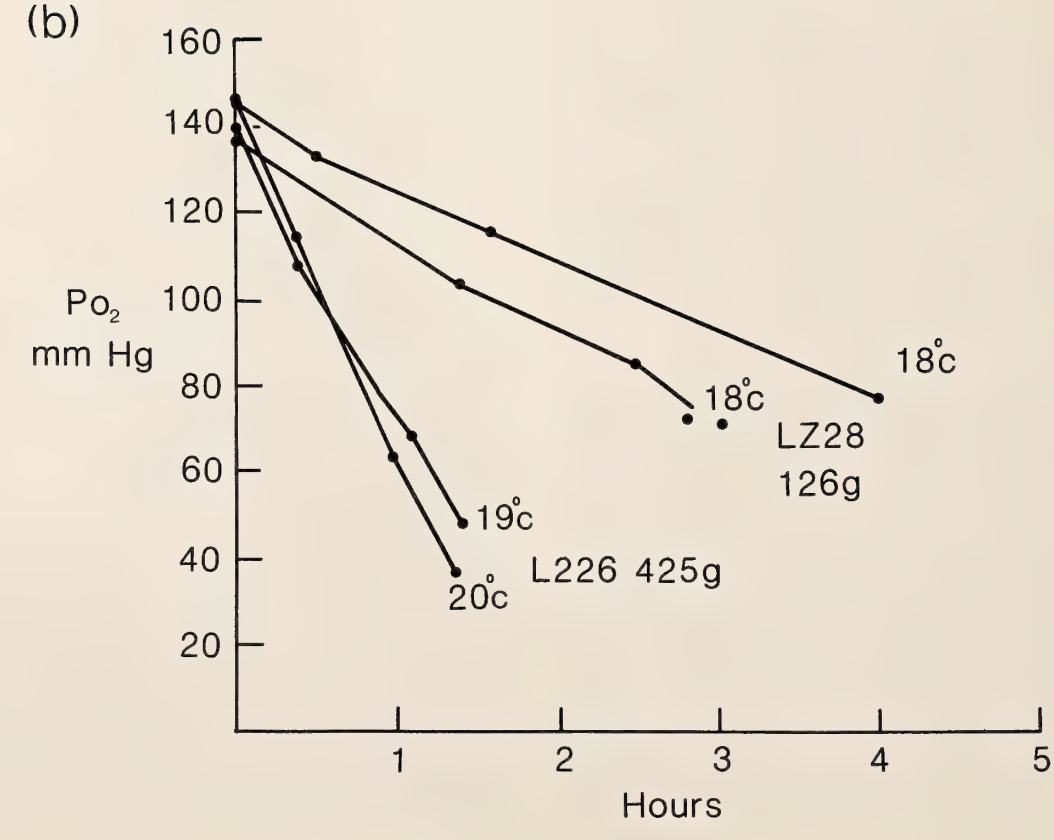
MATERIALS AND METHODS

Nautilus specimens were collected off Carter reef, 22 km (14 miles) NE of Lizard Island. Traps baited with dead fish and crabs were set on the fore-reef slope in 200 to 400 m from RVS *Sunbird* of the Lizard Island Research Station.

Animals for experiments were brought back to the laboratory in a refrigerated holding tank aboard RVS *Sunbird.* At the research station they were housed in a 220-L stock tank, aerated, and refrigerated; the flow of water through the stock tank (~250 mL/min) was used to adjust the temperature. Two 11-L respirometers were enclosed, and a refrigeration compartment built from polystyrene sheets around these and the holding tank, from which the respirometers were filled as required. Each respirometer had a floating lid of polystyrene, so that samples of the water could be run off through a compartment containing the electrode from an EIL 7130 oxygen analyzer and returned to the respirometer. Samples flowing past the oxygen probe were stirred magnetically. The electrode and collecting vessel (a beaker with a floating polystyrene lid) were enclosed in the same refrigerated space as the three aquaria.

Specific oxygen uptake figures are given in terms of flesh weight, measured when the animals were killed at the end


(a)
160
140
120
100
80
60
40
20
Po_2
mm Hg
LZ19
390g
18°c
18°c
17°c
17°c
14°c
1
2
3
4
5
Hours


(b)
160
140
120
100
80
60
40
20
Po_2
mm Hg
18°c
18°c
LZ28
126g
19°c
20°c
L226 425g
1
2
3
4
5
Hours

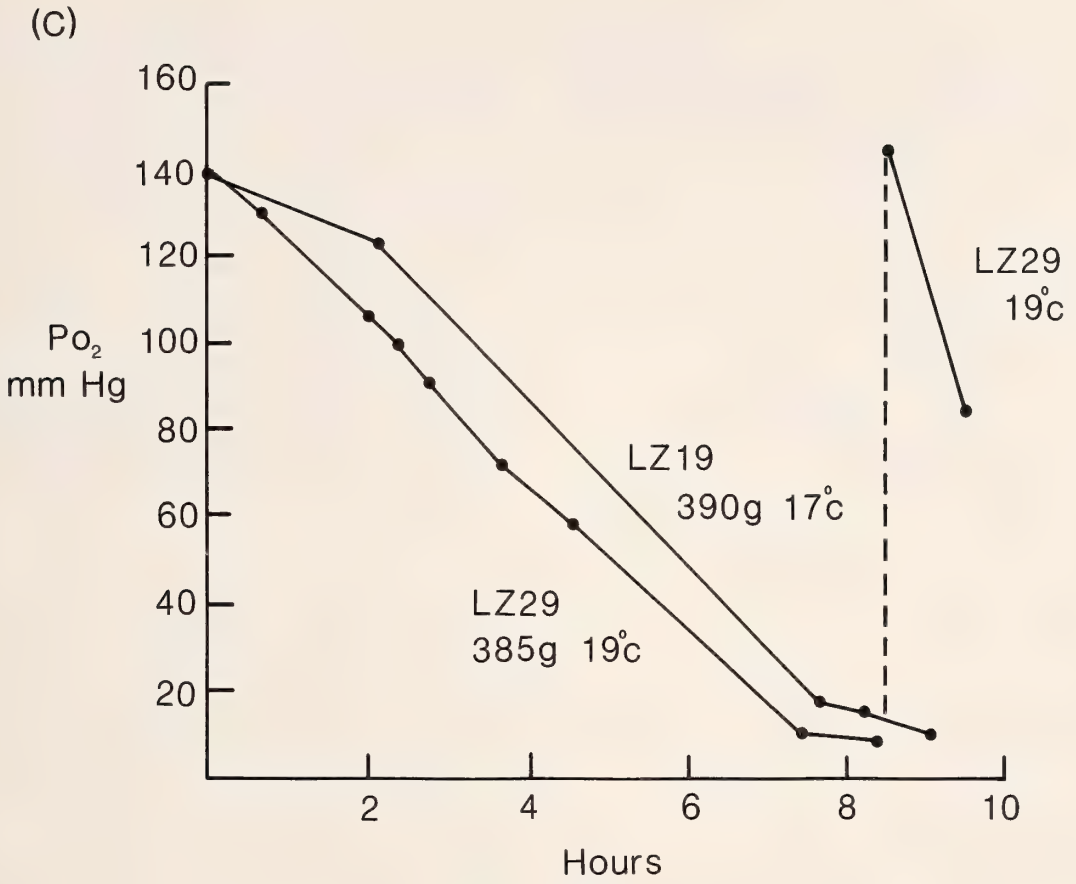


Figure 1

Regulation of oxygen uptake by *Nautilus* in closed respirometers. (a) five runs by a *N. pompilius,* LZ19 565 g, body wt. 390 g. (b) two runs by a juvenile *N. pompilius/stenomphalus* "hybrid," LZ28, 200 g, body wt. 126 g. And two by *N. pompilius,* LZ26, 655 g, body wt. 425 g. (c) two runs to very low oxygen levels by LZ19 and LZ29, another *N. pompilius/stenomphalus* "hybrid," 630 g, body wt. 385 g; in this plot, oxygen uptake is shown for a period immediately following transfer to well-aerated seawater. "Hybrids" are specimens showing a mixture of the characteristics of the two supposed species.

of the experiments. The oxygen content of the seawater at 100% saturation was taken from data given in CARPENTER (1966), assuming a chlorinity of 19.05, appropriate for Lizard Island in December.

The six animals used all remained in good condition throughout the period in the laboratory. Results from a seventh, which refused to feed at once when food was offered, were discarded.

RESULTS

Regulation of Oxygen Uptake

Because of the limitations imposed by refrigeration capacity, through-flow respirometry was impossible and oxygen uptake had to be measured from the reduction in PO_2 in a respirometer. It was therefore important to establish whether *Nautilus* can maintain its oxygen uptake in a declining ambient PO_2. Reports on its capacity to regulate in this manner have differed. REDMOND *et al.* (1978) showed that it could not do so at 25°C, whereas WELLS & WELLS (1985) found that the animals regulated successfully down at least to a PO_2 of 75 mm Hg in water at 17°C. Figure 1 summarizes a number of experiments made in which *Nautilus* progressively reduced the oxygen in their tanks down to PO_2s of 60 mm Hg and beyond (exceptionally to less than 20 mm Hg) without apparently changing their rates of uptake, at least until levels of 30 mm Hg and below were reached. Thus, there is no doubt that this animal can regulate over a wide range at the temperatures it normally meets in the sea.

Activity and Q_{10}

Oxygen uptake rises by a factor of two or three times when *Nautilus* is jetting rather than sitting quietly at 18–20°C.

Table 1

Nautilus. Activity, animal size, and oxygen uptake in mL·kg^{-1}·min^{-1}, along with temperature during run and number of days since last feeding; representative values from runs lasting for 1 h or more and ending with PO_2s above 60 mm Hg.

		No. days since last feeding
LZ19. *N. pompilius*. Mature male (565 g, body wt. 390 g).		
Active, while feeding	1.006 (19°C)	
Quiet	0.532 (19°C)	0
Quiet	0.207 (12°C)	4
LZ24. *N. stenomphalus*. Mature female (480 g, body wt. 310 g).		
Feeding	1.151 (21°C)	
Quiet	0.390 (18.5°C)	4
Quiet	0.189 (13°C)	5
LZ26. *N. pompilius*. Mature male (655 g, body wt. 425 g).		
Active	1.072 (20°C)	1
Quiet, following activity	0.814 (19°C)	1
LZ28. *N. pompilius/stenomphalus* "hybrid." Immature male (200 g, body wt. 126 g).		
Active	1.516 (18°C)	2
Quiet	0.499 (17.5°C)	4
LZ29. *N. pompilius/stenomphalus* "hybrid." Mature male (630 g, body wt. 385 g).		
After extreme hypoxia (see Figure 1c)	0.852 (19°C)	
Quiet	0.268 (17.5°C)	6
LZ30. *N. pompilius/stenomphalus* "hybrid." Mature male (810 g, body wt. 607 g).		
Active	0.605 (18°C)	4
Quiet	0.256 (17°C)	3

"Hybrids" were individuals showing a mixture of the characteristics of the two supposed species.

Figure 2 shows specific oxygen consumption plotted against temperatures for all runs lasting longer than 30 min made with mature animals at rest (or at least not noted as "active"; they were not kept under continuous observation). Oxygen uptake rises with increasing temperature, a matter that could be important to an animal that makes daily vertical migrations on reef slopes (Ward *et al.*, 1984). The Q_{10} computable from this data is 4.3, but the scatter is large and little reliance should be placed on the accuracy of this figure.

Numbers alongside the outlying values in Figure 2 show the number of days since the individual concerned was last fed. Feeding increases the metabolic rate, fasting reduces it.

The Capacity to Survive Periods of Acute Hypoxia

Nautilus can withdraw into its shell, blocking the entrance with the hood. As it cannot then ventilate, one would expect the animal to be resistant to intermittent hypoxia. In the present series of experiments animals were allowed to deplete the oxygen in their respirometers down to PO_2s of 20 mm Hg and lower, on six occasions. In the two most extreme cases, ventilation eventually ceased. The tentacles of these animals were extended, flaccid, and the animals were, to all external appearances, dead. They nevertheless reacted at once when touched, drawing back into the shell and (or) beginning to ventilate afresh. Vigorous ventilation began when the seawater in the respirometer was aerated. In the single instance when oxygen uptake was measured immediately after the restoration of oxygen-rich seawater (see Figure 1), this was greatly enhanced, suggesting repayment of an oxygen debt. No attempt was made to quantify this.

Effects of Feeding on Oxygen Uptake

Figure 3 summarizes the effect of feeding one animal five times in the course of nine days, four of the meals being on successive days. On three of the five occasions there was a marked rise in oxygen uptake just after feeding. This, however, appeared to be due to activity stimulated by feeding rather than feeding per se. Reasons for believing this are (1) the absence of a rise on the two days when the animal was *not* active after feeding and (2) the very short-term nature of the rise; it was over within an hour or two of feeding. It should be noted, too, that the peak at 10 days after capture occurred shortly *before* the animal was fed rather than after. In the longer term there is some indication that the average resting metabolic rate is elevated by repeated feedings. During the period of daily feedings on days 7–10 the resting rate rose to 0.6 mL·kg^{-1}·min^{-1} and then declined to 0.3 mL·kg^{-1}·min^{-1} in the three days fasting after this. Figure 2 shows the same effect; animals tested 2–6 days after feeding take up oxygen at only one-half to one-third of the rate of those tested within 24 h of a meal.

DISCUSSION

Some of the results summarized above confirm statements already made elsewhere. Thus, it is now quite certain, despite some earlier doubts on the matter, that *Nautilus* can regulate its oxygen uptake over a wide range of ambient oxygen tensions.

The results following feeding were new and unexpected. By analogy with *Octopus vulgaris*, another opportunistic feeder, one might reasonably have expected a marked transient increase in oxygen uptake to follow the ingestion of a meal. No such surge was seen. Very little is known about digestion in *Nautilus* and nothing is published. The absence of large salivary glands (which produce quantities of proteolytic enzymes in coleoids), the small caecum, and the

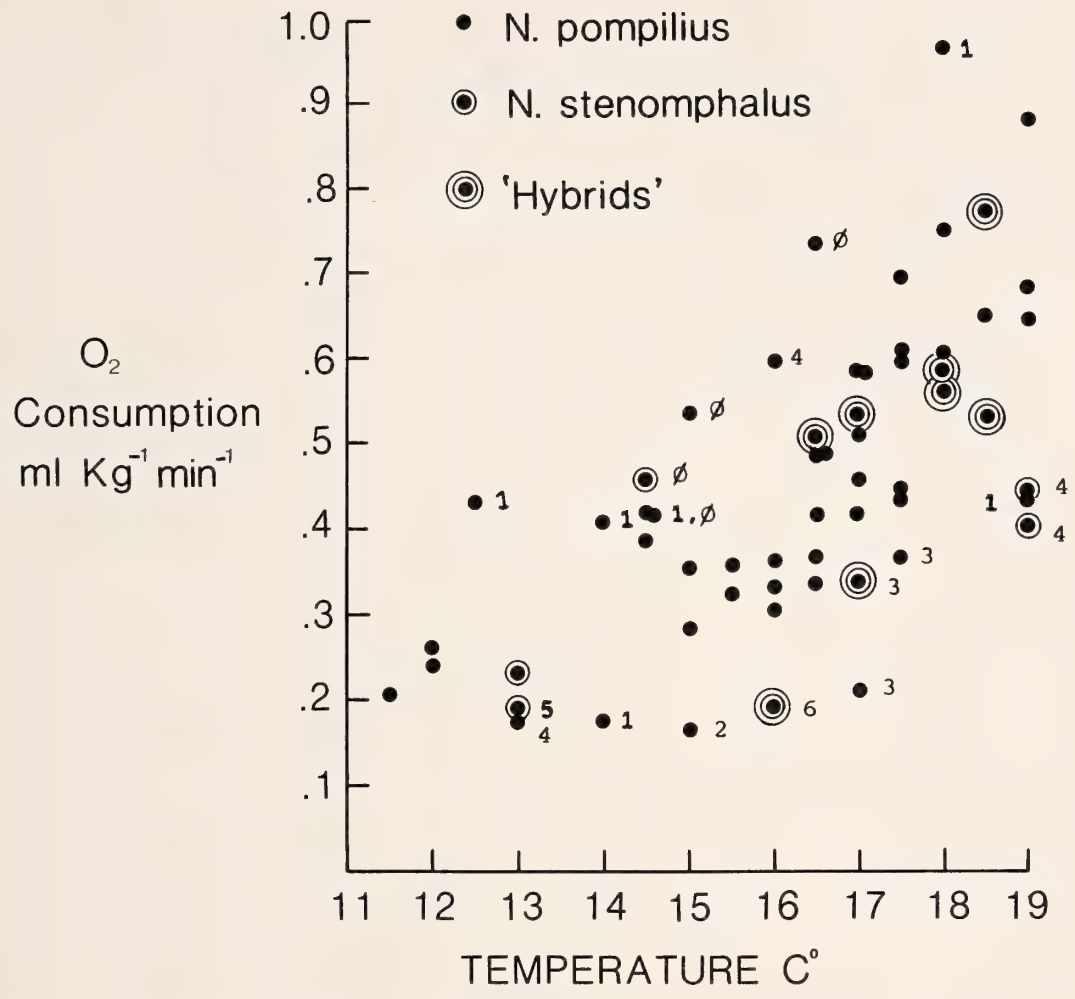


Figure 2

Oxygen uptake and temperature in *Nautilus*. Metabolic rate increased rapidly with temperature. Figures against outlying values show days since last fed.

unusual structure of the digestive gland (MANGOLD *et al.*, in press) all suggest that digestion is rather different from the system in coleoids (for review, see BOUCAUD-CAMON & BOUCHER-RODONI, 1983). Two facts from the present series of observations confirm the impression from the oxygen uptake experiments, that digestion in *Nautilus* is probably rather slow. One is the amount that animals would eat. All the individuals tested fed readily if presented with dead fish or pieces of crab, but they never took more than about 25 g of flesh. ZANN (1984) reported crop weights averaging more than 50 g from smaller animals caught in traps off Fiji. The implication is that the Lizard Island animals, first tested within a few days of arrival, were still "topping up" crops only part emptied after the last meal, having gorged themselves to repletion in the traps. The slow emptying of the crop was confirmed when animal LZ19 was killed. This *Nautilus* had not been fed for 3 days (see Figure 3) but it still had crab remains in the crop.

If digestion is as leisurely as these results suggest, it is likely that the great majority of the oxygen consumption figures that we have so far collected for *Nautilus* (REDMOND *et al.*, 1978; WELLS & WELLS, 1985, and in this account) are typical of fed rather than fasted animals, because all are derived from animals tested within a few days of capture in traps, where presumably, they gorged themselves. By analogy with *Octopus*, one would expect the metabolic rate to fall considerably in starvation. In view of the slow growth rate of *Nautilus* compared with other cephalopods (WARD, 1983) and the possible scarcity of catchable food in the depths where *Nautilus* lives, the possibility that the animal can cut its standard metabolic rate to low levels in lean times is important to our understanding of its ecology. The present series shows (Figures 2, 3) that oxygen uptake

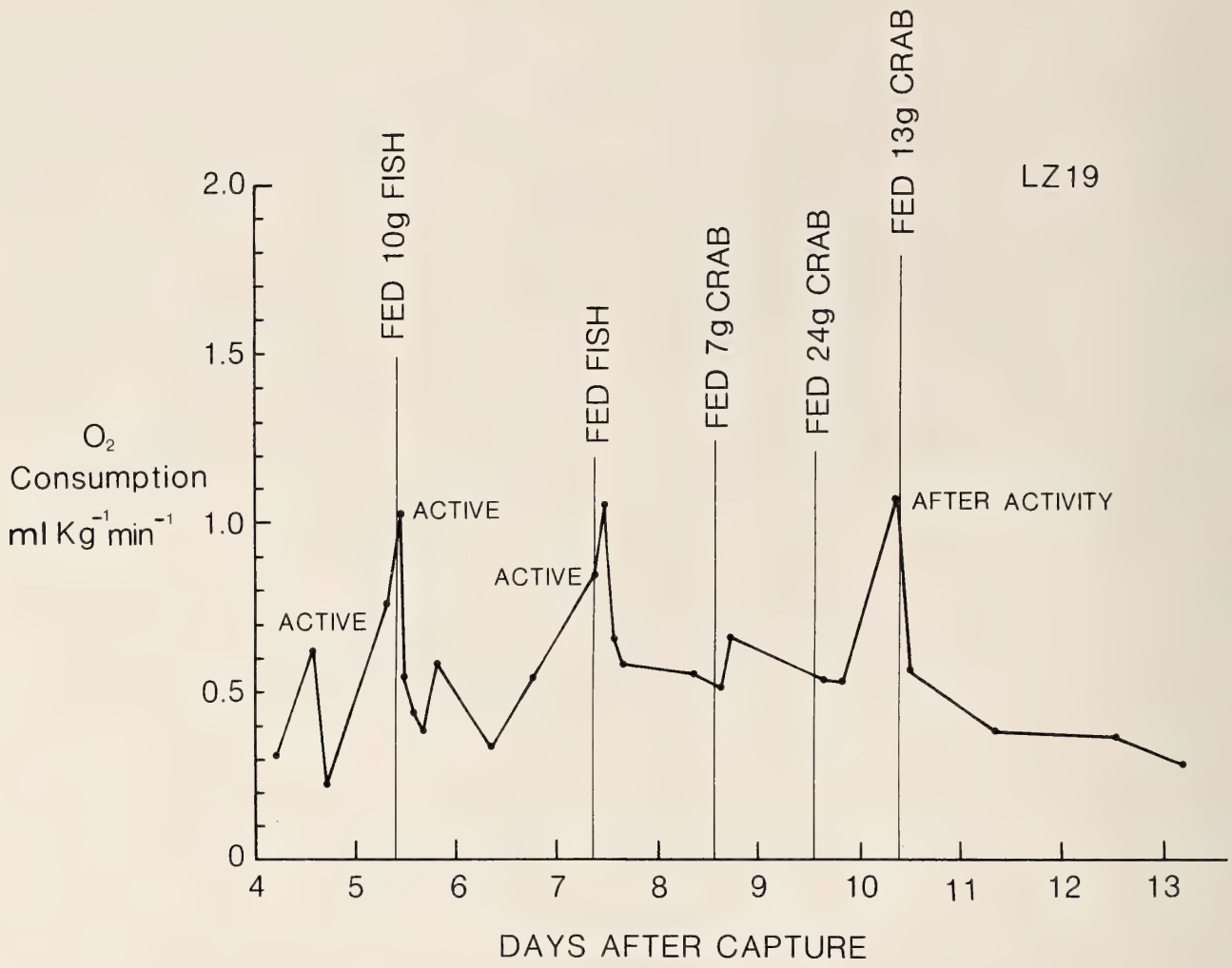


Figure 3

Metabolic rate and feeding history of *Nautilus pompilius* LZ19, body weight 390 g. "Active" means seen to be jetting about its respirometer at one or more spot checks made during oxygen uptake runs. The animal still had crab remains in the crop when killed 13 days after capture and 3 days after the last meal.

is reduced to one-half or even less by three days of fasting. We need a much longer series of oxygen uptake experiments to find out just how flexible *Nautilus* is in this respect.

Nautilus oxygen uptake is sensitive to temperature change (Figure 2). The animal is known to move into shallower water at night, with vertical changes of as much as 200 m not uncommon on such occasions (Ward *et al.*, 1984). Given the steep temperature profiles found along reef slopes (see, for example, Ward & Martin, 1980) and the lack of time for temperature adaption during these excursions, *Nautilus* is likely to be altering its standard metabolic rate by a factor of two or three in daily cycles. We do not know what part these changes may play in the economic strategy of *Nautilus,* but it is conceivable that the animal is economizing by feeding during its nightly excursions into regions of higher temperature and then dropping down to the cooler deeps to digest, as young salmon, for instance, are known to do in similar diurnal cycles (Brett, 1983).

Given the information now available about oxygen consumption at rest and in activity, the Q_{10} and vertical migrations, temperature profiles off the reef face, and activity patterns, it is possible to construct an elementary energy budget for *Nautilus.* Crudely, with an oxygen uptake of around 0.5 $mL \cdot kg^{-1} \cdot min^{-1}$ at rest at 17°C and twice that at 22°C, and the animal spending half of every 24 h at each temperature (as indicated by records of vertical migrations in Ward *et al.*, 1984 and the temperature profiles given in Ward & Martin, 1980) the likely oxygen consumption over 24 h will be around 1080 $mL \cdot kg^{-1}$. To this must be added the cost of locomotion, being the difference between the active and resting oxygen consumptions, about 0.75 $mL \cdot kg^{-1} \cdot min^{-1}$ (the cost of transport will not vary

significantly with temperature). Accepting ZANN's (1984) figures for the proportion of time spent actively swimming (2.6 $min \cdot h^{-1}$ during the day and 7 $min \cdot h^{-1}$ at night, with slightly higher figures at dawn and dusk) the added cost of locomotion is around 110 $mL \cdot kg^{-1} \cdot day^{-1}$. Taking one litre of oxygen to equal 4.6 kcal on a mainly protein diet broken down to ammonia, and a value for fish flesh of 1.27 $kcal \cdot g^{-1}$ wet weight (an average from values given in WATT, 1968), and 95% absorption of food ingested at a cost of 0.04 $kcal \cdot g^{-1}$ (as for *Octopus*, see O'DOR *et al.*, 1984), the daily requirement for a 500-g (flesh weight) *Nautilus* would be around 2 g of fish. A cropfull would keep the animal going for a month. This, it should be remembered, is based on the metabolic rates of fed animals. We know that the animal reduces its oxygen uptake by 50% after only three days of fasting. At this rate a square meal might last for a couple of months assuming zero growth but no loss of weight. *Nautilus* is evidently well suited to a scavenging life-style and an irregular food supply.

LITERATURE CITED

BOUCAUD-CAMOU, E. & R. BOUCHER-RODONI. 1983. Feeding and digestion in cephalopods. *In:* A. S. M. Saleuddin & K. M. Wilbur (eds.), The Mollusca, Vol. 5:149–187. Academic Press: New York.

BRETT, J. R. 1983. Life energetics of the sockeye salmon, *Oncorhynchus nerka*. *In:* W. P. Asprey & S. I. Lustick (eds.), Behavioral energetics. Ohio State Univ. Press.

CARPENTER, J. H. 1966. New measurements of oxygen solubility in pure and natural waters. Limnol. Oceanogr. 11: 264–277.

JOHANSEN, K., J. R. REDMOND & G. B. BOURNE. 1978. Respiratory exchange and transport of oxygen in *Nautilus pompilius*. Jour. Exp. Zool. 205:27–36.

MANGOLD, K., A. PORTMANN & A. M. BIDDER. In press. Traité de Zoologie. Grassé (ed.).

O'DOR, R. K., K. MANGOLD, R. BOUCHER-RODONI, M. J. WELLS & J. WELLS. 1984. Nutrient absorption, storage and remobilisation in *Octopus vulgaris*. Mar. Behav. Physiol. 11: 239–258.

REDMOND, J. R., G. B. BOURNE & K. JOHANSEN. 1978. Oxygen uptake by *Nautilus pompilius*. Jour. Exp. Zool. 205:45–50.

SAUNDERS, W. B. 1981. The species of living *Nautilus* and their distribution. Veliger 24:8–17.

WARD, P. D. 1983. *Nautilus macromphalus*. *In:* P. R. Boyle (ed.), Cephalopod life cycles, Vol. 1:11–28.

WARD, P. D., B. CARLSON, M. WEEKLY & B. BRUNBAUGH. 1984. Remote telemetry of daily vertical and horizontal movement of *Nautilus* in Palau. Nature 309:248–250.

WARD, P. D. & A. W. MARTIN. 1980. Depth distribution of *Nautilus pompilius* in Fiji and *Nautilus macromphalus* in New Caledonia. Veliger 22:259–264.

WATT, B. K. 1968. Composition of foods, raw and processed. Pp. 9–20. *In:* P. L. Altman & D. S. Dittmer (eds.), Metabolism. Fed. Amer. Soc. Exp. Biol.: Bethesda, Maryland.

WELLS, M. J., R. K. O'DOR, K. MANGOLD & J. WELLS. 1983. Feeding and metabolic rate in *Octopus*. Mar. Behav. Physiol. 9:305–317.

WELLS, M. J. & J. WELLS. 1985. Ventilation and oxygen uptake by *Nautilus*. Jour. Exp. Biol. 118:297–312.

ZANN, L. P. 1984. The rhythmic activity of *Nautilus pompilius* with notes on its ecology and behavior in Fiji. Veliger 27: 19–28.

The Veliger 30(1):76–81 (July 1, 1987)

THE VELIGER

The Indo-West Pacific Species of the Genus *Trigonostoma sensu stricto* (Gastropoda: Cancellariidae)

by

RICHARD E. PETIT AND M. G. HARASEWYCH

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract. Three Indo-West Pacific species referable to the nominotypical subgenus *Trigonostoma* are compared and figured. *Trigonostoma antiquatum* (Hinds, 1843) is shown to have been misidentified in the literature, and *T. antiquatum* of most authors other than Hinds is newly described herein. The three Indo-West Pacific species recognized are: *Trigonostoma scalare* (Gmelin, 1791), *T. antiquatum* (Hinds, 1843) and *T. **thysthlon*** sp. nov.

INTRODUCTION

A study of the cancellariid subgenus *Trigonostoma s.s.* in the Indo-West Pacific reveals that there are three distinct species. The species identified in the recent literature as *T. antiquatum* (Hinds) is not that species, but a previously unnamed species, described herein as *T. **thysthlon*** sp. nov. The lectotype of *T. antiquatum* is figured, the first time it has been illustrated photographically.

ABBREVIATIONS

Abbreviations for museum collections cited in this paper are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BM(NH), British Museum (Natural History), London; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum National d'Histoire Naturelle, Paris; NSMT, National Science Museum, Tokyo; USNM, National Museum of Natural History, Washington.

SYSTEMATICS

Genus *Trigonostoma* Blainville, 1827

Trigonostoma BLAINVILLE, 1827:652.
Type species (monotypy) *Delphinula trigonostoma* Lamarck, 1822 [=*Buccinum scalare* Gmelin, 1791].
Trigona PERRY, 1811:pl. 51, non *Trigona* Jurin, 1807.

Subgenus *Trigonostoma s.s.*

Trigonostoma scalare (Gmelin, 1791)

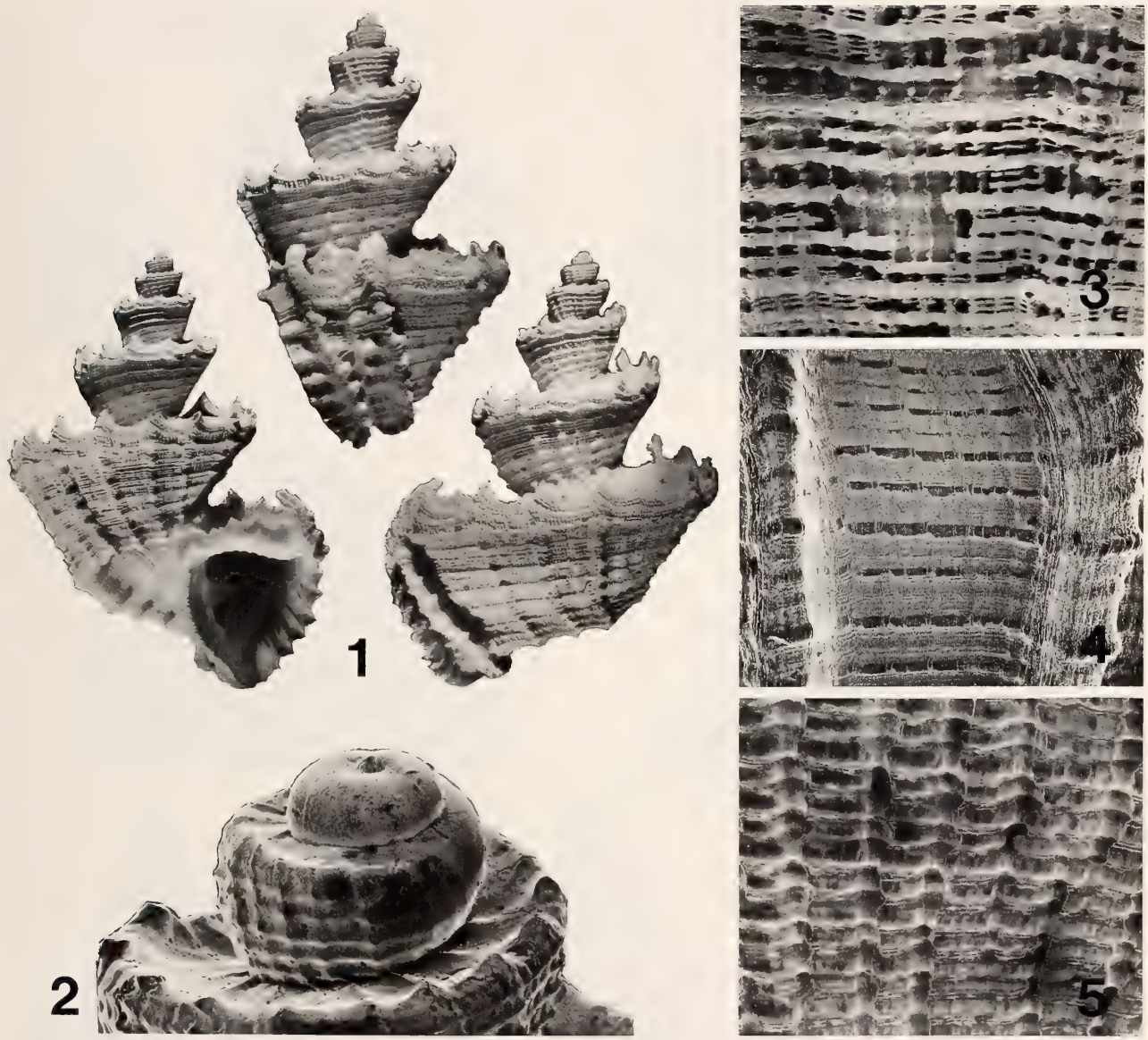
(Figures 1–3)

Buccinum scalare GMELIN, 1791:3495.
Trigona pellucida PERRY, 1811: pl. 51, figs. 1, 2.
Delphinula trigonostoma LAMARCK, 1822:231; BLAINVILLE, 1827:652; MERMOD & BINDER, 1963:170, fig. 234.
Cancellaria trigonostoma (Lamarck): DESHAYES, 1830:180; SOWERBY, 1833:7, fig. 44; KIENER, 1841:41, pl. 1, figs. 1, 1a; DESHAYES, 1843:409; SOWERBY, 1849b:457, pl. 94, figs. 45, 46; REEVE, 1856, pl. 11, figs. 51a–b; TRYON, 1885:78, pl. 5, fig. 79; LÖBBECKE, 1886:50, pl. 15, figs. 1, 2.
Trigonostoma pellucida (Perry): PETIT, 1967:217; ABBOTT & DANCE, 1982:229 [figured].
Trigonostoma antiquata (Hinds): GARRARD, 1975:20, pl. 3, fig. 16 [not of Hinds].
Trigonostoma trigonostoma (Deshayes): CHENU, 1859:276, fig. 1828; KIRTISINGHE, 1978:79, pl. 45, fig. 5.
Trigonostoma scalare (Gmelin): PETIT, 1984:58; VERHECKEN, 1986:59, fig. 27.

Diagnosis: *Trigonostoma scalare* may be readily distinguished from its congeners by its large size, concave sides, and characteristic imbricate sculpture (Figure 3).

Range: Sri Lanka to the Philippines, southeast to northeast Australia.

Remarks: The nomenclatural history of this distinctive species has been given by PETIT (1984). GARRARD (1975: 20) misidentified the species as *Trigonostoma antiquata* (Hinds) and later (1983:6) considered *T. antiquata* to be a synonym of *T. trigonostoma,* compounding his error by attributing the latter name to "Linnaeus, 1758."



Explanation of Figures 1 to 5

Figures 1, 2. *Trigonostoma* (*Trigonostoma*) *scalare* (Gmelin, 1791).

Figure 1. USNM 845609, taken by nets in 73 m, off Balut Is., Mindanao, Philippines. ×2.5.

Figure 2. Protoconch of specimen in Figure 1. ×50.

Figure 3. Detail of surface sculpture of specimen in Figure 1. ×50.

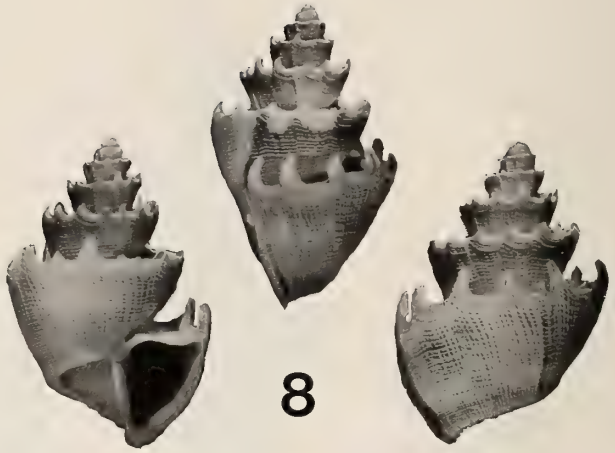
Figure 4. *Trigonostoma* (*Trigonostoma*) *antiquatum* (Hinds, 1843). Detail of surface sculpture of paralectotype BM(NH) 1968416/2, "Island of Corregidor, Manila Bay, Philippines." ×50.

Figure 5. *Trigonostoma* (*Trigonostoma*) ***thysthlon*** sp. nov. Detail of surface sculpture of specimen in Figure 8. ×50.

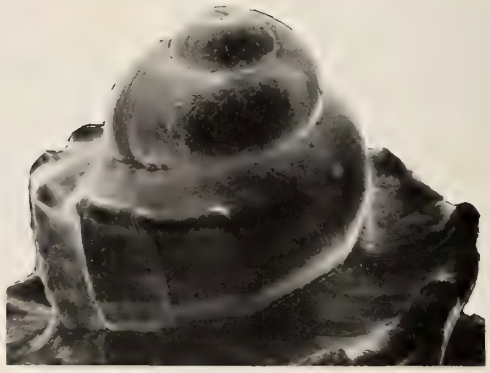
Early locality citations for this species were given simply as "Ceylon." The Australian records given by GARRARD (1975:21) cannot be accepted in their entirety owing to his misidentification. However, his figured specimen (pl. 3, fig. 16), definitely *Trigonostoma scalare,* is stated to be from "3 metres off Black Is., Whitsunday Group, Qld." In the past few years specimens have been taken from tangle nets off Bohol Island, central Philippines. VERHECKEN (1986: 59) reported a specimen from the Moluccas.

The location of the type of *Trigonostoma scalare* is not known. Gmelin based the name on an illustration in a Meuschen sales catalog (see PETIT, 1984:58) and the disposition of that specimen is not known. The location of the type of Perry's *T. pellucida,* stated to be in "Miss


6


8

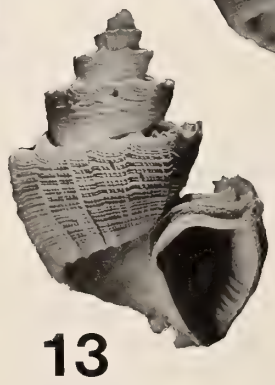

7


9


10


11


12


13

Mitford's collection," is also unknown. MERMOD & BINDER (1963) described and figured the holotype of *Delphinula trigonostoma* Lamarck, which is in MHNG.

Trigonostoma antiquatum (Hinds, 1843)

(Figures 4, 6, 7)

Cancellaria antiquata HINDS, 1843:49, 1844:43, pl. 12, figs. 17, 18.

Cancellaria antiquata Hinds: SOWERBY, 1849b:458, pl. 93, fig. 27; REEVE, 1856, pl. 16, figs. 74a, b; TRYON, 1885: 79, pl. 5, fig. 88; LÖBBECKE, 1886:57, pl. 16, figs. 9, 10.

Not *Trigonostoma antiquatum* (Hinds): HABE, 1961a:435, pl. 24, fig. 14; pl. 23, fig. 8; 1961b:73, pl. 36, fig. 8; LAN, 1980:95, pl. 41, figs. 93, 93a; ABBOTT & DANCE, 1982: 229 (all =*T.* ***thysthlon*** sp. nov.).

Not *Trigonostoma antiquata* (Hinds): GARRARD, 1975:20, pl. 3, fig. 16 (=*T. scalare* (Gmelin, 1791)).

Trigonostoma antiquata (Hinds): VERHECKEN, 1986:60 (in part).

Diagnosis: This species may be recognized by its smoothly convex whorls as well as by the presence of about 9 evenly spaced varices per whorl. Intervarical surface sculpture (Figure 4) consists primarily of numerous spiral ridges of irregular size.

Range: Along northern Indian Ocean to New Guinea. Philippines?

Remarks: In his original description HINDS (1843) gave the locality as "New Guinea; in twenty-two fathoms, coarse sand." He further stated that it had been "also observed by Mr. Cuming at the island of Corregidor, Bay of Manila, in seven fathoms, coarse sand." The next year Hinds gave only New Guinea as the habitat, not mentioning the Cuming specimens. The Hinds material was not deposited in the BM(NH) and its location is not known, leaving only the Cuming specimens to serve as type material. The British Museum (Natural History) has the Cuming specimens (BM(NH) 1968416) from which VERHECKEN (1986:60) selected as lectotype BM(NH) 1968416/1 (Figure 6), the remaining two specimens (1968416/2–3) becoming paralectotypes. The Philippine locality given for the Cuming specimens is suspect, as additional specimens have not been found even though the Corregidor Island area has been well collected. The possibility of incorrect locality data cannot be ignored, especially as other Cuming material stated to be from the Philippines, such as *Cancellaria semidisjuncta* SOWERBY (1849a), has been shown to be from localities far removed from the Philippines. All Philippine specimens of *Trigonostoma s.s.* that have come to our attention are assignable to either *T. scalare* (Gmelin) or to *T.* ***thysthlon*** sp. nov. described herein. VERHECKEN (1986: 60) cites *T. antiquatum* as occurring in India, the Strait of Hormuz, and the Gulf of Oman. We have examined several additional specimens from the northwestern Indian Ocean. These have regular varices and surface sculpture characteristic of *T. antiquatum,* although the shells tend to be thinner and less convex.

Table 1

Trigonostoma (*Trigonostoma*) ***thysthlon*** sp. nov. Measurements of shell characters. Linear measurements in mm. $n = 5$.

Character	Mean	SD	Range
Shell length	20.0	2.6	16.3–23.7
Shell width	13.0	1.5	10.9–15.6
Aperture length	8.0	1.0	6.4–9.5
$\frac{\text{Aperture length}}{\text{Shell length}}$	0.40	0.01	0.39–0.42
No. whorls, protoconch	1.95	0.19	1.75–2.25
No. whorls, teleoconch	5.0	0.22	4.75–5.2
Spire angle	60.7	4.9	54–69

Trigonostoma (*Trigonostoma*) ***thysthlon***
Petit & Harasewych, sp. nov.

(Figures 5, 8–13, Table 1)

Description: Shell small, reaching 24 mm in height, conispiral, deeply umbilicate. Protoconch (Figure 9) of 2 smooth whorls, deflected slightly from coiling axis. Transition to teleoconch delineated by fine lamellose varix with short open spine at the shoulder followed by onset of spiral

←

Explanation of Figures 6 to 13

Figures 6, 7. *Trigonostoma* (*Trigonostoma*) *antiquatum* (Hinds, 1843).

Figure 6. Lectotype, BM(NH) 1968416/1, "Island of Corregidor, Manila Bay, Philippines." ×2.5.

Figure 7. Protoconch of paralectotype BM(NH) 1968416/2. ×50.

Figures 8–13. *Trigonostoma* (*Trigonostoma*) ***thysthlon*** sp. nov.

Figure 8. Holotype, USNM 747301, in 56–73 m, off west coast of Wasir Is., West Wokam, Aru, Moluccas (5°30′S, 134°12′E). ×2.5.

Figure 9. Protoconch of specimen in Figure 8. ×50.

Figure 10. Paratype, Petit collection, in 15–20 m, Rio Cordo Del Sur, Philippines. ×2.5.

Figure 11. Paratype, Petit collection, in 182 m, S of Makung Is., Taiwan. ×2.5.

Figure 12. Paratype, NSMT 63633, in 90 m, off Wakayama Prefecture, Japan. ×2.5.

Figure 13. Paratype, MNHN, in 143–178 m, off NW Mindoro, Philippines (13°59′N, 120°14.5′E). ×2.5.

sculpture. Teleoconch with up to 6 tabulate whorls. Suture deeply impressed. First 2 postnuclear whorls with 11 or 12 finely lamellose varices per whorl. Thereafter 11 or 12 open shoulder spines per whorl, varices absent. Two thick varices in close apposition appear to mark the end of growth in adult specimens. Surface sculpture (Figure 5) of intersecting axial and spiral elements, with the axial elements being more prominent and consisting of fine, rounded riblets. Spiral sculpture of numerous weak cords, each composed of 2 or 3 fine threads. Aperture roughly triangular. Siphonal canal very short, forming shallow indentation in abapical corner of aperture. Outer lip of adult specimens with 12–15 thin lirae between the double-varix, smooth in subadults. Posterior portion of inner lip adpressed against siphonal fasciole. Inner lip with 2 columellar and 1 siphonal folds. One additional columellar thread occasionally occurring between the two columellar folds in large adult specimens. Umbilicus deep, reaching protoconch. Shell color white to pinkish brown. Aperture white. Internal structure, periostracum, and soft parts unknown.

Holotype: USNM 747301, in 56–73 m, off west coast of Wasir Island, West Wokam, Aru, Moluccas (5°30′S, 134°12′E), M. King Memorial Exp. sta. AWI 9P10, L = 16.5 mm.

Paratypes (8): Petit collection, in 15–20 m, Rio Cordo Del Sur, Philippines, L = 21.9 mm; Petit collection, in 182 m, S of Makung Is., Taiwan, L = 24.2 mm; NSMT 63633, in 90 m, off Wakayama Prefecture, Japan, L = 19.3 mm, 20.7 mm; MNHN, in 143–178 m, off NW Mindoro, Philippines (13°59′N, 120°14.5′E), L = 18.4 mm; ANSP 234758, in 90 m, Wakayama, Japan, L = 16.5 mm; AMNH 161104, off Kii Peninsula, Honshu, Japan, L = 23.5 mm; AMNH 122818, off Kii, Honshu, Japan, L = 16.5 mm.

Range: Southern Japan south to the Philippines.

Comparisons: This species most closely resembles *Trigonostoma antiquatum* from which it may be distinguished by its lack of pronounced varices beyond the second postnuclear whorl. Its flat or slightly convex whorls further distinguish it from *T. antiquatum* which has rounded whorls. The surface sculpture of *T.* ***thysthlon*** consists of strong axial and weaker spiral cords, while the surface sculpture of *T. antiquatum* consists of strong spiral and very weak axial cords.

Etymology: From the Greek *thysthlon,* a torch carried in the Bacchic festival.

ACKNOWLEDGMENTS

Mr. Donald Dan, West Friendship, Maryland, photographed numerous specimens of *Trigonostoma* in foreign museums at our request. Dr. Akihiko Matsukuma, National Science Museum, Tokyo, Dr. Robert Robertson, Academy of Natural Sciences of Philadelphia, Dr. Philippe Bouchet, Muséum National d'Histoire Naturelle, Paris, Dr. William K. Emerson, American Museum of Natural History, New York, and Ms. Kathie Way, British Museum (Natural History), London, all made available material from their museums' collections. Mr. Ron Parsons, Burlingame, California and Mr. P. W. Clover, Glen Ellen, California, loaned specimens from their personal collections. Mr. André Verhecken, Mortsel, Belgium, corresponded and furnished a photograph of *T. antiquatum* from the Strait of Hormuz. To all of the above we express our appreciation for their assistance and cooperation.

LITERATURE CITED

Abbott, R. T. & S. P. Dance. 1982. Compendium of seashells. E. P. Dutton: New York. 411 pp.

Blainville, H. M. D. de. 1825–1827. Manuel de malacologie et de conchyliologie. Paris. Two Vols., 190 pls. [Text pp. 1–647 issued 1825; pp. 649–664 and plates issued 1827].

Chenu, J. C. 1859. Manuel de conchyliologie et de paléontologie conchyliologique. Tome 1, pp. i–vii and 1–508, textfigs. 1–3707. Paris.

Deshayes, G. P. 1830. Encyclopédie méthodique. Histoire Naturelle des Vers 2(1):1–256. Paris.

Deshayes, G. P. 1843. Histoire naturelle des animaux sans vertèbres. 2nd ed. Vol. 9. Paris. 725 pp.

Garrard, T. A. 1975. A revision of Australian Cancellariidae (Gastropoda: Mollusca). Rec. Austr. Mus. 30(1):1–62.

Garrard, T. A. 1983. Notes on the family Cancellariidae. Austr. Shell News (42):6.

Gmelin, J. F. 1791. Caroli a Linné Systema Naturae per regna tria naturae. Editio decima tertia. Vol. 1, Pt. 6 (Vermes): 3021–3910. Lipsiae.

Habe, T. 1961a. Coloured illustrations of the shells of Japan (II). 148 pp., Appendix 42 pp., 66 pls. Osaka.

Habe, T. 1961b. Description of four new cancellariid species, with a list of the Japanese species of the family Cancellariidae. Venus 21(4):431–441, pls. 23, 24.

Hinds, R. B. 1843. Description of ten new species of *Cancellaria,* from the collection of Sir Edward Belcher. Proc. Zool. Soc. Lond. 11:47–49.

Hinds, R. B. 1844–45. The zoology of the voyage of H.M.S. Sulphur. Mollusca, Pts. 1–3. London. 72 pp., 21 pls.

Kiener, L. C. 1841. Spécies général et iconographie des coquilles vivantes. Genre Cancellaire. Paris. 44 pp., 9 pls.

Kirtisinghe, P. 1978. Sea shells of Sri Lanka. Charles E. Tuttle Co.: Vermont. 202 pp., 61 pls.

Lamarck, J. B. P. A. 1822. Histoire naturelle des animaux sans vertèbres. Vol. 6(2):1–232. Paris.

Lan, T. C. 1980. Rare shells of Taiwan in color. Taipei. 144 pp., 63 pls.

Löbbecke, T. 1881–87. Das genus *Cancellaria.* Systematisches Conchylien-Cabinet von Martini und Chemnitz 4:1–108, pls. 1–24.

Mermod, G. & E. Binder. 1963. Les types de la collection Lamarck au Muséum de Genève. Mollusques vivants. V. Revue Suisse de Zoologie 70(7):127–172.

Perry, G. 1811. Conchology, or the natural history of shells; containing a new arrangement of the genera and species. . . . London. 4 pp., 61 pls. (with pl. expl.).

Petit, R. E. 1967. Notes on Cancellariidae (Mollusca: Gastropoda). Tulane Stud. Geol. 5(4):217–219.

Petit, R. E. 1984. Some early names in Cancellariidae. Amer. Malacol. Bull. 2:57–61.

Reeve, L. 1856. Conchologia iconica, 10, *Cancellaria*. London. 18 pls. (with pl. expl.).

Sowerby, G. B. 1832–33. The conchological illustrations. *Cancellaria*. Pts. 9–13. London. 5 pls. with explanations + catalogue, 10 pp. [Pts. 9–12, figs. 1–35, published 1832; pt. 13, figs. 36–44 and catalogue published 1833].

Sowerby, G. B. 1849a. Descriptions of some new species of *Cancellaria* in the collection of Mr. H. Cuming. Proc. Zool. Soc. Lond. [for 1848] XVI(189):136–138.

Sowerby, G. B. 1849b. Thesaurus conchyliorum. *Cancellaria*. Pp. 439–461, pls. 92–96.

Tryon, G. W. 1885. Manual of conchology 7:65–98, pls. 1–7. Philadelphia.

Verhecken, A. 1986. The Recent Cancellariidae of Indonesia (Neogastropoda, Cancellariacea). Gloria Maris 25(2):29–66.

The Veliger 30(1):82–89 (July 1, 1987)

THE VELIGER

Two New Aeolid Nudibranchs from Southern California

by

DAVID W. BEHRENS

Pacific Gas and Electric Company, Biological Research Laboratory,
P.O. Box 117, Avila Beach, California 93424, U.S.A.

Abstract. Two species, *Cuthona* ***hamanni*** sp. nov. and *Eubranchus* ***steinbecki*** sp. nov., from southern California are described.

INTRODUCTION

Southern California has historically been a very active area for opisthobranch research. The vicinity of San Diego, California, has produced numerous new species, as recently as 1986: Gosliner (1981) described *Cuthona phoenix* and Bertsch & Osuna (1986) added *Tritonia myrakeenae*. This paper describes the morphology of two new aeolidacean nudibranchs belonging to the genera *Cuthona* Alder & Hancock, 1855, and *Eubranchus* Forbes, 1938.

Tergipedidae Thiele, 1931

Cuthona Alder & Hancock, 1855

Cuthona ***hamanni*** Behrens, sp. nov.

(Figures 1–5)

La Jolla aeolid (*Cuthona* sp.): Behrens, 1980:105, fig. 158.

Materials examined: (1) Holotype: one specimen approximately 9 mm long (preserved), collected intertidally

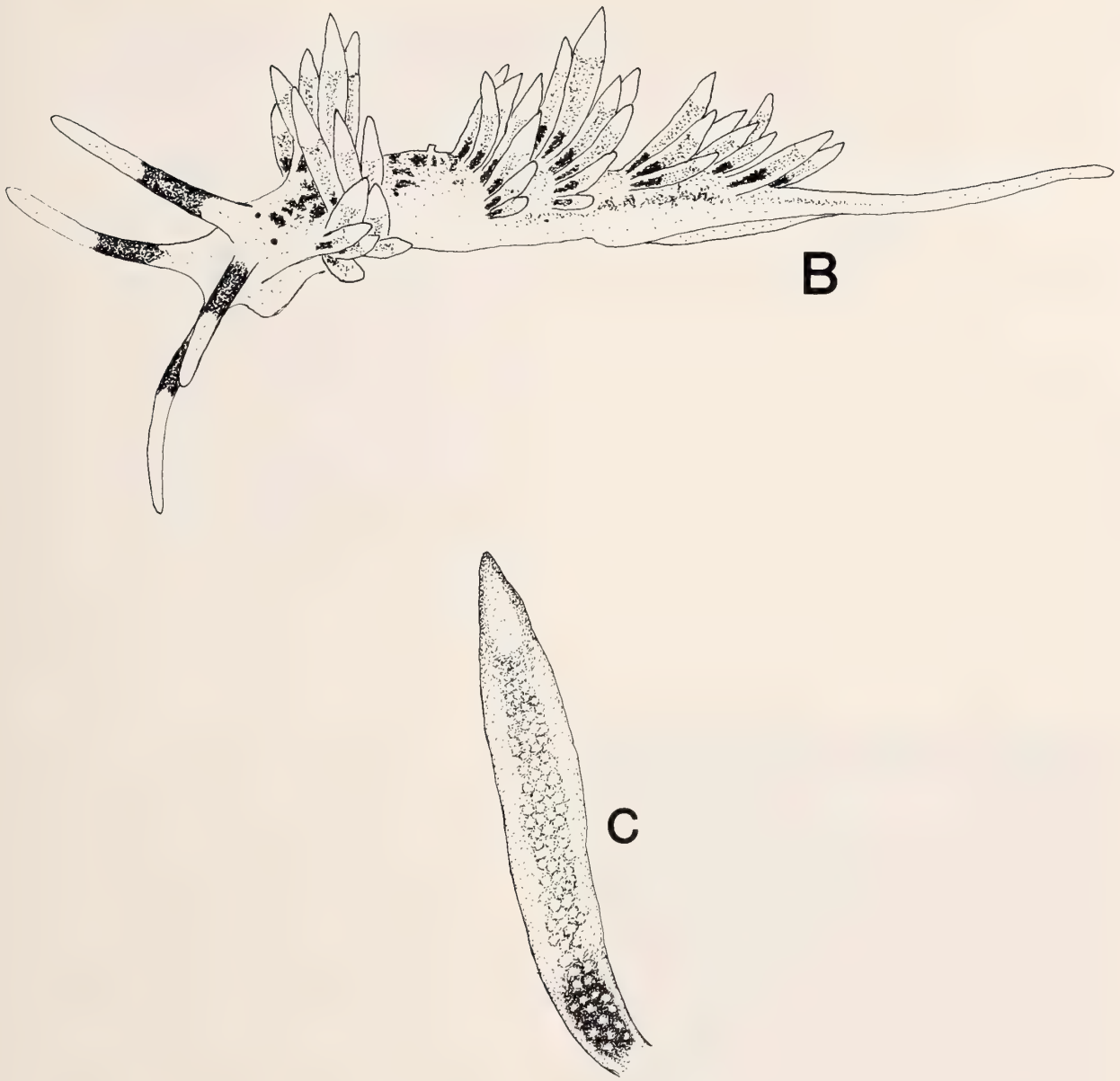


Figure 1

Cuthona ***hamanni*** Behrens, sp. nov. A. Living animal, 9-mm specimen collected from La Jolla, California. Photograph by Jeff Hamann. B. Living animal drawn from a color transparency. C. Detail of a ceras.

at La Jolla, California (32°51′N, 117°15′W) in July 1983 by Mr. Jeff Hamann. This specimen is deposited in the collection of the California Academy of Sciences, Department of Invertebrate Zoology and Geology (CAS), CASIZ 061410.

(2) Paratypes: two specimens, each 7 mm long (preserved) and collected concurrently with the holotype, are also deposited in the CAS collection, CASIZ 061411.

(3) One specimen, 5 mm long (preserved), collected intertidally at La Jolla, California, in May 1982 by Jeff Hamann. This specimen is also deposited in the CAS collection, CASIZ 061412. Color transparencies of living *Cuthona* ***hamanni*** are on file at CAS.

Description: Living animals may reach 14 mm long. The body is typically aeolidiform, elongate and graceful, tapering posteriorly (Figure 1). The foot is narrow, linear, tapering to a point posteriorly. The tail is long. The foot corners are square and somewhat laterally produced. The cephalic tentacles are cylindrical, tapering to a blunt point,

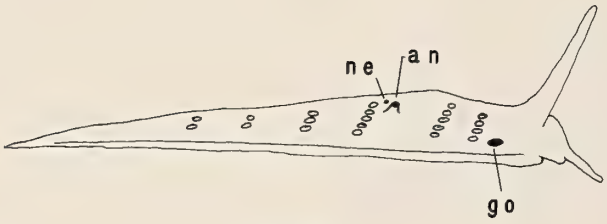


Figure 2

Cuthona ***hamanni.*** Lateral view. an, anus; go, genital orifice; ne, nephroproct.

and when extended to their fullest are equal in length to the rhinophores. The rhinophores are closely set, long, smooth, and tapering to a rounded tip. The cerata are slightly clavate and attain a length equal to that of the rhinophores (Figure 1C). In one specimen the ceratal half formula was I 4, II 5 (pre-pericardial), III 5, IV 3, V 2, VI 2 (post-pericardial). The ceratal arrangement is shown in Figure 2. The anal pore is located immediately anterior to the uppermost ceras of the first post-pericardial row, to the right of the pericardial elevation (Figure 2). The nephroproct is just medial to the anal pore (Figure 2). The genital orifice is located just below the pre-pericardial cerata on the right side of the body (Figure 2).

The ground color of the body is transparent white. The internal organs are easily seen through the body wall. Irregular patches of white and dark-brown pigment occur dorsally from the rhinophores to the tip of the tail. The white patches are more laterally distributed than the brown pigmentation. Some white spots occur on the head. The distal ⅓ of the rhinophores and cephalic tentacles is encrusted with white pigment, followed by a band of dark brown more proximally. The remaining ⅓ is similar to the ground color of the body. White speckling may overlay the proximal ⅔ of these appendages. The coloration of the cerata is complex (Figure 1B). The tip of each ceras is white, followed by a granular appearing medial region. The granular appearance of this region, which makes up ¾ the length of each ceras, is created by a series of uniformly spaced white specks overlaying the semi-translucent liver diverticulum. The color of the liver varies from tan to orange and salmon. Basally, the coloration of the liver abruptly changes to kelly green, forming a characteristically dark band. Occasional brown specks were observed on the cerata of several specimens.

The radular formula is 13–20 × 0.1.0. There are no

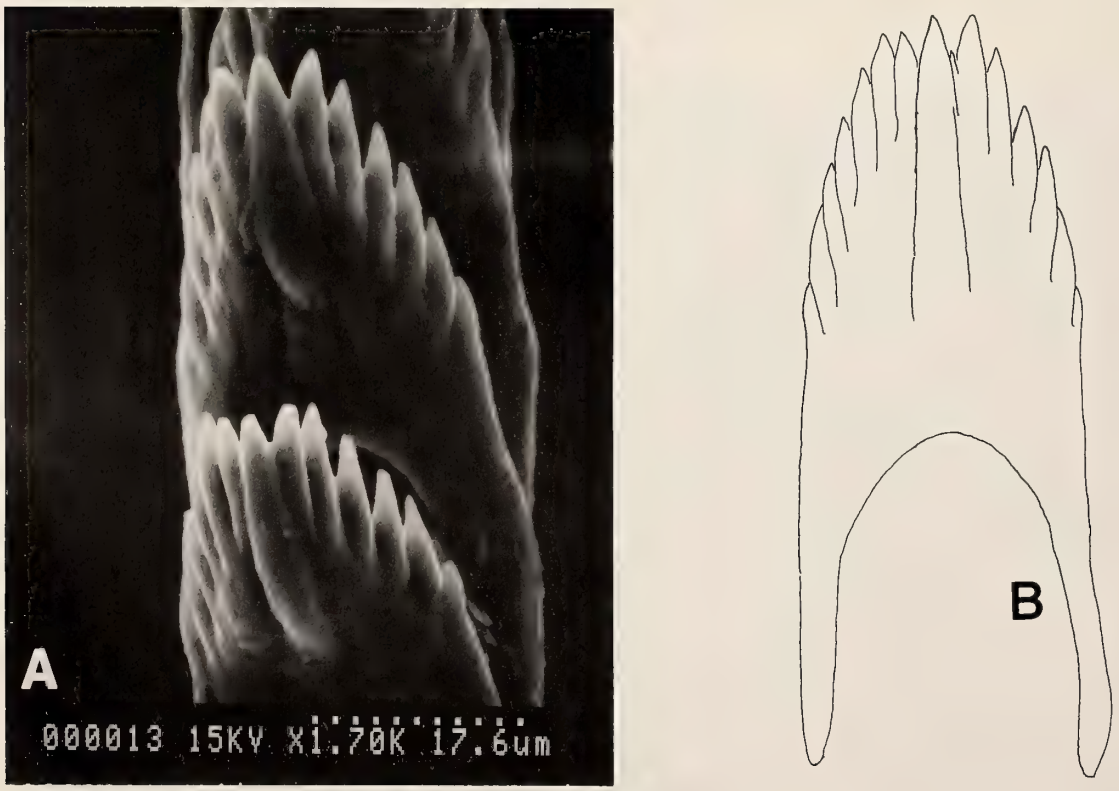


Figure 3

Cuthona ***hamanni.*** A. Scanning electron micrograph of radula. B. Drawing of a rachidian tooth.

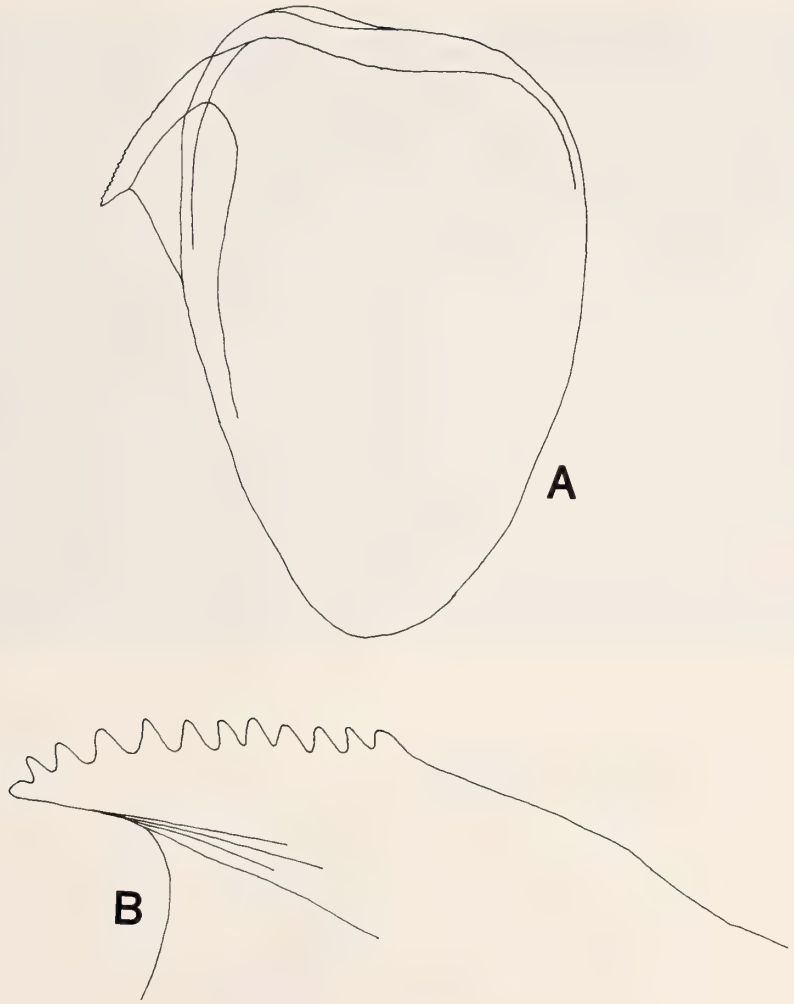


Figure 4

Cuthona ***hamanni.*** A. Jaw. B. Masticatory border of the jaw.

preradular teeth. Each rachidian tooth is a tall horseshoe-shaped arch, with a long articulatory socket on the anterior surface on either side (Figures 3A, B). The central cusp is barely differentiated from the denticles, but does form a low ridge. There are 6 or 7 strong, equal-size denticles to each side of the cusp. The jaws are lightly tinted gold and broadly oval (Figure 4A). The masticatory border is short and angular with 10 irregular denticles (Figure 4B).

The reproductive system is typically cuthonid (Figure 5). The penial papilla is conical, bearing a stylet, and is associated with a large bulbous penial gland. The vas deferens is prostatic. The receptaculum seminis comprises a single lobe and inserts into a common junction at the orifice of the large lobate female gland mass through a short duct. The ampulla is bulbous and connects with the receptaculum seminis through a long duct.

Discussion: Placement of *Cuthona* ***hamanni*** is based upon the presence of a non-tapering radula and the absence of a preradular tooth (Gosliner & Griffiths, 1981). The presence of a penial stylet is variable within the genus (Miller, 1977).

Cuthona ***hamanni*** can be separated from northeastern Pacific species by its distinctive body and ceratal coloration and by the number of teeth in the radula. Pigmentation on the body region in the form of opaque white patches or spots occurs in *C. abronia* (MacFarland, 1966), *C. albocrusta* (MacFarland, 1966), and *C. perca* (Marcus, 1958) (McDonald, 1983; Behrens, 1984). None of these species bears white and brown patches of pigmentation simultaneously, however. The uniform spotting and the bold green coloration of the liver diverticulum at the insertion of the cerata differ strikingly from the ceratal coloration of all

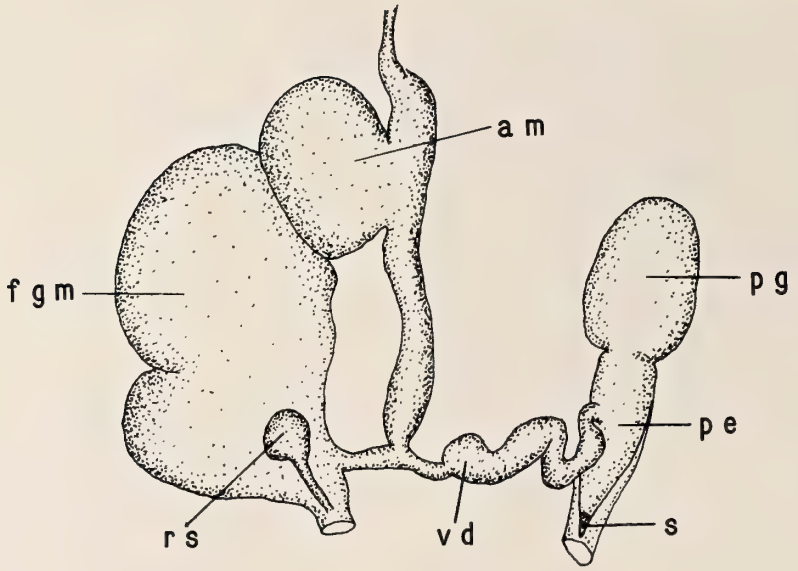


Figure 5

Cuthona ***hamanni***. Reproductive system. am, ampulla; fgm, female gland mass; pe, penis; pg, penial gland; rs, receptaculum seminis; s, stylet; vd, vas deferens.

described species. The number of radular teeth in *C.* ***hamanni*** (13–20) is very low, approached only by *C. fulgens* (MacFarland, 1966), which has from 16 to 59 teeth, and *C. perca,* bearing 16 to 35 radular teeth.

The specific name ***hamanni*** is chosen to acknowledge the energetic and enthusiastic efforts of Mr. Jeff Hamann to increase our knowledge of opisthobranch mollusks, not only from southern California but throughout the world. Jeff's collections of opisthobranch species, described and undescribed, have assisted researchers in bringing many fascinating discoveries to the attention of the scientific community as a whole. For myself and others, we thank him.

EUBRANCHIDAE Odhner, 1934

Eubranchus Forbes, 1938

Eubranchus ***steinbecki*** Behrens, sp. nov.

(Figures 6–9)

Eubranchus sp.: BEHRENS, 1980:105, fig. 157.

Material examined: (1) Holotype: one specimen approximately 4 mm long (preserved) collected off boat floats at Dana Landing, Mission Bay, San Diego, California (32°42′N, 117°11′W) 18 August 1978 by Dr. T. M. Gosliner. This specimen is deposited in the collection of the California Academy of Sciences, Department of Invertebrate Zoology and Geology (CAS), CASIZ 061413.

(2) Paratype: one specimen approximately 4 mm (preserved), collected intertidally at Palos Verdes, Los Angeles County, California (34°00′N, 118°47′W) on 23 March 1985 by William Jaeckle. This specimen is also deposited in the CAS collection, CASIZ 061414. Color transparencies of a living *Eubranchus* ***steinbecki*** are on file at CAS.

Description: Living animals reach 6 mm long. The body is typically aeolidiform (Figure 6). The foot is slightly wider than the body, linear and tapering posteriorly into a long tail. The foot corners are square. The cephalic tentacles are cylindrical and short, about ½ the length of the rhinophores (Figures 6, 7). The rhinophores are long, smooth, and taper to a blunt tip. The cerata are cylindrical and irregularly nodular (Figure 6B). The liver diverticulum is nodular within each ceras. The cerata are arranged in 6 or 7 oblique rows dorsolaterally on either side of the dorsum. An example of the branchial half formula is I 2–4, II 2–4 (pre-pericardial), III 3–5, IV 3–4, V 2, VI 2 (post-pericardial). The largest cerata are dorsomedial, with smaller ones situated marginally. The anal pore is anterior to the medial ceras of the third row and ventral to the pericardial elevation (Figure 7). The genital orifice lies posteriorly to the first ceratal row on the right side (Figure 7).

The ground color of the body is tan with dark olive-green mottling. The dark green pigmentation is concentrated dorsomedially, forming a series of longitudinal stripes along the dorsum connecting the ceratal groups. This striping varies greatly, both in darkness and in width, depending on the specimen. The head and proximal regions of the rhinophores and cephalic tentacles are speckled with olive-green. There are wide lateral translucent areas around the eyes. The rhinophores are tipped with white, followed by a dark olive-green band. In some specimens a clear band exists about ⅓ the length from the distal end, followed

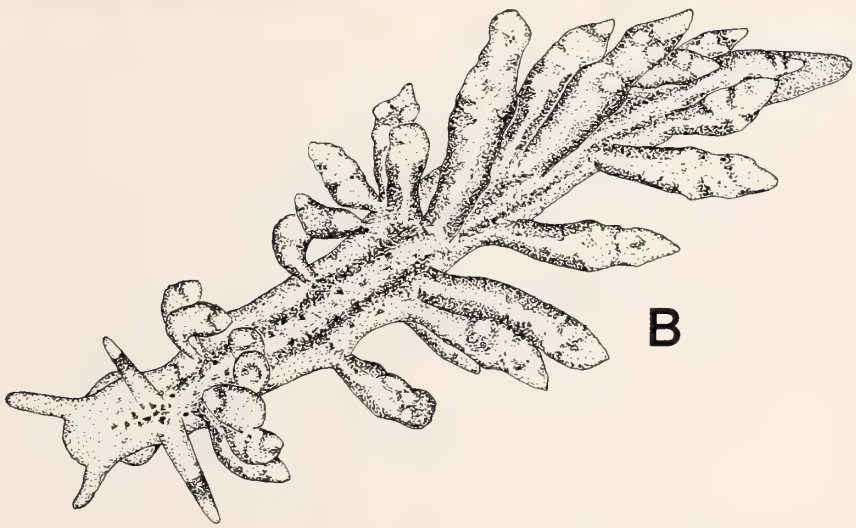


Figure 6

Eubranchus ***steinbecki*** Behrens, sp. nov. A. Living animal. 4-mm specimen collected from Dana Landing. Photograph by T. M. Gosliner. B. Living animal drawn from a color transparency.

by the speckled olive-green head color. The cephalic tentacles are white tipped and may have a green–brown subapical band. The cream-colored liver diverticulum is clearly discernible in the cerata. The cnidosac is cream to white. The cerata are covered with various amounts of dark green specks that may disperse, forming rings around the nodulations.

The buccal mass is muscular and the salivary glands large. The radular formula is 73 × 1.1.1. The central cusp of the rachidian tooth is set lower than the tips of the adjacent denticles and forms a low, central ridge (Figure 8A). There are 4 strong denticles on each side of the central cusp. The lateral teeth are thin rectangular plates with a single cusp on the inner side (Figure 8B), and are typical of the genus *Eubranchus.* The basal leg of the lateral tooth is long, and only slightly tapering, measuring 3 to 4 times the height of the tooth. The jaws are narrow, tapering posteriorly (Figure 8C). The masticatory border bears 19 or 20 denticles (Figure 8D).

The reproductive system is typically eubranchid (Figure 9). The hermaphroditic duct opens into the ampulla terminally. There is a penial gland, and the penis bears an

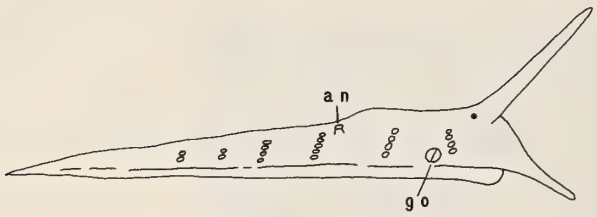


Figure 7

Eubranchus ***steinbecki.*** Lateral view. an, anus; go, genital orifice.

apparently cuticular stylet. The vas deferens is not prostatic. The ovotestes bear about 12 acini. The region midway between the small receptaculum seminis and the opening of the vagina may function as a bursa copulatrix as described in *Eubranchus farrani* (Alder & Hancock, 1844) by EDMUNDS & KRESS (1969:891, 897). The egg mass is a white-colored coil of ¾–⅞ of a whorl attached to the substrate at the center of the whorl. This mass is longer than that described by HURST (1967) for *E. olivaceus* (O'Donoghue, 1922), but is similar in morphology to the egg mass described for *E. cucullus* Behrens, 1985. Egg masses collected 10 August 1976 at Dana Landing were approximately 1 mm in diameter and were on the hydroid *Plumularia laganiforma.*

Discussion: The characteristics delineating the genus *Eubranchus* are well defined (EDMUNDS & KRESS, 1969). BEHRENS (1985) summarized recent additions to this genus. Of the 28 species known world-wide, many bear green pigmentation. *Eubranchus doriae* (Trinchese, 1874) from the Mediterranean and Atlantic coasts of France is the only other species to concentrate the dorsal pigmentation to form two dark stripes connecting the ceratal groups. Among the five west American species, the radular count of 73 places *E.* ***steinbecki*** midway between *E. cucullus* (82) and *E. rustyus* (Marcus, 1961) (50–60), with the remaining species having fewer teeth (ROLLER, 1972; MCDONALD, 1983). In this species also the central cusp of the rachidian is shorter than the lateral cusps. Additionally, the number of denticles (19 or 20) on the masticatory border of the jaw of *E.* ***steinbecki*** falls between those of the above-mentioned species, with *E. cucullus* having 25 and *E. rustyus* having 12–20 (ROLLER, 1972; MCDONALD, 1983).

The specific name ***steinbecki*** is chosen to give recognition to the author and philosopher John Steinbeck (1902–

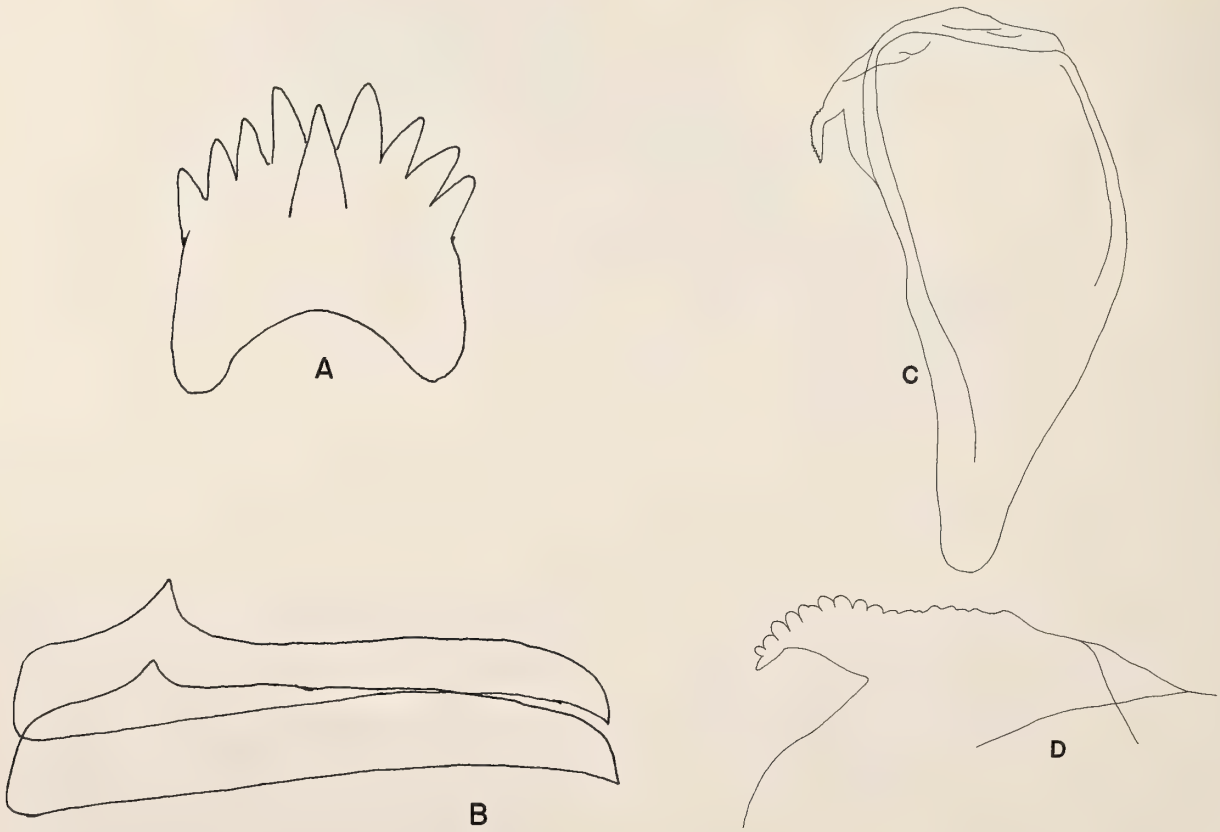


Figure 8

Eubranchus ***steinbecki.*** A. Rachidian tooth. B. Lateral tooth. C. Jaw. D. Masticatory border of the jaw.

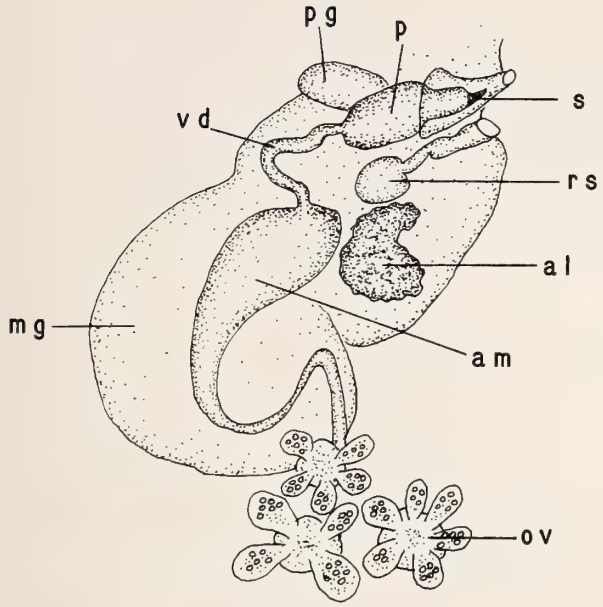


Figure 9

Eubranchus ***steinbecki.*** Reproductive system. al, albumen gland; am, ampulla; mg, mucus gland; ov, ovotestis; p, penis; pg, penial gland; rs, receptaculum seminis; s, stylet; vd, vas deferens.

1969), the man who not only influenced the works of Edward "Doc" Ricketts, but was himself so greatly influenced by Doc that some have speculated that Steinbeck may have joined the ranks of our colleagues had it not been for Ricketts untimely death. Together they wrote *The Sea of Cortez* and were nearing completion of *The Outer Shores* (see HEDGPETH, 1978a, b).

ACKNOWLEDGMENTS

I would like to express my thanks to Jeff Hamann, Will Jaeckle, and Terry Gosliner for providing me with the type material for these species, and to Jeff for his photograph of *Cuthona* ***hamanni*** and to Terry for the scanning electron micrograph and his photograph of *Eubranchus* ***steinbecki.***

LITERATURE CITED

BEHRENS, D. W. 1980. Pacific coast nudibranchs: a guide to the opisthobranchs of the northeastern Pacific. Sea Challengers Inc.: Los Osos, Calif. 112 pp.

BEHRENS, D. W. 1984. Notes on the tergipedid nudibranchs of the northeastern Pacific, with a description of a new species. Veliger 27(1):65–71.

BEHRENS, D. W. 1985. A new species of *Eubranchus* Forbes, 1838, from the Sea of Cortez, Mexico. Veliger 28(2):175–178.

BERTSCH, H. & A. M. OSUNA. 1986. A new species of *Tritonia* (Nudibranchia) from southern California and Baja California. Nautilus 100(2):46–49.

EDMUNDS, M. & A. KRESS. 1969. On the European species of *Eubranchus* (Mollusca: Opisthobranchia). Jour. Mar. Biol. Assoc. U.K. 49:879–912.

GOSLINER, T. M. 1981. A new species of tergipedid nudibranch from the coast of California. Jour. Moll. Stud. 47:200–205.

GOSLINER, T. M. & R. J. GRIFFITHS. 1981. Description and revision of some South African aeolidacean Nudibranchia (Mollusca, Gastropoda). Ann. S. Afr. Mus. 84(2):105–150.

HEDGPETH, J. W. (ed.) 1978a. The outer shores. Part 1. Ed Ricketts and John Steinbeck explore the Pacific Coast. Mad River Press Inc.: Eureka, Cal. 128 pp.

HEDGPETH, J. W. (ed.) 1978b. The outer shores. Part 2. Breaking through. Mad River Press Inc.: Eureka, Cal. 182 pp.

HURST, A. 1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. Veliger 9(3):255–288, 13 pls.

MCDONALD, G. R. 1983. A review of the nudibranchs of the California coast. Malacologia 24(1–2):114–276.

MILLER, M. C. 1977. Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Tergipedidae from New Zealand waters. Zool. Jour. Linn. Soc. 60(3):197–222.

ROLLER, R. A. 1972. Three new species of eolid Nudibranch from the west coast of North America. Veliger 14(4):416–423.

The Veliger 30(1):90–94 (July 1, 1987)

THE VELIGER

First Records of the Pteropods *Clio scheelei* (Munthe, 1888) and *Clio andreae* (Boas, 1886) (Opisthobranchia: Thecosomata) from the Western Pacific Ocean

by

L. J. NEWMAN AND J. G. GREENWOOD

Zoology Department, University of Queensland,
St. Lucia, Brisbane, Australia 4067

Abstract. Single individuals of *Clio andreae* (=*C. polita*), taken in three oblique plankton hauls from depths to 1000 m in the Coral Sea and Solomon Sea, are described and figured. This is the first published record of the species from the Pacific Ocean. Three individuals of *Clio scheelei* similarly taken from depths to 2000 m in the Coral Sea are also described and figured. This species was previously known from a single individual captured off Patagonia.

INTRODUCTION

Thecosomatous pteropods are found in all oceans, being most diverse in tropical waters and mainly epipelagic in distribution (BÉ & GILMER, 1977). There have been few studies of pteropods from waters off northeastern Australia other than those arising from the "Siboga" (TESCH, 1904) and "Challenger" (PELSENEER, 1888) expeditions, and from the studies of RUSSELL & COLEMAN (1935), TESCH (1948), TANAKA (1970), and SOLIS & WESTERNHAGEN (1978).

The present study arose from an examination of plankton samples taken from depths in excess of 1000 m in waters of the Coral Sea off northeastern Australia, and of the Solomon Sea to the north of Australia. Amongst the pteropods taken from those samples were two rare bathypelagic forms, neither of which has previously been recorded from the western Pacific Ocean, and one of which was previously known only from a single specimen taken in the southeastern Pacific. The present paper describes and illustrates western Pacific specimens of *Clio scheelei* (Munthe, 1888) and *Clio andreae* (Boas, 1886), extending greatly the known distribution ranges of both.

MATERIALS AND METHODS

All specimens were taken from plankton samples collected from the Solomon Sea and Coral Sea in 1981–1982, primarily for ichthyoplankton studies. Tows were made with nets of 4.0-mm mesh through the water column from depths greater than 1000 m to the surface. Samples were preserved in 2–3% formalin and deposited in the Museum of Victoria, Melbourne. Pteropods from those samples were made available for the present study and all specimens examined are lodged in the Museum of Victoria. Measurements were made with the aid of Wild M5 and M20 microscopes. Surface features were photographed using scanning electron microscopy (SEM). Thecate hydroids attached to the protoconchs of both *Clio andrea* and *C. scheelei* were not removed from our specimens prior to SEM treatment because of the extremely delicate nature of the shells. Thecate hydroids also have been found attached to other thecosome species (MILLARD, 1975). Only one of the three available specimens of each species was subjected to SEM treatment (and consequent damage). The best specimens were examined and drawn, but retained intact for museum deposition. Radulae were extracted from the specimens prior to the shell being subjected to SEM. The radula and buccal tissue were left in 10% KOH for 24 h, stained in acid fuchsin and prepared for light microscopy. Drawings were made with the aid of a camera lucida.

Sample data and species occurrences are given in Table 1.

RESULTS AND DISCUSSION

Clio andreae (Boas, 1886) (=*C. polita* Pelseener, 1888)

Single specimens of *Clio andreae* were taken in samples from depths to greater than 1000 m at two stations in the

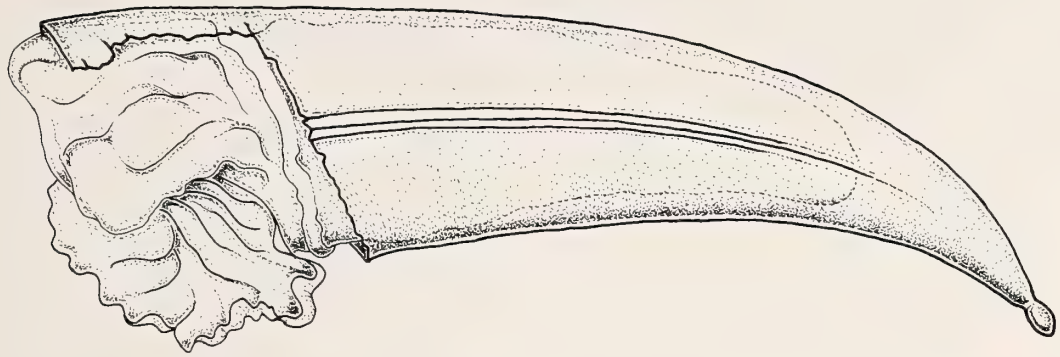


Figure 1

Clio andreae, lateral view of shell specimen that measured 7.3 mm long, aperture width 3.4 mm maximum.

Coral Sea and one station in the Solomon Sea (see Table 1). The animals were intact but their shells were damaged. All three specimens have been deposited in the Museum of Victoria (reference No. F 53081–53083).

All our specimens showed good agreement with shell features described by VAN DER SPOEL (1967, 1976) for specimens of up to 14 mm in length and 7 mm in width. The shell is transparent, fragile and colorless, and the shape is long and slender. The surface is completely smooth and without striae, but there is a protrusively rounded lateral rib on each side (Figure 3D). These ribs extend to the aperture rim, and are most prominent in the anterior half of the body, diminishing more posteriorly and being indiscernable in the posterior quarter (Figures 1, 3A–C). The shell has a distinct dorsal curvature, this curvature being more pronounced in the posterior third; the ventral border is therefore convex. The protoconch is not uniformly rounded distally, having an oval shape with an obtusely pointed distal end. The radula has 10 rows of teeth, which is typical of the genus, the teeth being similar in shape to those described for this species by VAN DER SPOEL (1967).

Clio andreae is known to be bathypelagic, occurring in depths below 1000 m. Populations are known to occur in tropical, subtropical, and transitional waters of the North and South Atlantic (VAN DER SPOEL, 1967, 1976). The only previous record of this species from the Pacific Ocean is contained in an unpublished report by MCGOWAN (1960, see BÉ & GILMER, 1977) who reported it from a depth of 135–250 m in the Gulf of Panama.

Clio scheelei (Munthe, 1888)

Single specimens were found in each of three samples collected from the Coral Sea (see Table 1). In each case the samples were taken by oblique hauls from a maximum depth of approximately 2000 m. All three specimens were found with the animal intact although some shell damage was evident. All three specimens are deposited in the Museum of Victoria (reference No. F 53084–53086).

The shell is transparent, straight and slender, with the surface annulated by equally spaced transverse lirations (Figures 2, 3E–G). A lateral rib extends on each side from the aperture rim to the protoconch; these ribs have a distinct

Table 1

Sample and shell data for occurrences of *Clio andreae* and *C. scheelei.*

Species & date	Sample no.	Latitude	Longitude	Max. tow depth (m)	Time		Shell dimensions (mm ± 0.1)	
					Start	Finish	Length	Aperture width
C. andreae								
18 May 81	1007-3	6°40.1′S	150°32.8′E	?	0010	?	12.6	5.1
1 Dec. 81	1043-5	12°21′S	146°30′E	1000	0105	0600	13.6	7.0
2 Dec. 81	1046-8	12°38′S	148°55′E	1450	1740	2355	7.3	3.4 (SEM)
C. scheelei								
2 Dec. 81	1046-8	12°38′S	148°55′E	1450	1740	2355	Specimen damaged	
3 Dec. 81	1047-7	12°31′S	148°41′E	1650	0015	0635	8.9	4.3
4 Dec. 81	1049-8	13°50′S	148°18′E	2100	2400	0624	7.0	3.4 (SEM)

SEM indicates these specimens as photographed in Figure 3.

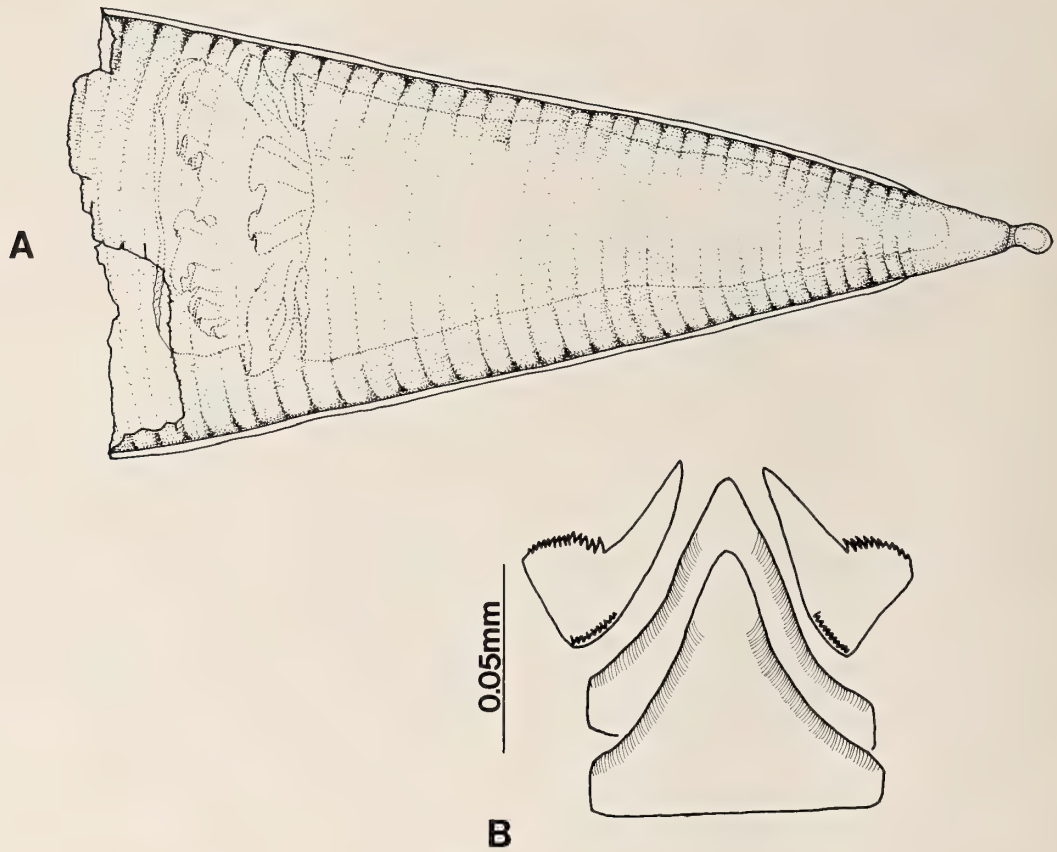


Figure 2

A. *Clio scheelei,* dorsal view of shell specimen that measured 7.0 mm long, 3.3 mm aperture width. B. Portion of radula showing median and marginal teeth.

median longitudinal indentation making them "gutter-shaped" (Figure 3F, H). The protoconch is rounded and separated from the teleoconch by a pronounced constriction.

The radula is composed of 10 rows of teeth. The lateral teeth show spines on both margins and the median tooth is bluntly pointed with fine serrations (Figure 2B).

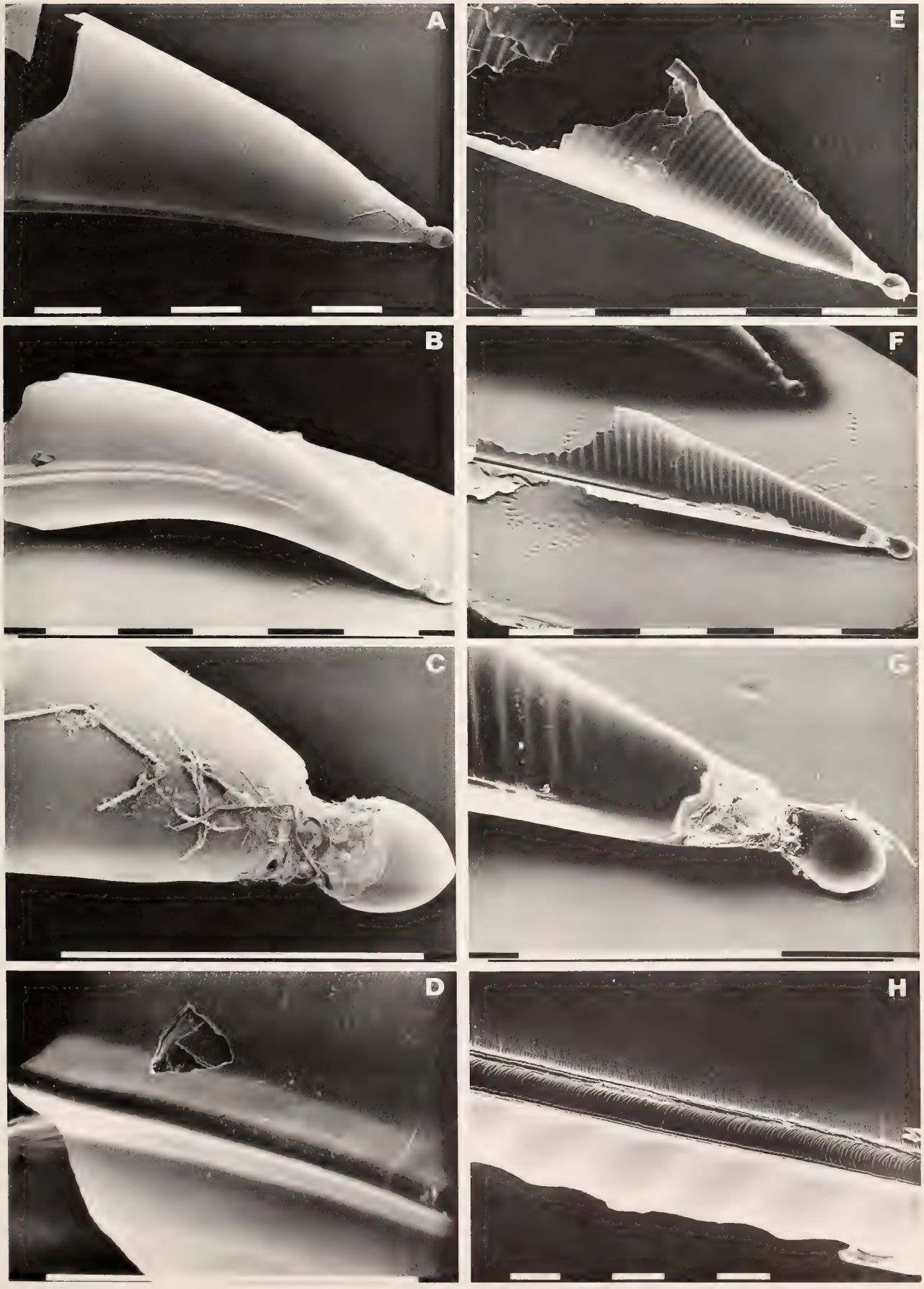
Only one specimen of *Clio scheelei* has previously been reported in the literature, and that was collected off the coast of Patagonia (148°0′S, 77°0′W) near Cape Horn (MUNTHE, 1888). This holotype cannot be located (van der Spoel, personal communication). Munthe described his specimen of *C. scheelei* as having a distinctive, broad longitudinal "ridge" widening towards the aperture. The dorsal side of the shell was also described as having three convex longitudinal ridges, the middle one being most pronounced, but not being present on the posterior portion of the shell. These broad ridges could not be discerned in our Coral Sea specimens. However, because Munthe's specimen was considerably larger than ours (being 16 mm in shell length), it is possible that our specimens are at a younger growth stage and that the formation of longitudinal "ridges" only becomes evident as greater size is achieved. In all other respects, our specimens agree with MUNTHE's (1888) original description of *C. scheelei* in: having a straight shell shape; being dorsoventrally flattened; having uniformly spaced transverse lirations; and in having a distinct groove running lengthwise down the center of the lateral ribs. Our specimens are therefore attributed to that species.

Clio scheelei differs from all other *Clio* species in having

→

Figure 3

A–D, shell of *Clio andreae*: A, ventral view; B, lateral view; C, protoconch detail; D, detail of rounded lateral rib. E–H, shell of *Clio scheelei* shell (damaged during SEM preparation): E, ventral view; F, lateral view; G, protoconch detail; H, detail of indented lateral rib. Scale bars = 1 mm.


A
B
C
D
E
F
G
H

a combination of the following shell characteristics: a straight shell with a 2:1 length-to-width ratio, a distinct constriction separating the protoconch and teleoconch, and transverse surface liration. The only two species of *Clio* that show any close similarity to *C. scheelei* are *C. recurva* (Childern, 1823) and *C. orthotheca* (Tesch, 1948). TESCH (1913) illustrated differences in shell shape between *C. scheelei* and *C. recurva*. The shell of the latter is curved ventrally at the posterior end, and its protoconch lacks a constriction. *Clio orthotheca* has a shell that is straight in shape, but does not have the distinctive liration as found in *C. scheelei*. The only known record of *C. orthotheca* is from the Indian Ocean (TESCH, 1948).

ACKNOWLEDGMENTS

Pteropod material was kindly made available by the Museum of Victoria. The study was funded by grants from the 1984 Australian Biological Resource Study, and from the University of Queensland. Mr. J. Hardy and Mr. R. Grimmer, Electron Microscope Centre, University of Queensland are thanked for their assistance. We also thank Dr. S. van der Spoel and reviewers for their comments on a draft of this paper.

LITERATURE CITED

BÉ, A. W. H. & R. W. GILMER. 1977. A zoogeographic and taxonomic review of euthecosomatous Pteropoda. Pp. 733–808. *In:* A. T. S. Ramsey (ed.), Oceanic micropalaeontology, Vol. 1. Academic Press: London.

BOAS, J. E. V. 1886. Spolia Atlantica. Bidrag til Pteropodernes. Morfologi og systematik samt til kundskaben om deres geografiske udbredelse. Vidensk. Selsk. Skr., 6 Raekke, naturvidensk. mathemat. Afd. IV. I:1–231, pls. 1–8.

MCGOWAN, J. A. 1960. The systematics, distribution and abundance of Euthecosomata in the North Pacific. Doctoral Thesis, Univ. California. 197 pp.

MILLARD, N. A. H. 1975. Monograph of the Hydroida of southern Africa. Ann. S. Afr. Mus. 68:215–216.

MUNTHE, H. 1888. Pteropoder i Upsala Universitets Zoologiska Museum, samlade af Kapt. G. von Scheele. Bih. K. Sv. Vet. Akad. Handlingar 13(4)(2):1–33.

PELSENEER, P. 1888. Report on the pteropods collected by H.M.S. "Challenger" during the years 1873–1876. II. The Thecosomata. Rep. Sci. Res. Voy. H.M.S. "Challenger" during the years 1873–1876. Zoology, 23(i):1–132.

RUSSELL, F. S. & J. S. COLEMAN. 1935. The zooplankton IV. The occurrence and seasonal distribution of the Tunicata, Mollusca and Coelenterata (Siphonophora). Sci. Rept. of the Great Barrier Reef Exped. 1928–1929. 2(7):203–276.

SOLIS, N. B. & H. VON WESTERNHAGEN. 1978. Vertical distribution of euthecosomatous pteropods in the upper 100 m of the Hilutangan channel, Cebu, The Philippines. Mar. Biol. 48(1):79–87.

TANAKA, T. 1970. Geographical and vertical distribution of Pteropoda and Heteropoda in the western Pacific. 2nd C.S.K. Symposium, Tokyo, Sept. 1970.

TESCH, J. J. 1904. The Thecosomata and Gymnosomata of the Siboga Expedition. Siboga Rept. 52:1–92.

TESCH, J. J. 1913. Pteropoda. Das Tierreich 36:1–154.

TESCH, J. J. 1948. The thecosomatous pteropods. II. The Indo-Pacific. Dana Rept. 5(30):1–45.

VAN DER SPOEL, S. 1967. Euthecosomata. A group with remarkable developmental stages (Gastropoda, Pteropoda). J. Noorduijn en Zoon. N.V. Gorinchem. 375 pp.

VAN DER SPOEL, S. 1976. Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda). Bohn, Scheltema and Holkema: Utrecht. 484 pp.

The Veliger 30(1):95–101 (July 1, 1987)

THE VELIGER

NOTES, INFORMATION & NEWS

Mass Mortality of the Bubble Snail *Bulla gouldiana* Pilsbry, 1893 (Gastropoda: Opisthobranchia)

by
Timothy D. Stebbins
Department of Biological Sciences,
University of Southern California, and
Invertebrates Section,
Los Angeles County Museum of Natural History,
Los Angeles, California 90007, U.S.A.

Bulla gouldiana Pilsbry, 1893, is the largest of the California bubble shells and ranges from Morro Bay, California, to Ecuador (McLean, 1978; Beeman & Williams, 1980). This snail is often very abundant in bays and lagoons, and is one of the most common of all gastropods in the Newport Bay and Mission Bay regions of southern California (Ricketts *et al.*, 1985).

Mass mortality of *Bulla gouldiana* occurred following a week of heavy rains during February 1986 in Morro Bay, California, the northernmost extreme of this snail's range. Seventy-one percent of the *B. gouldiana* population (n = 283) was observed either dead or dying on the Morro Bay mudflats during an intertidal survey (23 Feb. 1986; −0.3 m tide). The scattered remains of individuals without shells were discovered at the higher tidal levels, while numerous shelled specimens were observed dead or dying in the lower tidal regions. Few snails appeared healthy and active.

It is unknown what caused this mass die-off of *Bulla gouldiana*. The effects of an unidentified pathogen or freshwater are possible factors. A bacterial infestation may have not only killed off much of the local *B. gouldiana* population, but also rendered the animals unpalatable to local predators and scavengers (Western Gulls and other shorebirds did not appear to be feeding on the abundant snail remains). Such disease outbreaks have been implicated in catastrophic die-offs of shallow-water marine organisms at other locations (see Menge, 1979; Dungan *et al.*, 1982). The significant influx of freshwater resulting from severe storm activity the week preceding the observations may have caused the local mortality of *B. gouldiana*. Support for this hypothesis is that nine dead or dying echiuran worms, *Urechis caupo* Fisher & MacGinitie, 1928, were also observed on the tidal flats. I have seen similar mortality of *U. caupo* following heavy rains in Humboldt Bay, northern California.

It is premature to determine the exact cause of the mass mortality of *Bulla gouldiana*. Whatever the cause, several other common mudflat invertebrates did not appear to be affected. These included two other large opisthobranchs, the predatory *Navanax inermis* (Cooper, 1862) and the herbivorous *Aplysia californica* Cooper, 1863, as well as the ghost shrimps *Callianassa californiensis* Dana, 1854, and *Upogebia pugettensis* (Dana, 1852). It would be useful to know whether similar mortalities of *B. gouldiana* have occurred at other California locations following heavy storm activity.

Acknowledgments

I thank R. C. Brusca, P. M. Delaney, R. S. Houston, and several anonymous reviewers for comments on the manuscript.

Literature Cited

Beeman, R. D. & G. C. Williams. 1980. Opisthobranchia and Pulmonata: the sea slugs and allies. Pp. 308–354. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Dungan, M. L., T. E. Miller & D. A. Thomson. 1982. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. Science 216:989–991.

McLean, J. H. 1978. Marine shells of southern California. Los Angeles Co. Mus. Natur. Hist., Sci. Ser. 24, Revised edition:1–104.

Menge, B. A. 1979. Coexistence between the seastars *Asterias vulgaris* and *A. forbesi* in heterogenous environment: a non-equilibrium explanation. Oecologia 41:245–272.

Ricketts, E. F., J. Calvin & J. W. Hedgpeth, revised by D. W. Phillips. 1985. Between Pacific tides. 5th ed., Stanford Univ. Press: Stanford, Calif. 652 pp.

"*Punctum pusillum*" (Gastropoda: Pulmonata: Punctidae)—a Correction

by
Barry Roth
Santa Barbara Museum of Natural History,
Santa Barbara, California 93105, U.S.A.

In two recent papers (Roth, 1985, 1986), I introduced the name *Punctum* (*Toltecia*) *pusillum* (Lowe, 1831) to the literature of west North American land mollusks as a senior synonym of *Punctum conspectum* (Bland, 1865). This taxon has been recognized as a very widely disseminated, "weedy" species that has received many names in various parts of the world (Gittenberger *et al.*, 1980; Guntrip, 1986; Roth, 1986). Its correct name, however, is *Paralaoma caputspinulae* (Reeve, 1852).

The earliest name proposed is apparently *Helix pusilla* Lowe (1831:46), based on specimens from Madeira. However, the combination *Helix pusilla* is at least twice preoccupied and cannot be used for the species. Vallot (1801: 5) described a Recent European land gastropod as *H. pusilla*, as follows: "10. H. mignone. H. pusilla. Coquille

globuleuse, légèrement conique, à quatre spires; lêvres sans rebord." Twenty-seven years later, FLEMING (1828:265) described a Carboniferous fossil as *Helix pusilla*: "7. H. *pusilla*.—Depressed, smooth, umbilicated, convex beneath. Volutions round and tapering; their number about three. Mouth roundish.—*Mart.* Pet. Derb. t. lii. f. 3.—In a fossil pericarp, in *Clay Ironstone,* Derbyshire."

Helix pusilla Lowe, 1831, is thus a junior primary homonym of *H. pusilla* Vallot, 1801, and *H. pusilla* Fleming, 1828, and unavailable.

The earliest available name, as pointed out to me by Dr. F. M. Climo of the National Museum of New Zealand, is evidently *Helix caputspinulae* Reeve, 1852, based on specimens from New Zealand. *Helix caputspinulae* was proposed in the explanatory text to a plate of Reeve's *Conchologia Iconica* dated at foot as "October 1851." However, this plate is in the midst of a sequence of plates dating from 1852, and the date 1851 is most likely a misprint. The probable publication date is October 1852.

The original description of *Helix caputspinulae* cites "*Helix epsilon* Pfeiffer, Pro. Zool. Soc. 1851" as a synonym. *Helix epsilon* was first described in a paper (PFEIFFER, 1854) that, according to a collation of the *Proceedings of the Zoological Society of London* (SCLATER, 1893), could have been published no earlier than 22 March 1854.

The type species of *Paralaoma* Iredale, 1913, is *P. raoulensis* Iredale, 1913, from the Kermadec Island Group, New Zealand, another synonym of *P. caputspinulae,* according to CLIMO (1981). The type species of *Toltecia* Pilsbry, 1926, is *Thysanophora* (*Toltecia*) *jaliscoense* Pilsbry, 1926, which has most recently been considered (PILSBRY, 1948) a subspecies of *Punctum conspectum* (*i.e., Paralaoma caputspinulae*). *Toltecia* is therefore a junior synonym of *Paralaoma.* (It should be pointed out that our anatomical knowledge of *T. jaliscoense* is based on BAKER's (1927) dissections of specimens from Chapultepec Park, Mexico, D.F., rather than on topotypes from Guadalajara, Jalisco.)

Current practice is to rank *Paralaoma* as a genus of Punctidae, rather than as a subgenus of *Punctum*; see, for example, SMITH & KERSHAW (1979), CLIMO (1981), and SOLEM & CLIMO (1985). The two genera apparently have substantially different distributions and histories (F. M. Climo, personal communication).

I am indebted to F. M. Climo and E. Gittenberger for discussion of the synonymies involved in this case. Dr. Gittenberger kindly supplied a photocopy of the scarce Vallot reference.

Literature Cited

BAKER, H. B. 1927. Minute Mexican land snails. Proc. Acad. Natur. Sci. Phila. 79:223–246, pls. 15–20.

CLIMO, F. M. 1981. Classification of New Zealand Arionacea (Mollusca: Pulmonata). VIII. Notes on some charopid species, with description of new taxa (Charopidae). Natl. Mus. New Zealand Records 2:9–15.

FLEMING, J. 1828. A history of British animals. Bell & Bradfute: Edinburgh. 565 pp.

GITTENBERGER, E., H. P. M. G. MENKHORST & J. G. M. RAVEN. 1980. New data on four European terrestrial gastropods. Basteria 44:11–16.

GUNTRIP, D. W. 1986. *Toltecia pusilla* (Lowe, 1831) living in Britain. Jour. Conchol. 32:200–201.

LOWE, R. T. 1831. Primitiae faunae et florae Maderae et Portus-Sancti. Trans. Cambridge Philos. Soc. 4(1):1–70.

PFEIFFER, L. 1854. Descriptions of sixty-six new land shells, from the collection of H. Cuming, Esq. Proc. Zool. Soc. Lond. 20:56–70.

PILSBRY, H. A. 1948. Land Mollusca of North America (north of Mexico). Acad. Natur. Sci. Phila., Monogr. 3, 2(2):521–1113.

REEVE, L. A. 1851–1854. Conchologia Iconica or, illustrations of the shells of molluscous animals. Vol. VII. Containing a monograph of the genus *Helix*. Pls. 1–62 (1851), 63–146 (1852), 147–174 (1853), 175–210, title p., index (1854).

ROTH, B. 1985. A new species of *Punctum* (Gastropoda: Pulmonata: Punctidae) from the Klamath Mountains, California, and first Californian records of *Planogyra clappi* (Valloniidae). Malacol. Rev. 18:51–56.

ROTH, B. 1986. Notes on three European land mollusks introduced to California. Bull. So. Calif. Acad. Sci. 85:22–28.

SCLATER, P. L. 1893. List of the dates of delivery of the sheets of the 'Proceedings' of the Zoological Society of London, from the commencement of 1830 to 1859 inclusive. Proc. Zool. Soc. Lond. (1893):435–440.

SHERBORN, C. D. 1902–1933. Index Animalium. C. J. Clay & Sons: London. Sect. 1, 1195 pp., sect. 2, 7056 + 1098 pp.

SMITH, B. J. & R. C. KERSHAW. 1979. Field guide to the nonmarine molluscs of south eastern Australia. Austral. Natl. Univ. Press: Canberra. 285 pp.

SOLEM, A. & F. M. CLIMO. 1985. Structure and habitat correlations of sympatric New Zealand land snail species. Malacologia 26:1–30.

[VALLOT]. 1801. Exercice sur l'histoire naturelle. École Centrale du Département de la Côte-d'Or: Dijon. 8 pp. [SHERBORN (1902–1933) attributes authorship of this work to Vallot, but the latter's name does not appear in the copy seen by me, only (p. 8) the names of ten students who evidently prepared the text as part of their studies at the École Centrale.]

Synonymy of *Rabdotus sonorensis* (Pilsbry, 1928) With *Rabdotus nigromontanus* (Dall, 1897) (Gastropoda: Pulmonata: Bulimulidae)

by
James E. Hoffman
Department of Ecology & Evolutionary Biology,
University of Arizona,
Tucson, Arizona 85721, U.S.A.

Rabdotus sonorensis (Pilsbry, 1928) was described from shells collected by Francis C. Nichols, with the type locality listed as "Copete Mine, near Carbo, Sonora, Mexico." The holotype (ANSP 142647a) and the paratypes (ANSP 142647) were deposited in the collection of the Academy of Natural Sciences at Philadelphia.

PRATT (1974) stated that *Rabdotus sonorensis* was a syn-

onym of *R. nigromontanus* (Dall, 1897), but gave no information about what basis was use for his synonymy.

In November of 1984, Walter B. Miller, Edna Naranjo García, and I made the first of several trips to the Carbo area of Sonora, Mexico, in order to try to find the type locality of *Rabdotus sonorensis*. Although we could find no reference to Copete Mine on maps of the Carbo area, we searched the localities of the abandoned mines near Carbo for signs of *R. nigromontanus* or *R. sonorensis,* without success. We also asked, in Carbo, whether anyone knew of Copete Mine. One retired miner said that he had heard of Copete Mine near the town of Rayón, Sonora; no one, however, had knowledge of a Copete Mine in the vicinity of Carbo. Rayón is approximately 60 km, by road, east of Carbo.

After our return to Tucson from Carbo, Georganne Fink, a colleague of ours, found a reference to Minas del Copete on an old map of the Rayón area. Based upon further study of old maps and our subsequent field work, the locality of the Copete Mines is undoubtedly the type locality of *Rabdotus sonorensis*. The mines are located approximately 17 km by road SSW of Rayón, in Cerro el Cielo (29°37.3′N, 110°38.0′W) at an elevation of 700 m.

Our first expedition to the Copete Mines in November 1985 yielded many live adult *Rabdotus baileyi* (Dall, 1893), and a number of *Sonorella sitiens* Pilsbry & Ferriss, 1915, plus a few shells of *R. sonorensis*. Unfortunately, during this trip we were not able to find a live *R. sonorensis* for anatomical comparison with *R. nigromontanus*. The plants at the locality include species of *Jatropha, Bursera, Ceiba, Stenocereus, Prosopis, Olnea,* and several species of *Acacia* including *A. cymbispina.*

During our second expedition to the mines in February 1986, we found the same species as before, except that Dr. Miller found one live juvenile *Rabdotus* in leaf litter in a north-facing rockslide approximately 5 km NNE of the Copete Mines. After raising this snail to maturity, I dissected it. Its shell is 15.9 mm high and 10.6 mm in diameter, with 5.0 whorls; its penis is 10.2 mm, penile sheath 2.7 mm, epiphallus 2.4 mm, epiphallic cecum 4.0 mm, and penial retractor muscle 1.9 mm in length—all within or near the range of variation of *R. nigromontanus,* whose shell measurements have varied from 15.4 to 18.8 mm high, from 10.6 to 12.4 mm in diameter, and from 5.0 to 5.8 whorls, and whose range of measurement of reproductive anatomies also largely encompasses those of the above specimen (Hoffman, 1987). Additionally, the shells from Cerro el Cielo and the surrounding area are within the range of variation of *R. nigromontanus,* as are the shells of the holotype and paratypes in the ANSP collection (a photograph of the shell of *R. sonorensis* may be found in Pilsbry, 1928; photographs of a typical *R. nigromontanus* shell are located in Hoffman, 1987). Therefore, I confirm Pratt's conclusion that *Rabdotus sonorensis* (Pilsbry, 1928), is a junior subjective synonym of *Rabdotus nigromontanus* (Dall, 1897) and, accordingly, is not valid.

Acknowledgments

I am indebted to Georganne Fink for locating Las Minas del Copete and to her husband, Jim Fink, for providing the map. I also acknowledge with pleasure the help of Dr. Walter B. Miller and Edna Naranjo García. They accompanied me on every trip to resolve this problem, and also provided much helpful advice. Jane E. Deisler located the type material for me in the collection of the Academy of Natural Sciences at Philadelphia, for which I will always be grateful.

Literature Cited

Hoffman, J. E. 1987. A new species of *Rabdotus* (Gastropoda: Pulmonata: Bulimulidae) from Sonora, with a description of the reproductive anatomy of *Rabdotus nigromontanus*. Veliger 29:419–423.

Pilsbry, H. A. 1928. Mexican mollusks. Proc. Acad. Natur. Sci. Phila. 80:115–117.

Pratt, W. L., Jr. 1974. A revision of the mainland species of the bulimulid land snail genus *Rabdotus*. Bull. Amer. Malac. Union, Inc., for 1973:24–25.

Range Extension for *Doridella steinbergae* (Lance, 1962) to Prince William Sound, Alaska

by
Nora R. Foster
University of Alaska Museum,
Fairbanks, Alaska 99775, U.S.A.

Doridella steinbergae (Lance, 1962) is a small nudibranch found on colonies of the bryozoan *Membranipora,* which encrusts fronds of the giant kelps *Macrocystis pyrifera* and *Nereocystis luetkiana.* Its known range was given by Millen (1983) as Bamfield, Vancouver Island, British Columbia (48°50′N) to Los Coronados Island, Baja California (30°25′N).

On 20 July 1986, I collected and examined a *Nereocystis luetkiana* plant from Gibbon Anchorage, Green Island, Prince William Sound (60°17′N, 147°25′W). Large colonies of a *Membranipora* tentatively identified as *M. serrilamella* Osburn, 1950, were present, along with *Doridella steinbergae* and its egg masses. The nudibranch was examined in the field with a hand lens. The shape and pigmentation were compared with illustrations of *D. steinbergae* and *Corambe pacifica* MacFarland & O'Donoghue, 1929, in *Between Pacific Tides* (Ricketts *et al.,* 1985:144). The preserved specimens were later compared with the original description.

Three specimens of the nudibranch, measuring 7.75 mm, 8.0 mm, and 8.75 mm in length after preservation, egg masses, and the bryozoan were collected and preserved for the Aquatic Collection, University of Alaska Museum, Fairbanks, Alaska. These are in the wet collection, accession number 1986-14.

This range extension to the north and west is not surprising because the small size and concealing color pattern of this nudibranch make it easy to overlook. *Doridella steinbergae* seems likely to be present elsewhere along the southeast and southcentral Alaskan coast where *Nereocystis* and *Macrocystis* are common.

Acknowledgments

I thank Glenn Juday for the opportunity to participate in the Green Island Research Natural Area survey, and Nancy Lethcoe for a successful trip to Green Island.

Literature Cited

Lance, J. R. 1962. A new *Stiliger* and a new *Corambella* (Mollusca: Opisthobranchia) from the northwestern Pacific. Veliger 5(1):33–38.

Millen, S. V. 1983. Range extensions of opisthobranchs in the northeastern Pacific. Veliger 25(4):383–386.

Ricketts, E. F., J. Calvin & J. W. Hedgpeth, revised by D. W. Phillips. 1985. 5th ed. Between Pacific tides. Stanford University Press: Stanford, Calif. 652 pp.

Hermaea vancouverensis O'Donoghue, 1924, from Kodiak Island and Unga Island, Alaska

by

Nora R. Foster

University of Alaska Museum,

Fairbanks, Alaska 99775, U.S.A.

Surveys of opisthobranch fauna from the northeastern Pacific note the absence of sacoglossans from Alaskan waters (Millen, 1980, 1983; Lee & Foster, 1985). Because of their small size and seasonal occurrence, sacoglossans are easily overlooked by collectors so that their occurrence in Alaskan waters may be even more widespread than recorded here. This note is intended to remind workers of the possible presence of these small gastropods in low intertidal and shallow subtidal samples from Alaskan waters.

Hermaea vancouverensis O'Donoghue, 1924, has been identified from two southwestern Alaska localities: Humboldt Harbor, between Popof and Unga islands, Shumagin Islands (55°20.5′N, 160°32′W), and at Spruce Cape, Kodiak Island (57°47.25′N, 149°26.30′W).

The Humboldt Harbor sample was taken on 9 May 1985, using a pipe dredge in about 5 m of water, on a sand and mud bottom with scattered large kelps (*Agarum, Laminaria*). The sample was fixed in the field, then screened and sorted at the University of Alaska Museum in Fairbanks. Five specimens of *Hermaea vancouverensis,* ranging in size from 2 to 4 mm, were found.

The Kodiak Island sample (12 *Hermaea vancouverensis*: the largest 2 mm, the others less than 1 mm) was collected 23 May 1986 at Spruce Cape (57°47.25′N, 149°26.30′W) at low tide in an exposed rocky setting. The animals were associated with the alga *Neoptilota* sp. The epiphytic diatom *Isthmia nervosa,* mentioned as a food item for *H. vancouverensis* (Williams & Gosliner, 1973), was abundant on the alga.

The identification is based on characteristics of the radula, rhinophores, cerata, and pigmentation. Specimens are in the Aquatic Collection, University of Alaska Museum, accession numbers 1985-8 and 1986-8.

These observations extend the known range for this species from Vancouver Island, British Columbia, the northernmost locality given by Millen (1980). The animal has been found as far south as Bodega Head, California. The semiprotected shallow benthic and exposed rocky coast habitats reported here are similar to those mentioned for the species by Millen (1980) and Williams & Gosliner (1973).

Acknowledgments

For their assistance in the field I thank Jim McCullough, Alaska Department of Fish and Game, and Matthew Dick, Kodiak Community College. Philip Lambert, British Columbia Provincial Museum, loaned specimens of sacoglossans for comparison. Museum volunteers Jackie Herbert and Dixie Ostlind screened and processed the samples. Travel to Sand Point and Kodiak was made possible through acquisition funds provided to the University of Alaska Museum from the State of Alaska.

Literature Cited

Lee, R. S. & N. R. Foster. 1985. A distributional list with range extensions of the opisthobranch gastropods of Alaska. Veliger 27(4):440–448.

Millen, S. 1980. Range extensions, new distribution sites, and notes on the biology of sacoglossan opisthobranchs (Mollusca: Gastropoda) in British Columbia. Can. Jour. Zoology 58(6):1207–1209.

Millen, S. 1983. Range extensions of opisthobranchs in the northeastern Pacific. Veliger 25(4):383–385.

O'Donoghue, C. A. 1924. Notes on the nudibranchiate Mollusca from the Vancouver Island Region Part IV. Additional species and records. Trans. Royal Can. Inst. 15(1):1–33, pls. I–II.

Williams, G. C. & T. M. Gosliner. 1973. Range extensions for four sacoglossan opisthobranchs from the coasts of California and the Gulf of California. Veliger 16(1):112–116.

Pinna rugosa Sowerby, 1835 (Bivalvia: Pinnidae) at the Galápagos Islands

by

Yves Finet

Muséum d'Histoire naturelle, Case postale 434,

CH-1211 Genève 6, Switzerland

Distribution of the Species

Pinna rugosa Sowerby, 1835, is a pinnid bivalve occurring through most of the Panamic marine province. How-

ever, it has never been reported from the Galápagos Archipelago, nor from the other offshore islands of west Central America, except from Clipperton Island.

The type locality of the species is the Island of Rey, Panama, cited by SOWERBY (1835:34) as "Hab. in Sinu Panamensi (Isle of Rey) . . . they were procured from sand banks."

Subsequently, several authors have given new records for this species, extending its range from Baja California to Panama (TOMLIN, 1928:190; PILSBRY & LOWE, 1932:140; LOWE, 1933:75; BALES, 1938:45; WILKINS, 1953:28; OLSSON, 1961:143; KEEN, 1958, 1971; plus other literature cited in SALVAT & SALVAT, 1972).

In their study on the geographic distribution of *Pinna rugosa,* SALVAT & SALVAT (1972) report it also from Clipperton Island, a Pacific island off Mexico. According to the authors, although the species is known to occur in the eastern Pacific throughout most of the Panamic marine province, it is not known to occur on offshore islands like Cocos Island or the Galápagos Islands; according to the same authors, Clipperton seems to be "the only island with representatives of the family Pinnidae or with *Pinna rugosa.*"

Actually, other representatives of the family Pinnidae are known to occur in the Galápagos, including *Atrina texta* Hertlein, Hanna & Strong, 1943 (KEEN, 1971; BERNARD, 1983; FINET, 1985) and *Atrina tuberculosa* (Sowerby, 1835) (BERNARD, 1983).

The Galapagan New Records

During the F.N.R.S.-Belgian Expedition to the Galápagos in 1984, several empty shells of *Pinna rugosa* were collected or observed:

(1) One empty shell of a juvenile specimen was collected with the aid of SCUBA by Miss Burns and Mr. Stupakoff on 10 July 1984; locality is channel between Baltra and Santa Cruz Island, little island midway in channel, with mangroves; 3 m (10 feet), sandy bottom with boulders; water temperature 22.2°C.

(2) A large single valve was given to us by Señor Nestor Garáte Coronel, a local resident who helped us extensively collecting on Santa Cruz Island. The specimen was found at a depth of about 3 m at Tortuga Bay, Santa Cruz Island.

(3) Empty, but complete shells (two valves) are sold in groceries of Puerto Ayora, Santa Cruz; all are reported to be caught by fishermen near Tortuga Bay (southern coast of Santa Cruz Island). In addition, many complete but empty shells of *P. rugosa* can be seen hung for decoration on the walls of several restaurants at Puerto Ayora; these specimens are generally said to be caught by local fishermen.

These new records from the Galápagos, although not including live-collected specimens, add a species of bivalve to the list of the marine mollusks previously known to occur in this archipelago. They also extend the range of *Pinna rugosa* to another group of offshore islands in the eastern Pacific.

Literature Cited

BALES, M. D. 1938. Marine collecting on the west coast of Mexico. Nautilus 52(2):41–46.

BERNARD, F. R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. Canadian Spec. Publ. Fish. Aquat. Sci. No. 61:102 pp. Ottawa.

FINET, Y. 1985. Preliminary faunal list of the marine mollusks of the Galapagos Islands. Docums. Trav. Inst. R. Sci. Natur. Belg. No. 20:50 pp.

KEEN, A. M. 1958. Sea shells of tropical west America. Stanford Univ. Press: Stanford, Calif. xi + 624 pp.

KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford Univ. Press: Stanford, Calif. xiv + 1064 pp.

LOWE, H. N. 1933. The cruise of the "Petrel." Nautilus 46(3): 73–76.

OLSSON, A. A. 1961. Mollusks of the tropical eastern Pacific, particularly from the southern half of the Panama-Pacific faunal Province (Panama to Peru). Panamic-Pacific Pelecypods. Paleont. Res. Inst.: Ithaca, N.Y. 574 pp.

PILSBRY, H. A. & H. N. LOWE. 1932. West Mexico and Central American mollusks collected by H. N. Lowe, 1929–31. Proc. Acad. Natur. Sci. Phila. 84:33–144.

SALVAT, B. & F. SALVAT. 1972. Geographic distribution of *Pinna rugosa* Sowerby, 1835 (Mollusca: Bivalvia) and its occurrence on Clipperton Island. Veliger 15(1):43–44.

SOWERBY, G. B. 1835. [no title] Proc. Zool. Soc. Lond. 3:84.

TOMLIN, J. R. LE B. 1928. The Mollusca of the 'St. George' Expedition. Jour. Conch. Lond. 18(7):187–198.

WILKINS, G. L. 1953. Notes from the British Museum. I. *Pinna.* Proc. Malacol. Soc. Lond. 30:23–29.

California Malacozoological Society

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed 6 January 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger.* Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); or Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C.M.S., Inc., are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, and devises are deductible for Federal estate and gift tax purposes under sections 2055, 2106, and 2522 of

the Code. Upon request, the Treasurer of the C.M.S., Inc., will issue suitable receipts which may be used by donors to substantiate their tax deductions.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on 23 September 1986, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 30 of *The Veliger*. For affiliate members of the Society, the subscription rate for Volume 30 will be US$25.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will be US$50.00, also now with postage to domestic addresses included. An additional US$3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. There is a one-time membership fee of US$2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription.

Send all business correspondence, including subscription orders, membership applications, payments for them, and changes of address to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Page Charges

Although we would like to publish papers without charge, high costs of publication require that we ask authors to defray a portion of the cost of publishing their papers in *The Veliger*. We wish, however, to avoid possible financial handicap to younger contributors, or others without financial means, and to have charges fall most heavily on those who can best afford them. Therefore, the following voluntary charges have been adopted by the Executive Board of the California Malacozoological Society: $30 per *printed* page for authors with grant or institutional support and $10 per page for authors who must pay from personal funds (2.5 manuscript pages produce about 1 printed page). In addition to page charges, authors of papers containing an extraordinary number of tables and figures should expect to be billed for these excess tables and figures at cost. It should be noted that even at the highest rate of $30 per page the Society is subsidizing well over half of the publication cost of a paper. However, authors for whom the regular page charges would present a financial handicap should so state in a letter accompanying the original manuscript. The letter will be considered an application to the Society for a grant to cover necessary publication costs.

We emphasize that these are *voluntary* page charges and that they are unrelated to acceptance or rejection of manuscripts for *The Veliger*. Acceptance is entirely on the basis of merit of the manuscript, and charges are to be paid *after* publication of the manuscript, if at all. Because these contributions are voluntary, they may be considered by authors as tax deductible donations to the Society. Such contributions are necessary, however, for the continued good financial health of the Society, and thus the continued publication of *The Veliger*.

Reprints

While it was hoped at the "*birth*" of *The Veliger* that a modest number of reprints could be supplied to authors free of charge, this has not yet become possible. Reprints are supplied to authors at cost, and requests for reprints should be addressed directly to the authors concerned. The Society does not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

Patronage Groups

Since the inception of *The Veliger* in 1958, many generous people, organizations, and institutions have given our journal substantial support in the form of monetary donations, either to *The Veliger* Endowment Fund, *The Veliger* Operating Fund, or to be used at our discretion. This help has been instrumental in maintaining the high quality of the journal, especially in view of the rapidly rising costs of production.

At a recent Executive Board Meeting, we felt we should find a way to give much-deserved recognition to those past and future donors who so evidently have our best interests at heart. At the same time, we wish to broaden the basis of financial support for *The Veliger,* and thus to serve our purpose of fostering malacological research and publication. Accordingly, it was decided to publicly honor our friends and donors. Henceforth, donors of $1000.00 or more will automatically become known as **Patrons** of *The Veliger,* donors of $500.00 or more will be known as **Sponsors** of *The Veliger,* and those giving $100.00 or more will become **Benefactors** of *The Veliger*. Lesser donations are also sincerely encouraged, and those donors will be known as **Friends** of *The Veliger*. To recognize continuing support from our benefactors, membership in a patronage category is cumulative, and donors will be listed at the highest applicable category. As a partial expression of our gratitude, the names only of donors in these different categories will be listed in a regular issue of the journal. Of course, we will honor the wishes of any donor who would like to remain anonymous. The Treasurer of the California Malacozoological Society will provide each donor of $10.00 or more with a receipt that may be used for tax purposes.

We thank all past and future donors for their truly helpful support and interest in the Society and *The Veliger*. Through that support, donors participate directly and im-

portantly in producing a journal of high quality, one of which we all can be proud.

Notes to Prospective Authors

The increasing use of computers to prepare manuscript copy prompts the following notes. We request that the right margin of submitted papers be prepared "ragged," that is, *not* justified. Although right-justified margins on printed copy sometimes look "neater," the irregular spacing that results between words makes the reviewer's, editor's, and printer's tasks more difficult and subject to error. Similarly, the automatic hyphenation capability of many machines makes for additional editorial work and potential confusion; it is best not to hyphenate words at the end of a line. Above all, manuscripts should be printed with a printer that yields unambiguous, high-quality copy. With some printers, especially some of the dot-matrix kinds, copy is generally difficult to read and, specifically, the letters "a, p, g, and q" are difficult to distinguish, especially when underlined as for scientific names; again, errors may result.

Other reminders are (1) that three copies of everything (figures, tables, and text) should be submitted to speed the review process, and (2) absolutely everything should be double-spaced, including tables, references, and figure legends.

Because *The Veliger* is an international journal, we occasionally receive inquiries as to whether papers in languages other than English are acceptable. Our policy is that manuscripts must be in English. In addition, authors whose first language is other than English should seek the assistance of a colleague who is fluent in English *before* submitting a manuscript.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date and not less than *six weeks* before our regular mailing dates. Send notification to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges:

change of address and re-mailing of a returned issue—$5.00.

Sale of C.M.S. Publications

All back *volumes* still in print, both paper-covered and cloth-bound, are available only through "The Shell Cabinet," 12991 Bristow Road, Nokesville, VA 22123. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Morgan Breeden at the above address.

Volumes 1 through 13, 24, 26, and 27 are out of print.

Supplements still available are: part 1 and part 2, supplement to Volume 3, and supplements to Volumes 7, 11, 14, 15, and 16; these can be purchased from "The Shell Cabinet" only. Copies of the supplement to Volume 17 ("Growth rates, depth preference and ecological succession of some sessile marine invertebrates in Monterey Harbor" by E. C. Haderlie) may be obtained by applying to Dr. E. C. Haderlie, U.S. Naval Post-Graduate School, Monterey, CA 93940.

Some out-of-print editions of the publications of C.M.S. prior to Volume 26 are available as microfiche reproductions through Mr. Steven J. Long. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm, and can be supplied immediately. The following is a list of items now ready:

Volumes 1–6: $9.95 each.

Volumes 7–12: $12.95 each.

Supplement to Volume 6: $3.95; to Volume 18, $6.95. Send orders to Mr. Steven J. Long, Shells and Sea Life, 1701 Hyland, Bayside, CA 95524.

Single copies of back issues of *The Veliger* still in print are available *exclusively* from:

Conchylien Cabinet,
Grillparzerstrasse 22,
D-6200 Wiesbaden, BRD (West Germany).

International Commission on Zoological Nomenclature

The following applications have been received by the Commission and have been published in Vol. 43, Part 4, of the *Bulletin of Zoological Nomenclature* (11 December 1986). Comment or advice on them is welcomed and should be sent % The British Museum (Natural History), Cromwell Road, London, SW7 5BD, England. Comments will be published in the *Bulletin*.

Case No. 2571. *Belemnites paxillosa* Lamarck, 1801 (Mollusca, Coleoida): proposed suppression of both generic and specific names.

The Veliger 30(1):102–104 (July 1, 1987)

THE VELIGER

BOOKS, PERIODICALS & PAMPHLETS

North Atlantic Nudibranchs (Mollusca) Seen by Henning Lemche with Additional Species from the Mediterranean and the North East Pacific

by Hanne Just & Malcolm Edmunds. 1985. Ophelia Publications: Marine Biological Laboratory, Helsingør, Denmark. Supplementum 2:170 pp.

While Dr. Lemche was the Curator of Mollusca at the Zoological Museum, University of Copenhagen (1958–1974), he produced excellent water-color paintings of most of the opisthobranchs he was able to study alive. Dr. Lemche's intention was to compile a monograph of North Atlantic opisthobranchs illustrated with his own water-color plates of each species. Unfortunately, Dr. Lemche passed away in 1977 before he could complete his monograph. Mrs. Hanne Just was Dr. Lemche's graduate student at the time of his death; she has prepared Dr. Lemche's material for publication, including the selection of the most suitable paintings. The Preface and Introduction of the book describe very well the background history in publishing the book.

This publication presents the best of Henning Lemche's nudibranch drawings, beautifully reproduced in full color. One must certainly admire his artistic abilities to portray accurately such delicate, flamboyant, and polychromatic animals.

Species from the North Atlantic, the Mediterranean, and the northeast Pacific (near Friday Harbor, Washington) are illustrated. The 69 plates are excellent; 46 animals are identified to species, 22 only to genus (*e.g., Tritonia* sp. A), and 4 are identified to family (*e.g.,* Doridiidae sp. A). These were mainly the identifications by Dr. Lemche, and Just and Edmunds wisely did not change them. The unidentified species may represent color variations of species illustrated or of other North Atlantic forms, or some may well be new species. Detailed work and collection of additional material are necessary to clarify their taxonomy.

Four species illustrated are not listed in the Table of Contents (*Doto eireana, Doto columbiana, Doto cinerea,* and *Doris verrucosa*). Many of the species illustrated are compared anatomically with similar or related species. An index would have given a helpful entry to these taxa.

The text accompanying each plate (written by H. Just and M. Edmunds) includes collecting data on and description of the specimen illustrated, ecological information (usually diet and spawn), known distribution, and comments regarding the species. The text is informative and very well referenced.

The Appendix is an annotated list of North Atlantic opisthobranchs by Elizabeth Platts. Drawn from the literature, it indicates in tabular form the presence or absence of each species within 14 distribution areas. It has discussions of problems under "Notes on the Species," and its own section of references.

The difficulties of establishing a taxonomy that reflects phylogeny were underscored by this work. Dr. Lemche described a large number of *Doto* species with subtle color variations, each of which occurs on a highly specific food item (illustrated differences in egg masses between some species substantiates these decisions). Yet it is well known that the coloration of some species can vary greatly (plate 39 shows a large red and a yellow and brown juvenile of *Armina loveni*), often in response to diet (*e.g.,* p. 122, *Cuthona nana,* and p. 144, *Spurilla neapolitana*).

This is a useful, enjoyable, and aesthetic publication.

Hans Bertsch

A Field Guide to Caribbean Reef Invertebrates

by Nancy Sefton & Steven K. Webster. 1986. Sea Challengers: Monterey, California. 112 pp. $19.95 U.S.

On the front cover of this beautiful volume is a photograph of the red-legged hermit crab *Paguristes cadenati,* peering out of its gastropod shell. This picture sets the mood and tone for this guide book: the authors invite us to look closely at (and appreciate and understand) the marvelous invertebrate denizens of the Caribbean coral reefs.

Included in this brilliantly illustrated guide book are brief descriptions and color photographs of 179 invertebrate species and 16 plant species. The emphasis (over half the species in the book) is appropriately on sponges and cnidarians, as these are the predominant animals that SCUBA divers see in the Caribbean. The text for each species includes scientific and common names, a terse description identifying the organism's salient features, and some comments on its natural history. Often, notes on behavior, feeding, enemies, "noxious level," or habitat are given. Prefacing the main field guide portion of the text are a useful glossary (regrettably omitting "sessile"), a section on coral reef geology, taxonomy, zonation, reproduction, growth and feeding, and a brief introduction to the major invertebrate phyla.

The text is informative, often including the authors' own observations. Typographical errors are pleasantly rare. Although several congeneric species are separated, the layout is attractive. The color reproduction is excellent.

Having carried a camera underwater several times, I can attest that Sefton and Webster have published an impressive assemblage of underwater photographs. Because most of the animals are illustrated in their natural habitat, many of the photographs present important biological in-

formation about the species, as well as identifying characteristics. The camera angles and composition of some pictures show the animal so realistically that the reader is almost underwater looking at the animal!

I wish I could have had this reference with me on a recent expedition to the Caribbean.

Hans Bertsch

The Littorinid Molluscs of Mangrove Forests in the Indo-Pacific Region: The Genus *Littoraria*

by David G. Reid. 1986. British Museum (Natural History): London. Publication No. 978:xv + 228 pp. Price: 35 pounds.

In this scholarly work, the taxonomy of the "*Littorina scabra*" complex is revised. Twenty species, all assigned here to the genus *Littoraria,* are recognized from mangrove forests in the Indo-Pacific region. Provided for each species are synonymies, descriptions of shell, radula, and reproductive anatomy, as well as information on habitat and geographical distribution. Included are descriptions of one new subgenus, two new species, and one new subspecies.

Before the individual species accounts, an informative general account of the genus and its relation to others in the Littorinidae is provided, with sections on morphological characters (shell and anatomical), habitat (including zonation patterns), behavior, and biogeography. Features most useful in defining species are emphasized: those of the shell (sculpture, microsculpture, columellar form) and reproductive anatomy (penis, sperm nurse cells, pallial oviduct).

The volume is well written, with many superb line and halftone illustrations (plus a color frontispiece showing shell polymorphism). Much of interest to students of gastropods is contained within its pages, and the volume well deserves a place on the shelf.

D. W. Phillips

Seashells of Western Australia

by Fred E. Wells & Clayton W. Bryce. 1985. Western Australian Museum, Francis Street, Perth, W. Australia 6000. 207 pp.; 74 color plates.

Halfway through this book I was ready to schedule a flight to Western Australia. Rarely has shell collecting been presented in such an appealing, informative way. This book, based largely on collections of the Western Australian Museum, presents many of the common species of mollusks in Western Australia (and as the authors point out, animals rarely respect state borders, making the book useful as well in other regions of Australia).

After some introductory sections to acquaint the reader with the basics of resource conservation, local climates, and when and where to collect, the organization of the book is taxonomic, by class and family. For each family, given information includes the scientific name of the family, common name(s), a line drawing of a representative specimen, a brief description of the family and its biology, and, usually, references for further reading. For each species, a color photograph is provided, along with the scientific name (complete with author and date), maximum size, relative availability, and geographic distribution.

Both the illustrations and the text bear the clear marks of professionalism and craftsmanship. The splendid color plates (671 subjects on 74 plates) are as beautiful as they are informative, crisply printed on glossy paper. The text is concise and scientifically rigorous, while remaining interesting and fluid, not ponderous.

As a result, the authors have succeeded in the difficult task of producing a book, apparently designed primarily for the amateur, that is sure to please both the interested lay person and the scientist. This book is a sparkling invitation to shell collecting in Western Australia and to malacology.

D. W. Phillips

It's Easy to Say *Crepidula*! (kreh PID' yu luh)

by Jean M. Cate & Selma Raskin. 1986. Pretty Penny Press, P.O. Box 3890, Santa Monica, CA 90403. $19.95 plus shipping.

For those who have been intimidated by scientific names, help has arrived. Here is a handbook on pronunciation of scientific names of mollusks that is certain to be useful, and reassuring. No longer will there be an excuse to say "quahog clams" when it's so easy, and to my ear more pleasing, to say *Mercenaria* (mer' sen AIR' ee uh).

Included with the phonetic guide are a glossary of terms frequently used in malacology, a brief selection of conchological references, and an index of common names. These too will be of value to many.

The major constraints on utility of the book are the too frequent use of "*sensu lato*" genera and a rather skimpy general index. Combined, these can create some difficulties. For example, as chance would have it, the first three names I chose to look up were not found directly: *Ceratostoma foliatum* was listed under *Murex* (s.l.), *Collisella* under *Acmaea* (s.l.), and *Olivella* under *Oliva* (s.l.). Nor were the three chosen genera listed in the General Index, so that a student having just used a key to identify a specimen as *Ceratostoma foliatum* would be unlikely to find the pronunciation of *foliatum*. In addition, nowhere would be the pronunciation of *Ceratostoma,* the name in which I, for example, was actually interested. The inclusion of additional genera would increase the utility and facility of the manual.

Despite these omissions, hopefully to be addressed by future editions, this phonetic guide makes a valuable contribution by encouraging the use of scientific names. Fur-

thermore, although designed specifically for conchologists, students in other fields may also find it useful—the Greek and Latin word roots that are combined into the specific epithets of mollusks are, of course, often the same as those used for animals of other taxonomic groups.

D. W. Phillips

Biology and Distribution of Early Juvenile Cephalopods

edited by K. Mangold & S. v. Boletzky. 1985. Vie et Milieu 35(3/4):139–304. The volume, priced at 240 French Francs, can be ordered directly from the Editorial Office, Laboratoire Arago, Vie et Milieu, F-66650 Banyuls-sur-Mer, France.

This volume on cephalopods contains the proceedings of an international symposium organized by K. Mangold and S. v. Boletzky in 1985. It is published as a special issue of the journal *Vie et Milieu,* which as of Volume 37 will also bear the English "subtitle" of *Life and Environment.* The list of participants in the symposium reads much like an international "who's who" of cephalopod biology, and readers are sure to find much of interest within the 21 papers (some of them notes).

D. W. Phillips

Isla de Gorgona

edited by Henry Von Prahl & Michael Alberico. 1986. Banco Popular: Bogota, Colombia. 252 pp., illust.

This new book by scholars associated with the Universidad del Valle in Cali, Colombia, has a number of chapters that will be of interest to invertebrate zoologists: echinoderms (Raul Neira & Von Prahl), corals (Von Prahl), zoogeography of corals, crustaceans, mollusks (with a species list), and fish (Von Prahl), and the gastropod superfamily Muricacea (Francisco Borrero, Rafael Contreras & Jaime Cantera).

Eugene Coan

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

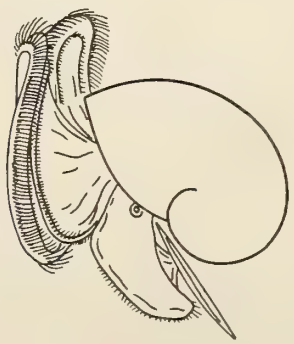
It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

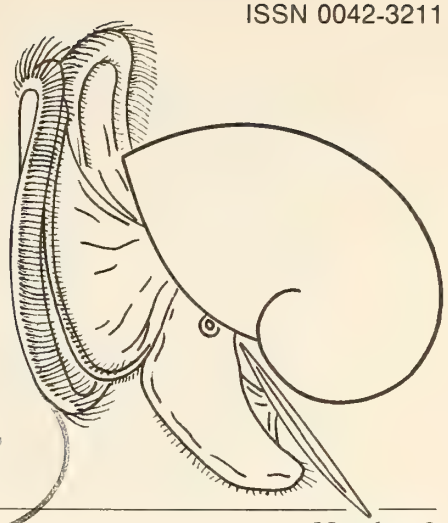
An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.



ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 30 October 1, 1987 Number 2

Contents

Contents — *Continued*

The Veliger (ISSN 0042-3211) is published quarterly on the first day of July, October, January and April. Rates for Volume 29 are $25.00 for affiliate members (*including* domestic mailing charges) and $50.00 for libraries and nonmembers (*including* domestic mailing charges). An additional $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Department of Zoology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Scope of the journal

The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

Membership and Subscription

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. As an affiliate member, a person may subscribe to The Veliger for US $25.00, which now *includes* mailing charges to domestic addresses. There is a one-time membership fee of US $2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription; a reinstatement fee of US $3.00 will be required if membership renewals do not reach the Society on or before April 1 preceding the start of the new Volume. If a receipt is required, a self-addressed, stamped envelope (or in the case of foreign members, the envelope and two International Postal Reply coupons) should be included with the membership or subscription request.

The annual subscription rate to The Veliger for libraries and nonmembers is US $50.00, which now *includes* mailing charges to domestic addresses.

An additional US $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Memberships and subscriptions are by Volume only (July 1 to April 1) and are payable in advance to California Malacozoological Society, Inc. Single copies of an issue are US $25.00 plus postage.

Send all business correspondence, including subscription orders, membership applications, payments for them, changes of address, to: C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709, USA.

Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616, USA.

The Veliger 30(2):105–126 (October 1, 1987)

THE VELIGER

Deep-Sea Gastropods of the Genus *Aforia* (Turridae) of the Pacific: Species Composition, Systematics, and Functional Morphology of the Digestive System

by

A. V. Sysoev and Yu. I. Kantor

A. N. Severtzov Institute of Animal Evolutionary Morphology and Ecology of the U.S.S.R. Academy of Sciences, Lenin Avenue, 33, Moscow 117071, U.S.S.R.

Abstract. The composition and distribution of deep-sea species of the genus *Aforia* from the Pacific are studied. Three new subgenera, ***Dallaforia***, ***Abyssaforia*** and ***Palaeoaforia***, are described. *Steiraxis* is considered as a taxon of the subgeneric level within *Aforia*. Three new species (*Aforia* ***abyssalis***, *A.* ***moskalevi*** and *A.* ***kupriyanovi***) and one new subspecies (*A. aulaca* ***alaskana***) are described.

The anatomies of seven species of *Aforia*, including the type species, are presented. On the whole, the structure of all main organ systems is similar in most of the species. None of the species has an invaginable part of the rhynchodaeum. It is shown that Toxoglossa possess an intraembolic proboscis characterized by a buccal mass situated near its base.

An explanation is proposed of the feeding mechanism in turrids having a well-developed subradular membrane and "nontoxoglossate" radular teeth. The explanation is based on findings of marginal teeth held by a sphincter of the tip of the proboscis of *Aforia* species. Thus, marginal teeth perform a double function, being used both in the buccal cavity and at the tip of the proboscis as in the higher Toxoglossa.

An analysis of the geographical distribution and history of members of *Aforia* shows that the main factor conditioning the evolution of the genus is its adaptation to low water temperatures.

INTRODUCTION

Gastropods of the genus *Aforia* are among the largest (adult shell sizes up to 92 mm) and most widely distributed members of the family Turridae in the Pacific. Species of *Aforia* are mostly found in relatively deep waters, and descriptions of the specific composition of *Aforia* in bathyal and abyssal faunas are fragmentary. There are very few data on the distribution of species, while data on anatomy are almost absent.

Several rare and undescribed species of *Aforia* have been found recently by Soviet deep-sea expeditions. Our investigations of the morphology of their shells, radulae, and soft parts have allowed us (1) to revise, to some extent, the generic composition and to erect infrageneric taxa, (2) to specify the identity and distribution of bathyal and abyssal species (of which three species and one subspecies appear to be new), and (3) to analyze the functional morphology of the digestive system of the species studied.

For the comparative analysis of *Aforia* morphology, an investigation was carried out of the anatomy of the genus type species, *A. circinata* (Dall), which is not a true deep-sea species.

All type specimens of described species are deposited in the Zoological Museum of Moscow State University. Registration numbers are indicated in the descriptions of species.

MATERIALS AND METHODS

Materials for the study were collected by Soviet expeditions on the research vessels *Vityaz, Dmitry Mendeleev, Akademik Kurchatov,* and *Gidrobiolog.* Coordinates of stations where mollusks were collected are listed in the descriptions of species.

The morphology of the digestive system was studied histologically. The anterior part of the system (including the proboscis with rhynchodaeum, poison gland, and a part of the oesophagus) or the molluscan body after removing the visceral mass and mantle were dehydrated and embedded in paraffin; sections 8–10 μm thick were cut. Sections were stained with haematoxylin-eosin and Mallory's stain. Semidiagrammatic representations of the anterior part of the digestive system were made. Poison and salivary glands, together with the radular sac, were represented stereoscopically, but the nerve ring was not figured. In studies of the odontophore of *Aforia circinata,* part of the buccal mass with radular sac was sectioned transversally.

Examinations of the mantle complex of organs and the penis were carried out with a stereomicroscope at magnifications of 16–32 times. Radulae for light microscopy were removed together with the radular sac and placed into a sodium hypochlorite solution to dissolve the tissues, with subsequent transfer to distilled water, cleaning, and embedding in glycerol. Radular teeth of two species were also prepared for scanning electron microscopy. After dehydration in alcohol and acetone, the teeth were mounted on sticky tape, coated with gold, and examined with a JSM-50A scanning electron microscope.

GENERAL ANATOMY OF EXAMINED SPECIES

The body of deep-sea species of *Aforia* lacks pigmentation. The head is well distinguished from the body; eyes are absent. The morphology of the mantle complex is similar in all species. The osphradium and gill are large, the hypobranchial gland is moderately developed, and an anal gland is absent. All species examined have an accessory pedal gland situated in the depression in the middle part of the marginal glandular cleft. The epithelial lining of the accessory gland is similar to the rest of the marginal cleft. The most probable function of the gland is lubrication of the foot.

Close attention was paid to the anterior part of the digestive system, as its morphology is the most variable among Turridae. The generalized scheme of organs of the body haemocoel of *Aforia* is represented in Figure 4A.

The species have a more or less long proboscis situated in the rhynchocoel (rhynchodaeal cavity or proboscis sheath). The proboscis can be stretched out through the rhynchostome, which is surrounded with a very large, powerful sphincter. The buccal mass lies at the base of the proboscis. The buccal tube leads from the buccal cavity to the mouth at the tip of the proboscis. The radular sac opens into the buccal cavity. Near the entrance of the radular sac two ducts of salivary glands open. Large salivary glands, which may unite to form a single large one, are placed near or above a large nerve ring (not figured). A long poison gland opens ventrally behind the buccal mass. The poison gland has a large and powerful distal muscular bulb that functions as a propulsive organ.

SYSTEMATIC DESCRIPTIONS

Class Gastropoda

Subclass Pectinibranchia Blainville, 1814

Order Toxoglossa Gray, 1853

Family Turridae Swainson, 1840

Subfamily Turriculinae Powell, 1942[1]

Genus *Aforia* Dall, 1889

Type species: *Pleurotoma circinata* Dall, 1873 (O.D.).

The mollusks under consideration have been described in such genera as *Pleurotoma, Leucosyrinx, Aforia, Irenosyrinx,* or *Steiraxis.* However, in recent works only the latter three names are used.

The genus *Irenosyrinx,* with type species *Pleurotoma (Leucosyrinx) goodei* Dall, 1890, was described by Dall (1908) for species close to those of *Aforia* but differing (at least as type species) by the structure of the operculum. In adult specimens of *I. goodei* the operculum has a subcentral nucleus and looks like that of *Buccinum* whereas the *Aforia* representatives have an elongate operculum with a terminal nucleus. Subsequently, however, authors considered these differences insignificant (Grant & Gale, 1931; Powell, 1942, 1966, 1969; McLean, 1971). We agree with this subsequent opinion because the considered group of species is rather homogenous and the species have similar morphologies of the shell, radular teeth and soft body, while the operculum with subcentral nucleus is known only for *A. goodei.* Such opercular morphology of the specimen studied by Dall can probably be considered an abnormal individual aberration caused by damage during growth, which also occurs sometimes in other turrids. This point of view is supported further by the fact that opercula of younger specimens also investigated by Dall (1908) have terminal nuclei similar to those of other species of *Aforia.* The division of *Aforia* and *Irenosyrinx* proposed by Bouchet & Waren (1980), based only on the fact that the type species of *Aforia* is a shallow-water boreal north Pacific species whereas that of *Irenosyrinx* is an abyssal eastern Pacific species, is considered groundless.

The monotypic genus *Steiraxis* was established by Dall

[1] Powell (1969) and Cernohorsky (1972) considered that the name Turriculinae Powell, 1942, cannot be used, being a junior homonym and, therefore, the available name for this taxon would be Cochlespirinae Powell, 1942. Recently, some authors have accepted this statement. However, according to the *International Code of Zoological Nomenclature,* the names Turriculinae Carpenter, 1861, and Turriculinae A. Adams, 1846, based on *Turricula* Fabricius, 1823 (Mitridae) (non *Turricula* Schumacher, 1817 [Turridae]) are not senior homonyms of Turriculinae Powell, 1942 (Article 54[1]), since the former two names are invalid (Article 39) and unavailable (Article 11[e]). Therefore, Turriculinae Powell, 1942, should be considered as an available and valid name.

(1896), with type species *Pleurotoma* (*Steiraxis*) *aulaca* Dall, 1896. According to Dall and all later authors, the principal feature separating this genus from *Irenosyrinx* (=*Aforia*) is stronger spiral sculpture equally developed on the whole surface of the shell whorls. However, the presence of the below-described abyssal species *A.* ***abyssalis*** sp. nov., which has sculpture intermediate between typical *Aforia* and *Steiraxis,* forces us to place *S. aulaca* in the genus *Aforia* while the name *Steiraxis* can be used for a subgenus within *Aforia.*

Peculiarities of the shell and radular tooth morphology and bathymetric distribution of the species of *Aforia* allow us to divide the genus into five subgenera. The diagnostic features of the subgenera are summarized in Table 1.

Subgenus *Aforia s.s.*

The shell spiral sculpture is represented by narrow, low ribs, being very slight on the shoulder. A weakly to moderately pronounced spiral keel is usually situated on the lower part of the shoulder. Marginal teeth of the radula are very small, and the shell height–tooth length ratio exceeds 100 (up to 180).

Species of the subgenus inhabit sublittoral and bathyal waters of the Pacific, the southwestern Atlantic, and the southeastern part of the Indian Ocean.

From our point of view the following nominal species should be included in the nominal subgenus: *Aforia circinata* (Dall, 1873), *A. insignis* (Jeffreys, 1883), *A. magnifica* (Strebel, 1908), *A. lepta* (Watson, 1881), *A. staminea* (Watson, 1881), *A. gonioides* (Watson, 1881), *A. goodei* (Dall, 1890), *A. persimilis* (Dall, 1890), *A. persimilis leonis* (Dall, 1908), *A. persimilis blanca* (Dall, 1919), *A. amycus* (Dall, 1919), *A. kinkaidi* (Dall, 1919), *A. hondoana* (Dall, 1925), *A. okhotskensis* Bartsch, 1945, *A. chosenensis* Bartsch, 1945, *A. sakhalinensis* Bartsch, 1945, *A. diomedea* Bartsch, 1945, *A. japonica* Bartsch, 1945, and *A.* ***moskalevi*** Sysoev & Kantor, sp. nov.

The above list includes names that have been only proposed, but at present we cannot estimate the validity of many of them because, on the one hand, we have too little material and, on the other hand, a detailed study on the shallow-water species systematics was beyond the scope of our work. It should be noted that, according to many authors, most if not all of the names proposed by BARTSCH (1945) should be synonymized with *A. circinata* (see POWELL, 1969) and all bathyal eastern Pacific species should be considered as a single species, *A. goodei* (see MCLEAN, 1971).

Aforia (*Aforia*) *circinata* (Dall, 1873)

(Figures 3A, C–E, 4B, C, 7A–D)

Material: Our specimens were collected near Iturup Island (Kurile Islands) at a depth of about 100 m (R/V *Gidrobiolog*).

Digestive system (Figure 7): The proboscis is long; in studied specimens it was stretched out through the rhynchostome. The buccal mass is large and pyriform, with a deep fold at the upper part. The walls of the buccal mass are thick, becoming thinner in the anterior part. The buccal tube is of a small diameter without folds along the buccal mass. The rhynchodaeum is strongly folded. The buccal tube forms a small expansion with a sphincter near the proboscis tip. The salivary glands are united as one large gland located above the oesophagus. Paired salivary ducts open into the radular sac near its entrance to the buccal cavity. The epithelium of the buccal cavity forms high folds, the largest of which are at the bottom of the cavity near the entrance of the radular sac (Figure 7B). The odontophore is of medium size with four subradular cartilages (Figure 7D) united in two pairs and connected by a muscular symphysis in the anterior part of the odontophore (Figure 7C). The radular sac is surrounded with a thick layer of muscles and is lined inside with a thick cuticular layer. The poison gland is large, with a greatly decreased diameter near its opening into the oesophagus. The muscular bulb is of medium size and oval. The oesophagus sharply increases in diameter posterior to the nerve ring. The stomach typically has a U-shape form and receives two ducts of the digestive gland. The radula is of typical form for the genus (Figures 3C–E). The central teeth are weak and thin. The marginal teeth are small. The shell height–tooth length ratio is 180.0.

Aforia (*Aforia*) *lepta* (Watson, 1881)

(Figures 1F, G, 5B, 6E–H, 8A–E)

Pleurotoma (*Surcula*) *lepta* WATSON, 1881:391, 1886:288, pl. XVIII, fig. 7.

Material: R/V *Dmitry Mendeleev,* station 1276, 48°25′S, 171°42′E (SE of New Zealand), depth 1100–1200 m, trawl Sigsbee, 1 specimen.

Shell: The shell of our specimen is very similar to that described by Watson (1886), differing in its smaller size (the shell height is 14.1 mm), less numerous whorls, and less well-developed spiral keel, especially on the penultimate whorl; spiral sculpture is more uniform, and intercalate threads between primary ones are absent.

The protoconch sculpture and also the operculum, radula and soft-body morphology, which were not studied previously, are described here. The operculum is small and drop-shaped (Figure 5B). The protoconch consists of 1.5 rapidly increasing whorls sculptured with very weak, thin, and inconspicuous spiral folds.

Anatomy (Figures 6E–H): The mantle is thin and the osphradium and gill are clearly seen through it. The siphon is short and contracts strongly during fixation. The propodium of the foot is narrow with a deep cleft; the accessory pedal gland is weak. The head is well distinguished from the body; the tentacles are short and rounded at the tip.

Table 1

Characters of the subgenera of *Aforia*.

Subgenus	Spiral ribs	Spiral keel	Shell height–tooth length ratio
Aforia s.s.	narrow, low, very slight on the shoulder	present, variously developed	107–180
Steiraxis	very strong, equally developed throughout the shell surface	present, strong	about 70
Abyssaforia	narrow, prominent, equally developed throughout the shell surface	none	57–90
Dallaforia	strongly inequal on the shoulder and on the rest of the whorl	none	about 100
Palaeoaforia	narrow, weak, smoothed on the shoulder	present, double	—

The rhynchostome has well-developed lips; its sphincter is very large.

Mantle complex (Figure 6G): The osphradium and gill are very large. The gill lamellae are tall and triangular; their height is nearly equal to the base width. At the inner side of the lamella a thickened cuticulized flagellum is situated. The flagellum adheres to the lamella. The gill extends nearly to the mantle outer edge but its lamellae are low there. The osphradium is flattened. The hypobranchial gland is poorly developed and is covered with a thick gel-like mucosal layer. The pallial oviduct is of small diameter and the female gonopore opens on a small rounded eminence. The rectum has a very small diameter. It lies along the surface of the oviduct; the anus opens nearer to the outer edge of the mantle than the gonopore does. There is a short and narrow transverse fold in the right part of the mantle.

Digestive system (Figure 8): The proboscis is small; its epithelium is formed by very tall gobletlike cells (Figure 8B). The buccal mass is of medium size with relatively thin walls. The buccal tube forms a fold along the buccal mass. In the anterior part, the buccal tube forms a small sphincter. Retractor muscles of the proboscis pass along its lumen and attach near the tip. The rhynchodaeum is folded and covered with a thick cuticular layer. The paired salivary glands are large, and their ducts are of small diameter, slightly coiling. The muscular bulb of the poison gland is small. Odontophore cartilages are absent, being replaced by a strong muscular fold. The oesophagus gradually widens posterior to the entrance of the poison gland. The stomach is typically U-shaped, containing two ducts of the digestive gland. The central radular teeth are very thin (Figure 8D). The marginal teeth are small (Figures 8D, E). The shell height–tooth length ratio is 100.7.

Distribution: The species was previously known from two localities—the Australian-Antarctic Rise (R/V *Challenger,* station 157, 53°55′S, 108°35′E, type locality) and near Kerguelen Island (Watson, 1886; Cantera & Arnaud, 1984). Our specimen was found in the New Zealand underwater plateau and, therefore, the species range is greatly extended eastward. The species lives at depths of 360 to 3560 m.

Aforia (*Aforia*) ***moskalevi***
Sysoev & Kantor, sp. nov.

(Figures 1E, H, 5A, 6A–D, 9A–G)

Material: R/V *Dmitry Mendeleev,* station 1314, 59°58′S, 158°07′E (SW Pacific), depth 3010–3030 m, trawl Sigsbee, 2 specimens—holotype (No. LC 5360) and paratype (No. LC 5361).

Description of holotype: The fusiform shell is thin and consists of 4.5 preserved whorls. The protoconch is lost, as the first preserved whorl is eroded. Whorls are slightly convex and angulate at the periphery. The whorl shoulder is flattened and sloping. There is a very weak spiral fold on the shoulder of the body whorl. Axial sculpture is represented only by numerous thin growth lines, some of them being rather more pronounced, especially below the shoulder. Spiral sculpture of the upper part of the whorl consists of threadlike, weak, flattened ribs irregularly displaced and separated by interspaces twice as wide. On the lower part of the whorl, spiral ribs are larger, narrow, rounded, irregularly disposed, and separated by interspaces that are 2–4 times wider than rib widths. In some interspaces, there are much weaker secondary ribs. As the spiral ribs cross the strongest growth lines, they form reticulate sculpture. The aperture is wide and oval. The outer lip is broken. The inner lip is smoothly curved, coated with thin callus. The siphonal canal is long, slightly curved. The sinus, judging by growth lines, is deep, wide, and rounded; its apex is situated some distance above the middle of the whorl shoulder. The shell color is gray. The shell height is 33.4 mm, the height of the body whorl is 25.5 mm, the aperture height is 20.8 mm, and the shell diameter is 12.2 mm.

The paratype is smaller (the shell height is 27.2 mm) and poorly preserved. Its shell is quite similar to the holotype. We have studied the anatomy of the paratype.

The operculum is small and roundly triangular, with a terminal nucleus (Figure 5A).

Anatomy (Figures 6A–D): The mantle is thick, and the osphradium and gill are seldom seen through it. The mantle edge is uneven; it has a distinct notch corresponding to

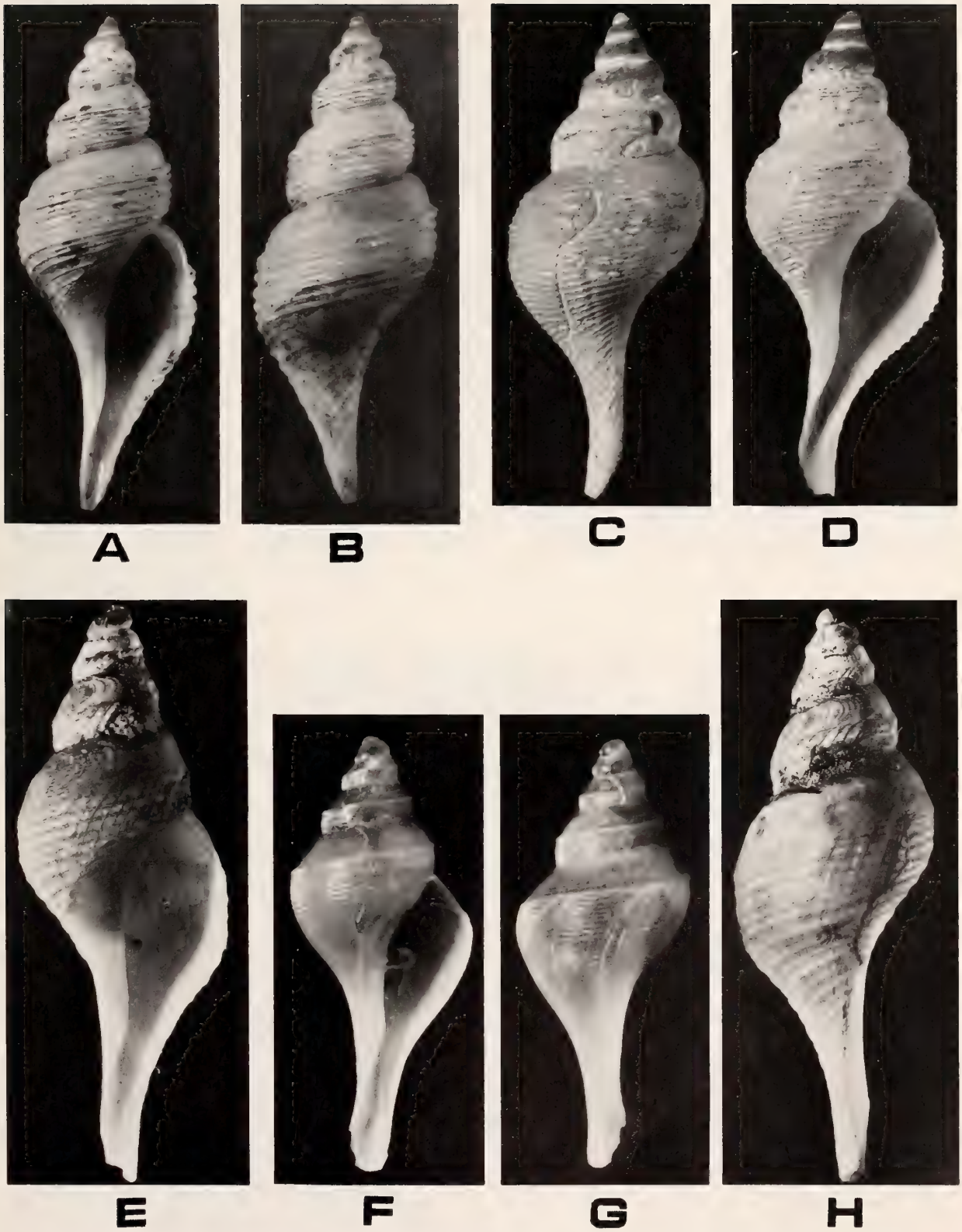


Figure 1

A and B, *Aforia crebristriata* (Dall), R/V *Vityaz*, stat. 4173, shell height of 40.4 mm. C and D, *A.* ***kupriyanovi*** sp. nov., holotype. E and H, *A.* ***moskalevi*** sp. nov., holotype. F and G, *A. lepta* (Watson), R/V *Dmitry Mendeleev*, stat. 1276, shell height of 14.1 mm.

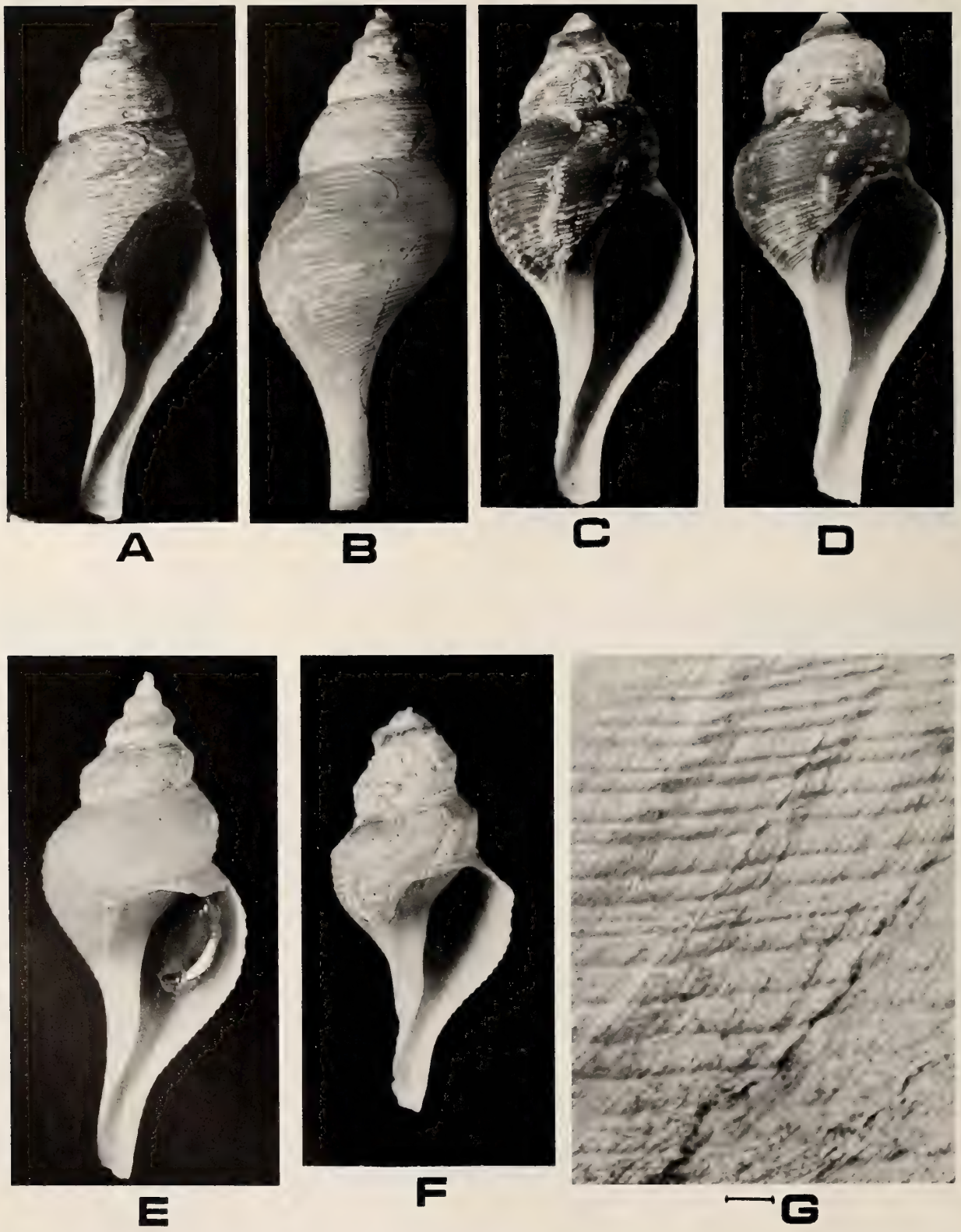


Figure 2

A–G, *Aforia* ***abyssalis*** sp. nov. A and B, holotype. C, paratype, R/V *Vityaz,* stat. 5624, shell height of 31.8 mm. D, paratype, R/V *Vityaz,* stat. 5624, shell height of 31.0 mm. E, paratype, R/V *Vityaz,* stat. 3594, shell height of 39.0 mm. F, paratype, R/V *Vityaz,* stat. 4104, shell height of 16.8 mm. G, paratype, shell sculpture. Scale bar = 1 mm.

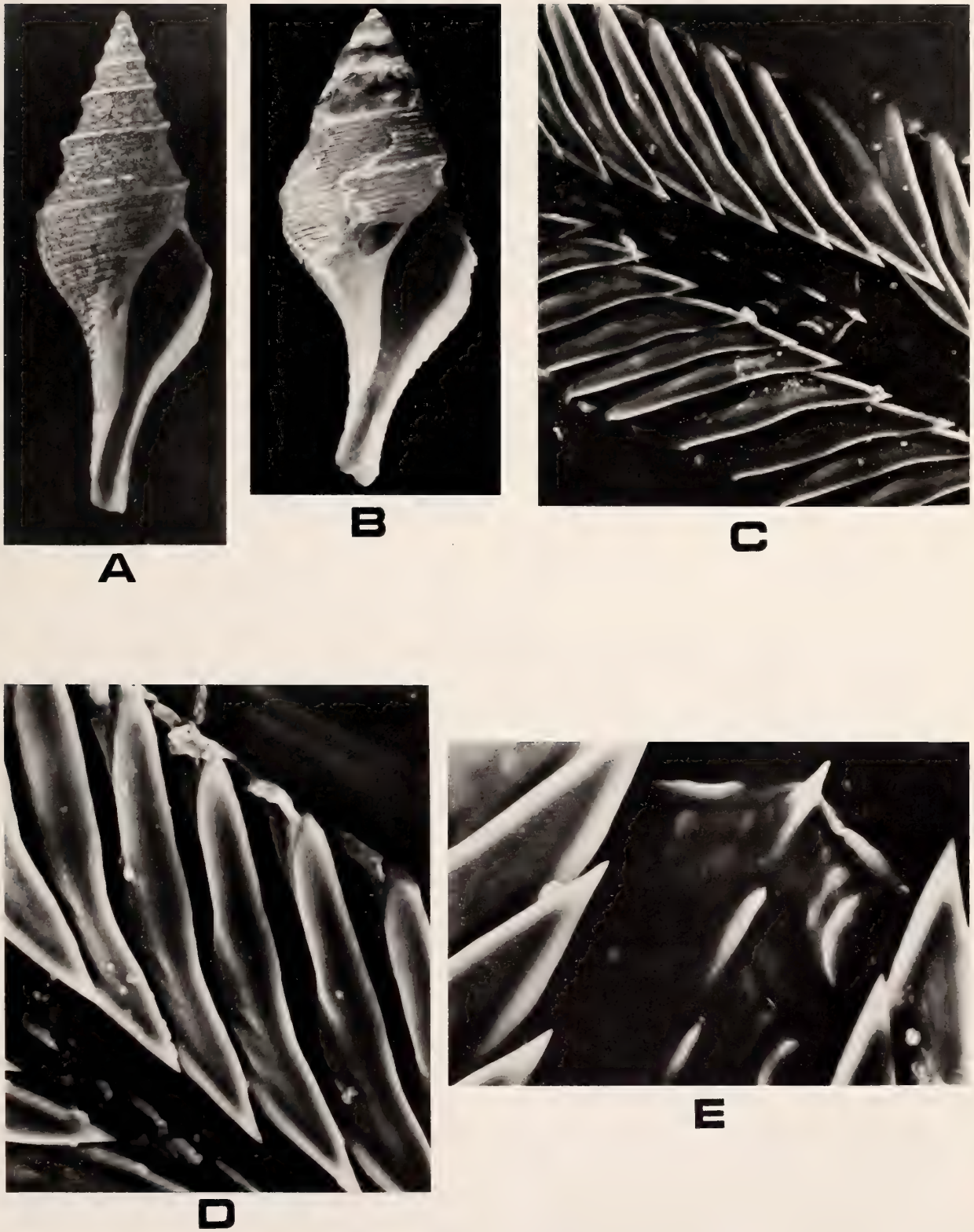


Figure 3

A, *Aforia circinata* (Dall), shell height of 52.4 mm. B, *A. aulaca* ***alaskana*** subsp. nov., holotype. C–E, SEM photographs of radula of *A. circinata*.

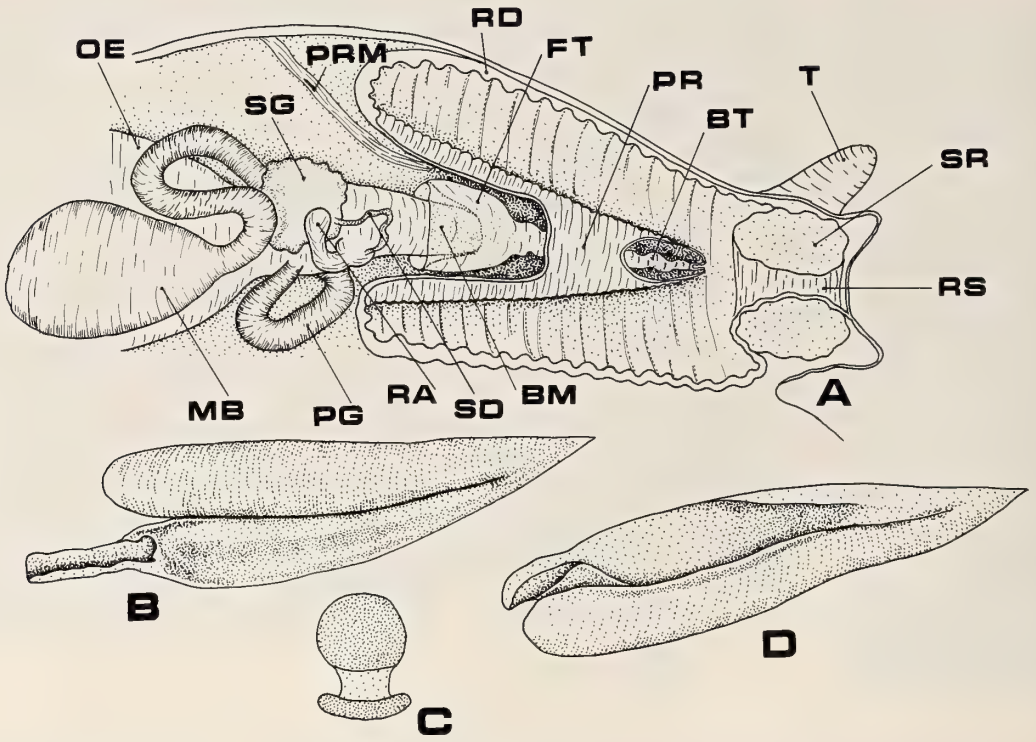


Figure 4

A, general diagrammatic section of the anterior part of *Aforia* digestive sytem. B–D, marginal teeth of *Aforia* (B, *A. circinata*. C, the same, transverse section. D, *A. **abyssalis***). Key to abbreviations for all figures: AG, accessory pedal gland; AO, anal opening; BT, buccal tube; BM, buccal mass; BW, body wall; CT, central tooth; DG, digestive gland; FT, fold of buccal tube; FG, female gonopore; G, gill; H, head; HG, hypobranchial gland; LM, longitudinal muscles; LR, lip of rhynchostome; MB, muscular bulb; MG, male gonopore; MT, marginal tooth; N, nephridium; OC, odontophoral cartilage; OE, oesophagus; OP, operculum; OS, osphradium; PG, poison gland; PO, pallial oviduct; PR, proboscis; PRM, retractor muscles of the proboscis; PP, propodium; PS, proboscidal sphincter; RA, radula; R, rectum; RD, rhynchodaeum; RS, rhynchostome; RT, radular tooth; S, siphon; SD, salivary duct; SG, salivary gland; SP, sublingual pouch; SR, rhynchostomal sphincter; ST, stomach; T, tentacles; TM, transverse muscles.

the anal sinus of the shell. The head is well distinguished from the body. The tentacles are long and flattened. The propodium is very narrow, and the accessory pedal gland is poorly developed. A large rhynchostomal sphincter is present.

Mantle complex (Figure 6C): The gill and osphradium are large, the latter being ⅔ of the gill length. Gill lamellae are tall and triangular. The thickened flagellum of the gill is free in its upper part to form a rounded growth. The hypobranchial gland is well developed, and forms about 30 closely placed folds. A long siphon with a large distributive valve at its base is well developed. The rectum is of small diameter with a small but distinct anal papilla.

Digestive system (Figure 9): The proboscis is long, narrowing towards its tip. Powerful proboscis retractor muscles are attached mostly to the integument of the body sinus roof. The buccal mass is not large. The buccal tube is surrounded with a relatively thin layer of circular musculature to form a long double fold along the buccal mass. There is a small sphincter of the buccal tube at its tip in which a radular marginal tooth was found to be held (Figure 9B). The muscular bulb of the poison gland is rather small and oval. The salivary glands join to form a single gland placed above the oesophagus and embracing it. The salivary ducts are relatively thick and twist slightly. The odontophore is small (Figure 9C); there are four subradular cartilages forming pairs on each side. The paired cartilages fuse in the anterior part of the odontophore and the fused pairs are connected with a muscular symphysis. The radular sac is lined with a thick layer of cuticle. The rachidian tooth of the radula is thin, weak, and curved, with a smooth anterior edge. The marginal teeth (Figures 9D, E) are short, broad, and their distal parts are optically more dense than the basal parts. The length of a marginal tooth is 0.24 mm. The shell height - tooth length ratio is 113.3. The oesophagus abruptly widens behind the entrance of the poison gland. The stomach is of the typical

U-shape, with two ducts of the digestive gland. The specimen dissected is an immature female.

Remarks: This species is closest to *Aforia* ***kupriyanovi*** sp. nov., differing by the weak development of spiral ribs on the body-whorl shoulder, the lesser number of ribs, the flattened whorl shoulder, and the much smaller marginal teeth (as measured in relative values).

Distribution: The species was found in the abyssal zone of the region southward from the Hyort trench (southwestern Pacific).

Subgenus *Steiraxis* Dall, 1896

Type species: *Pleurotoma* (*Steiraxis*) *aulaca* Dall, 1896 (O.D.).

Spiral sculpture consists of very strong, prominent, nearly rectangular in section ribs equally developed throughout the shell surface. The spiral keel is strong and situated at the whorl periphery. Marginal teeth of the radula are very large, and the shell height–tooth length ratio is about 70.

The subgenus includes a single species with two subspecies (*Aforia aulaca aulaca* (Dall) and *A. aulaca* ***alaskana*** subsp. nov.) living at abyssal depths of the eastern Pacific along the coast of North and Central America.

Aforia (*Steiraxis*) *aulaca* ***alaskana***
Sysoev & Kantor, subsp. nov.

(Figures 3B, 5D, 12F–H)

Material: R/V *Vityaz*, station 6109, 56°17.7′N, 139°43.3′W (Gulf of Alaska), depth 3460 m, Sigsbee trawl, 1 specimen (holotype, No. LC 5362).

Description of holotype: The shell is small, fusiform, and consists of 5 whorls. The upper whorls are significantly eroded. The whorls are slightly convex, angled at the periphery where a spiral keel is placed. The whorls are divided by very shallow, poorly visible sutures. The whorl shoulder is flattened. Axial sculpture is represented only by very thin, numerous growth lines. Spiral sculpture consists of the keel situated at the whorl periphery and also of strong, prominent, nearly rectangular in section ribs covering all the shell surface. The width of ribs varies insignificantly. Sometimes, there is an additional thin rib in the interspace between the more prominent ribs. There are two ribs on the spiral keel. The ribs are much lower on the shell base and on the anterior canal. Interspaces between ribs vary in their width, being in most cases equal to the ribs themselves or slightly wider. There are 15 spiral ribs on the penultimate whorl and 48 on the body whorl; 11 of the latter are disposed between the keel and the suture. The ovate aperture gradually transforms into the long siphonal canal, which is slightly curved and widens toward the end. The inner lip is coated with a wide but thin callus. The anal sinus, judging by growth lines, is wide, rounded, and not very deep, its apex being placed approximately in the middle of the space between the suture and the keel. The shell color is light brown. The shell height is 25.8, the body-whorl height is 20.0, the height of the aperture is 16.5, and the shell diameter is 11 mm.

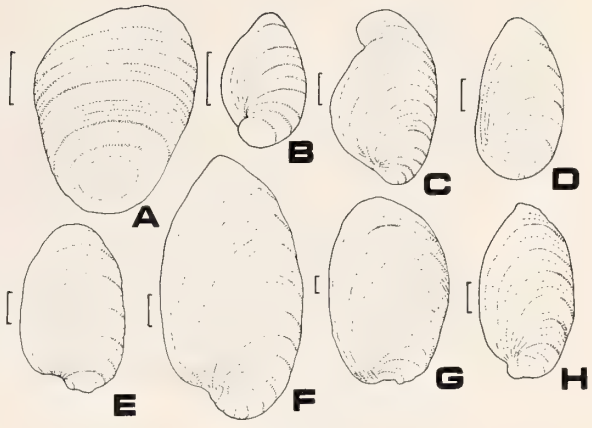


Figure 5

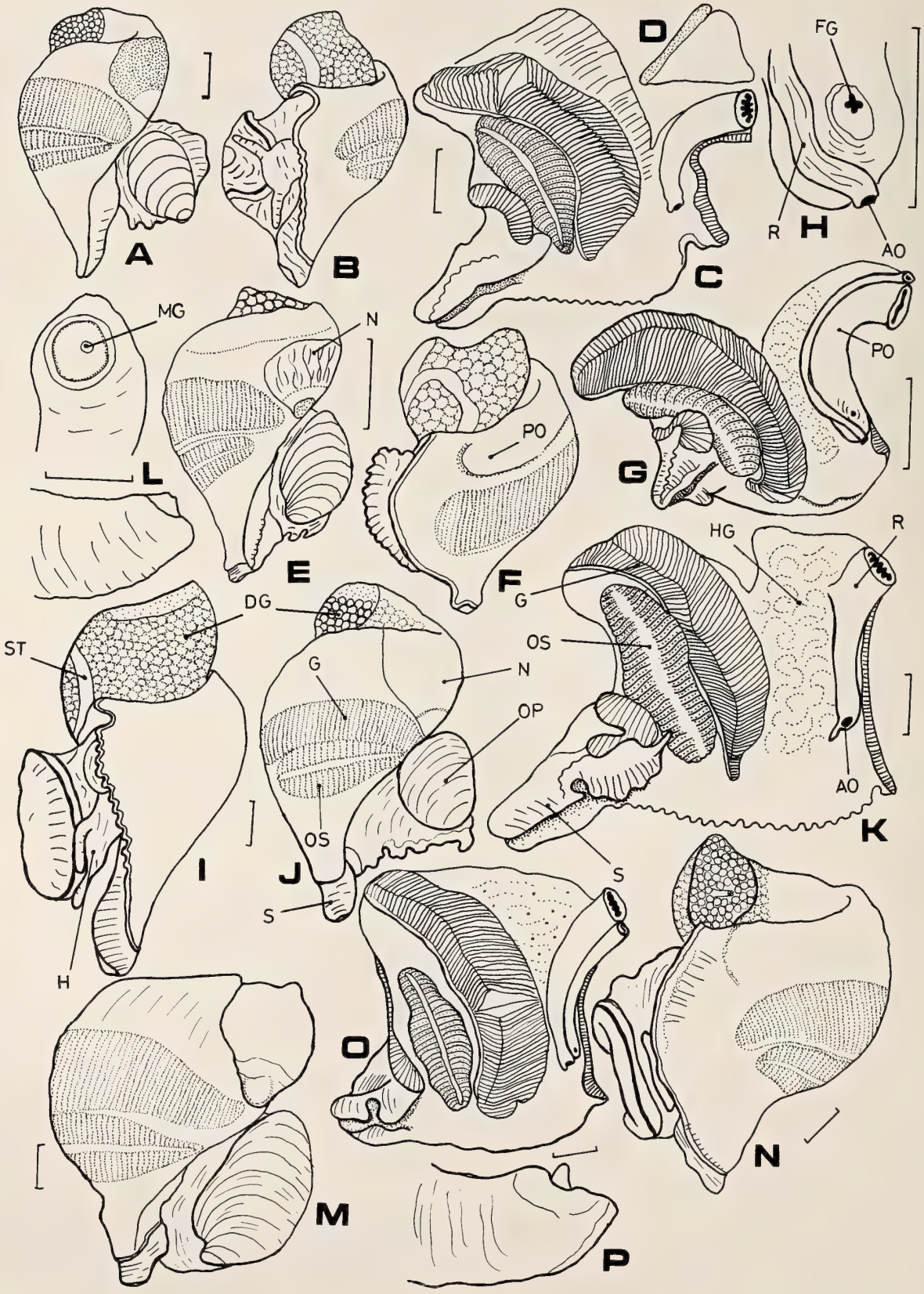
Opercula of *Aforia* species. *A, A.* ***moskalevi***, paratype. B, *A. lepta*. C, *A. crebristriata*. D, *A. aulaca* ***alaskana***, holotype. E–G, *A.* ***abyssalis*** (E, paratype, R/V *Vityaz*, stat. 5624. F, paratype, R/V *Vityaz*, stat. 3594. G, paratype, R/V *Vityaz*, stat. 2074). H, *A.* ***kupriyanovi***, holotype. Scale bar = 1 mm.

Anatomy: The rhynchostomal sphincter is very poorly developed, compared to other species. The rhynchostome has weak, small rhynchostomal lips. A small accessory propodial gland is placed on the bottom of the propodial cleft.

Mantle complex of organs: The mantle morphology is typical for the genus. The mantle edge is serrated. The ctenidial lamellae are high, and there is a thick cuticular basal flagellum at the inner edge. The hypobranchial gland is poorly developed.

Digestive system: The proboscis (Figure 12F) is typical for the genus. The buccal mass is small, and the buccal tube is surrounded by a rather thick layer of circular musculature. Near the tip of the proboscis the buccal tube forms a sphincter (Figure 12G). Powerful and large proboscis retractors are attached to the expansion of the buccal tube at some distance from the proboscis tip. It is possible that the end of the buccal tube can be everted. The poison gland is thick and has a very large muscular bulb. The central radular tooth is large; it has one cusp on its frontal edge and long, narrow, curved blades (Figure 12H). The marginal teeth are long and slightly curved (Figure 12H) (0.38 mm length). The shell height–tooth length ratio is 67.9.

Remarks and distribution: *Aforia aulaca* ***alaskana*** subsp. nov. differs from the nominal subspecies in having a smaller shell (the height of holotype shell of *A. aulaca aulaca* is 60 mm) that is covered with spiral ribs that are not sharp


A
B
C
D
FG
R
H
AO
MG
N
L
E
PO
F
G
HG
R
G
OS
DG
ST
G
N
OP
AO
K
I
J
OS
S
S
H
O
N
M
P

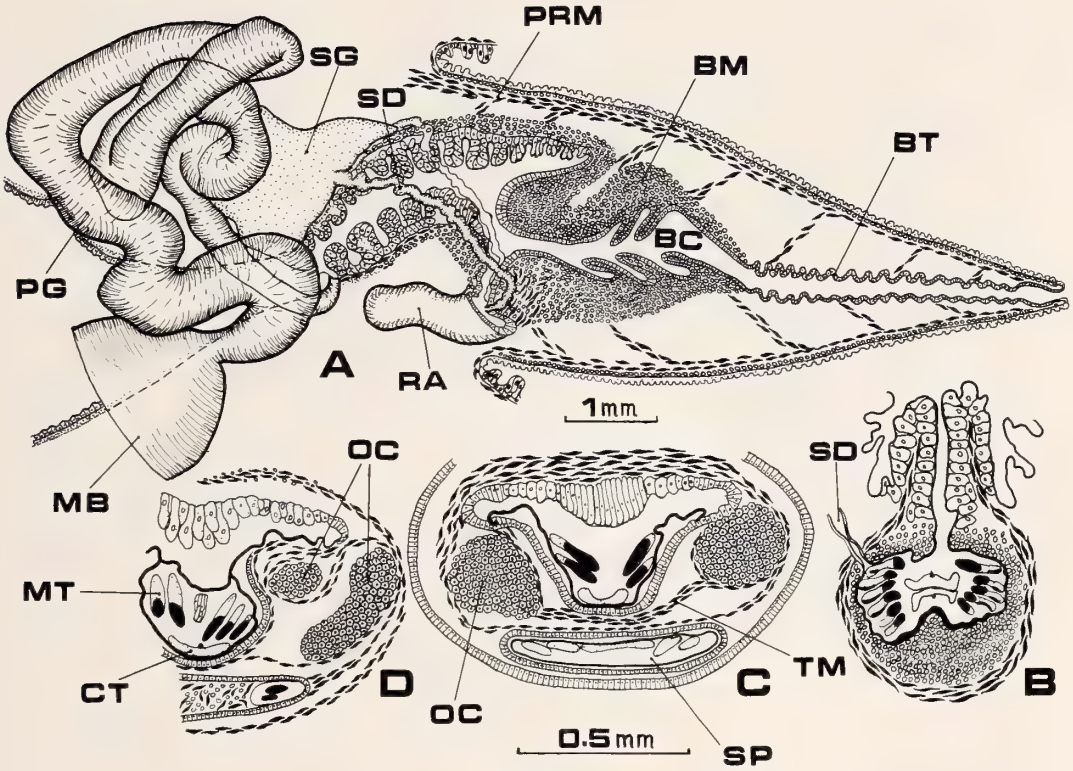


Figure 7

Morphology of digestive system of *Aforia circinata,* shell height of 49.0 mm. A, semidiagrammatic section of anterior part of digestive system. B, transverse section across the radular sac at the anterior part of odontophore. C, the same, medial part of odontophore. D, the same, basal part of odontophore. See Figure 4 for key to abbreviations.

but rectangular in side view, and with interspaces between them being equal or slightly wider than the rib width (*i.e.*, the interspaces between ribs are wider than in the nominal subspecies). The most striking difference between the subspecies is the shape of the radular teeth. The drawing of the radula of the holotype specimen of *A. aulaca aulaca* (according to the catalogue number) was published by Powell (1966:text fig. 26). The marginal teeth of the new subspecies are wider; the central tooth is large and crescentlike with a cusp on its frontal edge whereas the central tooth of the nominal subspecies is represented by a narrow small plate that is protracted along the subradular membrane and bipolarly sharply terminating. Moreover, the two subspecies differ in their geographic distribution. *Aforia aulaca aulaca* is found along the Pacific coast of North and Central America from northern California to the Gulf of Panama (Dall, 1908; Parker, 1964; Rokop, 1972). *Aforia aulaca* ***alaskana*** has been recorded so far only in the Gulf of Alaska. It is interesting to note that both subspecies have a similar vertical range, 3241–3798 and 3460 m respectively.

Subgenus ***Dallaforia***
Sysoev & Kantor, subgen. nov.

Type species: *Irenosyrinx? crebristriata* Dall, 1908.

Spiral sculpture is represented by very strong, wide, prominent ribs situated below the whorl shoulder and

←

Figure 6

Soft body of *Aforia* species. A–D, *A.* ***moskalevi,*** paratype (A and B, whole body. C, mantle complex. D, single lamella of the gill). E–H, *A. lepta* (E and F, whole body. G, mantle complex. H, distal part of female pallial gonoduct and rectum). I–L, *A. crebristriata* (I and J, whole body. K, mantle complex. L, penis). M–P, *A.* ***abyssalis,*** paratype, shell height of 39.0 mm (M and N, whole body. O, mantle complex. P, penis). Scale bar = 2 mm. See Figure 4 for key to abbreviations.

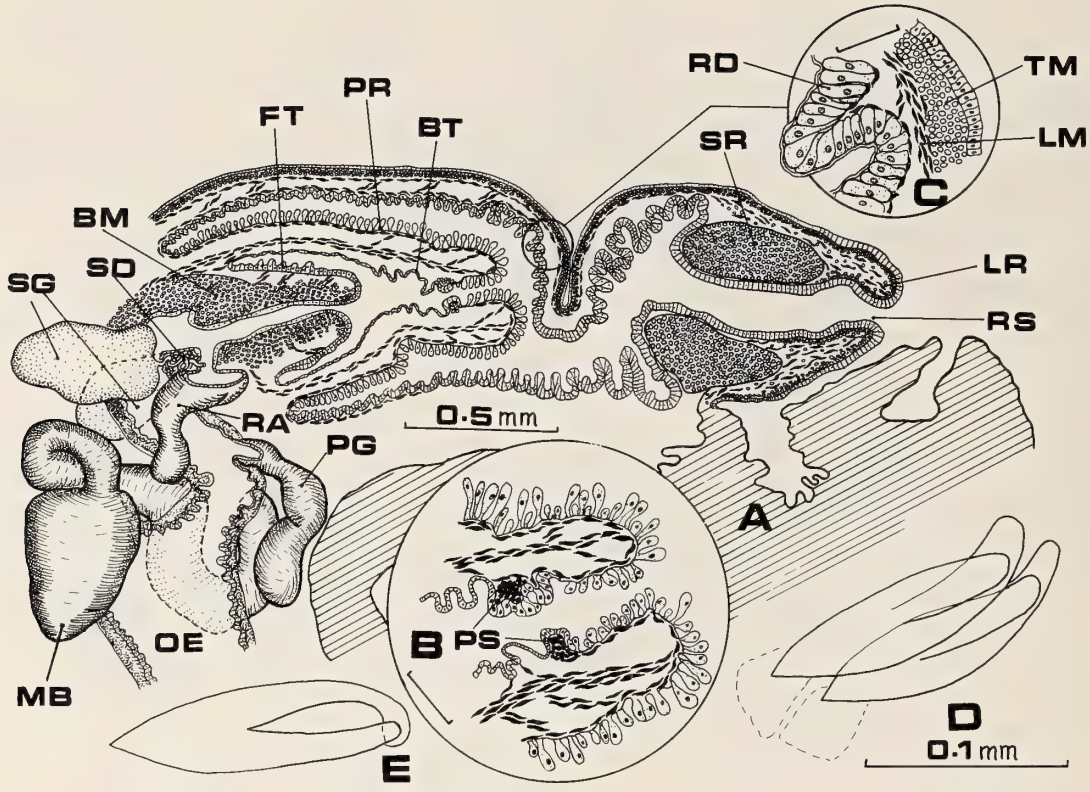


Figure 8

Morphology of digestive system of *Aforia lepta*. A, semidiagrammatic section of anterior part of body (the foot is hatched). B, magnified tip of the proboscis. C, magnified part of body wall. D and E, radula. Scale bar for B and C = 0.1 mm. See Figure 4 for key to abbreviations.

weak, flattened ribs on the shoulder. A spiral keel is absent. Marginal teeth of the radula are of middle size, and the shell height–tooth length ratio about 100.

The subgenus is represented only by the type species living in abyssal regions of the northeastern Pacific.

Aforia (***Dallaforia***) *crebristriata* (Dall, 1908)

(Figures 1A, B, 5C, 6I–L, 10A–C)

Irenosyrinx? crebristriata DALL, 1908:272, pl. 13, fig. 10.

Material: R/V *Vityaz,* station 4173, 44°54′N, 128°32′W (off Oregon), depth 2830–2840 m, trawl Sigsbee, 3 specimens.

A detailed description of the shell of *Aforia crebristriata* was given in the original description of the species. Therefore, we add data only on the operculum, anatomy and radula, which are absent in Dall's article.

Operculum: The operculum is small in comparison with other species of the genus; its shape is nearly triangular, with a terminal nucleus. The part most remote from the nucleus of the operculum of one of our specimens has a rounded projection (Figure 5C) that appears the probable result of a disturbance during its growth.

Anatomy (Figures 6I–L): The studied specimen has a shell height of 30.0 mm. The tentacles are long and cylindrical. The propodium is very narrow; the marginal cleft is shallow. The accessory pedal gland is poorly developed. At both sides of the propodium base, the metapodium forms rather long and large palps. The mantle is thin and the osphradium and gill are clearly seen through it. The mantle edge is scalloped; its projections correspond to spiral ribs. The mantle does not cover the head base.

Mantle complex (Figure 6K): The osphradium and the gill are large. The narrow gill is formed by tall triangular lamellae. The basal flagellum is weakly thickened and attached to the lamella along nearly its entire length. The gill axis is very thin. The osphradium is greenish. The hypodermal gland is covered with a thick layer of gel-like mucosa. The siphon is long and has a small distributive valve at its base. The rectum is of small diameter; there is a small palp formed by the rectal wall.

Digestive system (Figure 10): The proboscis is long. The buccal mass has rather thin walls. The buccal tube is surrounded by a moderately thick layer of circular muscles; it forms a long fold along the buccal mass. Salivary glands unite as one gland located above the oesophagus. The

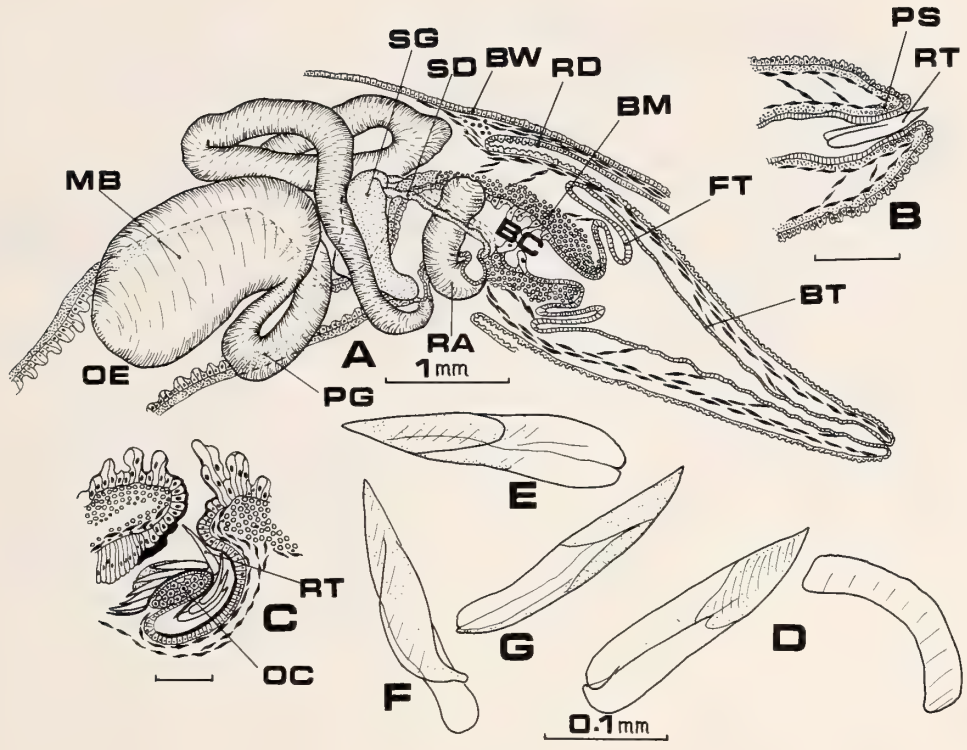


Figure 9

Morphology of digestive system of *Aforia* ***moskalevi***, paratype. A, semidiagrammatic section of the anterior part of digestive system. B, magnified tip of the proboscis. C, longitudinal section across the anterior part of radular sac. D, radula in natural position. E–G, marginal tooth, various projections. Scale bar for B and C = 0.2 mm. See Figure 4 for key to abbreviations.

salivary ducts are paired and of small diameter. Two odontophoral cartilages are very large; they unite in the anterior part of the odontophore (Figure 10B). The epithelium of the radular sac and the buccal cavity is lined with a thin cuticular layer. The large proboscis retractor muscles are placed near the proboscis walls and attach to the proboscis wall near its tip. The muscular bulb of the poison gland is large. The oesophagus abruptly widens behind the nerve ring. The poison gland opens into the oesophagus rather far from the radular sac. The radular sac is surrounded by a thick muscular layer. The central radular tooth has moderately wide, nearly straight, and almost rectangular blades, and one thin and long cusp on the frontal edge. The marginal teeth are wide, short, slightly curved, and very small (their length is 0.29 mm when the shell height is 30.2 mm). The shell height–tooth length ratio is 104.1. The stomach is of the typical U-shape, and contains paired closed ducts of the digestive gland.

Reproductive system: The vesicula seminalis is very large, formed by numerous very small loops of the seminal duct. The penis is relatively short and broad (Figure 6L), with slightly folded walls. The genital papilla is large, rounded, and surrounded by a circular fold. The male gonopore opens somewhat laterally in a small invagination.

Distribution: The species inhabits the upper abyssal zone along the northwestern coast of North America from the Gulf of Alaska to Oregon at depths of 2830 to 2869 m. Type locality—station 2859 of R/S *Albatross* (off Sitka, Alaska).

Subgenus ***Abyssaforia***
Sysoev & Kantor, subgen. nov.

Type species: *Aforia* (***Abyssaforia***) ***abyssalis*** Sysoev & Kantor, sp. nov.

Spiral sculpture is represented by numerous narrow, prominent ribs equally developed throughout the shell surface. A spiral keel is absent or a trace is retained as a slight angulosity of the whorl shoulder visible on early whorls. Marginal teeth of the radula are large, and the shell height–tooth length ratio is less than 100 (57–90).

Representatives of the subgenus live in abyssal regions of the Pacific and the northern Atlantic.

The subgenus includes three species—*A.* ***abyssalis*** Sysoev & Kantor, sp. nov., *A. hypomela* Dall, 1889, and *A.* ***kupriyanovi*** Sysoev & Kantor, sp. nov.

Most deep-water species of *Aforia s.s.* possess spiral sculpture close to that of ***Abyssaforia***.

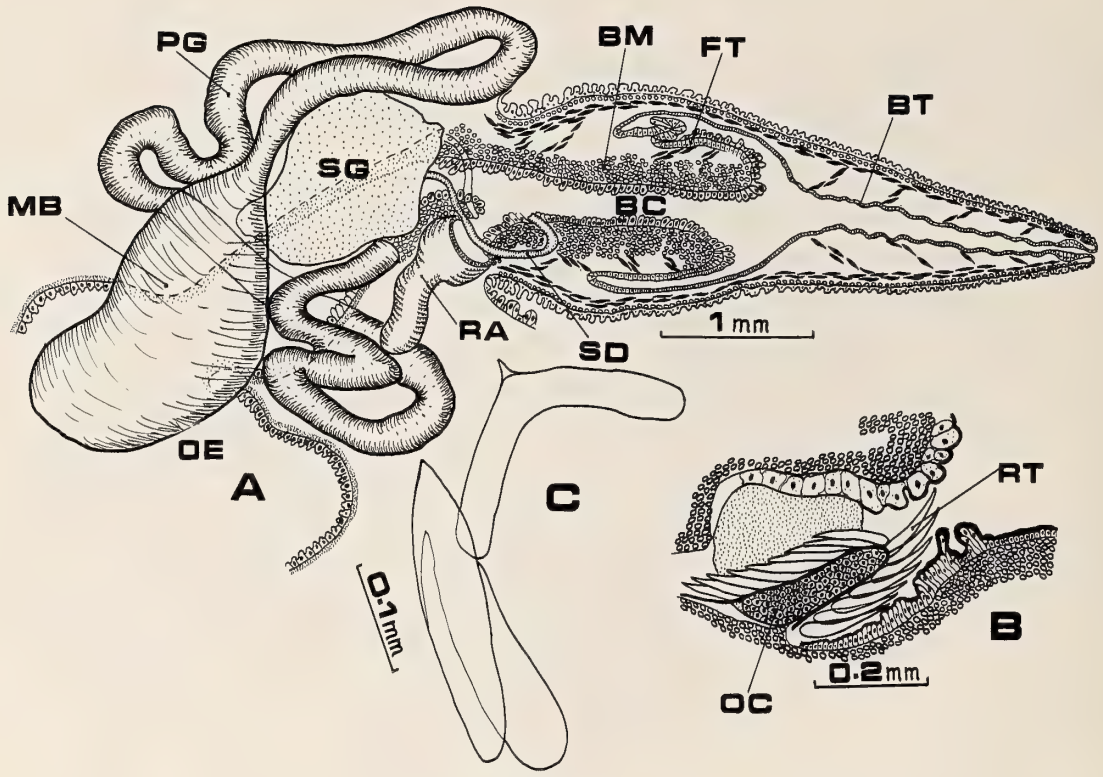


Figure 10

Morphology of digestive system of *Aforia crebristriata*. A, semidiagrammatic section of the anterior part of digestive system. B, longitudinal section across the anterior part of radular sac. C, radula. See Figure 4 for key to abbreviations.

Aforia (***Abyssaforia***) ***abyssalis***
Sysoev & Kantor, sp. nov.

(Figures 2A–G, 4D, 5E–G, 6M–P, 11A–F)

Material: R/V *Vityaz,* station 2074, 42°32′N, 150°41′E (SE of Iturup, Kurile Islands), depth 5140 m, trawl Sigsbee, 2 specimens; station 2119, 46°07.8′N, 155°16′E (E of Urup, Kurile Islands), depth 5070–5090 m, trawl Sigsbee, 1 specimen (holotype, No. LC 5363); station 3594, 40°55.2′N, 144°53.3′E (SE of Hokkaido, Japan), depth 3880–3900 m, trawl Sigsbee, 1 specimen and 1 shell; station 4104, 41°07.5′N, 159°53.9′W (NE Pacific), depth 5430–5456 m, trawl Sigsbee, 1 juvenile specimen; station 5624, 45°26′N, 154°12′E (E of Urup, Kurile Islands), depth 5220 m, trawl Galathea, 22 specimens (mostly juveniles) and 1 shell. All the paratypes are stored as No. LC 5364.

Description of holotype: The shell is medium in size for the genus, elongately fusiform, thin, and consists of 5 preserved whorls. The protoconch and upper whorls are seriously eroded. Whorls are weakly convex, somewhat angled at the periphery; the whorl shoulder is flattened. Axial sculpture is represented by growth lines that are numerous, clear, and very thin; some of them, probably reflecting significant interruptions of shell growth, clearly differ from others in their prominence. There are 6 of these growth lines on the body whorl. Spiral sculpture consists of thin, clear, pronounced, cordlike ribs separated by always larger interspaces. The ribs are separated from each other by uneven intervals; they are closest at the periphery of the whorl where the interspaces are 1.5–2 times wider than the width of the rib itself. They are most distant from each other on the whorl shoulder where interspaces are 3–7 times wider than those of the ribs. On the body whorl, 1 or 2 weak, thin accessory ribs may be situated in the interspaces. There are 15 spiral ribs on the penultimate whorl and about 60 on the body whorl, including the canal. The aperture is narrow and ovate; its outer lip is thin. The inner lip is gradually curved, covered by translucent callus, and develops a small projection when passing into the canal. The canal is long and curved. The shell color is grayish cream. The height of the shell is 56.3 mm, the height of the body whorl is 43.0 mm, the height of the aperture is 35.1 mm, and the shell diameter is 21.0 mm.

Younger paratype specimens are characterized by more convex and angled shell whorls. A tendency can be noted in some young specimens to develop a slight fold at the upper part of the whorl near the suture. The spiral ribs

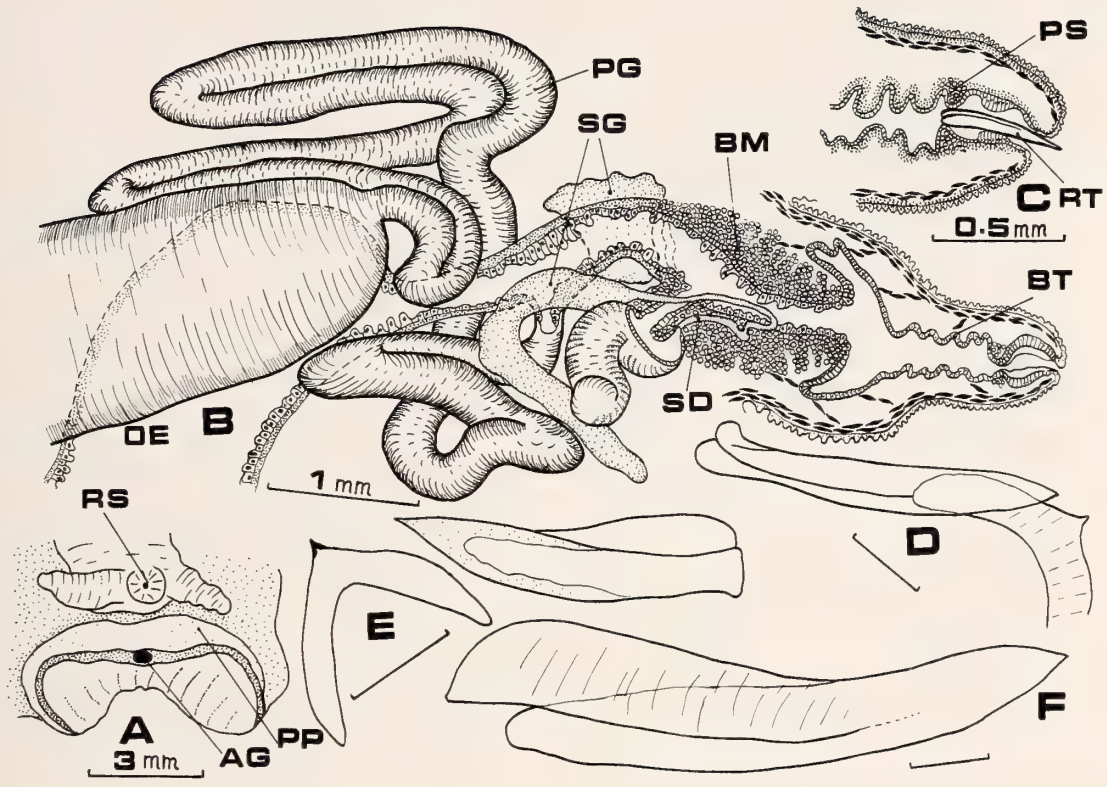


Figure 11

Morphology of digestive system of *Aforia* ***abyssalis***, paratype, shell height of 39.0 mm. A, head. B, semidiagrammatic section of the anterior part of digestive system. C, magnified tip of the proboscis. D, radula of paratype (R/V *Vityaz*, stat. 3594, shell height of 39.0 mm). E, the same (R/V *Vityaz*, stat. 5624, shell height of 25.7 mm). F, marginal tooth of paratype (R/V *Vityaz*, stat. 2074, shell height of 74.2 mm). Scale bar for D–F = 0.1 mm. See Figure 4 for key to abbreviations.

in paratypes, especially in young ones, sometimes are more flattened, wider, and closer to each other, especially on the whorl shoulder. The growth lines of smaller shells, particularly on upper whorls, may be more rough, prominent, and can form some kind of weak axial folds on the shell surface. The shell height of the largest paratype is 74.2 mm.

The operculum is ovate and large (Figures 5E–G).

Anatomy (Figures 6M–P): (The anatomy of a paratype from station 3594, having a shell height 39.0 mm, is shown in the most Figures except 6P). The propodium is narrow, and the marginal cleft is not deep. The accessory pedal gland is situated almost at the central part of the cleft. The mantle completely covers the head, which is well distinguished from the body. Tentacles are cone-shaped and rounded at the tip. The rhynchostomal lips form a funnel. The rhynchostome is small; its large and powerful sphincter constitutes the major part of the head volume.

Mantle complex (Figure 6O): The gill is very large; its length is nearly equal to the mantle length. The lamellae are tall and triangular, with poorly thickened lamellae at their inner sides which completely adhere to the lamellae. The osphradium is of medium size, and greenish. The hypobranchial gland forms inconspicuous folds covered with a thick layer of gel-like mucus. The rectum is of small diameter, and its wall forms a small palp near the anus.

Digestive system (Figure 11): The proboscis is rather short. The buccal mass is large and has thick walls. The buccal tube forms a small fold along the buccal mass. The salivary gland is paired; the right salivary gland is elongate and the left one is more ovate. The salivary ducts are slightly coiled, moderately thick, and open into the radular sac near its entrance into the buccal cavity. The odontophoral cartilages are very thin, narrow, and connected in the anterior part by a transverse muscle. There are 4 cartilages, which are united in 2 pairs. The muscular bulb of the poison gland is very large with a small lumen. The oesophagus gradually widens behind the opening of the poison gland. The stomach is of the typical U-shape and contains a single duct of the digestive gland. The radular

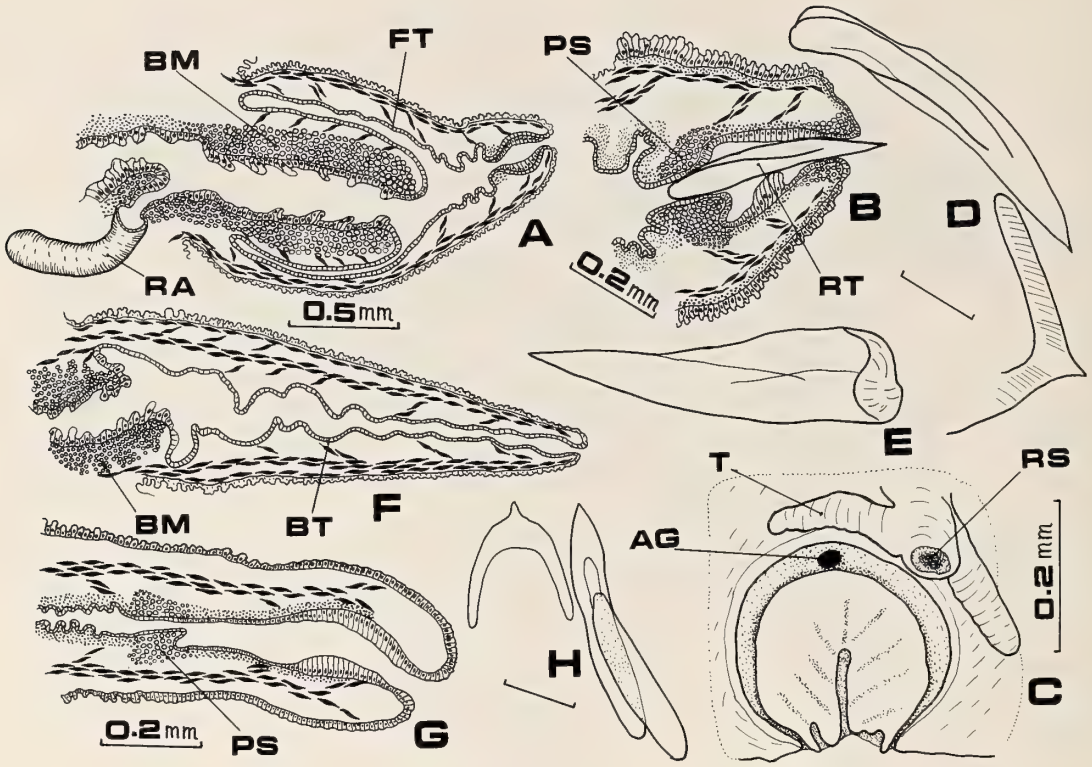


Figure 12

A–E, *Aforia* ***kupriyanovi,*** holotype. A, semidiagrammatic section of the proboscis. B, magnified tip of the proboscis. C, head and the anterior part of the foot. D, radula. E, marginal tooth in lateral projection. Scale bar for D and E = 0.1 mm. F–H, *A. aulaca* ***alaskana,*** holotype. F, semidiagrammatic section of the proboscis. G, magnified tip of the proboscis. H, radula. Scale bar = 0.1 mm. See Figure 4 for key to abbreviations.

teeth show variability based on age. The younger specimen has more short and broad marginal teeth (Figure 11E) than the older one (Figure 11F). The central tooth has one cusp which becomes sharper and longer during growth of the mollusk. The length of the marginal tooth of the specimen with the shell height of 25.7 mm is 0.30 mm, with the shell height of 39.0 mm it is 0.44 mm, and with the shell height of 74.2 mm it is 0.80 mm. The shell height–tooth length ratios are 82.9, 88.6, and 90.5 respectively.

Reproductive system: One of studied paratypes (station 3594) is an immature female. The paratype from station 5624 is a mature male. Its vesicula seminalis is very large, with numerous small loops of seminal duct. The penis (Figure 6P) is long, flattened, and sharp at the frontal edge. The male gonopore opens on a small papilla surrounded with a circular fold.

Remarks: The species is conchologically very close to *Aforia hypomela* Dall, differing in that the new species has more numerous and narrow spiral ribs, a more curved siphonal canal, different form and size of the radular teeth (for *A. hypomela* see BOUCHET & WAREN, 1980:fig. 7), and a different geographical distribution: *A. hypomela* is an Atlantic species while *A.* ***abyssalis*** sp. nov. is presently reported only from the Pacific.

Distribution: The species inhabits the lower abyssal zone of the northern Pacific at depths of 3880 to 5456 m; most records are from the northwestern Pacific.

Aforia (***Abyssaforia***) ***kupriyanovi***
Sysoev & Kantor, sp. nov.

(Figures 1C, D, 5H, 12A–E)

Material: R/V *Akademik Kurchatov,* station 240, 23°47′S, 71°03′W, (off Antofagasta, Chile), depth 4300 m, trawl Galathea, 1 specimen (holotype, No. LC 5365).

Description of holotype: The shell is of moderate size, fusiform, thin, fragile, and consists of 5.5 preserved whorls. A part of the protoconch is lost; the upper whorls are seriously eroded. The shell whorls are convex, rounded, and separated from each other by definite shallow sutures. The body whorl occupies about ¾ of the shell height. Growth lines are weak and poorly visible. The spiral sculpture consists of similar, low, cordlike, slightly wavy ribs covering all the shell surface and separated from each other

by interspaces that are 2–4 times wider than the ribs. The ribs are placed more closely to each other at the whorl periphery and more distant at the shell base. Two ribs of the periphery of the body whorl are situated on a weak eminence and look like a very poorly developed spiral keel. There are 15 ribs on the penultimate whorl and 44 on the body whorl including the canal. The aperture is wide and ovate. There is a large, low knob at the upper portion of the inner lip. The canal is long and curved. The anal sinus, judging by growth lines, is wide, deep, and rounded. The shell color is grayish white. The shell height is 26.4 mm, the body-whorl height is 19.9 mm, the aperture height is 16.2 mm, and the shell diameter is 11 mm.

The operculum is ovate; its growth axis is strongly curved.

Anatomy: The propodium is narrow, the marginal cleft is not deep, and the accessory pedal gland is situated at its middle part. Diameter of the pedal gland is about 0.25 mm. The metapodium forms small palps at both sides of the propodial base (Figure 12C). The head is elongate and well distinguished from the body. The tentacles are long and cylindrical. The rhynchostome is wide; its sphincter is large.

The mantle complex is typical for the genus. The osphradium and the gill are large, and the mantle edge forms a deep notch, corresponding to the anal sinus of the shell. The distributive valve of the siphon is small. The gill lamellae are tall, with a thickly cuticulized flagellum.

Digestive system: The proboscis is not large (Figure 12A). The buccal mass is very large; its length exceeds ½ of the proboscis length. The buccal tube forms a very long fold along the mass. The buccal tube is surrounded by a rather thick layer of circular muscles. At the tip of proboscis, the buccal tube forms a small enlargement in which a single radular marginal tooth was found to be held (Figure 12B). The tooth basal part is held by the sphincter that is situated at the base of the enlargement. Another sphincter is at the tip of the proboscis. The retractor muscles of the proboscis are rather small; they follow along the proboscis walls. The buccal tube is connected with the proboscis walls by numerous muscles. The central radular tooth has long curved blades and one broad cusp on the frontal edge. The marginal teeth are curved (Figures 12D, E), rather broad, and small (0.46 mm). The shell height–tooth length ratio is 57.4. The muscular bulb of the poison gland is large, and elongate-oval. The stomach is of the typical U-shape, containing two ducts of the digestive gland.

Remarks: The species is most similar to the abyssal species *Aforia hypomela* Dall and *A.* ***abyssalis*** sp. nov., but differs clearly by having a small shell, with rounded, strongly convex whorls, stronger spiral ribs, and a long, considerably curved siphonal canal, and different radular tooth (especially the central one) form.

Distribution: The species lives in the abyssal zone of the Peru-Chilean trench.

Subgenus ***Palaeoaforia***
Sysoev & Kantor, subgen. nov.

Type species: *Aforia campbelli* Durham, 1944.

Spiral sculpture consists of slight, narrow ribs that are smoothed on the whorl shoulder and of two strong spiral keels on the lower part of the whorl shoulder and on the shell base.

The subgenus is represented mostly by fossil species (*Aforia campbelli* Durham, 1944, *A. wardi* (Tegland, 1933), *A. addicotti* Javidpour, 1973, *A. clallamensis* (Weaver, 1916), *A. tricarinata* Addicott, 1966) reported from Oligocene and lower Miocene deposits of western North America (Javidpour, 1973). *Aforia trilix* (Watson, 1886) is the only Recent species that can be probably included in this subgenus. Nevertheless the species' taxonomic position (including its belonging to *Aforia*) at present is uncertain and needs further investigations.

An opinion on the possibility of isolating Oligocene *Aforia* as a separate subgenus was earlier expressed by Hickman (1976) based on the presence of the second keel on Oligocene shells.

DISCUSSION

General Morphology of Species of *Aforia*

Generally the organ morphology of studied systems is very similar among subgenera and species of *Aforia.* We could not find any significant differences at the subgeneric level. The digestive system manifests probably the most marked differences between species.

The rhynchodaeum, the wall of the proboscis sheath, is folded in all species; its epithelium is represented by tall secretory cells. In most species, the rhynchodaeum adheres to the wall of the body haemocoel whereas in *Aforia lepta* it is free all along its length to be connected only in places to the haemocoel wall with thin muscles. An invaginable part of the rhynchodaeum, such as is present in gastropods with a pleurembolic proboscis, is absent in *Aforia.* However, most *Aforia* species can stretch the proboscis out of the rhynchostome. This process is facilitated by secretions produced by the secretory epithelial cells lining the proboscis and the rhynchodaeum. *Aforia lepta* probably is an exception. The proboscis epithelium of this species is formed by very tall, thin, gobletlike cells (Figure 8B). It is difficult to imagine that such cells would remain undamaged during proboscis stretching and functioning in the environment. The relative small size of the proboscis, as compared to the proboscis sheath, seems also to be evidence that extension of this species' proboscis is limited only to the rhynchocoel. In all *Aforia* species, the proboscis retractor muscles are represented by several moderately thick muscle bands situated at the cavity perimeter along the proboscis lumen. The most powerful muscles are attached to the inner side of the body haemocoel wall. The retractors pass near the proboscis walls to join often with the inner (lon-

Table 2

Dependence of relative length of marginal teeth of *Aforia* radulae on depth of species habituation.

Groups of species	Depths of habituation of studied specimens (meters)	Shell height–tooth length ratio
A. circinata, A. kinkaidi	100–240	150–180
A. lepta, A. ***moskalevi,*** *A. crebristriata*	1200–3030	100–113
A. aulaca ***alaskana,*** *A.* ***kupriyanovi, A. abyssalis***	3460–5220	57–90

gitudinal) muscle layer of the proboscis wall. The retractors are always connected both with the proboscis walls and the buccal tube by numerous muscle fibers.

The buccal tube leads from the buccal mass to the mouth at the proboscis tip. In all species, the buccal tube is very thin, semitransparent and is formed by one layer of epithelial cells surrounded by a layer of circular muscles of different thickness. The possibility cannot be excluded that the buccal tube is capable of peristaltic movements. In all *Aforia* species except *A. circinata* the buccal tube forms a fold (sometimes double) directed backward along the buccal mass walls. The functional significance of this fold remains unclear. In its anterior part the buccal tube forms an enlargement of various sizes surrounded by a sphincter used for holding a single marginal tooth. The anterior part of the proboscis is capable, at least in some species, of introverting during contractions of the proboscis retractors. This is most obvious in the morphology of the proboscis tip in *A. lepta* and *A. aulaca* ***alaskana***. Retraction of the proboscis tip can be judged by the epithelium structure. The anterior part of the buccal tube in these species has the same kind of epithelium as the outer proboscis wall (Figures 8B, 12G). However, at some distance from the proboscis tip, the lining of the tube is as on the remainder of the buccal tube. We believe that this change in epithelial structure may be explained by introverting of the proboscis tip.

The size of the usually powerful buccal mass is variable in comparison with the proboscis length. The smallest relative size of the buccal mass is in *Aforia aulaca* ***alaskana*** and the largest is in *A.* ***kupriyanovi***.

The boundary line between the back part of the buccal mass and the oesophagus can be usually determined by the place of an abrupt enlargement of the digestive tube diameter near the opening of the poison gland. At that region the thick layer of circular muscles that constitute the major part of buccal mass wall becomes much thinner.

The radula is situated at the bottom of the buccal cavity. The radular sac, containing the radula frontal part and the odontophore, is connected with the buccal cavity through a relatively long and narrow duct. All species except *Aforia lepta* have more or less well developed odontophore cartilages. *Aforia circinata, A.* ***abyssalis,*** and *A.* ***moskalevi*** have four cartilages which lie symmetrically, two on each side of the odontophore. At the anterior part of the odontophore, the cartilages of each pair join and a thick, muscular symphysis connects the two newly formed cartilages. The radula bends over this symphysis. *Aforia crebristriata* has only two cartilages, which join in the anterior part of the odontophore. This species also has the largest cartilages (Figure 10B). *Aforia lepta* lacks the cartilage tissue but has a thick transverse muscle over which the radula bends. Relatively good development of the odontophore and the muscles connected with it seems to indicate that radular mobility is sufficient to allow the odontophore to protrude into the buccal cavity. The inner cavity of the anterior part of the radular sac is lined with a thick cuticular layer which prevents damage to the walls during radula movements.

The morphology of the radular marginal teeth was studied with the scanning electron microscope. Each tooth appears to consist of two parts or plates (Figures 3D, 4B–D) which are free at the base of the tooth and flow together at its tip. One of them has a thin ligament by which the tooth is connected with the radular membrane. Sections of the tooth show that in the proximal part both plates are also connected with a cuticular membrane (Figure 4C). The upper plate of the tooth is more rounded and the lower one is crescent-shaped. These plates and the membrane are differently stained by Mallory: the formers are bright orange and the latter is dark blue. The plates and membrane form a groove along both sides of the tooth. The relative length of the marginal tooth (the shell height–tooth length ratio) varies markedly among species, from 57 (*A.* ***kupriyanovi***) to 180 (*A. circinata*). By comparing this ratio with the bathymetric distribution of the species, one can see that tooth length increases with the transition from sublittoral to bathyal and to upper and lower abyssal species (Table 2).

The poison gland is long, well developed, and powerful in all species; it forms tight convolutions. The gland opens approximately at the border between the buccal mass and the oesophagus and rather distant from the opening of the radular sac into the buccal cavity. This may indicate that all of the inner cavity of the proboscis is filled with poisonous liquid. The size of the muscular bulb varies: *Aforia lepta* has the smallest one, *A.* ***abyssalis*** has the largest one, and the muscular bulbs of *A. crebristriata* and *A.* ***moskalevi*** are of medium size. All species have a rather small lumen in the bulb, usually adjacent to the opening of the poison gland. The walls of the muscular bulb are formed by two layers of muscles, longitudinal and circular, which are not separated by an intermediate layer of connective tissue as in Conidae (Hyman, 1967).

All *Aforia* species have large salivary glands situated under the nerve ring. In *A. circinata, A.* ***moskalevi,*** and *A. crebristriata,* the glands are united into a single mass. The salivary ducts are always paired and weakly coiled.

They open into a duct connecting the radular sac with the buccal cavity. Proximal parts of the salivary ducts run within the wall of the buccal cavity. Most parts of the ducts are lined with a ciliary epithelium, which provides transport for the gland secretion. As the duct opening is approached, the ciliary epithelium is replaced by a smooth one.

All *Aforia* species have differently developed rhynchostomal lips, which are rounded muscular folds forming a kind of funnel at the anterior side of the head. The rhynchostome has a large powerful sphincter obviously used in catching prey.

Other systems of organs of studied *Aforia* species are the same as in other families of neogastropods. Morphology of the mantle complex is similar in all species and is characterized by substantial development of the gill and the osphradium. The large sizes of the mentioned organs may be conditioned by a low density of food resources at great depths and by the necessity of an active mode of life. This requires (1) high oxygen consumption, which is provided by a large gill, and (2) the necessity of well-developed chemoreception, which demands a considerable development of the osphradium (KANTOR & SYSOEV, 1986).

Functional Analysis of Morphology of the Digestive System

Recently, many authors have paid attention to morphofunctional specializations of the digestive system of Turridae (SMITH, 1967; SHIMEK, 1975; SHERIDAN *et al.*, 1973; SHIMEK & KOHN, 1981). Most important is the examination of the anterior part of the digestive system and radula, which are the most variable among turrids. Morphological and functional types of turrid radulae were analyzed by SHIMEK & KOHN (1981). According to the classification proposed by those authors, *Aforia,* like other representatives of the subfamily Turriculinae, has a slicing radula used for tearing the prey body. The radulae of all other Turridae, with well-developed subradular membranes and mainly with "nontoxoglossate" solid marginal teeth, are classified as slicing, slicing-rasping, and slicing-stabbing types of radulae.

However, the functional types of "nontoxoglossate" radulae and the correspondent mechanisms of functioning proposed by Shimek & Kohn cannot explain many facts. The buccal mass with radula is situated at the base of the proboscis in all Toxoglossa and cannot be moved out through the mouth as in other prosobranchiate gastropods. Therefore, slicing the prey as supposed by Shimek & Kohn can take place only in the buccal cavity after the prey is already caught and partially swallowed. In this connection, the presence of a well-developed, large poison gland in "nontoxoglossan" Turridae cannot be explained, because envenomation of the prey inside the buccal cavity would seem useless. On the other hand, the poison gland disappears during reduction of the radula, and prey capture by species with a reduced radula occurs with the help of proboscis or enlarged rhynchostomal lips (KANTOR & SYSOEV, 1986). Using the classification of SHIMEK & KOHN (1981) it is impossible to explain the functioning of such a specialized radula as in *Imaclava unimaculata* (subfamily Clavinae) which has true "toxoglossate" hollow marginal teeth along with a central one and well-developed laterals. It is difficult to imagine the mechanism by which poison would be passed through the hollow marginal tooth or its usefulness, as soon the buccal cavity would be filled with the poisonous liquid. MAES (1983) has also put forward reasonable doubts about the slicing function of Clavinae radulae. She considered that the radula of *Drillia cydia* is used not for tearing but for holding and perforating the prey, a fact confirmed by finding almost intact polychaetes in the mollusk's stomach.

Thus, the hypothesis of a "slicing" or "slicing-stabbing" function of turrid radulae possessing a well-developed subradular membrane is not in agreement with many data.

In this connection, the findings of single marginal teeth held by a sphincter of the proboscis tip in three *Aforia* species (*A.* ***moskalevi***, *A.* ***kupriyanovi***, and *A.* ***abyssalis***) is of great interest. Morphology of the distal part of the proboscis of other species also confirms the possibility that the marginal tooth is held by the sphincter. The only possible explanation of the fact is that marginal teeth, removed from the subradular membrane in the sublingual pouch during radular degeneration, are used at the proboscis tip for stabbing prey and poisoning them with poisonous liquid in a fashion similar (but not identical) to that used in higher Toxoglossa. Grooves running along both sides of the tooth (see above) could be used for administering the poison. Thus, the radula of *Aforia* species has two functions. The first is to stab the prey with the single marginal tooth at the proboscis tip and to use the radula as a whole in the buccal cavity. The second function is to a great extent unclear for *Aforia.* It is possible that the radula, which can move out to some extent into the buccal cavity, is used to move the prey from the buccal cavity to the oesophagus and probably for damaging the prey tissues. In particular, this second function is confirmed by the structure of the central tooth, which has one rather large cusp on the frontal edge.

One can suppose that using the marginal teeth at the proboscis tip is almost universal among turrids with a well-developed subradular membrane. The fact is confirmed by our finding of a marginal tooth at the tip of the proboscis of *Splendrillia* sp. (subfamily Clavinae). The function of the hollow marginal tooth of *Imaclava unimaculata* also becomes obvious: the mollusk uses it at the proboscis tip as higher Toxoglossa do.

Evolution of the radular apparatus is closely associated with the evolution and morphology of the proboscis. SMITH (1967) described a new type of proboscis of prosobranch gastropods, an intraembolic one characterized by circular folds formed by proboscis walls in their contracted state. When describing the buccal apparatus of *Oenopota levidensis,* SHIMEK (1975) advanced the notion of the intraem-

bolic proboscis and postulated that its principal feature was the existence of a permanent rhynchodaeum; this means that not the whole rhynchodaeum of the intraembolic proboscis participates in the proboscis everting. However, in many gastropods with a pleurembolic proboscis, even when the proboscis is completley everted a part of the rhynchodaeum remains inside. A special subtype of pleurembolic proboscis, the extraembolic type, was proposed for gastropods in which the whole rhynchodaeum takes part in the proboscis eversion and the proboscis sheath is absent during the complete eversion of the proboscis (KANTOR, 1985).

Investigation of the proboscis morphology of several species of *Aforia* allows us to state that all species of the genus lack an invaginable part of the rhynchodaeum; that is, everting of the proboscis results only from its stretching. Comparison of *Aforia* with other turrids leads to a conclusion that the main characteristics of the intraembolic proboscis are the absence of the invaginable part of the rhynchodaeum and the localization of the buccal mass at the proboscis base.

Differences in the displacement of the buccal mass are the most important differences between the intraembolic and pleurembolic probosces as well as between rachiglossan and toxoglossan neogastropods in general. In fact, during the origination of the proboscis by elongation of the ancestral form snout, the elongation of the anterior oesophagus in front of the nerve ring occurred in rachiglossan families while elongation of the buccal tube connecting the buccal cavity with the mouth occurred in toxoglossan groups (PONDER, 1973). Thus, the two proboscis types have different origins and are not homologous. Formation of concentric telescopic folds within the walls of the intraembolic proboscis serve to enhance its elongation.

The origin of the intraembolic type of proboscis may be connected with the origin and development of the poison gland. This process may be presented in the following way: the poison gland that appeared in the toxoglossan ancestor at the first stages of evolution was closely associated with the radular apparatus. Probably the efficiency of the poison gland and the poison itself was much lower than in modern species. This required maximal proximity of the administered poison to the radula that was damaging the prey tissue. At the same time elongation of the proboscis and the appearance of the poison gland allowed "distant feeding" on actively moving prey. Elongation of the proboscis appears to be closely related to poison gland enlargement; as the inner volume of the proboscis grew, more poison was needed to fill it. Formation of a powerful poison gland, which already did not fit the proboscis, prevented the gland from everting together with the proboscis. At the same time, distancing the radular apparatus from the opening of the poison gland hampered the use of the poison. This caused, in turn, fixation of the buccal mass at the proboscis base. Most probably during that period of evolution the mechanism developed of using marginal teeth at the proboscis tip for stabbing the prey. Using the marginal teeth at the proboscis tip did not require any considerable morphological changes of the anterior part of the digestive apparatus: in all prosobranch gastropods, the subradular membrane degenerates in the sublingual pouch and worn teeth are removed via the digestive tract. By contrast in toxoglossan gastropods, teeth that separate from the subradular membrane are transferred to the proboscis tip where they were held by the sphincter. Using the single tooth at the proboscis tip allowed a considerable elongation of the proboscis because the function of stabbing the prey was no longer associated with the radular apparatus per se. Therefore, the appearance of the intraembolic proboscis is associated with the appearance of the poison gland, transition to "distant feeding" on actively moving animals, and using the marginal tooth at the proboscis tip.

If the proposed scheme of evolution of the anterior digestive apparatus is adopted, one can easily understand also the appearance of the typically "toxoglossan" mode of feeding as in higher Turridae and Conidae which possess only hollow marginal teeth acting as a syringe needle. As the proboscis elongated, the main radular function became stabbing the prey with the individual tooth at the proboscis tip. This led to reduction of the odontophore and, consequently, of the subradular membrane. Thus, *Aforia* is a kind of intermediate morphological stage transitional to the typical "toxoglossate" forms. However, *Aforia* cannot be considered as an intermediate evolutionary stage because modern turrids with a well-developed subradular membrane often are more numerous than the typical toxoglossan forms; "nontoxoglossate" turrids should be considered as a result of evolution of a separate evolutionary line (or lines), which is not the same as that resulting in "true toxoglossates." Probably, use of the radula not only at the proboscis tip but also in the buccal cavity has some advantages. If the radula were not used in the buccal cavity it would be difficult to explain the existence of numerous species of the subfamily Clavinae having, besides marginal teeth, also central and large, powerful lateral teeth.

The mechanism of transporting the tooth from the radular sac to the proboscis tip in *Aforia* is presently unclear. Pushing the tooth, separated from the membrane, into the buccal cavity occurs probably by the contraction of the powerful circular musculature of the radular sac. Transportation of the tooth to the proboscis tip may occur along with the flow of poisonous liquid during contraction of the muscular bulb or also by peristaltic movements of circular muscle fibers of the buccal tube. The position of the proboscis sphincter and the length of the marginal tooth are correlated so that the tooth, held at its base by the sphincter, extends outside the proboscis. In this connection it is interesting to analyze the morphology of the proboscis tip of *A. aulaca* ***alaskana*** (Figure 12G). If one supposes that the well-developed sphincter of the buccal tube is intended to fix the tooth base, then the point of the tooth would not protrude outside the proboscis. As has been mentioned above, in this species, the proboscis tip can be everted and after eversion the tooth point appears to be protruded outside. One can propose that such a mechanism was developed to protect the rhynchodaeum during eversion of the proboscis with the already held tooth and also to protect

the tooth itself, as searching for prey is probably carried out by a sense of touch of the proboscis tip. Transportation of the tooth from the radular sac to the proboscis tip most probably occurs at the moment of drawing the proboscis into the rhynchodaeum because in this case the distance from the buccal mass to the proboscis tip is much less than that in the everted proboscis.

History of the *Aforia* Fauna

The genus under consideration is closest to the genera *Leucosyrinx* Dall, 1889, *Comitas* Finlay, 1926, *Parasyrinx* Finlay, 1924, and *Turrinosyrinx* Hickman, 1976. These genera are apparently interrelated and have a common ancestor.

The earliest certain findings of fossil species of *Aforia* are known from the Oligocene. From the upper Oligocene of northwestern North America, a rather diverse fauna of *Aforia,* consisting of four species, has been recorded (Javidpour, 1973). At present, a single finding of a Paleogene species is known from the northwestern Pacific. The species related to *A. clallamensis* (Weaver, 1916) was found, according to unpublished data of V. N. Sinelnikova and A. E. Oleynik, in deposits of western Kamchatka (Rategin suite). However, dating of this suite currently is rather uncertain (upper Eocene or upper Oligocene—A. E. Oleynik, personal communication).

Apparently the geographical center of the species diversity is the northern Pacific, with the most intensive formation of species being in its northeastern region. This is evident both from the relatively high diversity of fossil *Aforia* species in this region and from the fact that the highest morphological diversity of recent species is from the Pacific coast of North America, the only region where representatives of all the subgenera live.

Recent species of *Aforia* demonstrate an association with low water temperatures, living generally in bathyal and abyssal zones and rising into shallow waters only in high boreal and Antarctic regions. One can confidently consider that life in cold waters was characteristic of this genus during all of its history and that adaptation to cold water has conditioned the formative history of the recent fauna of the genus.

The first Cenozoic phase of colder climates in the northern Pacific began in the second part of the Eocene (Kafanov, 1982). Precisely in this period, formation of the genus began. The temperature minimum was most pronounced in the middle Oligocene (Kafanov, 1982), and, after achieving it, various and numerous upper Oligocene *Aforia* fauna developed. However, some warming of the climate in the northeastern Pacific began later in the Oligocene (Wolfe & Hopkins, 1967), reaching its maximum in the northern Pacific at the end of the early or beginning of the middle Miocene (Kafanov, 1982). These facts are well correlated with the disappearance of most of *Afloria* species at the border between the Oligocene and Miocene in fossil formations of the northwestern part of the U.S.A., with the single species being recorded at the very early Miocene (Javidpour, 1973). Apparently this disappearance was related to the leaving of *Aforia* species for bathyal and abyssal regions of the northern Pacific. Representatives of the deep-sea Miocene fauna are not known, but a reason exists that forces us to consider that there was a rather well-developed deep-sea fauna of *Aforia* in the Miocene. At present there are two closely related species living in the abyssal regions of the northern Pacific and northern Atlantic respectively—*A.* ***abyssalis*** and *A. hypomela.* Obviously these two species are relicts of the early Miocene deep-sea fauna of Central America. Geographical separation of the species resulted from the forming of the central American isthmus and the closing of the deep-sea connection between the Pacific and the Atlantic, which are dated to the middle Miocene (for a review of this subject see Nesis, 1985).

One can suppose that, precisely in the Miocene, migrations of bathyal species began southward along the Pacific coast of North and South America. Similar migrations have been reconstructed in the geological history of many other groups of animals (Nesis, 1985). Presently, the movement of *Aforia* representatives southward is traced by the distribution of recent bathyal and abyssal species and subspecies from the eastern Pacific (Powell, 1951; present data).

The late Miocene Nuvok transgression (Kafanov, 1982) has led to the forming of a connection between the north Pacific and Polar basins, which in turn caused a cooling of the climate. In this respect, a gradual rising of *Aforia* species to more shallow zones, including the western Pacific, began during the Pliocene. An earlier Pliocene finding of *Aforia* is recorded from the Tomya Formation of Honshu (Otuka, 1949) which is characterized by a relatively deep-sea (bathyal) fauna (Okutani, 1968). Also at the Pliocene *A. circinata* appears on the shelf of the Gulf of Alaska (Javidpour, 1973) and in deposits of eastern Kamchatka (Petrov, 1982). Thus, just at the Pliocene, the fauna of *Aforia* obtained its principal features of its Recent appearance and distribution.

The rising of a part of the species to shallow but cold zones took place also in the southern Pacific. Some Antarctic species that migrated from the northern Pacific along the American coast have settled in the shallow zone for a second time, rising up to the sublittoral. The rising of *Aforia* species to shallow waters in Antarctic regions, while species distributed in tropical and subtropical latitudes retained their relation within deep-sea habits, has been analyzed in detail by Powell (1951).

Presently the main part of *Aforia* species live in the Pacific, being distributed almost circumoceanically except for the western Pacific (Rukue Islands at the north to Macquarie Island at the south). A single species (*A. hypomela*) is recorded from the northern Atlantic and two species (*A. gonioides* and *A. magnifica*) penetrate into the southwestern Atlantic. Another two species penetrate also into the southern part of the Indian Ocean (*A. lepta* and *A. staminea*). Most species show a near-continental distribution.

ACKNOWLEDGMENTS

We wish to express our cordial thanks to Dr. L. I. Moskalev and V. Ya. Lus (Institute of Oceanology of the U.S.S.R. Academy of Sciences) and to Dr. V. N. Goryachev (Zoological Museum of Moscow State University) for their kind assistance in access to material for study. An incalculable help in carrying out the histological study was given to us by Dr. S. Kupriyanov (Institute of General Genetics of the U.S.S.R. Academy of Sciences) and Dr. S. V. Saveljev (Institute of Human Morphology of the U.S.S.R. Academy of Sciences). We are also greatly indebted to Dr. V. N. Sinelnikova and A. E. Oleynik (Geological Institute of the U.S.S.R. Academy of Sciences) for consultations on fossil species.

We also wish to thank Dr. David W. Phillips, Editor of *The Veliger* for assistance with the manuscript.

LITERATURE CITED

BARTSCH, P. 1945. The west Pacific species of the molluscan genus *Aforia*. Jour. Wash. Acad. Sci. 35(12):388–393.

BOUCHET, P. & A. WAREN. 1980. Revision of the north-east Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). Jour. Moll. Stud. Suppl. 8:1–119.

CANTERA, J. R. & P. M. ARNAUD. 1984. Les Gasteropodes Prosobranches des iles Kerguelen et Crozet (sud de l'ocean Indien). Comparaison ecologique et particularities biologiques. Comit. Nat. Franc. Rech. Antarct. 56:1–169.

CERNOHORSKY, W. O. 1972. Comments on the authorship of some subfamilial names in the Turridae. Veliger 15(2):127–128.

DALL, W. H. 1896. Diagnoses of new species of mollusks from the west coast of America. Proc. U.S. Natl. Mus. 18(1034): 7–20.

DALL, W. H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos .... XXXVIII. Reports on the scientific results of the expedition to the eastern tropical Pacific .... XIV. Reports on the Mollusca and Brachiopoda. Bull. Mus. Compar. Zool. 43(6): 205–487.

GRANT, U. S. & H. R. GALE. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Mem. San Diego Soc. Natur. Hist. 1:477–612.

HICKMAN, C. S. 1976. Bathyal gastropods of the family Turridae in the early Oligocene Keasey formation in Oregon with review of some deep-water genera in the Paleogene of the eastern Pacific. Bull. Amer. Paleontol. 70(292):1–119.

HYMAN, L. H. 1967. The Invertebrates. Vol. 6: Mollusca I—Aplacophora, Polyplacophora, Monoplacophora, Gastropoda. McGraw-Hill Book Co.: New York. 792 pp.

JAVIDPOUR, M. 1973. Some records on west American Cenozoic gastropods of the genus *Aforia*. Veliger 15(3):196–205.

KAFANOV, A. I. 1982. Cenozoic history of malacofauna of the north Pacific shelf. Pp. 134–175. *In:* Marine biogeography. Nauka: Moscow [in Russian].

KANTOR, YU. I. 1985. Feeding and some features of functional morphology of the molluscs in the subfamily Volutopsiinae (Gastropoda, Pectinibranchia). Zool. Zhurn. 64(11):1640–1647 [in Russian].

KANTOR, YU. I. & A. V. SYSOEV. 1986. New species of the family Turridae from the northern part of the Pacific ocean. Zool. Zhurn. 65(4):485–498 [in Russian].

MAES, V. O. 1983. Observations on the systematics and biology of a turrid gastropod assemblage in the British Virgin Islands. Bull. Mar. Sci. 33:305–335.

MCLEAN, J. H. 1971. A revised classification of the family Turridae, with the proposal of new subfamilies, genera and subgenera from the eastern Pacific. Veliger 14(1):114–130.

MCLEAN, J. H. 1971. Family Turridae. Pp. 686–766. *In:* A. M. Keen, Sea shells of tropical West America, marine mollusks from Baja California to Peru. 2nd ed. Stanford Univ. Press: Stanford, California.

NESIS, K. N. 1985. Oceanic cephalopod molluscs. Nauka: Moscow. 286 pp. [in Russian].

OKUTANI, T. 1968. Systematics, ecological distribution and palaeoecological implication of archibenthal and abyssal Mollusca from Sagami Bay and adjacent areas. Jour. Fac. Sci., Univ. Tokyo, sect. II 17(1):1–98.

OTUKA, Y. 1949. Fossil Mollusca and rocks of the Kigosumi group exposed at Minato-machi, Chiba Prefecture, and its environs (1st paper). Japan. Jour. Geol. Geogr. 24(1–4): 295–309.

PARKER, R. H. 1964. Zoogeography and ecology of some macro-invertebrates, particularly mollusks, in the Gulf of California and continental slope off Mexico. Viddensk. Medd. Dansk. Naturh. Foren 126:1–178.

PETROV, O. M. 1982. Marine molluscs of the anthropogene from the northern region of the Pacific. Trudy Geologicheskogo in-ta AN SSSR (Proc. Geol. Inst. USSR Ac. Sci.) 357:1–143 [in Russian].

PONDER, W. F. 1973. Origin and evolution of the Neogastropoda. Malacologia 12(2):295–338.

POWELL, A. W. B. 1942. The New Zealand recent and fossil Mollusca of the family Turridae with general notes on turrid nomenclature and systematics. Bull. Auckland Inst. Mus. 2: 1–192.

POWELL, A. W. B. 1951. Antarctic and subantarctic Mollusca. Pelecypoda and Gastropoda. Discovery Rept. 26:47–196.

POWELL, A. W. B. 1966. The molluscan families Speightiidae and Turridae. Bull. Auckland Inst. Mus. 5:1–184.

POWELL, A. W. B. 1969. The family Turridae in the Indo-Pacific. Part 2. The subfamily Turriculinae. Indo-Pacific Mollusca 1(7):207–416.

ROKOP, F. J. 1972. Notes on abyssal gastropods of the eastern Pacific, with description of three new species. Veliger 15(1): 15–20.

SHERIDAN, R., J.-J. VAN MOL & J. BOUILLON. 1973. Etude morphologique du tube digestif de quelques Turridae (Mollusca—Gastropoda—Prosobranchia—Toxoglossa) de la region de Roscoff. Cah. Biol. Marine 14:159–188.

SHIMEK, R. L. 1975. The morphology of the buccal apparatus of *Oenopota levidensis*. Ztr. Morphol. Tiere 80:59–96.

SHIMEK, R. L. & A. J. KOHN. 1981. Functional morphology and evolution of the toxoglossan radula. Malacologia 20(2): 423–438.

SMITH, E. H. 1967. The proboscis and oesophagus of some British turrids. Trans. Roy. Soc. Edinburgh 67(1):1–22.

WATSON, R. B. 1881. Mollusca of H.M.S. "Challenger" expedition. Part 8. Jour. Linn. Soc. 15:388–412.

WATSON, R. B. 1886. Reports on the Scaphopoda and Gastropoda collected by H.M.S. "Challenger" during the years 1873–76. Rept. Sci. Res. Challenger Exped., Zool. 42:1–756.

WOLFE, J. A. & D. M. HOPKINS. 1967. Climatic changes recorded by Tertiary land floras in northwestern North America. Pp. 67–76. *In:* Proc. 11th Pacific Sci. Congr., Symp. 25. Tokyo, 1966. Sasaki: Sandai.

The Veliger 30(2):127–133 (October 1, 1987)

THE VELIGER

The Effects of Aggregation and Microhabitat on Desiccation and Body Temperature of the Black Turban Snail, *Tegula funebralis* (A. Adams, 1855)

by

KAREN E. MARCHETTI

University of California, Bodega Marine Laboratory, Box 247, Bodega Bay, California 94923, U.S.A.

AND

JONATHAN B. GELLER[1]

Bodega Marine Laboratory[2], Box 247, Bodega Bay, California 94923, U.S.A. and
Department of Zoology, University of California, Berkeley, California 94720, U.S.A.

Abstract. We studied the roles of aggregative behavior and microhabitat differences in reducing desiccation of the rocky intertidal prosobranch gastropod *Tegula funebralis* (A. Adams, 1855) at Bodega Bay, California. Solute concentration of extra-corporeal water (ECW) was measured as an indication of desiccation through evaporative water loss. In the majority of field collected samples, aggregated *Tegula funebralis* had lower ECW solute concentrations than solitary individuals. In laboratory experiments, smaller individuals desiccated faster. In the field, microhabitats had a large influence on desiccation stress: both aggregated and solitary individuals in protected microhabitats during times of exposure had lower solute concentrations than individuals in exposed microhabitats. Microhabitat differences had no effect on body temperature, but aggregated snails were significantly cooler.

INTRODUCTION

Organisms inhabiting the rocky intertidal zone are continuously subject to a variety of physical stresses. During each tidal cycle, these organisms may be subject to conditions of essentially a terrestrial environment (DAVIES, 1969; VERNBERG & VERNBERG, 1972). Evaporative water loss upon exposure to wind and solar radiation may result in high levels of desiccation. Behavioral and physiological adaptations to desiccation are therefore important for survival in the rocky intertidal environment (GARRITY, 1984).

The purpose of this study was to investigate the effects of aggregative behavior on desiccation and body temperature in *Tegula funebralis* (A. Adams, 1855), and some of the factors influencing this behavior. *Tegula funebralis,* the black turban snail, is a common middle intertidal gastropod occurring from Vancouver Island, British Columbia, to Central Baja California (MORRIS *et al.,* 1980). Although its spatial distribution has been studied (see, for example, WARA & WRIGHT, 1964; PAINE, 1969; FAWCETT, 1984), little attention has been given to the aggregative behavior of this species and its possible role in reducing desiccation stress.

We examined this question by comparing extra-corporeal water (ECW) samples from aggregated and solitary snails. Extra-corporeal water, held within the mantle cavity, is a source of evaporative water loss in exposed snails. WOLCOTT (1973) showed that, for limpets, mortality during low tide exposure is associated with concentration of internal fluids resulting from evaporative water loss.

Microhabitat choice by snails may also play an important role in avoiding desiccation (GARRITY, 1984). It was therefore our further intent to investigate the relative importance of aggregation and microhabitat selection in reducing desiccation stress.

[1] Author for correspondence.
[2] Address for correspondence.

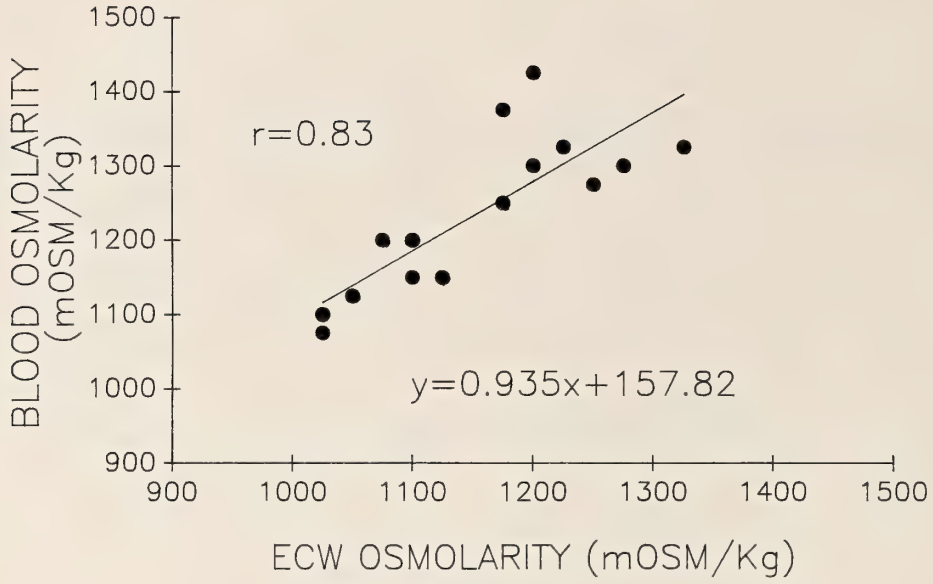


Figure 1

Relationship between blood osmolarity and extra-corporeal water osmolarity in *Tegula funebralis*. The plotted line and equation are the linear regression of these variables.

MATERIALS AND METHODS

This study was conducted during April and May 1986, on the Bodega Marine Life Reserve, Sonoma County, California. Laboratory studies were conducted at the Bodega Marine Laboratory. Field data were collected during low tides, at a tidal level of approximately 1.5 m above mean lower low water. Temperature, wind conditions, and time of day differed during collection of field data, but conditions were qualitatively similar. The substratum was heterogeneous, consisting of bare flat rock, crevices, and various degrees of algal cover (mainly *Endocladia muricata* [Postels and Ruprecht, 1840], *Pelvetiopsis limitata* Gardner, 1910, and *Porphyra* sp.). SUTHERLAND (1970) and WOLCOTT (1973) provide further details of the study site.

Field Studies

To use ECW as a measure of desiccation, it was first necessary to determine that *Tegula funebralis* is isoosmotic with its aqueous environment, and that osmolarity of internal fluids increases with increasing osmolarity of ECW. To confirm this relationship, we collected snails from the field and placed them in the sun for various lengths of time. This allowed testing over a wide range of evaporative water loss. Extra-corporeal water samples were collected by pressing lightly on the operculum with a capillary tube (0.9 mm diameter), allowing a small amount of ECW to be drawn into the tube as the snail withdraws and ECW is forced out of the mantle cavity. Capillary tubes were immediately plugged with plasticene clay, to prevent further evaporation of samples.

Blood samples were taken by removing individuals from their shells, pat-drying any residual ECW, and cutting the foot with a razor blade. A blood sample large enough for analysis could then be drawn by placing a small capillary tube (0.5 mm diameter) into the laceration and applying pressure to the foot. For each snail, 8 μL samples of both blood and ECW were analyzed using a Wescor 5130 C vapor pressure osmometer. Solute concentration (osmolarity) was measured in milli-osmoles per kilogram (mOsm/kg) blood or ECW.

Extra-corporeal water was sampled in the field in order to compare differences in extent of desiccation between aggregated and solitary *Tegula funebralis*. Sampled aggregations always consisted of at least 10 individuals, each in contact with at least one other snail. In the first trials, solitary individuals sampled were always within 30 cm of a given sampled aggregation, and at least 5 cm away from any other snail, following the criteria of GALLIEN (1985). This procedure assured that aggregated snails and surrounding solitary snails were from the same microhabitat. Seven sets of aggregations and nearby solitary snails were sampled. As a measure of size, the greatest shell width was recorded for each individual.

A second set of field samples tested the effect of microhabitat on level of desiccation. Extra-corporeal water samples were taken from snails within two distinct microhabitats: exposed (bare rock with no crevices) and protected (containing crevices and[or] algal cover). Temperatures of all individuals in the second field sampling were also measured using a Keithly 870 K-type thermocouple thermometer. The probe was placed against the foot, and the snail was allowed to retract into its shell, pulling the probe into the mantle cavity. Snails were in contact with only the

Table 1

Two-way analysis of variance testing the effects of different field sites and aggregation on extra-corporeal water solute concentration in *Tegula funebralis*. (Significance levels: ** $P < 0.01$; *** $P < 0.001$.)

Source	SS	DF	MS	*F*-ratio
Site	59,640.2	6	9940.0	3.2**
Aggregation	92,685.1	1	92,685.1	29.2***
Site × aggregation	64,878.2	6	10,813.0	3.4**

probe for the duration of the reading, with minimal contact with fingers which may warm the snail.

Laboratory Studies

The effect of aggregative behavior on decreasing desiccation stress was also examined in the laboratory. Artificial aggregations consisted of seven snails, five of which were randomly chosen to be sampled for ECW. Both solitary snails and artificial aggregations of small (9–12 mm) and medium sized (16–18 mm) snails were placed in 4-cm diameter cells in a plastic tray while being desiccated. Owing to their size, solitary snails and artificial aggregations of large (22–25 mm) snails were placed in larger 4.5 × 5.5-cm rectangular cells while desiccating. Snails were restrained in cells by a cover of 10-mm mesh nylon netting. Snails were desiccated under two lightbulbs (75 and 100 W) situated 35 cm almost vertically above them. Air was moved over the snails by placing a household electric fan 65 cm vertically above them. Ten aggregated individuals and 10 solitary individuals were sampled every hour for six hours. Measures of osmolarity and temperatures were recorded as an indication of level of desiccation stress. A different set of snails was used for each period of time.

Stress resulting from desiccation was assayed in a second group of snails (all 16–18 mm; desiccated for 4, 6, and 8 hr) by measuring the amount of time necessary for the individual to fully emerge from its shell, adhere to the container, and resume function of cephalic tentacles upon rehydration in normal seawater. For brevity, this behavior is henceforth referred to as emergence. Osmolarity of ECW was sampled before testing for time of emergence: these values were used as a further measure of desiccation.

Behavioral Tests

We examined two potential cues that may be involved in the aggregative behavior of *Tegula funebralis*. First, in order to determine possible preference for light or dark substrata, eight snails were placed uniformly (one per square; see below) in a 19 × 30 × 4-cm pan containing a checkerboard pattern of alternating black and white 9 × 5-cm squares. Locations of snails were noted after 30 min

Table 2

Analyses of covariance (snail size as covariate) testing the effects of aggregation and snail size on desiccation of *Tegula funebralis* as measured by solute concentration of extra-corporeal water. Snails were measured in seven sites on two consecutive days. Differences in slope for aggregated and solitary snails were tested before ANCOVA was performed: slopes within sites were not different except for site 6. (Significance levels: * $P < 0.05$; ** $P < 0.01$; ns, $P > 0.05$.)

Source	SS	DF	MS	*F*-ratio
Site 1				
Aggregation	1396.3	1	1396.3	0.55ns
Size	2160.7	1	2160.7	0.86ns
Residual	68,005.9	27	2518.7	
Site 2				
Aggregation	52,285.0	1	52,285.0	6.14*
Size	9707.7	1	9707.7	1.14ns
Residual	136,293.9	16	8518.4	
Site 3				
Aggregation	2889.4	1	2889.4	5.67*
Size	108.7	1	108.7	0.21ns
Residual	11,210.2	22	509.6	
Site 4				
Aggregation	7093.9	1	7093.9	2.36ns
Size	11,762.1	1	11,762.1	3.91ns
Residual	51,112.9	17	3006.6	
Site 5				
Aggregation	14,858.6	1	14,858.6	8.84**
Size	648.6	1	648.6	0.39ns
Residual	36,995.6	22	1681.6	
Site 6				
Aggregation	41,234.5	1	41,234.5	23.4***
Size	27,555.8	1	27,555.8	15.6**
Aggregation × size	23,625.8	1	23,625.8	13.4**
Residual	38,746.9	22	1761.2	
Site 7				
Aggregation	16,576.2	1	6576.2	6.6*
Size	8825.9	1	8825.9	3.5ns

(little movement was observed after this period). Twenty trials of this test were performed, and each individual snail was tested only once.

Secondly, we examined the role of mucus trail following in the formation of aggregations. The following experiment tested whether snails will choose to follow a conspecific mucus trail regardless of substrate color, or move to dark substrata regardless of the presence or absence of a mucus trail. Mucus trails were created by allowing one snail to move freely on a 19-cm diameter clear plastic sheet placed in a 19-cm petri dish divided into four equal-sized alternating black and white quadrants. This plastic disk could then be rotated such that the trail led to a white or a black

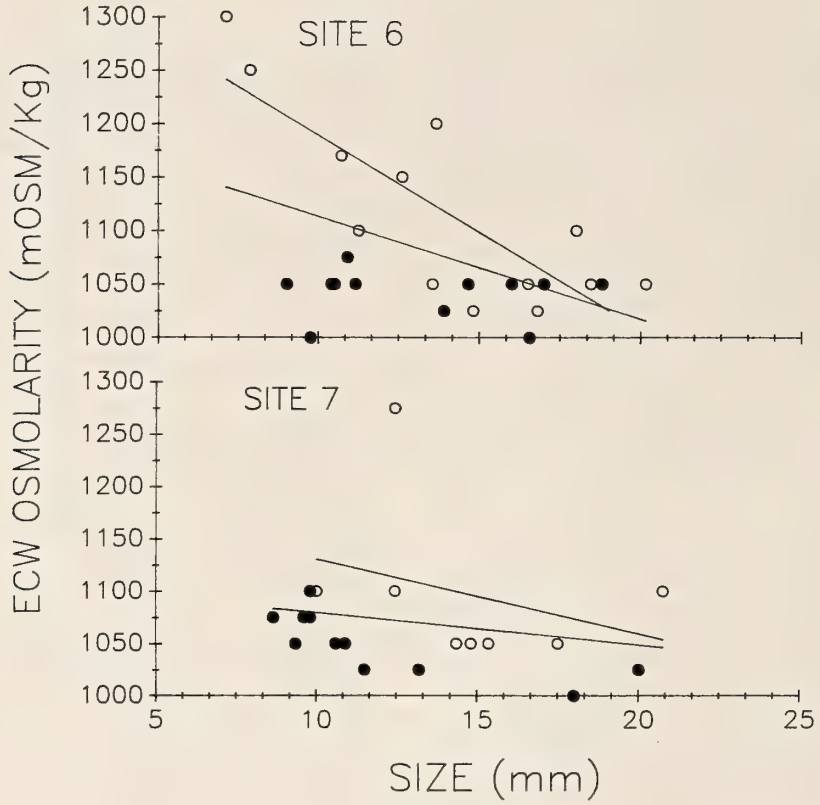


Figure 2

Relationship between snail size and osmolarity of extra-corporeal water of aggregated snails (solid circles and bottom line) and solitary snails (open circles and top line) snails. In site 6 (top graph), slopes are significantly different; in site 7 (bottom graph), slopes are not different but solitary snails are significantly more desiccated (see Table 2).

quadrant. For each mucus trail, a second snail was tested with the trail leading to a dark quadrant, and a third snail was tested with the trail leading to a white quadrant. This procedure was repeated 24 times.

RESULTS

Field Studies

The validity of extra-corporeal water as an indirect measure of blood concentration, and therefore desiccation, was confirmed (Figure 1). Results of a linear regression revealed that solute concentration (Y) of blood increased with that of ECW (X) ($r = 0.83$; $Y = 0.935X + 157.82$; $n = 18$, $P < 0.001$).

A preliminary two-way analysis of variance (ANOVA) of the results from the first field samples indicated significant differences in solute concentration among the seven sites and between solitary and aggregated individuals (Table 1). For easier interpretation, separate analyses of covariance (ANCOVA) were performed for each site, with snail size as the covariate. The results of these analyses are presented in Table 2, and representative data are shown in Figure 2. In two of the seven sites (sites 1 and 4), there were no significant differences in ECW solute concentration between aggregated and solitary snails, nor any relationship to snail size. In four of the seven sites (sites 2, 3, 5, 7), ECW solute concentration differed significantly between aggregated and solitary snails, but again had no relationship to snail size. In one site (site 6), the slopes of the regression lines for aggregated and solitary snails differed: inspection of the data (Figure 2) indicates that in this site, differences in osmolarity between aggregated and solitary snails vary with snail size, with solitary snails more desiccated and this difference most pronounced for small snails. It should be noted that in all seven sites, the slopes of regression lines relating snail size to ECW solute concentration were always negative, but significantly so only in site 6.

The results of the second field trials, which considered microhabitat as well as aggregation, indicated that the effect of microhabitat on desiccation is also important (Figure 3). A two-way ANOVA showed that the effect of microhabitat (protected vs. exposed) on ECW concentration was highly significant ($F_{1,93} = 33.40$; $P < 0.001$),

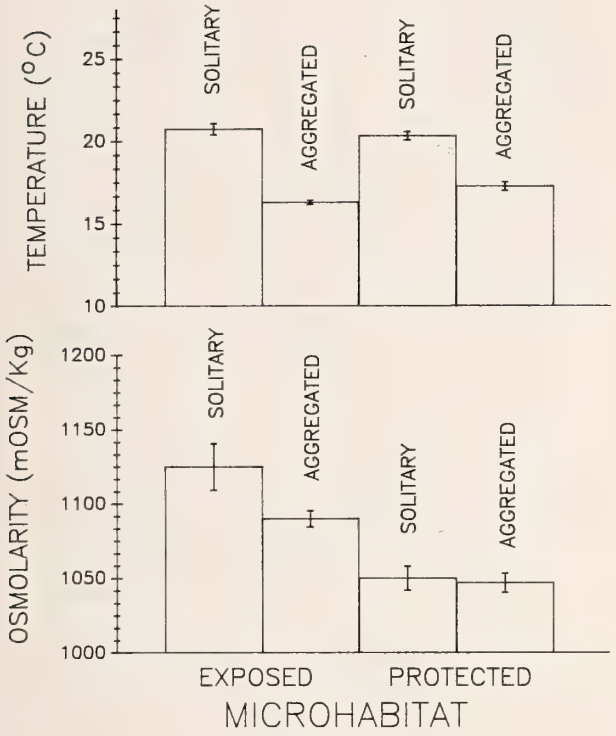


Figure 3

Temperatures (top graph) and extra-corporeal water osmolarity (bottom graph) of solitary and aggregated *Tegula funebralis* in protected (crevices or algal cover) and exposed (open surfaces) microhabitats. Temperature did not differ between microhabitats, but aggregated snails were significantly cooler. Osmolarity was lower in protected microhabitats, but solitary and aggregated snails did not differ.

while in this case the effects of aggregation and the interaction between aggregation and microhabitat were not significant (aggregation: $F_{1,93} = 3.29$; $0.08 > P < 0.05$; interaction: $F_{1,93} = 2.60$; $P > 0.1$). In these trials, both aggregated and solitary snails in protected habitats sustained lower levels of evaporative water loss than did aggregated or solitary snails in exposed microhabitats: mean values (±SD) for protected microhabitats were 1048 ± 38 mOsm/kg ($n = 24$) and 1050 ± 40 mOsm/kg ($n = 25$) for aggregated and solitary snails, respectively; for exposed microhabitats, mean values were 1090 ± 26 mOsm/kg ($n = 23$) for aggregated snails and 1125 ± 78 mOsm/kg ($n = 25$) for solitary snails (Figure 3).

Protective cover had no significant effect on snail body temperature (Figure 3). A two-way ANOVA showed no significant effect of microhabitat (exposed vs. protected) ($F_{1,93} = 1.26$; $P > 0.26$), while aggregated snails were significantly cooler than solitary snails ($F_{1,93} = 229.67$; $P < 0.001$). There was also a significant interaction between aggregation and microhabitat ($F_{1,93} = 11.51$; $P < 0.01$): inspection of the data indicates that the difference between aggregated and solitary snails is greatest in exposed microhabitats (Figure 3). Mean body temperatures (±SD) for aggregated snails were 17.2 ± 1.0°C in protected microhabitats and 16.3 ± 0.5°C in exposed microhabitats. For solitary snails, mean body temperatures were 20.3 ± 1.3°C (protected) and 20.7 ± 1.7°C (exposed). In addition to reducing evaporative water loss, as shown above, aggregative behavior may be a means of reducing body temperature.

Table 3

Two-way analysis of covariance (time of exposure as covariate) testing the effects of time of exposure, snail size, and aggregation on desiccation of *Tegula funebralis* as measured by solute concentration of extra-corporeal water. (Significance levels: * $P < 0.05$; *** $P < 0.001$; ns, $P > 0.05$.)

Source	SS	DF	MS	*F*-ratio
Aggregation	52,586.5	1	52,586.5	3.46ns
Snail size	103,725.6	2	51,862.8	3.41*
Time of exposure	4,428,927.7	1	4,428,927.7	291.48***
Aggregation × snail size	20,184.6	2	10,092.3	0.66ns
Aggregation × time	39,440.5	1	39,440.5	2.60ns
Snail size × time	527,567.2	2	263,783.6	17.36***
Aggregation × snail size × time	33,544.3	2	16,772.1	1.10ns
Residual	4,862,293.4	320	15,194.7	

Laboratory Studies

Results from the laboratory agreed with those from the field, further supporting the hypothesis that aggregative behavior reduces desiccation stress. For all size classes combined over all time periods (1–6 h), solitary snails had higher osmolarity of ECW than aggregated snails ($F_{1,264} = 19.49$; $P < 0.001$). A more detailed two-way ANCOVA (Table 3) (time as the covariate) indicates significant effects of time and snail size on ECW concentration ($P < 0.05$) and a near significant effect of aggregation ($P = 0.064$): under laboratory conditions, time of exposure appeared to have the greatest effect on desiccation. The only significant interaction in the three-way ANOVA was that of time and snail size (Table 3). This can be interpreted as a proportionally greater effect of time of exposure on small snails than on large snails.

Desiccation affected time for emergence: two separate one-way ANCOVAs, with aggregation as the main factor and time of exposure or final osmolarity as the covariate, showed that both time of exposure and osmolarity of ECW had significant effects on time for snails to emerge from their shells following rehydration (time: $F_{1,93} = 43.85$; $P < 0.001$; osmolarity: $F_{1,93} = 53.75$; $P < 0.001$). In neither case did aggregation significantly effect time for emergence

($0.09 > P > 0.05$), nor were there significant interaction terms.

Behavioral Tests

When snails were placed on a substratum with a checkerboard pattern of black and white squares, six or more of the eight snails were found to situate themselves on black squares in 18 of the 20 trials performed. Using this conservative criterion for preference (that is, six or more of eight snails), a chi-square test indicates that this result is significantly different from an null hypothesis of even frequency of preference for black or white ($\chi^2 = 12.8$, df = 1, $P < 0.001$).

In the experiment testing the role of mucus trails, snails placed on a mucus trail leading to a black quadrant went to a black quadrant 21 times, while 3 snails went to a white quadrant. This differs significantly from a random distribution ($\chi^2 = 13.5$, df = 1, $P < 0.001$). This first test, however, does not differentiate between preference for a black substratum vs. trail following. In the second test, most (21 of 24) of the disks had one or two mucus trails (depending on the path taken by individual snails) leading to a black quadrant. When the disk is rotated one quarter turn, these trails lead to white quadrants. If mucus trail following is of primary importance, the null hypothesis is that all of the snails should have followed a trail to a white quadrant. Instead, all 24 snails went to a black quadrant, and a chi-square test (confined to these 21 snails) rejects this null hypothesis ($\chi^2 = 21$, df = 1, $P < 0.001$).

DISCUSSION

This study suggests that aggregative behavior in *Tegula funebralis* may be of importance in reducing desiccation stress. Aggregated snails in the laboratory and in the field were shown to lose less water after a given period of time desiccated than solitary snails. In addition, although ECW concentration and not aggregation per se significantly affected the time taken for emergence, aggregated snails under field conditions should resume normal activity more rapidly than solitary snails owing to the correlation between aggregation and extent of desiccation. Previous studies on different organisms support the conclusion that aggregative behavior reduces desiccation stress. Warburg (1968) showed that aggregated terrestrial isopods lost water at one-half the rate of solitary individuals owing to a reduction in exposed surface area-to-volume ratio. Snyder-Conn (1980) demonstrated enhanced survivorship of aggregated hermit crabs under desiccating conditions. Formation of aggregations reduces water loss and enhances survivorship in a tropical neritid (Garrity, 1984; Garrity & Levings, 1984). Many studies have indicated that desiccation rates increase with decreased body size (see, for example, Davies, 1970; Wolcott, 1973). Our observations agree with these findings: small snails desiccated significantly faster than large snails regardless of aggregated or solitary conditions.

Aggregation may also be a means of regulating body temperature, and therefore metabolic rate, while exposed. In many invertebrates, metabolic rate varies with changes in salinity and(or) temperature. The ability to withstand a short-term rise in ambient temperature or salinity without a significant rise in metabolic rate may be essential to the maintenance of energetic gain in organisms that experience variable environmental temperatures and reduced food availability upon exposure (Newell, 1979). Aggregated *Tegula funebralis* in different microhabitats (protected or exposed) had similar temperatures, and these temperatures were lower than those of solitary snails in either microhabitat. This may be due to water held between individuals, thereby keeping snails at a more constant and lower temperature.

It is of interest to determine whether aggregative behavior functions primarily as a means of reducing desiccation, or whether aggregations are formed as a result of snails converging into protected areas upon exposure. Several observations from this study suggest that aggregations in protected microhabitats may be formed artifactually, owing to crowding into protected areas, while those in exposed microhabitats may be formed actively, owing to orientation toward other snails. First, differences in desiccation stress (due to evaporative water loss) were found to be largest between aggregated and solitary snails in exposed microhabitats, but were not found to exist between aggregated and solitary snails in protected microhabitats. That is, desiccation stress in solitary individuals in exposed microhabitats is relatively high, and a behavior for reducing this stress would be advantageous. Second, our laboratory investigation of preference for dark-colored vs. light-colored substrata indicates strong directionality toward dark areas of the substratum, potentially a cue for protective cover. Third, mucus trails seem to be of little importance to snails in the formation of aggregations: snails did not follow trails leading to white areas of the substratum. Therefore, cues indicative of protective cover may be of greater importance to exposed snails than cues indicating the presence of other snails. In the absence of protective cover, snails may orient to other snails with the dark shell as a primary cue.

The results of this study show that aggregation is an effective method for reducing desiccation stress due to evaporative water loss. Microhabitat choice also appears to be an effective method, however, and the question as to whether aggregations are formed as a means of reducing desiccation or as a result of crowding into protected microhabitats upon exposure during low tide may have more than one answer. In unprotected microhabitats, snails may actively seek to form aggregations. In protected microhabitats, aggregations may be the result of a common orientation toward cues representing protective cover.

ACKNOWLEDGMENTS

We wish to thank V. Chow, P. Connors, C. Declerck, B. Kraus, C. Petersen, and T. Suchanek and two anonymous

reviewers for helpful advice, discussions and(or) comments on the manuscript. We also thank Director J. Clegg and the staff of the Bodega Marine Laboratory for making facilities there available.

LITERATURE CITED

Davies, P. S. 1969. Physiological ecology of *Patella*. III. Desiccation effects. Jour. Mar. Biol. Assoc. U.K. 49(2):291–304.

Davies, P. S. 1970. Physiological ecology of *Patella*. IV. Environmental and limpet body temperatures. Jour. Mar. Biol. Assoc. U.K. 50:1069–1077.

Fawcett, M. H. 1984. Local and latitudinal variation in predation on an herbivorous marine snail. Ecology 65(4):1214–1230.

Gallien, W. B. 1985. The effect of aggregations on water loss in *Collisella digitalis*. Veliger 28(1):14–17.

Garrity, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65(2):559–574.

Garrity, S. D. & S. C. Levings. 1984. Aggregation in a tropical neritid. Veliger 27(1):1–6.

Morris, R. H., D. P. Abbott & E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press: Stanford, California. 690 pp.

Newell, R. C. 1979. Biology of intertidal animals. Marine Ecological Surveys LTD. 781 pp.

Paine, R. T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50(6):950–961.

Snyder-Conn, E. K. 1980. Tidal clustering and dispersal of the hermit crab *Clibanarius digueti*. Mar. Behav. Physiol. 8: 43–53.

Sutherland, J. P. 1970. Dynamics of high and low populations of the limpet *Acmaea scabra* (Gould). Ecol. Monogr. 40(1):169–188.

Vernberg, W. B. & F. J. Vernberg. 1972. Environmental physiology of marine animals. Springer-Verlag, Inc.: New York. 346 pp.

Wara, W. M. & B. B. Wright. 1964. The distribution and movement of *Tegula funebralis* in the intertidal region of Monterey Bay, California. Veliger 6(Suppl.):30–37.

Warburg, M. R. 1968. Behavioral adaptations of terrestrial isopods. Amer. Zool. 8:545–559.

Wolcott, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at limiting factors. Biol. Bull. 145:389–422.

The Veliger 30(2):134–137 (October 1, 1987)

THE VELIGER

Behavioral Control of Water Loss in the Terrestrial Slug *Deroceras reticulatum* (Müller): Body-Size Constraints

by

THOMAS A. WAITE

Department of Zoology, The Ohio State University, Columbus, Ohio 43210, U.S.A.

Abstract. I examined the hypothesis that the extent to which the terrestrial slug *Deroceras reticulatum* Muller uses behavioral tactics to minimize evaporative water loss is related to body size. Small slugs, relative to larger individuals, tended to lose more mass (% initial body mass) and tended to spend more time moving and less time in a contracted posture. However, when moist microhabitats were made available the correlation between loss in body mass and body size was positive, as small slugs tended to use these microhabitats more extensively and tended to spend less time moving and more time in a contracted posture than did larger slugs. The implications of body-size constraints on the water balance of slugs are discussed.

INTRODUCTION

Terrestrial pulmonate gastropods have moist, highly permeable integuments that render them vulnerable to evaporative water loss whenever ambient humidity is lower than the equilibrium humidity of their blood (approximately 99.5% r. h. at 20°C; MACHIN, 1975). Slugs then should be able to take in atmospheric moisture only when relative humidity approaches 100% or when a moist substrate can be contacted so that integumental absorption can occur (contact-rehydration; MAKRA & PRIOR, 1985). However, COOK (1981) reported that, apparently owing to water loss associated with the production of the mucus trail for locomotion, specimens of *Limax pseudoflavus* Evans continued to lose mass when kept over, but not in contact with, distilled water for 18 h, even after they had been dehydrated previously to only 30% of their initial body mass. This considerable tolerance to dehydration (DAINTON, 1954; PRIOR *et al.*, 1983), coupled with their labile haemolymph volume (HUGHES & KERKUT, 1956; ROACH, 1963), is of obvious adaptive significance for terrestrial pulmonates which are often active under desiccating conditions.

Water-conserving aggregations (huddles) have been observed in the terrestrial slugs *Limax pseudoflavus* (CHATFIELD, 1976; COOK, 1976; EVANS, 1978), *L. maximus* (PRIOR *et al.*, 1983), and *Deroceras reticulatum* Müller (unpublished results). COOK (1981) provided experimental evidence that (1) the extent and frequency of huddling was greater in low compared to high humidity conditions, and (2) slugs that huddled with one other slug experienced a 34% reduction in evaporation rate relative to solitary slugs. COOK (1981) also demonstrated that *L. pseudoflavus* responded to dehydration by moving less frequently and spending more time in a contracted posture. Huddling occurs in much the same predictable manner in *D. reticulatum* (unpublished results). PRIOR *et al.* (1983) demonstrated that solitary slugs lost more than twice as much mass as did slugs that had been allowed to huddle.

In this paper I examine a hypothesis concerning effects of body size on behavioral water-conserving tactics in the terrestrial slug *Deroceras reticulatum* Müller. *Deroceras reticulatum* is a small (generally less than 50 mm in extended length) nocturnal slug which is native to Europe but has spread throughout much of North America since its introduction (BURCH & PATTERSON, 1966; CHICHESTER & GETZ, 1973). Because small slugs have a greater volume-specific surface area than larger slugs, their rate of evaporative water loss, measured as percent of initial body mass, should be greater. In fact, in the absence of body-size-related differences in the behavioral control of water loss, the rate of evaporative water loss (% initial mass) would be predicted to vary inversely with initial body mass$^{2/3}$. Therefore, small slugs might be expected to compensate for their greater vulnerability to dry conditions by (1) more readily adopting a contracted posture, (2) spending less

time moving, and (3) using moist microhabitats with greater frequency. These tactics should permit small slugs to suppress their evaporative water loss below the predicted rate relative to larger slugs.

MATERIALS AND METHODS

Deroceras reticulatum individuals of various ages were collected at night in Franklin Co., Ohio. They were maintained in a terrarium at 26 ± 3°C ($\bar{X}$ ± SD) with a 16-h photoperiod. The slugs were kept on a gravel-loam mixture that was covered with common dandelion (*Taraxacum officinale*) greens. Wheat and barley cereal, rolled oats and water were provided ad libitum, and apple slices were provided periodically. The slugs were held from 23 April to 25 May 1985, and the experiments were conducted between 1400 and 1900 h at 28°C. Statistical analyses were performed using Spearman's rank correlation (SIEGAL, 1956). As this analysis uses ranks, the conversion of initial body mass (IBM) to $IBM^{2/3}$ was unnecessary. Statistical significance was set at the 0.05 level.

I determined the mass of 15 slugs, ranging from 0.057 to 0.944 g, and placed each one in a separate 10 × 1.5-cm (diameter × height) plastic petri dish. Each petri dish had, attached to the underside of its lid, a small bag (fashioned from a 5 × 5-cm piece of cheesecloth) containing anhydrous calcium sulfate. Beginning one min after the slugs were introduced to the petri dishes, I used a scan sampling technique (LEHNER, 1979), once each minute for 70 min, and recorded the postural state of each individual as "moving" (tentacles outstretched, body outstretched, and moving), "intermediate" (tentacles retracted, body contracted such that the individual's head was under the anterior edge of the mantle flap, and not moving), and "contracted" (tentacles retracted, head under the anterior edge of the mantle flap, and not moving). Immediately following this 70-min period of observation, I redetermined the mass of each slug. In order to be able to compute the mean posture of each individual for the 70 scan samples, I converted each observation of "contracted," "intermediate," and "moving" postures to the numeric values of 1, 2, and 3, respectively.

The results of the above experiment (see Figure 1B) prompted an experiment designed to examine the importance of microhabitat use with respect to body size. This experiment tests the prediction that small slugs should show a greater tendency than should larger individuals to use moist microhabitats as a means of compensating for their higher vulnerability to dehydration. The methods replicate those of the previous experiment with one important exception. In addition to the desiccant, each petri dish contained an 8-cm^3 porous, water-saturated polystyrene cube in which a 2-cm^3 "tunnel" had been fashioned on the underside. After determining the mass of 15 slugs, ranging from 0.150 to 0.914 g, I placed each one in a separate petri dish. Beginning 1 min thereafter, I recorded each minute for 60 min (1) the posture of each slug and (2) whether it was using the microhabitat (defined as making contact with either the interior or the exterior of the polystyrene cube). I then redetermined the mass of each slug.

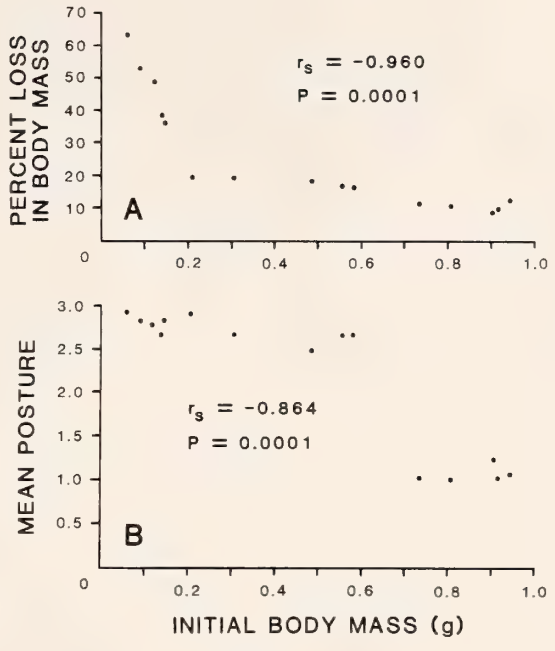


Figure 1

Correlations of (A) loss in body mass and (B) mean posture (where 1 = contracted, 2 = intermediate, and 3 = moving) with initial body mass of 15 *Deroceras reticulatum* individuals. *P*-values are from two-tailed Spearman's rank correlation (r_s) tests.

RESULTS AND DISCUSSION

Loss in body mass (% of initial mass) ($P = 0.0001$; Figure 1A) and mean posture ($P = 0.0001$; Figure 1B) both were negatively correlated with initial body mass when no moist microhabitat was available. In other words, small slugs tended to lose a greater percentage of their initial body mass and were more active than were large slugs. The results in Figure 1B contradict the notion that in desiccating conditions small slugs (1) should be more likely to assume a contracted posture, thereby effectively reducing their evaporative surface area, and (2) should spend less time moving, an activity that requires the secretion of a highly aqueous mucus trail. It may be that the small slugs in this experiment were under such severe body-size constraints (namely, their surface-area-to-volume ratios were prohibitively large) that any water-conserving tactic other than finding a moist microclimate would have been inadequate. That the two smallest individuals died during this experiment while all others survived lends further support for this postulation.

In contrast to the above results, when a moist micro-

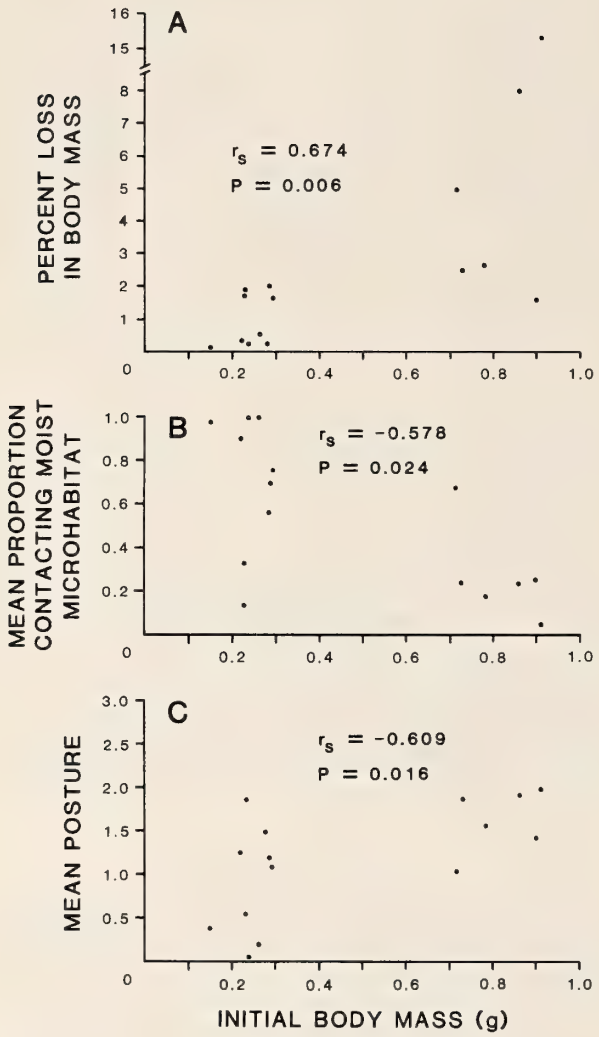


Figure 2

Correlations of (A) loss in body mass, (B) use of moist microhabitat (proportion of observations in which an individual made contact with the microhabitat) and (C) mean posture (where 1 = contracted, 2 = intermediate, and 3 = moving) with initial body mass of 15 *Deroceras reticulatum* individuals when a moist microhabitat was available. *P*-values are from two-tailed Spearman's rank correlation (r_s) tests.

habitat was available the correlation between loss in body mass and initial body mass was significantly positive (P = 0.006; Figure 2A). In addition, small slugs (1) tended to use the moist microhabitat to a greater extent (P = 0.024; Figure 2B) and (2) tended to adopt a contracted posture more frequently and move less often than larger individuals (P = 0.016; Figure 2C). Thus, when a moist microhabitat was accessible small slugs behaved as predicted on the basis of scaling considerations. It appears that the option of using such a microhabitat aided small slugs in solving their water loss problem. Admittedly, it could be argued that the moist microhabitat caused an increase in humidity within the petri dishes. This criticism, however, fails to account for the significant positive correlation between loss of body mass and initial mass; as all 15 individuals lost mass during the experiment, we still should expect a negative correlation if there were no body-size-related differences in behavior.

My results prompt the argument that under temporarily desiccating conditions large slugs have the option of conserving water by making postural adjustments. Smaller individuals exposed to the same conditions for the same length of time, because of their greater surface-area-to-volume ratio, should be quicker to reach the point at which contact-rehydration becomes necessary (60–70% initial body mass for *Limax maximus*; PRIOR, 1984). Small slugs thus should resort quicker than larger individuals to searching for moist microhabitats. Under such conditions the benefit of water conservation due to postural adjustments and reduced mucus production for locomotion presumably would not outweigh the cost associated with prolonged exposure for small individuals.

Moreover, my results allow some speculation concerning how activity budgets of slugs in nature might be related to body size. One might predict, for instance, that the mean body size of slugs active under dry conditions would be skewed upward relative to the mean body size of slugs active under more humid conditions.

ACKNOWLEDGMENTS

I am grateful to T. C. Grubb, Jr., D. W. Phillips, J. A. Smallwood, and two anonymous reviewers for their valuable comments on an earlier draft of the manuscript. This study was conducted while I was supported by NSF grant BSR-8313521 to T. C. Grubb, Jr.

LITERATURE CITED

BURCH, J. B. & C. M. PATTERSON. 1966. Key to the genera of land gastropods (snails and slugs) of Michigan. Museum of Zoology, University of Michigan Circular No. 5.

CHATFIELD, J. E. 1976. *Limax grossui* Lupu 1970, a slug new to the British Isles. Jour. Conchol. 29:1–4.

CHICHESTER, L. F. & L. L. GETZ. 1973. The terrestrial slugs of northeastern North America. Sterkiana 51:11–42.

COOK, A. 1976. Trail following in land slugs. Jour. Moll. Stud. 42:298–299.

COOK, A. 1981. Huddling and the control of water loss by the slug *Limax pseudoflavus* Evans. Anim. Behav. 29:289–298.

DAINTON, B. H. 1954. The activity of slugs: I. The induction of activity by changing temperatures. Jour. Exp. Biol. 31: 165–187.

EVANS, N. J. 1978. *Limax pseudoflavus* Evans: a critical description and comparison with related species. Ir. Nat. Jour. 19:231–236.

HUGHES, G. M. & G. A. KERKUT. 1956. Electrical activity in a slug ganglion in relation to the concentration of Locke solution. Jour. Exp. Biol. 33:282–294.

LEHNER, P. N. 1979. Handbook of ethological methods. Garland STPM Press: New York.

MACHIN, J. 1975. The evaporation of water from *Helix aspersa*. I. The nature of the evaporating surface. Jour. Exp. Biol. 41:759–769.

MAKRA, M. E. & D. J. PRIOR. 1985. Angiotensin II can initiate contact rehydration in terrestrial slugs. Jour. Exp. Biol. 119: 385–388.

PRIOR, D. J. 1984. Analysis of contact-rehydration in terrestrial gastropods: osmotic control of drinking behavior. Jour. Exp. Biol. 111:63–74.

PRIOR, D. J., M. HUME, D. VARGA & S. D. HESS. 1983. Physiological and behavioral aspects of water balance and respiratory function in the terrestrial slug, *Limax maximus*. Jour. Exp. Biol. 104:111–127.

ROACH, D. K. 1963. Analysis of the haemolymph of *Arion ater* L. (Gastropoda: Pulmonata). Jour. Exp. Biol. 40:613–623.

SIEGAL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill: New York.

The Veliger 30(2):138–147 (October 1, 1987)

THE VELIGER

Responses of a Mussel to Shell-Boring Snails: Defensive Behavior in *Mytilus edulis*?

by

THOMAS A. WAYNE

Oregon Institute of Marine Biology, University of Oregon,
Charleston, Oregon 97420, U.S.A.

Abstract. The mussel *Mytilus edulis* responded to shell-boring snails of the genus *Nucella* with valve gaping, mantle retraction, repetitive valve closures, foot extensions, and changes in byssus attachment rates. Valve closures frequently pinched snails and occasionally displaced them. Repetitive valve closures appeared to force snails away from the valve edges. *Mytilus edulis* attached more byssal threads to adjacent *Nucella* than to adjacent mussels. Attached byssal threads limited snail mobility and sometimes completely immobilized snails. When the foot of a *M. edulis* came into contact with *Nucella,* the snail tended to move. In addition to moving, snails responded to contact by a *M. edulis* foot with shell lifting, shell twisting, and radula strikes. A carnivorous snail that does not bore and two herbivorous snails did not elicit gaping in *M. edulis,* nor did another mussel, *M. californianus,* stimulate shell lifting or shell twisting by *Nucella.* Several alternative hypotheses may explain the behavioral responses of *M. edulis* to *Nucella*: (1) the responses are reactions to a paralyzing substance liberated by the snail, (2) they are shell-cleaning behaviors stimulated by the presence of the snail on the mussel's valves, and (3) they are defensive, anti-predator behaviors. The responses of *M. edulis* to *Nucella* appear most consistent with an anti-predator interpretation of their function.

INTRODUCTION

Bivalves are vulnerable to shell-crushing, prying, and piercing predators such as crabs, seastars, and snails (SEED, 1976). Within the constraints of the bivalve body plan, which might appear severely to limit behavior, bivalves have diverse behavioral defenses. ANSELL (1969) documented the leaping behavior of several clam species which, when stimulated by seastars, rapidly extend their foot and lift themselves off the substratum. LAWS & LAWS (1972) found that the clam *Donacilla* responds to a burrowing gastropod predator by crawling to the surface. Scallops repeatedly open and close their valves when stimulated by seastars, thus expelling jets of water sufficient to produce a type of swimming (FEDER & CHRISTENSEN, 1966).

In contrast to these bivalves, mussels have been thought to have no such defenses (FEDER, 1972). KIM (1969) observed that the mussel *Mytilus edulis* exhibited no behavior other than a prolonged closure of its valves when attacked by the seastar *Asteria amurensis.* NIELSON (1975) similarly observed only prolonged valve closure when *M. edulis* was attacked by the predatory gastropod *Buccinum undatum.* However, a more recent observation indicates that shell-boring snails stimulate *M. edulis* to perform valve movements, prolonged foot-extensions, and attachment of byssal threads to the snails' shell. These responses have been interpreted as defensive behaviors by WAYNE (1980, abstract). MCCONNAUGHEY & ZOTTOLI (1983) similarly interpreted behaviors of *M. edulis* filmed by Wayne. While the claim of a behavioral defense in *M. edulis* has not been confirmed, such is consistent with bivalve behavior and ecology.

The purpose of this paper is to describe the previously identified behaviors of *Mytilus edulis* (WAYNE, 1980, abstract) and to test for an association between those behaviors and stimulation by shell-boring gastropods.

MATERIALS AND METHODS

Preliminary Observations

Experiments were done following several years of preliminary observations, begun in 1976, during which time the responses of thousands of mussels and hundreds of snails were viewed. Descriptions and diagrams of behavior were assembled from observations, photographs, and motion picture films of mussels and snails interacting in aquaria under a variety of conditions.

Experimental mussels and snails were collected at Cape Arago, the Siuslaw Marina, Pirate's Cove, and the south jetties of Coos and Siuslaw bays. These collection sites are within 80 km of the Oregon Institute of Marine Biology (Charleston, Oregon), where the observations and experiments were conducted. Running seawater was provided in all set-ups; seawater temperatures did not exceed ocean temperatures by more than 2°C. All mussels were *Mytilus edulis* Linnaeus, 1758.

Gaping Response of Mussels Exposed in Aggregate to Free-Moving Snails

A clump consisting of 200–300 *Mytilus edulis* was placed in a 10-gal. (38-L) aquarium. After the mussels attached byssi and the clump had stabilized, 30–40 snails, *Nucella emarginata* (Deshayes, 1839) and *N. lamellosa* (Gmelin, 1791) (formerly placed in *Thais*), were introduced into the aquarium. A 16-mm Bolex camera with a close-up lens was used to film the activity on the surface of the clump at 1 frame per 8 sec. The film was repeatedly viewed at regular speed in both forward and reverse motions by projecting the image on a large sheet of paper. The positions of mussels were drawn on the paper, and the paths of snails were traced to obtain counts of mussels in each of two categories: mussels touched by snails and mussels not touched by snails. For each category, mussels gaping and mussels not gaping were counted. Mussels were judged to be gaping when their valves appeared to be open twice as wide as the valves of adjacent mussels. The results were entered into a 2 × 2 contingency table and the *G*-statistic (Sokal & Rohlf, 1969) was used to test for independence.

Gaping Response of Mussels Tested Individually

Forty numbered finger bowls (10.5 cm diameter × 4.5 cm) were haphazardly interspersed in a water table. Two mussels (2–3 cm long) were placed in each finger bowl and were left undisturbed for 4 h. After this acclimation period the mussels in 20 of the finger bowls were stimulated with the smooth tip of a glass rod; the remainder were stimulated by contact with *Nucella emarginata*. Stimulation consisted of light touches to the posterior region of the mussel's mantle and valve edges. Each mussel was touched a total of 15 times at intervals of approximately 1 min with either the glass rod or a snail. Touches with snails were accomplished by holding a snail slightly out of water until it extended its foot; then the extended foot was brought into contact with a mussel. Mussels gaping and those not gaping after 15 touches were tabulated for each category of stimulation. The results were analyzed using the *G*-statistic as indicated above.

Byssus Production by Mussels Stimulated with *Nucella emarginata*

At the conclusion of the experiment described above, byssi produced by the glass-rod-stimulated mussels and the snail-stimulated mussels were counted. Mussels producing one or fewer byssi were discarded, leaving 29 mussels in each set (one extra mussel was chosen at random and excluded to make both sets equal). These mussels were returned to the water table for 12 h, after which time the byssi were counted again. The production of new byssi in the two sets of mussels was tested for similarity (one-tailed) with the Wilcoxon two-sample test (Sokal & Rohlf, 1969).

Choice Between Mussel and Snail Shell Substrata for Byssus Attachment

Seventy mussels (2–3 cm long) were placed in individual, small finger bowls (8 cm diameter × 3 cm) which were haphazardly distributed in a watertable. Four hours later, 50 of the most firmly attached mussels were stimulated by *Nucella emarginata* (stimulation was as previously described). A plastic grid (1-cm^2 openings) was placed over each mussel's finger bowl; then, one new non-stimulated mussel and one *N. emarginata* were wedged into the grid openings. The grid was positioned so that both the inserted mussel and snail were in comparable proximity to the attached mussel below. Each mussel and snail inserted into the grid was chosen and placed so as to provide approximately equal surfaces extending down from the grid into the finger bowl. These setups were returned to the watertable where they remained undisturbed for 12 h, after which time the byssal threads attached to each substratum choice (the mussel and the snail inserted into the grid) were counted. Because the mussels had a third choice of attachment (the finger bowl) that was likely to be selected because of greater area and closer proximity, outcomes in which mussels failed to attach at least one byssal thread to a test substratum were excluded in order to minimize this potentially confounding effect. There were 12 such results. Seventeen more of the original 50 setups were not acceptable for counting owing to mussel escape, snail escape, and dislodgment of the grid. The frequencies of byssal thread attachment to the two substrata were tested for similarity (one-tailed) with the Wilcoxon two-sample test.

Specificity of the Gaping Response

Mussels secured to a substratum by byssi may have different orientations and can move. It is difficult to stimulate such mussels equally or apply consistent criteria for interpreting their responses. To improve upon this situation, a method for immobilizing mussels was devised. One valve was lightly filed to produce a small flat spot, a drop of cyanoacrylate glue was placed on the flat spot, and the mussel was held against a plastic slide until firmly attached. The slide was then inserted into a slot (with the posterior valve edges upright and the valve opening facing the experimenter) in a specially constructed plastic carriage. The mussels remained out of water for 30–60 min during preparation. The entire carriage with a set of mus-

sels (3.0–4.5 cm long) so prepared was lowered into a 5-L chamber. Control mussels were placed near the chamber's seawater inflow (upstream from the experimental mussels) to avoid stimulating them with water-borne substances that might emanate from the snails or from the experimental mussels. Mussels that showed signs of damage or that failed to open their valves and resume their normal behavior during a period of acclimation were discarded.

Gaping was defined to include both a visible increase in the valve opening and a simultaneous mantle retraction. Stimulation was carried out as previously described. Each experiment included a negative control (stimulation by glass rod) and a positive control. *Nucella emarginata* was used as the positive control in the first experiment; in subsequent experiments, *N. lamellosa* was used because it was easier to handle. In addition to testing *N. lamellosa* in the first experiment, four other snail species, *N. canaliculata* (Duclos, 1832), *Searlesia dira* (Reeve, 1846), *Tegula funebralis* (A. Adams, 1853), and *Calliostoma ligatum* (Gould, 1849), were tested for their ability to stimulate gaping. Mussels gaping and those not gaping after 15 stimulations were tabulated. The data from each experiment were tested for independence with the *G*-statistic.

Valve Opening, Mantle Retraction, Valve Closures, and Foot Extension in Mussels Stimulated by *Nucella emarginata*

Mussels used for these experiments were 3.0–4.5 cm long, and were immobilized on plastic slides and prepared in a manner similar to that described above. Valve openings and mantle retractions were measured at the posterior valve edges using a small section of plastic ruler held with a long pair of forceps. Mantle retractions to the inside of the valves were recorded as negative numbers (that is, they were considered negative extensions). Valve closures were recorded as observed. Foot extensions and retractions were voice recorded on an audio tape recorder. The time that a mussel's foot remained extended from the valves was then obtained by review of the tape. After 30–40 min into the experiment, experimental mussels were intermittently stimulated for about an hour with *Nucella emarginata.* Stimulation was administered as previously described. Data were recorded before, during, and after the period of stimulation. Another set of mussels prepared in the same manner was used to control for time-dependent variables; these mussels were not stimulated.

Data were collected in five separate trials, each with four to six mussels. There were small time differences (10–30 min) in the pre-stimulation periods among the first few trials. Valve closures and foot extensions were not recorded in the first two. Furthermore, some foot-extension data were lost. All mussels for which both before and after data were obtained were used in the statistical analysis. Paired sets of before and after values for valve opening, mantle retraction, valve closure, and foot extension were tested for equality in a paired analysis of variance (Sokal & Rohlf, 1969). The before values were means of measurements made in the time period before stimulation began. The after values were means of measurements from an equivalent time period immediately after stimulation ended.

Some of the above data consisted of uninterrupted records of sets of valve opening, mantle retraction, valve closure, and foot extension measured during the pre-stimulation period and continuing until several hours after stimulation ended. The data in these sets were combined and plotted to provide a visual illustration of the mussels' responses.

Shell Lifting and Shell Twisting in *Nucella emarginata*

Individuals of *Nucella emarginata* were filmed at 1 frame per 4 sec while they were stimulated by contact with a freshly excised mussel foot; this was followed, after a 5-min wait, by a second period of stimulation with the foot of a second mussel species. The mussels used were *Mytilus edulis* and *M. californianus* Conrad, 1837. The order of stimulation was randomly varied to control for order dependence. The anterior region of the snail's foot, near the siphon, was touched repeatedly with a mussel foot for 3 min.

In order to keep the snails in front of the camera, the snail's shell was lightly filed and glued (with cyanoacrylate) to the end of an acrylic rod, which was inserted into a hole in the top of a 2-L acrylic filming chamber, thus suspending the snail from the end of the rod into the seawater below. A small plastic sphere (2.5-cm diameter) was brought into contact with the snail's foot, providing a surface upon which the snail could "move." Snails invariably accepted this surface and began rotating the sphere with their crawling motions.

Frame-by-frame analysis was done by placing the 16-mm film over a stage micrometer and viewing the backlighted image at ×25. The vertical distance from the lower edge of a snail's shell to the lowest part of its foot was measured directly on the film. The mean of 10 randomly chosen frames was used to estimate the shell-lifting response of each snail. Responses to each type of stimulation (*M. edulis* foot vs. *M. californianus* foot) were tested for significance in a paired analysis of variance (Sokal & Rohlf, 1969).

The maximum horizontal displacement of the snail's tissue was also measured directly from the film to obtain an estimate of shell twisting. Because a twisting snail will alternately show front and side views (differing in width), the mean difference in tissue width between successive, randomly chosen frames (10 frames were chosen at random and then arranged in ascending order) was used for the estimate of shell twisting. The responses to the two types of stimulation were compared in a paired analysis of variance as indicated above.

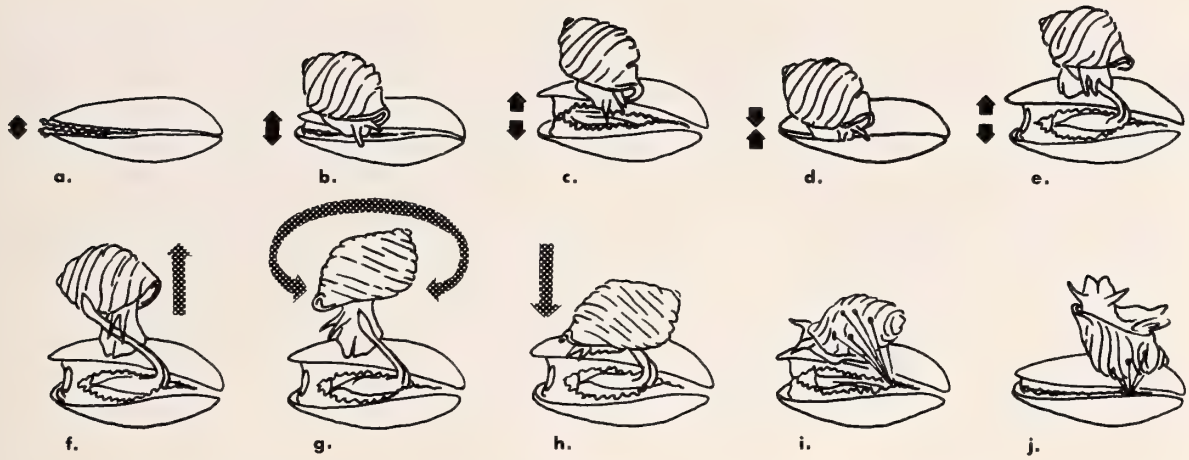


Figure 1

Behavioral interactions between the mussel *Mytilus edulis* and a shell-boring snail of the genus *Nucella*. This sequence (drawn from still photographs and motion picture film) illustrates behaviors that occurred when snails moved freely among mussels. The dark arrows indicate mussel valve movements; the light arrows indicate snail shell movements. a. Undisturbed appearance of *M. edulis*. b and c. Valve opening and mantle retraction following contact by *Nucella*. d. Valve closure on *Nucella* foot. e to h. Mussel foot activity and snail shell lifting and shell twisting. i. Byssal threads attached to the snail. j. Snail immobilized by attached byssus. In addition to the events illustrated here, the snail may be displaced, it may leave its prey, or it may drill and consume the prey.

RESULTS

Preliminary Observations and Descriptions

The interactions between *Mytilus edulis* and *Nucella* included behaviors that differed in kind and degree from those observed for mussels or snails alone (Figure 1). Undisturbed mussels kept their valves slightly open and extended their mantle just beyond the valve edges (Figure 1a). Mussels did not react to many organisms that crawled across their valves, nor did they react when their mantle was gently touched with a glass rod. They did, however, retract their mantle and close their valves when strongly prodded; and, even when undisturbed, they closed their valves at intervals.

In contrast, mussels gaped widely after contact with shell-boring snails; the gape was so extreme and the mantle so strongly retracted that much of the mussels' internal anatomy could be seen (Figures 1b, c). Initial contact with a snail usually produced a momentary valve closure; then, the valves gradually opened, increasing until an extreme gape was produced. This condition resembled that of a dead mussel; yet, gaping mussels reacted to contact and, once the snails were removed, gradually returned to their undisturbed appearance.

In addition to gaping, mussels increased their foot activity, and they also exhibited intermittent, repetitive valve closures (the valves closed without any apparent stimulus and then reopened within seconds) following contact with shell-boring snails. Snails crawling near a mussel's valve edges were sometimes pinched and subsequently moved away (Figure 1d); some snails fell off when the mussel's valves closed.

Unlike the stereotyped patterns of gaping and valve closures, foot activity was varied and complex. A mussel might extend its foot over its valves or reach beneath them as though exploring. Contact with a snail often resulted in probing and wiping of the snail's shell and soft tissue (Figures 1f, g, h). Snails responded to such contact by moving away, by lifting and twisting their shell (Figures 1f, g, h), or by directing radula strikes toward the mussel's foot.

Mussels also attached byssal threads to snails. On occasion, a snail's twisting motions broke recently attached threads. The majority of snails placed into aquaria with large clumps of mussel were eventually immobilized by byssi or found with broken byssal threads attached to them. Some snails were found with so many attached threads that it is doubtful they could have pulled free (Figure 1i). Furthermore, many of the immobilized snails were positioned with their foot upward (Figure 1j), and appeared unable to grasp either mussel or substratum.

Gaping Response of Mussels Exposed in Aggregate to Free-Moving Snails

Ninety-four individual mussels could be seen well enough on the 16-mm film to be counted (Table 1). Of those that had been incidentally touched or crawled over by snails during the filming, 27 were judged to show valve gaping. Of the mussels that were observed to have no contact with

Table 1

Results of two experiments testing for independence of the gaping response in *Mytilus edulis*. The results of the first experiment show counts taken from a film record in which incidental snail contact was observed and subsequent gaping recorded. The snails were *Nucella emarginata* and *N. lamellosa*. The second experiment compares gaping in mussels individually touched 15 times with either a glass rod or *N. emarginata*.

Treatment	Not gaping	Gaping	*G*-statistic
Experiment 1			
No snail contact	24	0	
Snail contact observed	43	27	15****
Experiment 2			
Touch by glass rod	40	0	
Touch by *N. emarginata*	19	21	31.3****

**** = $P < 0.001$.

snails during the filming, none gaped. The probability of the null hypothesis that gaping in *Mytilus edulis* is independent of contact with the snails (*Nucella* spp.) is low ($P < 0.001$) and the null hypothesis can be rejected.

Gaping Response of Mussels Tested Individually

Stimulating mussels with a glass rod produced no valve gaping; by comparison, over half the mussels stimulated with *Nucella emarginata* gaped (Table 1). Again, the probability that gaping is independent of the stimulus is low ($P < 0.001$).

Byssal Thread Production by Mussels Stimulated with *Nucella emarginata*

Mussels initially stimulated by contact with *Nucella emarginata* produced fewer byssal threads (5.2 per mussel) during a subsequent 12-h period than mussels that were similarly stimulated with the tip of a glass rod (8.1 per mussel). The two sample distributions differed significantly ($n = 58$, $t = 1.86$, $P < 0.05$), and the hypothesis that byssus production is unaffected by the stimulus can be rejected.

Choice Between Mussel and Snail Shell Substrata for Byssus Attachment

Mussels initially stimulated by contact with *Nucella emarginata* attached more byssal threads during a subsequent 12-h period to live *Nucella emarginata* (2.8 per mussel) than to live *Mytilus edulis* (1.3 per mussel). The two sample distributions differed significantly ($n = 42$, $t = 2.19$, $P < 0.025$) and the hypothesis that mussels will attach the same number of byssal threads to nearby *N. emarginata* as to nearby *M. edulis* can be rejected. On the other hand, at the conclusion of the experiment many *Nucella* were found with their foot gripping the experimental mussel. This result changed the original conditions of the experiment, which provided the experimental mussels with equal proximity to both substrata.

Table 2

Five different gastropods and their effect on gaping in *Mytilus edulis*. Touches with a glass rod were used for the negative control. The positive control was *Nucella emarginata* in the first experiment and *N. lamellosa* in the remainder. Stimulation is described in the text.

Treatment	Not gaping	Gaping	*G*-statistic
Experiment 1			
Negative control	36	0	
N. lamellosa	0	36	135.8****
Positive control	0	34	
Experiment 2			
Negative control	24	0	
N. canaliculata	0	24	91.6****
Positive control	0	24	
Experiment 3			
Negative control	19	1	
Searlesia dira	19	1	81.4****
Positive control	0	20	
Experiment 4			
Negative control	30	0	
Tegula funebralis	32	0	101.3****
Positive control	1	27	
Experiment 5			
Negative control	20	0	
Calliostoma ligatum	19	1	58.7****
Positive control	0	16	

**** = $P < 0.001$.

Specificity of the Gaping Response

Each of the five experiments testing different gastropods for their ability to produce gaping gave highly significant results (Table 2), in part because of the distinctive contrasts provided by the positive and negative controls. From a total of 126 mussels stimulated with the positive control (*Nucella* spp.), 125 produced a gape; whereas, only one mussel was judged to gape out of 130 stimulated with the negative control (glass rod). Each test of a gastropod's ability to produce gaping can be evaluated by inspecting Table 2 and comparing the snail's effect with that of the positive and negative controls.

In the first experiment, the effect of *Nucella lamellosa* was the same as the positive control. In the second experiment, the effect of *N. canaliculata* was the same as the positive control. In the last three experiments, the effects of *Searlesia dira, Tegula funebralis,* and *Calliostoma ligatum* were the same as the negative controls.

Valve Opening, Mantle Retraction, Valve Closure, and Foot Extension in Mussels Stimulated by *Nucella emarginata*

Valve opening and mantle retraction were initiated in *Mytilus edulis* immediately after contact with *Nucella emarginata*. When both attributes are plotted on the same graph (Figure 2A), they provide a distinctive "fingerprint" of the gaping behavior. The magnitude of the gaping decreased when stimulation ceased, and it returned to pre-stimulation values after several hours. Foot extensions were more frequent and prolonged after 30–40 min of stimulation; they continued long after stimulation ended (Figure 2B). Valve closures exhibited a similar latent response to stimulation; they also continued long after stimulation ended (Figure 2C).

Statistical analyses of the complete data set (not the subset used for illustration and discussed above) show that before and after values for the experimentals are significantly different (Table 3) for valve opening, mantle retraction, valve closures, and foot extension time. There were no significant time-dependent changes in the control values compared over the same period as the experimentals (valve opening, $n = 11$, $F = 0.32$, $P > 0.5$; mantle retraction, $n = 11$, $F = 1.32$, $P > 0.25$; valve closure, $n = 10$, $F = 1.99$, $P > 0.10$; foot extension, $n = 9$, $F = 0.69$, $P > 0.25$). Assuming this was also true of the experimentals, the hypothesis that *Mytilus edulis* behavior is the same before and after contact by *Nucella emarginata* can be rejected.

Shell Lifting and Shell Twisting in *Nucella emarginata*

Nucella emarginata lifted its shell significantly higher above the substratum ($P < 0.005$) when stimulated by a *Mytilus edulis* foot than when stimulated by a *M. californianus* foot. The mean change in the snail's horizontal displacement was also significantly greater ($P < 0.025$) when stimulated by a *M. edulis* foot than when stimulated by a *M. californianus* foot (Table 4). The hypothesis that *N. emarginata* responds similarly to foot contact by *M. edulis* and by *M. californianus* can be rejected.

DISCUSSION

By themselves, the behaviors of *Mytilus edulis* reported in this paper are not unusual. Similar results are easily explained and are probably commonly observed. For example, one could expect mussels to attach byssi to snails by chance alone. Furthermore, both byssus production and foot activity probably increase while mussels periodically re-attach themselves to the substratum. Mussels are known to close their valves in response to chemicals (DAVENPORT, 1977), and they may also close them following physical disturbance. Some mussels gape on exposure to air (LENT, 1968), and mussels might be expected to gape when in water with low oxygen. Because bivalves have hinges that exert a tension to open, mussels will also gape as a result of death, or perhaps injury.

However, such explanations fail to account for the present observations. Gaping behavior of *Mytilus edulis* occurred following contact with the shell-boring gastropods *Nucella emarginata, N. lamellosa,* and *N. canaliculata.* Gaping was not produced by contact with a glass rod, with a predator that does not bore (*Searlesia dira*) or with the herbivorous gastropods *Tegula funebralis* and *Calliostoma ligatum.* Mussels, whether attached by their own byssi or glued to plastic slides, gaped in response to snails of the genus *Nucella.* Although limited in extent, these results suggest that gaping is a reaction to stimuli associated with shell-boring gastropods. Additional observations of a preliminary nature indicated that three more shell-boring snails, *Ceratostoma foliatum, Ocenebra interfossa,* and *O. lurida,* stimulated gaping, while additional snails that do not bore, *Olivella biplicata, Lirularia succincta,* and *Amphissa* sp., did not. Furthermore, two East coast shell-boring snails, *Nucella lapillus* and *Urosalpinx cinerea,* stimulated gaping in East coast *Mytilus edulis* (P. Frank, personal communication).

Gastropods generally have well-developed chemosensory abilities (CROLL, 1983), and one should expect sessile prey to respond to such olfactory searching predators by closing (PALMER *et al.,* 1982). Consequently, the fact the *Mytilus edulis* gaped in the presence of *Nucella* suggests that the mussel was affected by a toxic or paralytic substance. A choline ester that slows muscle contraction has been isolated from the hypobranchial gland of *N. emarginata* (BENDER *et al.,* 1974). The barnacles *Balanus glandula* and *Chthamalus* sp. gape when attacked by *Acanthina punctulata,* and the gape has been linked to toxins from the snail's hypobranchial gland (SLEDER, 1981). Perhaps the repetitive valve closures of *M. edulis* help remove such substances by increasing water exchange. However, interpreting *M. edulis* gaping as a reaction to snail toxins is inconsistent with several other observations suggesting that gaping mussels are not vulnerable to attack: gaping *M. edulis* closed their valves when their soft-tissue was touched by either a snail or a glass rod; gaping mussels increased their foot activity; *Nucella* frequently abandoned mussels that were gaping; and *Nucella* did not feed on live mussels through their gaping valves during any of the hundreds of gapes observed in these experiments, nor are *Nucella* known to do so from any reports in the literature. Furthermore, no gaping was observed in *M. californianus* during preliminary observations of about 30 individuals stimulated by *Nucella.*

The gaping behavior, then, presents a contradiction. This contradiction could be resolved by one of several possibilities. First, gaping might be an incidental response to substances in *Nucella* that paralyze other prey. Second, *Nucella* may induce gaping and then sample mussels to test their suitability as prey. Third, because choline esters are known to stimulate escape and avoidance responses (literature cited by CROLL, 1983), defensive behavior is

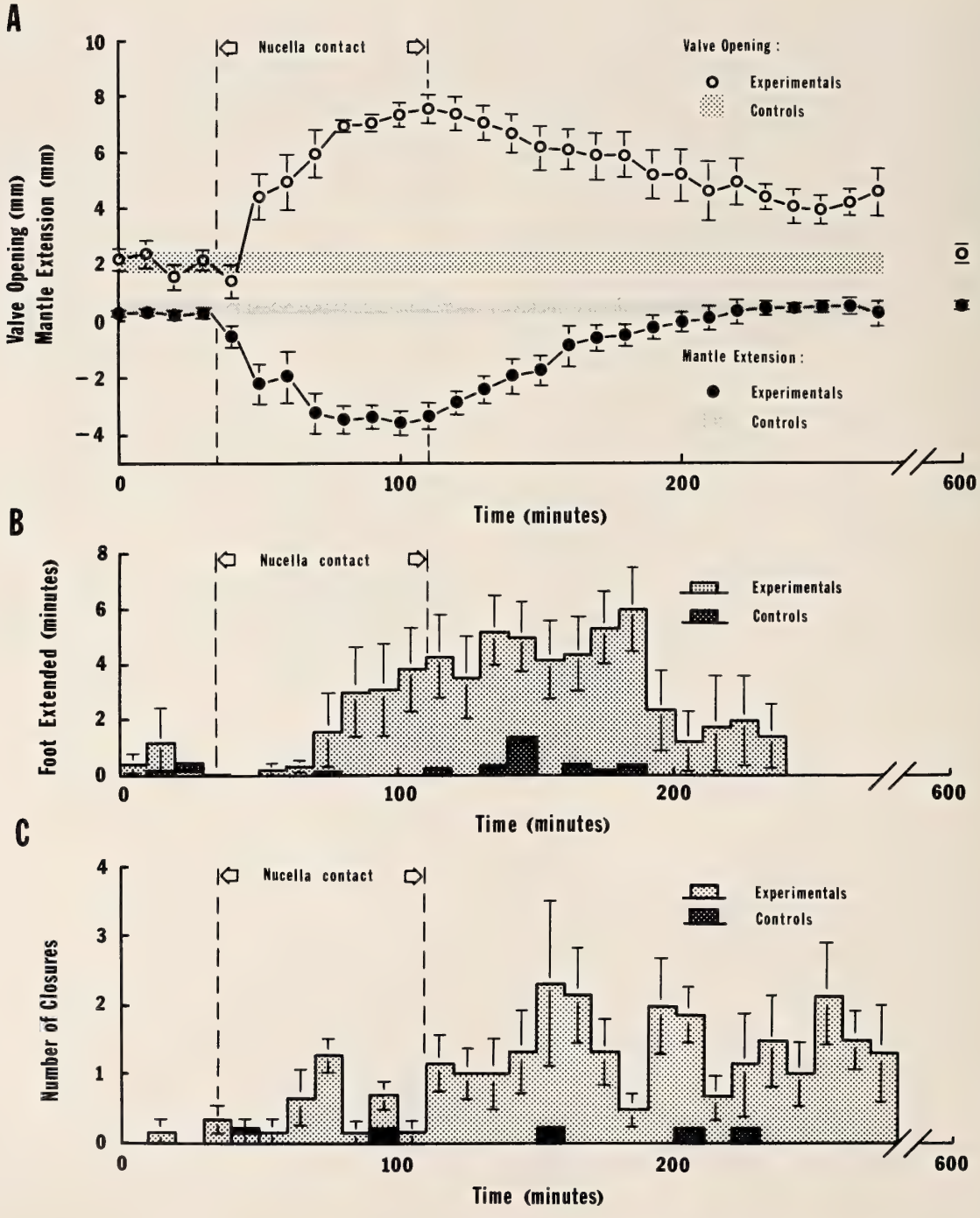


Figure 2

Temporal changes in the behavior of *Mytilus edulis* as a function of contact by the shell-boring snail *Nucella emarginata*. The values plotted are the means from 6 experimental and 5 control mussels. The vertical bars represent ±1 S.E.; however, note that these data are a subset of those used for significance testing and are themselves not suitable for such. See text for further information. A. *Gaping*. The gaping behavior includes valve opening and mantle retraction (mantle retractions are plotted as negative mantle extensions). The control data are shown as gray bands to better illustrate the gaping behavior; actual control data points match the pre-stimulation values of the experimentals. B. *Foot activity*. Time in minutes that a mussel foot extended outside the valves during each 10-min period. C. *Valve movements*. Number of valve closures during each 10-min period.

Table 3

Results of paired analyses of variance used to test for changes in valve opening ($n = 10$), mantle extension ($n = 10$), valve closures ($n = 9$), and foot extension ($n = 8$) in *Mytilus edulis* following contact with *Nucella emarginata*. Means are given for before (pre-stimulation) and after (post-stimulation) data. See text for method of stimulation and information on controls.

Source of variation	Mean		df	SS	*F*
	Before	After			
Valve opening	2.9 mm	6.2 mm			
Snail contact			1	56.1	15.4***
Individuals			9	42.4	1.26
Remainder			9	32.8	
Mantle extension	0.3 mm	−2.4 mm			
Snail contact			1	33.8	11.6**
Individuals			9	21.5	0.82
Remainder			9	26.2	
Valve closure	0.2	1.2			
Snail contact			1	4.49	8.16*
Individuals			8	4.57	1.04
Remainder			8	4.40	
Foot extended	0.23 min	1.23 min			
Snail contact			1	32.0	10.1*
Individuals			7	29.8	1.35
Remainder			7	22.1	

* = $P < 0.025$.
** = $P < 0.01$.
*** = $P < 0.005$.

suggested. PALMER *et al.* (1982) suspect that prolonged withdrawal in *Balanus glandula* is a chemically mediated avoidance response. *Nucella emarginata* is one of the predators that elicits the response. It is possible that gaping is an avoidance behavior that obscures information required by *Nucella* for prey identification, or perhaps the gape interferes with the snail's attack by pushing the snail against adjacent substrata. However, if gaping is a mussel defense, then the function of gaping in *M. edulis* is contrary to what is found in barnacles, and ability of *Nucella* to use olfactory information from *M. edulis* is contrary to what is expected.

When one considers how mussel valve movements, foot motions, and byssal thread attachments might affect a shell-boring snail, it is difficult not to conclude that such behaviors increase the snail's time and energy costs. For example, from the standpoint of time and energy, the best place for a snail to drill a mussel is near the valve edges. Yet, snails seldom drill there. The majority of drill holes in mussel valves are found in the thicker central region (CAREFOOT, 1977). In the present study, snails invariably moved away from the valve edges in apparent reaction to their movement. Perhaps the valve movement forces snails into the central region where more time and energy are required for penetration. Another explanation for the location of drill holes in mussels is that the snails may be attempting to maximize access to the underlying tissues.

Table 4

Shell lifting and shell twisting in *Nucella emarginata* after contact by *Mytilus edulis* and by *M. californianus*. A paired analysis of variance was used to test the responses for similarity ($n = 6$). See text for method of stimulation and details of measurement.

Source of variation	Mean response of snail when stimulated by		df	SS	*F*
	M. edulis	*M. californianus*			
Shell lifting	0.74 cm	0.47 cm			
Mussel foot			1	0.33	28.4***
Individuals			5	0.21	3.64
Remainder			5	0.06	
Shell twisting	0.22 cm	0.05 cm			
Mussel foot			1	0.13	10.4*
Individuals			5	0.09	1.5
Remainder			5	0.06	

* = $P < 0.025$.
*** = $P < 0.005$.

Yet, the snails' possession of an extensible proboscis would seem to relax such a strategy. Furthermore, several other bivalves move their valves in the presence of predators (CARRIKER & VAN ZANDT, 1972; KIM, 1969) suggesting a defensive role for valve movement. In addition, STIMSON (1970) notes that *Nucella* has a tendency to retract its foot, lose its grip on the substratum, and be washed away when pinched by the shell of the owl limpet, *Lottia gigantea*. *Nucella* behaved similarly when pinched by *M. edulis* valves, again suggesting that valve movements affect the location of drill holes. That such pinches dislodged *Nucella* also suggests a means by which the sessile mussel may "escape" its predator.

The foot motions of *Mytilus edulis* were similar to those previously described by THEISEN (1972) as shell cleaning behavior. Shell cleaning involves "licking" motions of the foot, which remove small particles from the valves. A possible explanation for the foot activity of *M. edulis* observed in the present study is that it was shell cleaning behavior, and it was stimulated by presence of *Nucella* on the mussel's valves. On the other hand, several aspects of the foot activity were more suggestive of interference behavior than they were of shell cleaning. First, the foot was frequently extended above the valves; thus, "licking" was not the only behavior observed. Second, several mussels were heavily encrusted with barnacles; consequently, one should expect the stimulus for shell cleaning to be obscured. Third, filing their valves and gluing plastic slides to the mussels did not stimulate shell cleaning. Fourth, the wiping and probing motions of the foot appeared to be directed at the snail; and fifth, the snail frequently moved following contact by the mussel's foot.

Mytilus edulis can immobilize *Urosalpinx cinerea* by attaching byssi to the snail's shell. These immobilizations

are not thought to have ecological significance because they occur at temperatures at which bivalves are active but snails have gone into hibernation (CARRIKER, 1981). In the present study, however, *M. edulis* attached byssi to *N. emarginata* and to *N. lamellosa* at temperatures at which both mussels and snails were active. As in the case with *U. cinerea, Nucella* were often immobilized. These observations suggest byssal threads are used defensively, inasmuch as byssus attachment to an active snail could, by restricting the snail's movement, prolong the attack, cause the attack to be aborted, or increase the snail's risk to predators and physical stress. When provided with two substratum choices, *M. edulis* attached more byssal threads to live *Nucella* than to live *M. edulis,* thus indicating that byssus attachment is biased toward the predator. However, this result must be interpreted cautiously because the snails increased their proximity to the mussels during the experiment. On the other hand, such changes in proximity are an inevitable consequence of a snail's attack.

The shell-lifting and shell-twisting behaviors of *Nucella* could defend it from byssus attachment. Byssal threads were broken by such motions, and the same motions probably make byssus attachment more difficult. Similar shell twisting and shell lifting in other gastropods has been interpreted as defensive behavior (CLARK, 1958; FEDER, 1967, 1972; PRATT, 1974). Alternately, such behavior in *Nucella* might be considered a reaction to food, but this argument is weakened by the fact that a second, although not a preferred prey, *Mytilus californianus,* does not stimulate the same behavior.

CONCLUSIONS

Demographic studies of mussels indicate that they experience heavy predation in most environments. Some mussels have morphological defenses against predation. Greatly thickened valves are associated with resistance to shell-boring gastropods (VERMEIJ, 1978) and such thickened valves are characteristic of *Mytilus californianus.* Horse mussels, *Modiolus modiolus,* produce tapering hairs or awns on their periostracum which discourage attachment by the predatory whelk *Thais lapillus* (WRIGHT & FRANCIS, 1984). Predation pressure is especially severe for *M. edulis*; it is the preferred prey of at least 10 different invertebrate predators and is consumed in large numbers by many of them (SEED, 1969; HARGER, 1972; SUCHANEK, 1978).

Heavy predation by specialized predators should provide strong selection pressure for the evolution of defensive, anti-predator mechanisms; however, *Mytilus edulis,* with its relatively thin, smooth valves, appears to have poor morphological defenses against shell-boring snails. On the other hand, these small, specialized predators stimulate valve movements, foot motions, and byssus attachment by *M. edulis,* all of which could interfere with the snail's selection of a drill site and eventual penetration of the mussel's valve. Several explanations, including toxic secretions from snails and shell-cleaning behavior, may account for such responses in *M. edulis,* but the mussel's behaviors appear more consistent with an anti-predator function. While *M. edulis* seems to have a poor morphological defense, the mussel's responses strongly suggest a behavioral defense. A comparable situation exists for *Tegula aureotincta* (SCHMITT, 1981). Like *M. edulis, T. aureotincta* is a preferred prey with an inferior morphological defense. Significantly, perhaps, *T. aureotincta* utilizes a behavioral defense.

ACKNOWLEDGMENTS

I thank Paul Rudy, Robert Terwilliger, and James Carlton for their help and encouragement. Bayard McConnaughey and Clifton Gass provided helpful commentaries on an earlier version of the manuscript. Peter Frank, A. R. Palmer, and Johnathan Geller provided additional suggestions that I have gratefully used in the present version. I also thank Lynn Rudy who critiqued the graphs and diagrams and Kathryn Young who helped with several experiments and proofread the various drafts. Thanks are also due Don Rogers for modifying and maintaining laboratory utilities. I am especially grateful to Paul Rudy, director of the Oregon Institute of Marine Biology, for the use of laboratory facilities and equipment.

LITERATURE CITED

ANSELL, A. D. 1969. Leaping movements in the Bivalvia. Proc. Malacol. Soc. Lond. 38:387–399.

BENDER, J. A., K. DERIEMER, T. E. ROBERTS, R. RUSHTON, P. BOOTH, H. S. MOSER & F. A. FUHRMAN. 1974. Choline esters in the marine gastropods *Nucella emarginata* and *Acanthina spirata.* Comp. Gen. Pharmacol. 5:191–198.

CAREFOOT, T. H. 1977. Pacific seashores. Univ. Wash. Press: Seattle. 208 pp.

CARRIKER, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. Malacologia 20:403–422.

CARRIKER, M. R. & D. VAN ZANDT. 1972. Predatory behavior of a shell-boring muricid gastropod. Pp. 157–244. *In:* H. F. Win & B. L. Olla (eds.), Behavior of marine animals. Vol. I. Plenum Press: New York.

CLARK, W. C. 1958. Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. Nature 181:137–138.

CROLL, R. P. 1983. Gastropod chemoreception. Biol. Rev. 58: 293–319.

DAVENPORT, J. 1977. A study of the effects of copper applied continuously and discontinuously to specimens of *Mytilus edulis* exposed to steady and fluctuating salinity levels. Jour. Mar. Biol. Assoc. U.K. 57(1):63–74.

FEDER, H. M. 1967. Organisms responsive to predatory sea stars. Sarsia 29:371–394.

FEDER, H. M. 1972. Escape responses in marine invertebrates. Sci. Amer. 227:92–100.

FEDER, H. M. & A. M. CHRISTENSEN. 1966. Aspects of asteroid biology. Pp. 87–127. *In:* R. A. Boolootian (ed.), Physiology of Echinodermata. Wiley Interscience: New York.

HARGER, J. R. 1972. Competitive co-existence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus.* Veliger 14:387–410.

Kim, Y. S. 1969. An observation on the opening of bivalve mollusks by the starfish, *Asteria amurensis*. Bull. Fac. Fish. Hokkaido Univ. 20(2):60–64.

Laws, H. M. & D. F. Laws. 1972. The escape response of *Donacilla angusta* Reeve in the presence of a naticid predator. Veliger 14(3):289–290.

Lent, C. M. 1968. Air gaping by the ribbed mussel, *Modiolus demissus* (Dillwyn); effects and adaptive significance. Biol. Bull. 134:60–73.

McConnaughey, B. H. & R. Zottoli. 1983. Introduction to marine biology. Mosby: London. 638 pp.

Nielsen, C. 1975. Observations on *Buccinum undatum* L. attacking bivalves and on prey responses with a short review on attack methods of other prosobranchs. Ophelia 13:87–108.

Palmer, A. R., J. Szymanska & L. Thomas. 1982. Prolonged withdrawal: a possible predator evasion behavior in *Balanus glandula* (Crustacea: Cirripedia). Mar. Biol. 67:51–55.

Pratt, D. M. 1974. Behavioral defenses of *Crepidula fornicata* against attack by *Urosalpinx cinerea*. Mar. Biol. 27:47–49.

Schmitt, R. J. 1981. Contrasting anti-predator defenses of sympatric marine gastropods (family Trochidae). Jour. Exp. Mar. Biol. Ecol. 54:251–263.

Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. Part II. Growth and mortality. Oecologia 3:317–350.

Seed, R. 1976. Ecology. Pp. 13–65. *In:* B. L. Bayne (ed.), Marine mussels: their ecology and physiology. International Biological Programme 10. Cambridge Univ. Press: Cambridge, London.

Sleder, J. 1981. *Acanthina punctulata* (Neogastropoda: Muricacea): its distribution, activity, diet, and predatory behavior. Veliger 24(2):172–180.

Sokal, R. R. & F. J. Rohlf. 1969. Biometry. W. H. Freeman: San Francisco. 776 pp.

Stimson, J. 1970. Territorial behavior of the owl limpet, *Lottia gigantea*. Ecology 51:113–118.

Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Jour. Exp. Mar. Biol. Ecol. 31:105–120.

Theisen, B. F. 1972. Shell cleaning and deposit feeding in *Mytilus edulis* L. (Bivalvia). Ophelia 10:49–55.

Vermeij, G. T. 1978. Biogeography and adaptation: patterns of marine life. Harvard Univ. Press: Cambridge, Massachusetts. 332 pp.

Wayne, T. A. 1980. Antipredator behavior of the mussel *Mytilus edulis*. Amer. Zool. 20(4):789 (abstract).

Wright, M. M. & L. Francis. 1984. Predator deterence by flexible shell extensions of the horse mussel *Modiolus modiolus*. Veliger 27(2):140–142.

The Veliger 30(2):148–158 (October 1, 1987)

THE VELIGER

Skeletal Growth Histories of *Protothaca staminea* (Conrad) and *Protothaca grata* (Say) Throughout Their Geographic Ranges, Northeastern Pacific

by

ROBERT J. HARRINGTON

Department of Geological Sciences, University of California Santa Barbara, Santa Barbara, California 93106, U.S.A.

Abstract. The skeletal growth histories of only a few bivalve species have been documented throughout most or all of their latitudinal ranges. This paper considers growth parameters based on new growth measurements made throughout the geographic ranges of two bivalve species, *Protothaca staminea* (Conrad) and *P. grata* (Say). Growth data for a third species, *Siliqua patula* (Dixon, 1788) by Weymouth *et al.* are employed extensively in the study for comparative purposes. The collective range of all three species extends from the Gulf of Alaska to Panama. The parameters studied include: shell height vs. age (H_t), the rate of decrease in growth rate with ontogeny (defined as the slope of Walford plots and as e^{-k} in the von Bertalanffy growth equation), mean maximum height (H_a), and mean maximum longevity of individuals. Latitudinal trends in the number of daily growth increments formed during the first full season of growth are contrasted for individuals of both *Protothaca* species.

All three species exhibit similar growth history trends throughout their respective ranges. Northern individuals grow slowly but at more uniform rates averaged over ontogeny, and live longer than do southern phenotypes. High initial growth rates correspond to more rapid decreases in annual growth rate. The rate of growth deceleration is highly correlated with mean annual sea-surface temperatures. The number of daily growth increments formed during the first full season of growth is apparently related to the planetary gradient in sunlight and productivity. The latitudinal rate of change in the number of daily growth increments is not affected across species boundaries.

INTRODUCTION

Only a few studies have considered skeletal growth patterns over large segments of the latitudinal ranges of molluscan species (*e.g.,* WEYMOUTH *et al.,* 1931; NEWELL, 1964; ANSELL, 1968; GILBERT, 1973; BEUKEMA & MEEHAN, 1985), but attempts have not been made to relate skeletal growth aspects to latitudinal gradients in major oceanographic factors. Reduced growth rates among higher latitude phenotypes are expected based on thermodynamic arguments and the effects of pronounced seasonality in trophic resource supply. This paper presents evidence that the effects of temperature and seasonality can be at least partially distinguished based on analyses of specific skeletal growth parameters, and that the analysis of skeletal growth trends can be useful in reconstructing the life histories of fossil individuals and the states of past oceans.

The research presented is based on growth-history determinations made by the author for two northeastern Pacific, intertidal, infaunal bivalves, *Protothaca staminea* (Conrad) at thirteen localities, and *P. grata* (Say) at six localities, throughout most of their composite geographic ranges from Prince William Sound, Alaska, to Panama Bay. The growth history of a third congener, *P. asperrima* (Sowerby), from a single locality in Panama Bay is included. Also included are growth histories of six Pleistocene sample populations of *P. staminea* representing collections ranging geographically from Bay Center, Washington, to central Baja California, and a single collection of *P. staminea* from the Middle to Late Pliocene Etchegoin Formation of central California. Growth data provided in WEYMOUTH *et al.* (1931) based on their study of latitudinal trends in the growth of *Siliqua patula* (Dixon, 1788) are included in the analysis for comparative purposes. Geographic trends in growth-history parameters

documented for *Protothaca* include annual shell height (H_t), the rate at which growth rate decelerates with ontogeny (defined as the slope of Walford plots of growth curves and as e^{-k} of the VON BERTALANFFY [1938] growth equation), maximum mean size (H_a), and maximum mean longevity. Also included are daily growth-increment data which suggest that their number during the first full season of growth is closely tied to the planetary gradient in available sunlight and productivity, and as such may be of value in the determination of paleolatitudes, and(or) long-term trends in seasonality at specific latitudes. In all, the growth histories of more than 500 specimens of *Protothaca* are included in the analysis, approximately one-half of these from the Recent and one-half from the Pleistocene.

Protothaca staminea is the widest ranging and most intensively studied of the congeners (FRASER & SMITH, 1928; QUAYLE, 1943; SCHMIDT & WARME, 1969; FEDER & PAUL, 1973; PAUL & FEDER, 1973; PAUL *et al.*, 1976; NICKERSON, 1977; FEDER *et al.*, 1979; see also PETERSON, 1977). The species ranges from Prince William Sound, Alaska, to the southernmost tip of the Baja California penninsula, but does not occur in the Gulf of California north of La Paz. *Protothaca grata,* one of several tropical to subtropical congeners, ranges from the Pacific coast of central Baja California where its range overlaps with *P. staminea,* through the Gulf of California and as far south as Peru. In the region of overlap, both species bear striking similarities in size, shape, coloration, and surface texture. As will be shown, growth histories of both congeners within their zone of overlap are sufficiently distinct to separate the species from one another. The third species, *P. asperrima,* ranges from the Gulf of California to Peru but does not overlap with *P. staminea.* It is easily distinguished from the other species of this study by its rasplike, fine surface texture, but is otherwise closer to *P. grata* in shell characteristics.

MEASUREMENT AND SAMPLING PROCEDURES

Shell heights were measured to the nearest 0.1 mm at annuli along a curved line from the umbo to the ventral margin (Figure 1). Specimens were obtained from the University of California, Los Angeles (UCLA) Department of Earth and Space Sciences Museum, the Los Angeles County Museum of Natural History (LACMNH) sections of malacology and invertebrate paleontology, and the University of California, Berkeley Museum of Paleontology (UCMP). Efforts were made to locate specimen lots that were large and composed of relatively well-preserved specimens representative of all size classes. After a series of preliminary growth-rate determinations were made, it was determined that large sample sizes were not necessary to generate representative growth curves for all localities, and several small lots (less than 10 individuals) were interposed with larger (25 or more specimens) collections. Collections of fossil specimens were selected following the same criteria as for the Recent. An additional criterion was the availability of precise stratigraphic data, particularly in relation to isotopic stage determinations (see SHACKLETON & OPDYKE, 1976; KENNEDY, 1978).

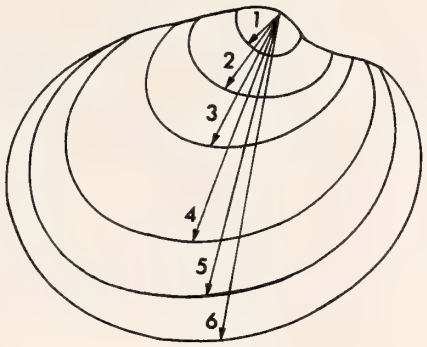


Figure 1

Measurement of shell heights at the intersections of annuli with a curved line from the umbo to the ventral margin.

The preservation of Pleistocene shell material is generally adequate for the purpose of determining rates of annual growth. However, the quality of many Pliocene specimens was too poor to permit accurate direct determinations of growth break positions. In some cases this problem was overcome by plotting specimens on a Walford plot (SHELDON, 1965, and see below). In other cases, annuli weathered out as resistant ridges on the surface of otherwise poorly preserved specimens, undoubtedly an artifact of the denser packing of growth increments during the slow-growth season, and this provided useful data.

SOURCES OF GROWTH-ANNULUS VARIATION

Several sources of variation in mean annual height vs. age data can be identified: sample size, the number of individuals surviving to a specific age, geographic dispersion in the length of the spawning season (and therefore, in conditions experienced when juvenile growth is initiated), carry-over effects of earlier growth increases into later growth stages, and the latitudinal gradient in the length of the growing season. Standard deviations in data compiled for *Protothaca staminea* throughout its range (HARRINGTON, 1986) indicate that sample size is not a major factor in the variability of height vs. age. Because survivorship falls with increasing age, the number of individual data points determining a given age class's mean size declines, but normally this does not affect the smoothness of the growth curve until less than about five specimens represent a given age class. Standard deviations in height vs. age data do not measurably increase in *Protothaca* with ontogeny.

Geographic differences in the duration of the spawning season and dispersion in the time of settlement have a more dramatic effect on latitudinal trends in the variance of size

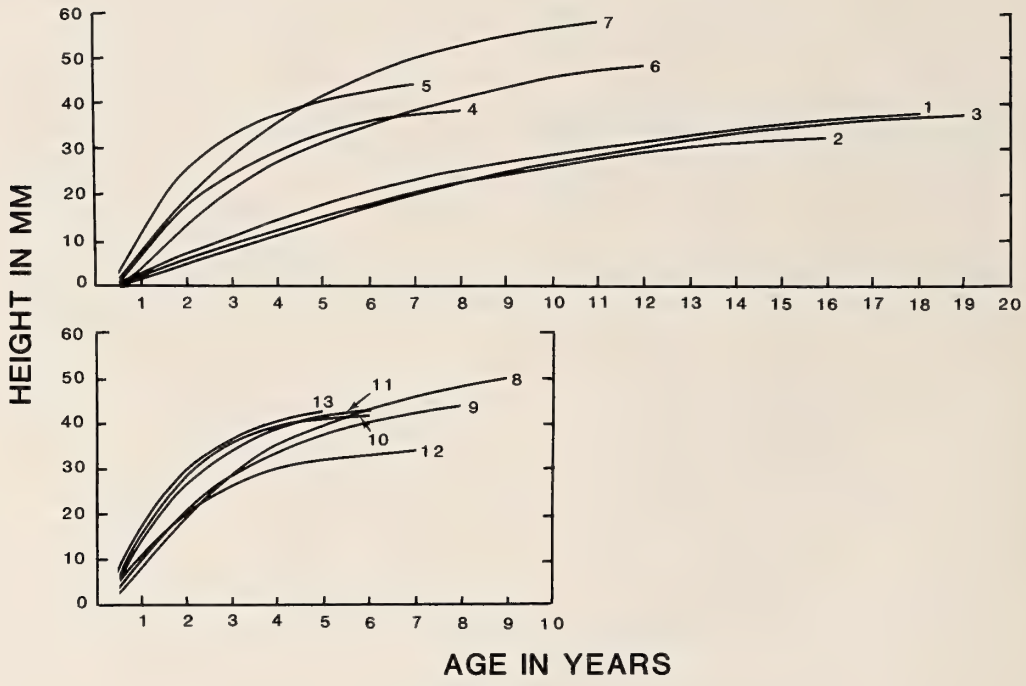


Figure 2

Shell height vs. age curves of 13 Recent collections of *Protothaca staminea* throughout its range. 1, Whittier, AK; 2, Kayak Is., AK; 3, Dall Is., AK; 4,5, Puget Sound, WA; 6, coastal Oregon; 7, Humbolt, CA; 8, Cayucos, CA; 9, Morro Bay, CA; 10, Long Beach, CA; 11–13, Baja California, Mexico: 11, Estero Punta Banda; 12, Rosarita Bay; 13, Santa Maria Bay. Note the general increase in the convexity of curves and reduced longevity progressing from northern to southern localities.

vs. age data. At high latitudes, spawning in *Protothaca staminea* is limited to the month of June and standard deviations in size vs. age data are exceptionally small (Feder *et al.*, 1979; and see Nickerson, 1977). At lower latitudes near Victoria, B.C., however, spawning takes place from April to October (Quayle, 1943) and standard deviations there are substantially greater. Kinne (1972) has noted progressive increases in the duration of the spawning season for many temperate invertebrates with decreasing latitude. Craig (1967) observed more scatter in the position of growth rings in bivalve species sampled at Bimini lagoon when compared to higher latitude (temperate) species and suggested that this may reflect more continuous recruitment throughout the year in the Bimini species. Hence, where spawning is spread throughout more of the year greater standard deviations in shell heights are predicted among individuals of a given age.

GROWTH HISTORIES

Growth curves of Recent *Protothaca* specimens are summarized in Figures 2 and 3. Table 1 contains a listing of Walford slopes for *Protothaca* and *Siliqua patula* throughout the study region as a function of sea-surface temperature. Walford plots were constructed for each sample in order to estimate the rate of growth deceleration, maximum mean size, and maximum longevity of average individuals (Walford, 1946; Hancock, 1965; Sheldon, 1965, Cerrato, 1980) (Figure 4). Because of the asymptotic approach of growth curves to a horizontal line, maximum shell heights must be estimated when employing Walford plots. In this study, maximum height is taken where 98% of H_{t+1} (shell height at time t plus one year) has been obtained by H_t. The age that corresponds to this shell height is taken as the mean maximum longevity of individuals from the habitat.

Latitudinal Trends in Growth Histories

At the northern range end points of all three species studied the rate of growth is slower, growth rate deceleration is less pronounced (see below), and longevity is greater than at their southern range end points. Maximum sizes of *Protothaca staminea* are not observed at extreme high latitudes, but somewhat south (Table 1). This reflects almost negligible height increases during the first few years of growth for this species in the Gulf of Alaska. In *P. grata* and *Siliqua patula,* initial growth rates are not as markedly reduced at their northern range end points and the maximum sizes are obtained there.

Walford plot slopes represent a quantification of the rate at which growth decelerates with ontogeny equivalent

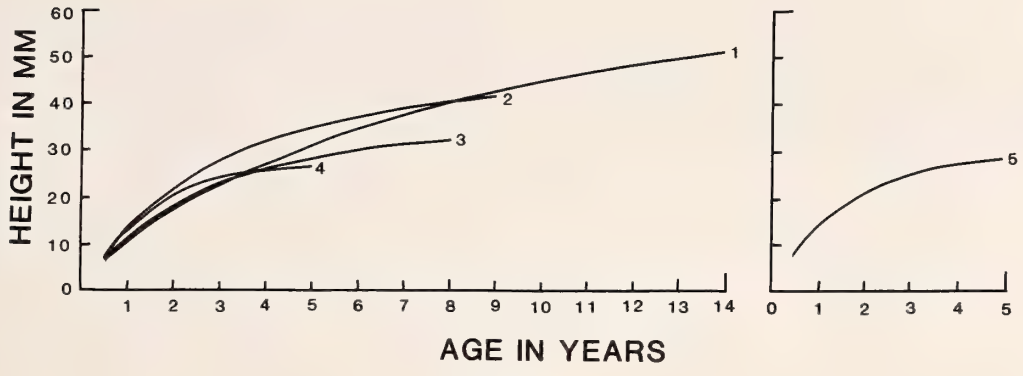


Figure 3

Representative shell height vs. age curves of *Protothaca grata* (1–4), and *P. asperrima* (5). 1, Cholla Bay, head of the Gulf of California; 2, Magdalena Bay, Mexico; 3, Mazatlan, Mexico; 4, Panama Bay; 5, Panama.

to e^{-k} in VON BERTALANFFY's (1938) growth equation. High Walford slopes represent relatively steady growth increases from year to year while progressively lower slopes reflect increasingly pronounced convexity in size vs. age curves. For *Protothaca,* slopes decrease from north to south beginning with a value of 0.91 for *P. staminea* from Prince William Sound, Alaska, decreasing to a minimum value of 0.49 for a sample from Santa Maria Bay (central Baja California). *Protothaca grata* specimens also exhibit a maximum Walford slope (0.89) at the taxon's northern range end point at the head of the Gulf of California, and a minimum value (0.55) near the southern range end point of the species at Panama Bay. A Walford plot for the species *P. asperrima* from a single locality at Venado Island in the Canal Zone (near that taxon's southern range end point) was constructed yielding a slope of 0.52. Thus, in the northern hemisphere, Walford slopes on the order of 0.90 typify post-inflection growth of northern range end-point individuals of *Protothaca,* while values of 0.50 (or slightly less) typify the growth of individuals near southern range end points.

Slopes for *Siliqua patula* range from a maximum of about 0.70 at the northern range end point in the Gulf of Alaska, and gradually decrease to a minimum of about 0.33 at the southern range end point near Pismo, California. Although these end-point values are less than those of *Protothaca,* it is interesting to note that the *range* of values is approximately the same (roughly 0.40). The reasons for this discrepancy in range end-point values are not understood. It is possible that the differences arise from the significantly more compressed shell geometry of *Siliqua.*

Walford slope values for *Protothaca staminea, P. grata,* and *Siliqua patula* are plotted against mean annual sea-surface temperature estimates taken for each region by interpolating between 0.5°C surface isotherms determined for the northeastern Pacific by ROBINSON & BAUER (1976) (Figure 5). A slightly higher temperature (*i.e.,* 8.6°C vs. 7.5°C) was taken for Prince William Sound, Alaska, representing April through September mean monthly temperatures only (NICKERSON, 1977). This step was taken so that the temperature estimate was approximately in line with that actually experienced by *Protothaca* during its growth season in the region. Excellent correlations were obtained with $r = -0.938$ for *P. staminea,* $r = -0.842$ for *P. grata,* and $r = -0.935$ for *S. patula,* suggesting that mean annual temperature is a principal environmental factor determining the slope of the Walford plot, and hence the rate of annual growth deceleration.

Two samples from Puget Sound yielded seemingly anomalous slopes of 0.68 and 0.62. As a check for consistency, data from Fraser and Smith (1928) for *Protothaca staminea* at Victoria, B.C., yield a value of 0.70. However, K. Cheu at the University of Washington Department of Ecology (personal communication, 1985) advises that mean temperatures within the sound are easily 4°C warmer on many of the tidal flats than along the Washington outer coast. This indicates mean annual temperatures for Puget Sound tidal flats are approximately 12.5°C. Hence, Walford slopes close to those observed at Cayucos and Morro Bay, California (*e.g.,* 0.74 and 0.69, respectively) (Table 1) should in fact be expected for the Puget Sound area.

A second latitudinal anomaly in Walford slopes occurs along northern Baja California, Mexico, where they are higher than expected for the latitude. As indicated on ocean-surface temperature maps (ROBINSON & BAUER, 1976), however, the northern Baja California region is a site of pronounced coastal upwelling, and mean surface temperatures there are nearly identical to the more northern Long Beach, California locality (Table 1). South of these areas of upwelling, the decreasing trend in Walford slopes with latitude may be resumed; the southernmost sample of *Protothaca staminea* from central Baja California possesses a Walford slope (0.49) slightly lower than any of the other collections. Here temperatures are substantially warmer, averaging about 17.5°C.

As previously noted, the southernmost range of *Protothaca staminea* overlaps along the central and southernmost outer coast of southern Baja California with the north-

Table 1

Walford slopes (e^{-k}), mean annual sea-surface temperatures, and geographic locations of samples. Temperatures from ROBINSON & BAUER (1976) except for Alaskan localities of *Protothaca staminea,* which are from NICKERSON (1977).

Species	Walford slope (e^{-k})	Water temperature °C	Location
Protothaca staminea	0.91	8.6	Whittier, AK
Protothaca staminea	0.87	8.6	Kayak Island, AK
Protothaca staminea	0.90	8.6	Dall Island, AK
Protothaca staminea	0.68	12.5	Puget Sound, WA
Protothaca staminea	0.62	12.5	Puget Sound, WA
Protothaca staminea	0.83	11.8	Oregon
Protothaca staminea	0.78	12.2	Humbolt, CA
Protothaca staminea	0.74	13.5	Cayucos, CA
Protothaca staminea	0.69	13.5	Mooro Bay, CA
Protothaca staminea	0.51	16.0	Long Beach, CA
Protothaca staminea	0.59	14.5	Punta Banda, Mex.
Protothaca staminea	0.59	14.5	Rosarita Bay, Mex.
Protothaca staminea	0.49	17.5	S. Maria Bay, Mex.
Protothaca grata	0.89	21.5	Cholla Bay, Mex.
Protothaca grata	0.68	23.0	Guaymas, Mex.
Protothaca grata	0.74	22.0	Magdalena Bay, Mex.
Protothaca grata	0.69	25.5	Mazatlan, Mex.
Protothaca grata	0.63	27.5	Nicaragua
Protothaca grata	0.55	27.3	Panama
Siliqua patula	0.68	6.8	Hallo Bay, AK
Siliqua patula	0.69	6.8	Swickshak, AK
Siliqua patula	0.71	7.2	Karls Bar, AK
Siliqua patula	0.64	9.2	Masset, AK
Siliqua patula	0.48	11.5	Copalis, WA
Siliqua patula	0.54	12.2	Crescent City, CA
Siliqua patula	0.33	13.5	Pismo, CA

ernmost range of *P. grata,* and the taxonomic separation of the two species based on gross morphological grounds is difficult within their zone of range overlap. Growth histories are useful in distinguishing these species, however. Two collections from the Magdalena Bay region exhibit markedly different Walford slopes of 0.49 and 0.74 for *P. staminea* and *P. grata,* respectively.

PALEOTEMPERATURE DETERMINATIONS

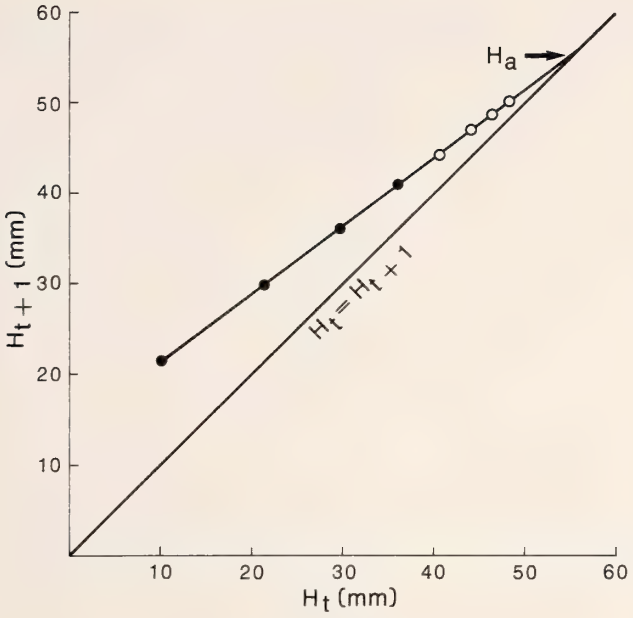
Growth-history curves are presented for six Pleistocene and a single Pliocene collection in Figure 6. Slopes were used to infer paleotemperatures (from Figure 5) and these were compared with paleotemperature determinations based on isotopic stage data (see SHACKLETON & OPDYKE, 1976; KENNEDY *et al.,* 1982) (Figure 7) and the distribution of cold and warm temperature molluscan faunas (KENNEDY, 1978, 1979; KENNEDY *et al.,* 1979, 1982; EMERSON *et al.,* 1981) for the Pleistocene of the Pacific coast. In general, paleotemperature estimates based on the regression of Walford slopes with modern sea temperatures are in good agreement with data provided from the sources cited above. The following discussion is organized from the youngest to the oldest specimen localities.

One of the youngest samples (LACMNH loc. 6913) is from the 40,000–60,000 year-old, mid-Wisconsin terrace at Isla Vista (Goleta) near Santa Barbara, California. The age would place the collection in isotopic stage 3 of SHACKLETON & OPDYKE (1976), a period of very cold water even at this comparatively low latitude. The Walford slope obtained for this sample is 0.84, indicative of a mean annual temperature on the order of 10.3°C, about 4°C colder than the mean for this section of the coast today. KENNEDY (1978) has noted that the faunas at this locality and along the Santa Barbara and Ventura coastlines contain several cold-water species presently restricted to the Columbian Molluscan Province.

Cold water is implied by the growth histories of two specimens from Cape Blanco, Oregon (UCMP A-8712) that are of approximately the same age as the cold-water Isla Vista collection (above). KENNEDY (1978) has noted a number of species with modern-day Aleutian affinities at Cape Blanco. Walford slopes suggest slightly colder paleotemperatures compared to those of Isla Vista. For Cape Blanco a slope of 0.87 was determined suggesting a mean annual temperature of about 9.6°C. Although the slope is based on only two specimens, both exhibited nearly identical skeletal growth histories.

Two localities, UCLA loc. 4722 from Santa Cruz, California, and LACMNH loc. 5662 from Bay Center, Washington, have been assigned by KENNEDY (1978) to isotopic stage 5a (SHACKLETON & OPDYKE, 1976), a time of cooler conditions than occur today. According to Kennedy, Columbian temperatures may have persisted at least as far south as central California (*e.g.,* not as far south as during the colder isotopic stage 3, above); however, the faunal compositions at Santa Cruz indicate water temperatures somewhat warmer than expected when compared to the fauna at Point Año Nuevo only a few miles north. Kennedy has attributed this to the coastal physiography of Monterey Bay, and the lack of upwelling there. J. F. Wehmiller (unpublished, *in* KENNEDY, 1978) notes anomalous warm air temperatures for the latitude at Santa Cruz occurring today. The Walford slope for the Santa Cruz collection indeed reflects warmer than expected paleotemperatures given the climatic framework of isotopic stage 5a. The computed slope of 0.60 would suggest an approximate mean annual paleotemperature of 14.5°C. Based on very limited data for the Bay Center region, Kennedy suggests paleotemperatures very close to modern temperatures. The paleotemperature suggested in the Walford plot of the Bay Center specimens supports this interpretation; a slope of 0.86 suggests a paleotemperature of about 9.8°C.

Two other Pleistocene localities are approximately 120,000 years old, a time of unusually warm temperatures (isotopic stage 5e). The first (UCLA loc. 2314) is from



AGE	HEIGHT
1	10.2
2	21.5
3	29.7
4	36.2
5	40.8
(6)	44.2
(7)	46.8
(8)	48.7
(9)	50.1

Figure 4

Construction of a Walford plot from height vs. age data (right). The horizontal axis represents shell height (mm) at a given age (years). The vertical axis represents shell height one year later. Open circles are values derived from the growth equation ($H_{t+1} = b + mH_t$), where m is the slope of the Walford plot and b is the intercept with the vertical axis. H_a describes the intersection of the Walford plot line with a line of no growth where $H_t = H_{t+1}$.

the Palos Verdes Sand, type locality of the Pleistocene Verdean Province. Specimens yield a Walford slope of 0.58, indicative of temperatures approaching 15°C. The second (a composite of UCLA locs. 3447 and 3445) was taken slightly to the north at the type locality of the Pleistocene Cayucan Province, and indicates a paleotemperature of about 11.2°C based on a Walford slope of 0.79. The large temperature change over this relatively short geographic distance during isotopic stage 5e is not surprising. The collections are separated by a major physiographic transition centering today on Point Conception, and this results in the clustering of sea-surface isotherms there. If the paleotemperature estimates above are correct, they suggest the currently steep latitudinal thermal gradient was maintained between the Verdean and Cayucan Provinces during isotopic stage 5e.

The single Pliocene collection (UCLA loc. 3491) is from the Etchegoin Formation of Kern County, California. For these probable Middle to Late Pliocene age specimens, growth under relatively cool-water conditions is expected (Addicott, 1970). A Walford slope of 0.65 was determined for a sample of 30 specimens, suggesting a mean annual temperature of about 13.5°C.

Despite the unknowns concerning the precision of temperature values projected from Walford plots, and the first-order approximations of temperature based on maps of sea-surface isotherms, the use of Walford slopes as an estimate of paleotemperatures appears promising. The obvious next step in the research should be to determine Walford slopes based on a large number of Recent species throughout their geographic ranges, especially from locations where mean annual temperatures have been previously determined. A second future line of research should be to contrast Walford temperature estimates with determinations based on isotopic compositions of shell material.

LATITUDINAL TRENDS IN DAILY GROWTH-INCREMENT NUMBERS

Criteria employed in the recognition of daily growth increments for *Protothaca* follow Kennish (1980) for *Mercenaria mercenaria* and other references cited in Rhoads & Lutz (1980). Latitudinal trends in daily growth-increment data (Figure 8) are based on observations in thin-section, acetate peels, and in polished shells embedded in resin blocks. The determination of the number of increments formed within the first growing season is important because numbers decline with ontogeny. Preliminary evidence suggests that the rate of this decline also varies with latitude (Figure 9). In some specimens small areas of the umbonal region were abraded and the number of increments had to be estimated. This was done by measuring the distance across the abraded area and then dividing by the average thickness of adjacent increments. This procedure should have introduced an error of no greater than about 10 increments.

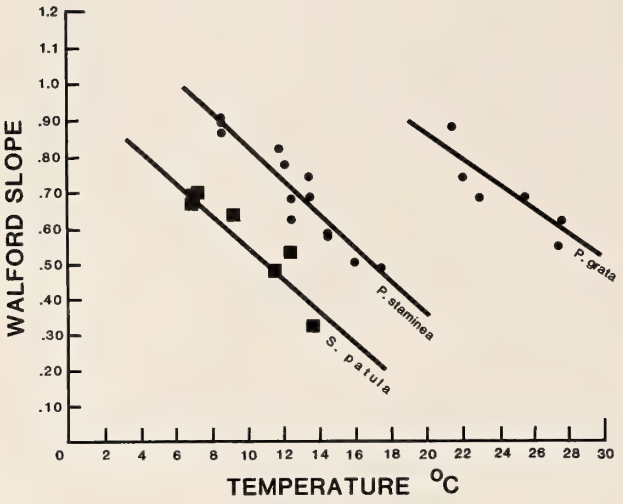


Figure 5

Walford slopes plotted against mean annual sea-surface temperature (see text) for *Protothaca staminea, P. grata,* and *Siliqua patula* samples collectively ranging from the Gulf of Alaska to Panama.

The maximum number of daily increments formed during the first full growing season increases systematically with decreasing latitude (Figure 8), and the trend is not interrupted where congeners overlap. In the Gulf of Alaska, the maximum number of daily growth increments is about 150, suggesting that *Protothaca staminea* is metabolically growth-active for only about five months out of each year. Progressing southward, the numbers of increments increase gradually such that at Panama Bay, they number about 331.

The latitudinal trend in increment numbers parallels the global seasonal pattern of primary productivity in the world's oceans (Cushing, 1959a, b; Menzel & Ryther, 1960; Ryther & Menzel, 1960; Raymont, 1963). A regular trend in the duration and amplitude of primary productivity undoubtedly affects the length of the growing season. At high latitudes the season is short and peaked. Progressing toward the equator, the amplitude of the productivity curve flattens substantially, often consists of two modes at mid-latitudes, and very near the equator is extremely low, but of much greater duration. The global distribution of available sunlight is considered of principal importance in the initiation of annual productivity, whereas the role of temperature is relatively minor. This being the case, then it should be expected that the regular trend in daily increment numbers vs. latitude (Figure 8) should more closely reflect trophic resource seasonality patterns than temperature effects.

DISCUSSION

Several factors structure the growth histories of post-larval individuals throughout the northeastern Pacific range of *Protothaca.* Two of the most important factors are the range of temperatures experienced by individuals, and the seasonal pattern of primary productivity. Other factors such as salinity and water chemistry are considered to contribute a relatively insignificant effect on growth-history differences over the broad geographic scale evaluated in the study.

Temperature is known to determine the rate at which food may be metabolized, and hence, should substantially affect the seasonal pattern of increasing and decreasing daily increment thicknesses. Such trends have been well documented for a number of bivalve taxa (*e.g.,* Pannella & MacClintock, 1968; Rhoads & Pannella, 1970; Arthur *et al.,* 1983). The effect of seasonal patterns in trophic resource abundance on the thicknesses of daily growth increments, and questions involving the energetics of calcium carbonate precipitation over the range of temperatures that bivalve species experience, remain as important areas of future research.

Figure 6

Pleistocene (1–6) and Pliocene (7) shell height vs. age curves of *Protothaca staminea.* 1, Isla Vista, CA; 2, Cape Blanco, OR; 3, Santa Cruz, CA; 4, Bay Center, WA; 5, Palos Verdes, CA; 6, Cayucos, CA; 7, Etchegoin Fm., central CA.

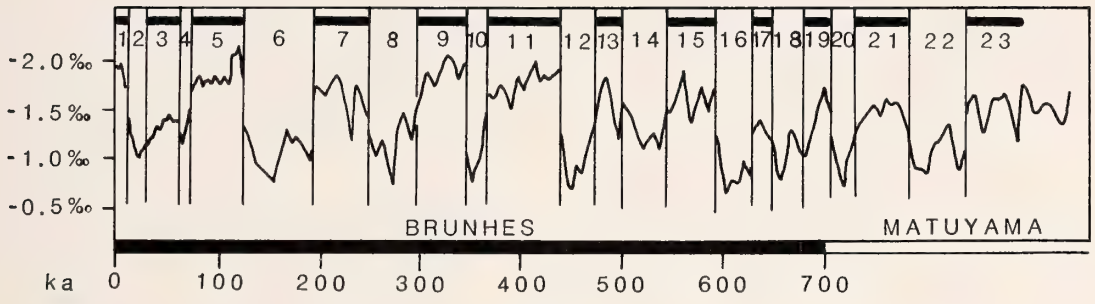


Figure 7

Isotopic stages redrawn from SHACKLETON & OPDYKE (1976). Peaks represent relatively warmer paleotemperatures.

The seasonal pattern of trophic resource supply is clearly important in determining the length of the growing season at different latitudes and this is apparently best recorded in the number of growth increments formed during the first full season of growth experienced by individuals. However, as shown earlier (Figure 9) the number of increments recorded within annual growth bands decreases systematically with increasing age. One explanation for this decline could be that ever-increasing energy is expended each year in other metabolic activities such as reproduction and maintenance. It has yet to be determined, however, if fewer days are recorded at the beginning of the growth season, at the end, or if the pattern of growth increment formation is simply more intermittent throughout the year. This hypothesis could be tested by contrasting some measure of the seasonal pattern of reproductive effort against growth expenditures for a series of age classes.

Near the southern range end point of a species, the growing season is relatively longer, and temperatures warmer on the average, than along more northern segments of its range. The combination of these factors acts to maximize the initial annual growth rate of *Protothaca.* Whether the higher rate of growth deceleration and reduced longevity at lower latitudes are consequences of initial (perhaps wasteful) growth expenditures as has been suggested by WEYMOUTH *et al.* (1931), or whether they result from the relaxation of selection for continued size increases after a minimum adaptive size is obtained, is unclear. Transplantation experiments (*e.g.,* SEED, 1968) that document rejuvenated growth late in life argue against models based on pre-determined lifetime metabolic allocations.

One explanation arises if the relatively reduced rate of ontogenetic growth deceleration (and increased longevity) is viewed from the standpoint of potential lifetime reproductive commitments. For example, if high latitude phenotypes followed a similar schedule of growth rate decline as their low latitude counterparts, their size and potential reproductive contributions at any given age would be volumetrically reduced (Harrington, in preparation). Hence, high-latitude individuals may rely on a strategy that acts, perhaps through allelic substitutions, to maximize the duration of growth activity each season, and perhaps to increase longevity. Table 2 contrasts predicted total lifetime reproductive contributions for individuals near the range end points and range midpoint of *Protothaca staminea,* assuming that fecundity is uniformly a 50% function of soft-tissue volume. Although this tabulation represents only gross estimates of lifetime reproductive effort, it is significant in two respects. First, the reproductive contributions for individuals located near the respective range end points are nearly identical. This suggests that range end points may not be determined by thermal effects per se (*i.e.,* heat or cold death) but by population recruitment effects stemming from (temperature and seasonality-dependent) growth-history patterns. Secondly, individual reproductive contributions and potential population recruitment levels are maximized near the range midpoint of the species. Thus, it should be expected that population sizes are greatest and perhaps most stable there (see BROWN, 1984).

Viewed from the standpoint of relative life-history strategies (STEARNS, 1976), it is apparent that northern range end-point representatives, in effect, hedge their reproductive bets by virtue of delayed contributions (due to slower

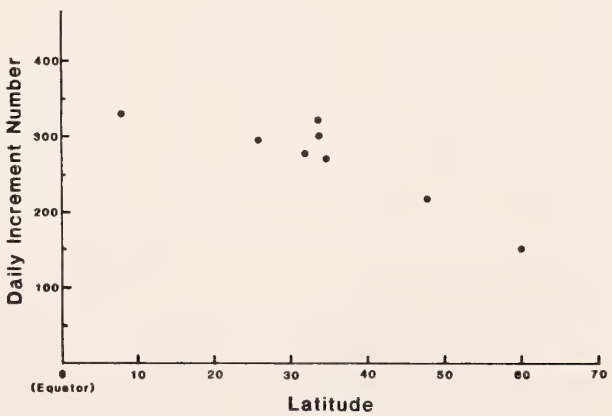


Figure 8

The number of daily growth increments formed during the first full season of growth (see text) based on single specimens of *Protothaca* from the Gulf of Alaska to Panama.

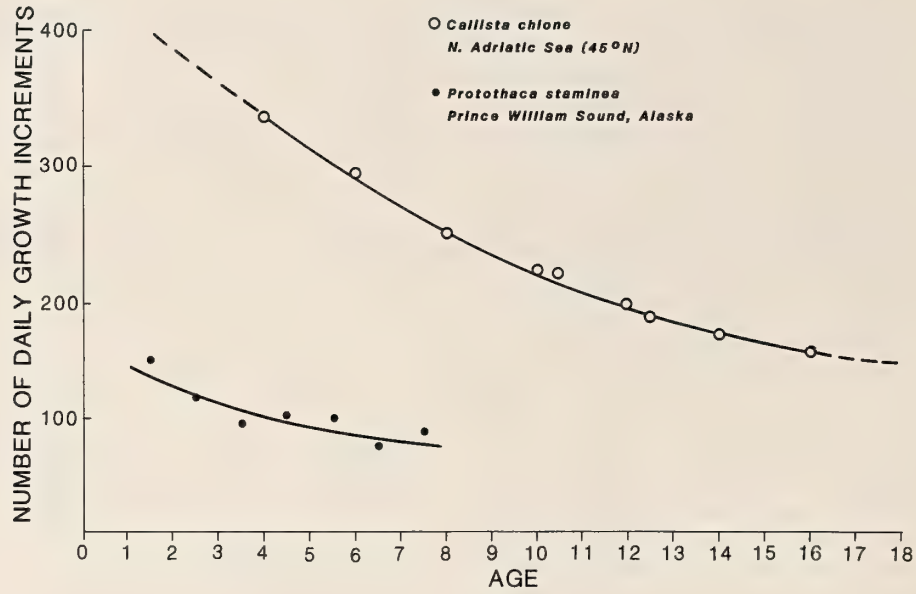


Figure 9

Ontogenetic decrease in the number of daily growth increments for a specimen of *Prototheca staminea* from the Gulf of Alaska (lower curve) and *Callista chione* (upper curve) from the northern Adriatic Sea. Data for *C. chione* are extracted from HALL (1975) by combining the number of growth increments in the "fast growth band" and the "biocheck" at given ages from Hall's curve (HALL, 1975:fig. 4). Note that the rate of decrease is greater for *C. chione*.

growth) and significantly greater longevity. Meanwhile, southern phenotypes can be viewed as relative *r*-strategists; reproductive contributions are maximized among relatively young individuals. For example, by age 4 the southern phenotypes have produced as many potential offspring per capita as do northern phenotypes by age 12 (Table 2). In terms of actual population recruitment potentials for *Prototheca staminea* this analysis awaits data based on latitudinal differences in survivorship. For *Siliqua patula,* however, the general pattern is of progressively lower age-specific mortality at higher latitudes (WEYMOUTH *et al.*, 1931). If this survivorship trend also applies to *Prototheca,* then smaller age-specific reproductive efforts among young, northern individuals should be at least partially overcome by the more significant reproductive contributions of relatively larger, older age classes.

The employment of growth-history patterns may provide useful data to a variety of paleontological problems. Potential paleotemperature applications have been suggested in a previous section. As a paleobiogeographic tool the patterns observed suggest a means by which the geographic position of a fossil sample with respect to its species range end points might be suggested. For example, Walford slopes of approximately 0.90 should indicate proximity to northern, and values of approximately 0.50 to southern range end-point positions.

Latitudinal trends in the number of daily growth increments formed during the first full season of growth may

Table 2

Estimated age-specific shell volumes for individuals of *Prototheca staminea* from northernmost, mid-range, and southernmost localities. Total reproduction is taken as one-half of the sum of shell volumes at age. Volumes derived from curve in HARRINGTON (1986).

	Gulf of Alaska		Cayucos, CA		Baja California	
Age (yr)	Height (mm)	Volume (mL)	Height (mm)	Volume (mL)	Height (mm)	Volume (mL)
1	2.69	<1.0	10.23	1.2	14.90	1.8
2	5.76	<1.0	21.54	2.7	27.10	4.3
3	8.93	1.0	29.70	6.0	34.30	9.0
4	12.63	1.5	36.20	10.5	38.53	12.8
5	15.68	1.9	40.76	16.0	41.04	16.4
6	18.20	2.3	44.13	20.0	42.51	18.2
7	20.58	2.5	46.73	24.2	—	—
8	22.82	2.9	48.66	27.8	—	—
9	24.50	3.5	50.10	30.7	—	—
10	26.10	3.9	51.18	31.5	—	—
11	27.49	4.4	51.97	33.0	—	—
12	28.71	5.1	—	—	—	—
13	29.78	6.0	—	—	—	—
14	30.70	6.5	—	—	—	—
15	31.51	7.0	—	—	—	—
16	32.22	7.5	—	—	—	—
Total volume		58.0		175.8		62.5
Total production		29.0		87.9		31.2

provide information useful in documenting latitudinal translations of crustal blocks. Because high-latitude phenotypes should typically record a low number of increments, shells from high-latitude fossil deposits bearing anomalously high increment numbers in the first annulus should signal that large-scale latitudinal translations may have occurred. However, much more data are needed in order to determine the generality of the association between increment numbers and latitude. In addition, increment numbers may be useful in the evaluation of finer-scale trends in seasonality over given latitudinal regions.

As a potential tool in the correlation of rock units, growth-history analysis may lead to more precise local correlations reflecting localized temperature effects. Refined stratigraphic subdivisions of fossiliferous rock units may be based on at least three growth-history criteria: (1) the rate of growth deceleration, (2) initial annual growth rates, and (3) the thickness of growth increments and their rate of decline in numbers during ontogeny.

ACKNOWLEDGMENTS

My grateful appreciation is extended to J. W. Valentine, S. M. Awramik, and J. A. Mattinson of the Department of Geological Sciences, University of California, Santa Barbara, who served on the author's dissertation committee. A. Clarke, British Antarctic Survey, P. W. Frank, University of Oregon, G. L. Kennedy, Los Angeles County Museum of Natural History, J. W. Valentine, and an anonymous reviewer each contributed many constructive criticisms of earlier versions of the manuscript.

Partial financial support was obtained through the University of California Institute of Marine Resources, a Geological Society of America Research Grant, the National Science Foundation NSF-EAR 17011, and the Department of Geological Sciences, University of California, Santa Barbara. Mary Parrish, United States Museum of Natural History, provided assistance in drafting the figures, and Lorie Harrington provided substantial support in the preparation of the original manuscript.

LITERATURE CITED

Addicott, W. O. 1970. Latitudinal gradients in the Tertiary molluscan faunas of the Pacific coast. Palaeogeog., Palaeoclimatol., Palaeoecol. 8:287–312.

Ansell, A. D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographic range. Jour. Cons. Perm. Int. Explor. Mer 31:364–409.

Arthur, M. A., D. F. Williams & D. S. Jones. 1983. Seasonal temperature-salinity changes and thermocline development in the mid-Atlantic Bight as recorded by the isotopic composition of bivalves. Geology 11:655–659.

Beukema, J. J. & B. W. Meehan. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. Mar. Biol. 90:27–34.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Amer. Natur. 124:255–279.

Cerrato, R. M. 1980. Demographic analysis of bivalve populations. Pp. 417–465. *In:* D. C. Rhoads & R. H. Lutz (eds.), Skeletal growth of aquatic organisms. Plenum: New York.

Craig, G. Y. 1967. Size-frequency distributions of living and dead pelecypods from Bimini, Bahamas, B.W.I. Jour. Geol. 75:34–45.

Cushing, D. H. 1959a. On the nature of production in the sea. Fish. Invest. Lond. Series II. 22:1–40.

Cushing, D. H. 1959b. The seasonal variation in oceanic productivity as a problem in population dynamics. Jour. Cons. Perm. Int. Explor. Mer 24:455–464.

Emerson, W. K., G. L. Kennedy, J. F. Wehmiller & E. Keennan. 1981. Age relations and zoogeographic implications of Late Pleistocene marine invertebrate faunas from Turtle Bay, Baja California Sur, Mexico. Nautilus 95:105–116.

Feder, H. M. & A. J. Paul. 1973. Abundance estimates and growth rate comparisons for the clam *Protothaca staminea* from three beaches in Prince William Sound, Alaska with additional comments on size-weight relationships, harvesting and marketing. Univ. Alaska Inst. Mar. Sci. Tech. Report No. R73-3:34 pp.

Feder, H. M., J. C. Hendee, P. Holmes, G. J. Muellar & A. J. Paul. 1979. Examination of a reproductive cycle of *Protothaca staminea* using histology, wet-dry weight ratios, and condition indices. Veliger 22:182–187.

Fraser, C. M. & G. M. Smith. 1928. Notes on the ecology of the littleneck clam, *Paphia staminea* Conrad. Trans. Roy. Soc. Can. Ser. 3, 22, Sect. V:249–269.

Gilbert, M. A. 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). Biol. Bull. 145:119–126.

Hall, C. A., Jr. 1975. Latitudinal variation in shell growth patterns in bivalve molluscs: implications and problems. Pp. 163–175. *In:* G. D. Rosenberg & S. K. Runcorn (eds.), Growth rhythms and the history of the earth's rotation. John Wiley and Sons: London.

Hancock, D. A. 1965. Graphical estimation of growth parameters. Jour. Cons. Perm. Int. Explor. Mer. 29:340–351.

Harrington, R. J. 1986. Growth patterns within the genus *Protothaca* (Bivalvia: Veneridae) from the Gulf of Alaska to Panama: paleotemperatures, paleobiogeography, and paleolatitudes. Doctoral Thesis, University of California, Santa Barbara. 235 pp.

Kennedy, G. L. 1978. Pleistocene paleoecology, zoogeography and geochronology of marine invertebrate faunas of the Pacific Northwest coast (San Francisco Bay to Puget Sound). Doctoral Thesis, University of California, Davis. 824 pp.

Kennedy, G. L. 1979. Pleistocene marine faunal provinces of California. Appendix to K. R. LaJoie, J. P. Kern, J. F. Wehmiller, S. A. Mathieson, A. M. Sarna-Wojcicki, R. F. Yerkes & P. A. McCrory (1979), Quaternary marine shorelines and crustal deformation, San Diego to Santa Barbara, California. Pp. 3–15. *In:* P. L. Abbott (ed.), Geological excursions in the southern California area (Dept. Geol. Sci., San Diego State Univ., San Diego).

Kennedy, G. L., K. R. LaJoie & J. F. Wehmiller. 1979. Late Pleistocene and Holocene zoogeography, Pacific northwest coast. Geol. Soc. Amer. Abstr. Prog. 11:87.

Kennedy, G. L., K. R. LaJoie & J. F. Wehmiller. 1982. Aminostratigraphy and faunal correlations of late Quaternary marine terraces, Pacific coast, USA. Nature 299:545–547.

Kennish, M. J. 1980. Shell microgrowth analysis: *Mercenaria mercenaria* as a type example for research in population dynamics. Pp. 255–294. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms. Plenum: New York.

KINNE, O. 1972. Temperature. Pp. 321–616. *In:* O. Kinne (ed.), Marine ecology Vol. 1. Wiley Interscience: London.

MENZEL, D. W. & J. H. RYTHER. 1960. The annual cycle of primary production in the Sargasso Sea, Bermuda. Deep Sea Res. 6:351–367.

NEWELL, N. D. 1964. Physiological aspects of the ecology on intertidal molluscs. Pp. 59–81. *In:* R. M. Wilbur & C. M. Yonge (eds.), Physiology of Mollusca. Vol. 1. Academic Press: London.

NICKERSON, R. B. 1977. A study of the littleneck clam (*Prototothaca staminea* Conrad) and the butter clam (*Saxidomus giganteus* Deshayes) in a habitat permitting coexistence, Prince William Sound, Alaska. Proc. Natl. Shellfish Assoc. 67:85–102.

PANNELLA, G. 1975. Paleontological clocks and the history of the earth's rotation. Pp. 253–284. *In:* G. D. Rosenberg & S. K. Runcorn (eds.), Growth rhythms and the history of the earth's rotation. John Wiley and Sons: London.

PANNELLA, G. & MACCLINTOCK. 1968. Biological and environmental rhythms reflected in molluscan shell growth. Jour. Paleontol. 42:64–80.

PAUL, A. J. & H. M. FEDER. 1973. Growth recruitment and distribution of the littleneck clam, *Prototothaca staminea* in Galena Bay, Prince William Sound, Alaska. Fish Bull. 7: 665–677.

PAUL, A. J., J. M. PAUL & H. M. FEDER. 1976. Recruitment and growth in the bivalve *Prototothaca staminea* at Olson Bay, Prince William Sound ten years after the 1964 earthquake. Veliger 18:385–392.

PETERSON, C. H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43:343–359.

QUAYLE, P. B. 1943. Sex, gonad development and seasonal gonad changes in *Paphia staminea* (Conrad). Jour. Fish. Res. Bd. Canada 6:140–151.

RAYMONT, J. E. G. 1963. Plankton and Productivity in the Oceans. Pergamon Press: New York. 660 pp.

RHOADS, D. C. & R. H. LUTZ (eds.). 1980. Skeletal growth of aquatic organisms. Plenum: New York. 750 pp.

RHOADS, D. C. & G. PANNELLA. 1970. The use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3:143–161.

ROBINSON, M. K. & R. A. BAUER. 1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. Naval Oceanographic Office, Washington, D.C.

RYTHER, J. H. & D. W. MENZEL. 1960. The seasonal and geographic range of primary production in the Western Sargasso Sea. Deep Sea Res. 6:235–238.

SCHMIDT, R. R. & J. E. WARME. 1969. Population characteristics of *Prototothaca staminea* (Conrad) from Mugu Lagoon. Veliger 12:193–199.

SEED, R. 1968. Factors influencing shell shape in *Mytilus edulis* L. Jour. Mar. Biol. Assoc. U.K. 48:561–584.

SHACKLETON, N. J. & N. D. OPDYKE. 1976. Oxygen isotope and paleomagnetic stratigraphy of Pacific core V28-239, late Miocene to latest Pleistocene. Geol. Soc. Amer. Mem. 145: 449–464.

SHELDON, R. W. 1965. Fossil communities with multi-modal size-frequency distributions. Nature 206:1336–1338.

STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51:3–47.

VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws II). Human Biol. 10:181–213.

WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90:141–147.

WEYMOUTH, F. W., J. C. MCMILLIN & W. H. RICH. 1931. Latitude and relative growth in the razor clam *Siliqua patula*. Jour. Exp. Biol. 8:228–249.

The Veliger 30(2):159–166 (October 1, 1987)

THE VELIGER

Age and Growth of the Subantarctic Limpet *Nacella (Patinigera) magellanica magellanica* (Gmelin, 1791) from the Strait of Magellan, Chile

by

LEONARDO F. GUZMAN AND CARLOS F. RIOS

Instituto de la Patagonia, Universidad de Magallanes,
Casilla 113-D, Punta Arenas, Chile

Abstract. Age and growth rate of the subantarctic limpet *Nacella (Patinigera) magellanica magellanica* (Gmelin, 1791) from intertidal cobble–boulder fields of the Strait of Magellan were determined. Growth was defined using exterior shell growth lines and employing the Ford-Walford relationship and von Bertalanffy model. Males and females did not show significant differences in growth and, according to estimated growth parameters, which varied geographically along the Strait, the ten studied populations can be segregated into four distinct groups. A seasonal growth pattern, with higher growth rates during spring–summer and lower rates during autumn–winter, was present which correlates with seasonal fluctuations of physical and biological conditions of the Strait. Initiation of annulus formation might occur between the end of summer and the beginning of autumn. A low annual growth rate (K = 0.0263 – 0.1913), a low instantaneous rate of natural mortality (M = 0.026 – 0.191), and a long life (15.7–37.8 yr) were characteristics of the studied populations. Growth rate and longevity were inversely correlated. The western populations of the studied area had the highest growth rates and the lowest longevities, while the eastern populations showed the opposite trend. The observed growth pattern was inversely correlated with tidal range, but this single physical factor alone did not explain the trend.

INTRODUCTION

Comprehensive studies on growth and age have been undertaken for many marine gastropods at different latitudes (FRANK, 1969; BRANCH, 1974; BRETOS, 1980; COCKCROFT & FORBES, 1981), including the Antarctic region (PICKEN, 1979, 1980). However, comparatively little information exists for gastropods inhabiting the subantarctic zone (*e.g.*, BLANKLEY & BRANCH, 1985).

Among the subantarctic gastropods, the *Nacella (Patinigera)* complex is well represented within southern Patagonia and Tierra del Fuego of Chile and Argentina (*i.e.*, the Magellanic molluscan province; POWELL, 1973). Powell considers this complex to be constituted by cold water limpets with the greater part of their range being subantarctic. *Nacella (Patinigera) magellanica magellanica* (Gmelin, 1791) is one of the 14 species of the genus *Nacella* Schumaker, 1928, recognized in the subantarctic zone, and one of the most common inhabitants of the beaches of Tierra del Fuego, the Strait of Magellan, and the Falklands Islands (POWELL, 1973).

Biological information for this species is scarce, although its geographical and bathymetric distributions (CARCELLES & WILLIAMSON, 1951), diagnostic features (DELL, 1971; POWELL, 1973; OTAEGUI, 1974), density, and spatial pattern of distribution (GUZMAN, 1978) have been studied. The aim of the present study was to determine age and growth for 10 intertidal populations of *Nacella (P.) magellanica* and to provide baseline data from which predictions and comparisons could be made.

MATERIALS AND METHODS

Samples of *Nacella (P.) magellanica* were obtained from 10 sites located in the Strait of Magellan, from the second narrow to its eastern entrance (Figure 1). Except for Punta Catalina, where the physical habitat is characterized by a hard clay terrace, the other sites are typical cobble–boulder beaches. The sites have a wide range of sediment sizes, exposures to wave action, slopes, and tidal amplitudes (see GUZMAN, 1978).

Fifty limpets at each site were randomly collected from

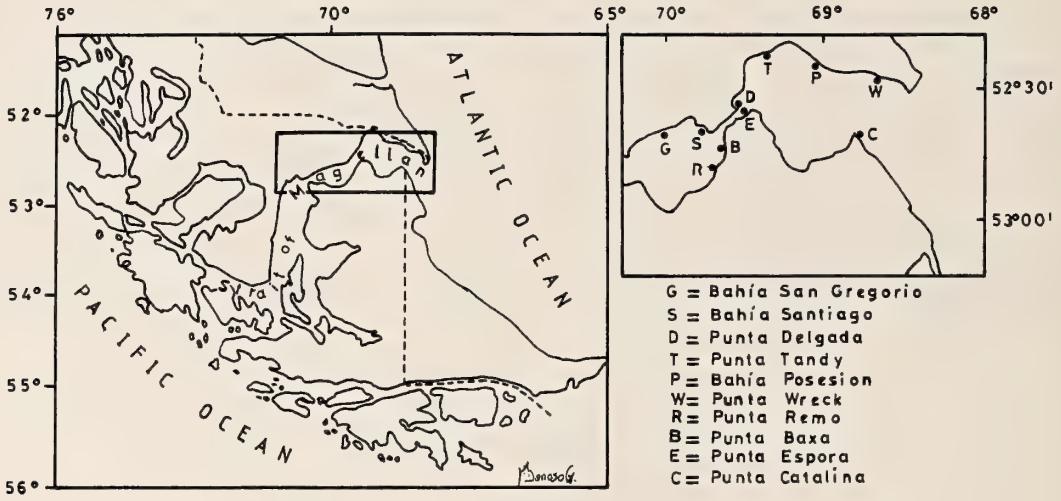


Figure 1

Location of the study area including sampling sites in the Strait of Magellan.

the mid-intertidal zone during spring 1977, winter 1978, and summer 1978 and 1979. Specimens from Punta Tandy were sampled in fall and spring 1980. In the laboratory the specimens were sexed by direct observation of the gonads, and the shell was used for growth measurements.

Growth was estimated by the growth ring method, which requires the establishment of rings as annual marks on the shell of the species under study (WILBUR & OWEN, 1964). This approach has been employed successfully in growth and age estimations in patellid (PICKEN, 1980), fissurellid (BRETOS, 1980, 1982), trochid (WILLIAMSON & KENDALL, 1981), and muricid (MIRANDA, 1975) species.

On the exterior shell surface of *Nacella* (*P.*) *magellanica* growth marks are present. It was assumed that the marks correspond perfectly to true annuli and, consequently, they were used for aging purposes (see Discussion). The maximum length of each consecutive growth ring from the front of the ring to its posterior margin was measured to the nearest 0.1 mm with vernier calipers. Separate information for females, males, and sexually undetermined specimens was recorded.

Measurements of consecutive rings were not assigned to specific ages owing to difficulties in assessing the rings on the shell apex, which is usually eroded. Thus, growth was inferred by plotting the correspondent pairs of consecutive ring lengths measured in each specimen, grouped by sampling periods and by sexes, according to the Ford-Walford method (WALFORD, 1946). This method basically consists of the linear relation of size at t years against size at t + 1 years.

Age was inferred from VON BERTALANFFY's (1938) growth model. The parameters K (growth coefficient) and L_∞ (asymptotic length) were derived from the regression coefficients of the Ford-Walford plots, while the theoretical age at length zero (t_ϕ) was computed following GULLAND (1965). The age at which 95% (p) of the asymptotic length or theoretical age limit (A_p) was reached, the instantaneous rate of natural mortality (M), and the fraction of an initial stock that would die during a year or conditional mortality rate (A) were derived from t_ϕ and K parameters following TAYLOR (1959). In this study, M is equivalent to the total instantaneous mortality rate (Z).

In order to evaluate both annual ring formation and seasonality in growth, the yearly marginal shell increment at six sites was evaluated. For this purpose, 10 shells from winter, spring, and summer samples were randomly chosen within an age range (7–9 yr) defined by the correspondent growth equation. Marginal increments were determined on the posterior edge of the shell, by measuring the distance from the last distinguishable growth ring to the edge of the shell using a stereomicroscope (16×) with a precision of ±0.02 mm.

RESULTS

The ranges of shell lengths of the specimens used in this study and those recorded during a 4-yr study program in the same sampling localities (unpublished data) are presented in Table 1.

Considering the residual variance, the best fit to the 10 Ford-Walford plots was given by an AM functional regression computed following Nair-Bartlett's procedure (BARTLETT, 1949). Taking into account the homogeneity of variances (Bartlett's test; $P > 0.05$), an analysis of covariance (ANCOVA) showed no significant difference in slopes and intercepts between sexes and sampling periods ($P > 0.05$). Consequently, the data were pooled and a global AM functional regression for each site was calculated.

In all cases the regressions of L_{t+1} on L_t were highly

Table 1

Range of shell lengths (mm) of *Nacella (P.) magellanica* collected during sampling periods in each study site (I: October–November 1977; II: January 1978; III: July–August 1978; IV: December 1978–February 1979). In parentheses are given the size ranges (mm) of limpets inhabiting the mid-intertidal zone. Locality codes are given in Figure 1.

Localities	I (Spring)	II (Summer)	III (Winter)	IV (Summer)
G	10.9–46.7 (9–48)	10.2–46.5 (7–46)	12.4–43.5 (7–50)	14.2–46.5 (9–48)
S	16.5–47.4 (11–48)	11.0–62.7 (7–62)	15.0–52.5 (13–52)	23.1–44.5 (9–46)
D	17.5–45.0 (14–46)	8.3–54.8 (5–54)	13.8–50.0 (6–53)	15.0–51.0 (12–50)
P	20.5–47.4 (11–48)	11.7–36.2 (7–40)	10.3–43.2 (7–44)	11.3–50.8 (9–50)
W	9.5–60.8 (7–68)	12.7–59.3 (5–64)	14.9–57.5 (3–57)	17.3–56.8 (9–64)
C	19.0–41.2 (16–45)	20.4–48.9 (7–50)	14.8–56.9 (13–56)	22.6–42.5 (17–46)
E	37.0–49.2 (33–52)	18.0–51.8 (9–52)	18.9–49.0 (6–50)	10.6–51.9 (7–52)
R	37.0–48.8 (37–52)	16.6–48.8 (13–56)	20.1–49.1 (17–50)	43.5–48.8 (10–50)
B	31.1–42.0 (29–43)	30.8–40.5 (21–42)	17.6–41.3 (13–43)	16.1–41.5 (9–50)
T*	13.2–30.8 (12–41)		17.0–31.9 (12–32)	

* Sampled on April (autumn) and December (spring) 1980, respectively.

Table 2

Single and common Ford-Walford regressions for *Nacella (P.) magellanica*. b = slope; a = intercept; r^2 = determination coefficient; n = sample size. Locality codes are given in Figure 1.

Localities	b	a	r^2	n
G	0.826	9.368	0.941	362
R	0.863	7.481	0.974	601
S	0.881	7.964	0.949	432
E-D-B	0.896	6.332	0.964	300
T-P	0.924	4.636	0.963	412
W-C	0.974	3.127	0.991	200

significant and explained over 92% of the observed variances, reflecting a good predictive relationship. The variances about the regression lines were heteroscedastic ($P > 0.05$), although three groups with homogeneous variances can be segregated; the population at Remo was heterogeneous with respect to all others. According to the ANCOVA applied within each homogeneous group, it is possible in some cases to calculate a common AM regression line, although the majority of the regression coefficients were significantly different ($P > 0.05$; Table 2).

A lower annual growth rate (slope) was estimated for the Gregorio and Remo populations, while higher values were obtained at Wreck-Catalina, reflecting an increasing tendency from west to east, *i.e.,* from the interior sites toward those near the eastern entrance of the Strait. The shell length at the first year of growth (intercept) follows an opposite tendency to the slope values, being larger in the inner sites. The value of the Gregorio population is almost three times larger than that of Wreck-Catalina.

The results obtained with the von Bertalanffy growth model reflect different growth rates of the studied populations. A greater growth rate was found at Gregorio, Santiago, and Remo, and the opposite at Wreck-Catalina (Table 3; Figure 2). The largest specimen collected in each locality, the theoretical age limit, the instantaneous rate of natural mortality, and the conditional mortality rate are also included in Table 3.

Although Wreck-Catalina populations presented the highest asymptotic length (120 mm) and those at Gregorio the lowest (54 mm), this parameter did not show a geographic tendency. According to a two-tailed Spearman rank correlation test (Snedecor & Cochran, 1964) the asymptotic length and the actual maximum size registered at each sampling site are positively correlated ($r = 0.652$; $P < 0.05$). Von Bertalanffy growth coefficients (K) varied between 0.0263 and 0.1913, decreasing toward the sites located near the eastern entrance of the Strait. The higher K value was determined for Gregorio, and it is approximately nine times larger than the lowest value recorded at Wreck-Catalina. The estimated annual growth rate indicated that different ages reached the 95% asymptotic length (A_p); and that these ages ranged between 15 and 37 yr, excluding Wreck-Catalina where the value was extremely high (113 yr). Because as K increases asymptotic length decreases, the lowest theoretical age limit was estimated for Gregorio, while the highest was determined for Wreck-Catalina.

The mortality rates were low, varying between 0.026 at Wreck-Catalina (2.6%) and 0.191 at Gregorio (17.4%), and showing an inverse relationship with growth rate. Mortality at Gregorio (inner site) was almost seven times higher than that at Wreck-Catalina (outer sites).

Along the study areas, tidal range shows a clear gradient from the eastern entrance to the second narrow (approximately from 10 to 4 m during spring tides), and correlates with the limpet's annual growth rate, size at the first year of growth, longevity, and mortality. In contrast, an independent relationship between K, L_∞, relative height of sampling areas, and tidal range at each site (following Kendall's nonparametric concordance analysis $W = 0.10$; $P > 0.05$) was found. Annual growth rate, size at the first year of growth, mortality rate, and asymptotic length are not correlated with limpet population density (mean val-

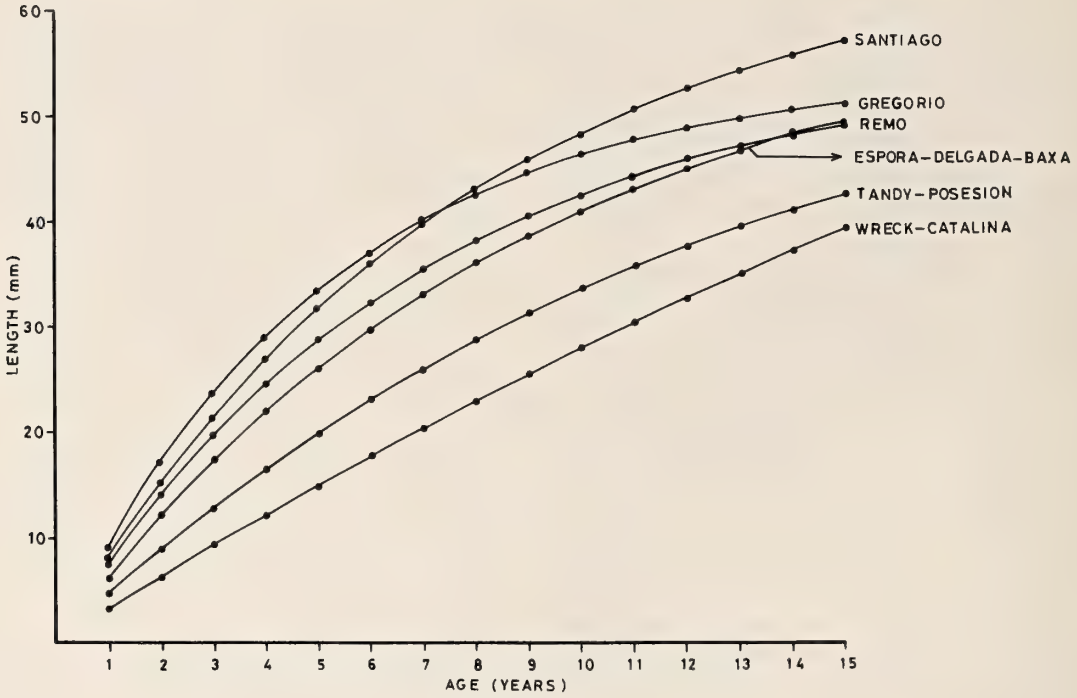


Figure 2

Von Bertalanffy growth curves for six populations of *Nacella* (*P.*) *magellanica* in the Strait of Magellan.

ues, unpublished data) according to a two-tailed Spearman's rank correlation test ($P > 0.05$). These variables, excluding asymptotic length ($P < 0.05$), are also independent of the intensity of aggregation estimated according to the Morisita index (SOUTHWOOD, 1975) ($P > 0.05$; unpublished data).

According to an analysis of variance (ANOVA), the mean marginal growth for limpets collected during different seasons was significantly different ($P < 0.05$), being higher during summer in comparison to spring and winter seasons (ANOVA; $P < 0.05$) (Table 4). The largest differences were observed between summer and winter, while no difference was detected between summer periods ($P < 0.05$). A geographical gradient in marginal growth is also distinguishable and follows the trend described for the annual growth estimation, *i.e.*, a tendency to decrease from west to east.

The seasonality in mean marginal growth follows the same pattern observed in some physical and biological growth-related parameters of the Strait (Figure 3). Data on macroalgal abundance have demonstrated a clear seasonal pattern, with maximum coverage in spring–summer and minimum coverage in winter (unpublished data). Also, photoperiod length interpolated from FRANCIS (1972) for the 52°S latitude is characterized by 17 h in early summer (December) and 8 hr in winter (July). Meanwhile, the surface seawater temperatures (from National Petroleum Company records) show the highest values in February (11.9°C) and the lowest in August (2.4°C).

DISCUSSION

Several factors can affect age and growth estimates when they are based on the shell ring method. In our study it must be noted that (1) limits are imposed by the assumption that growth ring formation occurs only once a year, and (2) there are difficulties in assessing consecutive growth rings, especially at the shell apex.

The criteria adopted to assess consecutive rings seem to be appropriate according to the determination coefficient values and the non-significant differences in slopes and elevations of the Ford-Walford relationships when periods within each locality were compared. On the other hand, the difficulty in assessing the first three or four growth rings is reflected in a poor representation of the left part of the Ford-Walford plots. In this case, asymptotic length should be overestimated and growth rhythm could not be as low as that obtained. Nevertheless, excluding the Wreck-Catalina estimation, all other cases show the asymptotic length to be close to the actual maximum size recorded at each sampling site. The difference between predicted and actual size at Wreck-Catalina can be explained, as has been pointed by KNIGHT (1968), by the growth line curvature which mathematically leads to an extremely large asymptotic length and, consequently, has no biological meaning.

A seasonal growth pattern in *Nacella* (*P.*) *magellanica* has not been experimentally shown, but some results suggest that such a pattern might occur in this limpet species.

Table 3

Von Bertalanffy parameters for *Nacella (P.) magellanica*. t_ϕ = theoretical age at length zero; K = instantaneous growth rate; L_∞ = asymptotic length; A_p = 95% theoretical limit age; M = instantaneous rate of natural mortality; A = conditional mortality rate; LT = maximum recorded length. Locality codes are given in Figure 1.

Localities	L_∞ (mm)	K	t_ϕ	A_p (yr)	M	A (%)	LT (mm)
G	54	0.1913	0.00910	15.7	0.191	17.4	55.1
R	55	0.1470	0.01153	20.4	0.147	13.7	55.2
S	67	0.1271	0.00910	23.6	0.127	11.9	61.0
E-D-B	61	0.1098	−0.00432	27.3	0.110	10.4	54.7-62.0-51.0
T-P	61	0.0792	−0.00289	37.8	0.079	7.6	41.8-52.0
W-C	120	0.0263	−0.00463	113.9	0.026	2.6	74.7-59.1

In fact, marginal summer growth increments were consistently higher than those estimated for winter and also, but to a lesser extent, than those of spring. We assumed that the beginning of ring formation occurs between the end of summer and early autumn, *i.e.*, between March and April. Initiation of annulus formation cannot occur during mid winter, because this would require a very short lapse of time to explain the relatively high marginal growth increment of spring samples. Breeding of *N. (P.) magellanica* in the Strait occurs annually between December and January (unpublished data), and the formation of a reproductive growth ring must be discarded because the marginal growth increment in summer samples is relatively too high. This seasonality in growth is in concordance with the annual fluctuation of physical and biological environmental conditions registered in the eastern part of the Strait of Magellan. Strong seasonal constraints by these factors (*e.g.*, incident light, temperature, and algal coverage) could result in restrictions in molluscan shell growth during these critically limiting months. A seasonal growth pattern has been observed in a number of marine gastropods (*e.g.*, Seapy, 1966; Bretos, 1978; McQuaid, 1981; Phillips, 1981; Race, 1981; Cockcroft & Forbes, 1981; McLachlan & Lombard, 1981); but growth rate seasonality reported for several Antarctic invertebrates as a response to the marked seasonal fluctuations of physical parameters is especially enlightening. Among these, the Antarctic littorinid *Laevilacunaria antarctica* (Martens, 1885) (Picken, 1979) and the Antarctic limpet *N. (P.) concinna* (Strebel, 1908) (Picken, 1980) have been reported.

The growth parameters obtained here fall well within the reported range for several species of marine gastropods, although *Nacella (P.) magellanica* can be considered among those species with a low growth rate. This feature is in accordance with estimates for *N. (P.) concinna* (Picken, 1980) but differs from *N. delesserti* (Blankley & Branch, 1985), which shows a much higher growth rate. The first year of growth of *N. delesserti* is almost four times greater than the highest estimation obtained for *N. (P.) magellanica*.

An inverse relationship between growth rate and longevity is evident for *Nacella (P.) magellanica*. This relation is in agreement with Fisher-Piette's (1941) conclusion on growth of several European marine species (*i.e.*, the faster growth, the shorter longevity). A similar inference was reached by Branch (1974) working with five South African *Patella* species, demonstrating that this relationship occurs at an intraspecific and interspecific level.

The longevities we report are among the highest recorded for marine gastropods (see review by Powell & Cummins, 1985). It is interesting to point out that, in a littoral population of the Antarctic limpet *Nacella (P.) concinna*, longevity is approximately 21 yrs (Picken, 1980), while in a sublittoral population of the same species, it

Table 4

Mean marginal growth (mm) ± SE for *Nacella (P.) magellanica* at selected sites of the study area. Locality codes are given in Figure 1.

Localities	Oct. '77 (Spring)	Jan. '78 (Summer)	Jul.–Aug. '78 (Winter)	Dec. '78–Feb. '79 (Summer)
G	0.58 ± 0.054	1.14 ± 0.155	0.62 ± 0.094	1.28 ± 0.172
S	0.88 ± 0.122	0.96 ± 0.098	0.51 ± 0.051	1.46 ± 0.144
D	0.68 ± 0.107	1.18 ± 0.156	0.34 ± 0.104	1.00 ± 0.084
W	0.59 ± 0.120	0.65 ± 0.070	0.14 ± 0.048	0.78 ± 0.028
P	0.83 ± 0.124	1.13 ± 0.104	0.53 ± 0.095	0.85 ± 0.114
R	0.68 ± 0.097	0.89 ± 0.097	0.34 ± 0.075	0.86 ± 0.107

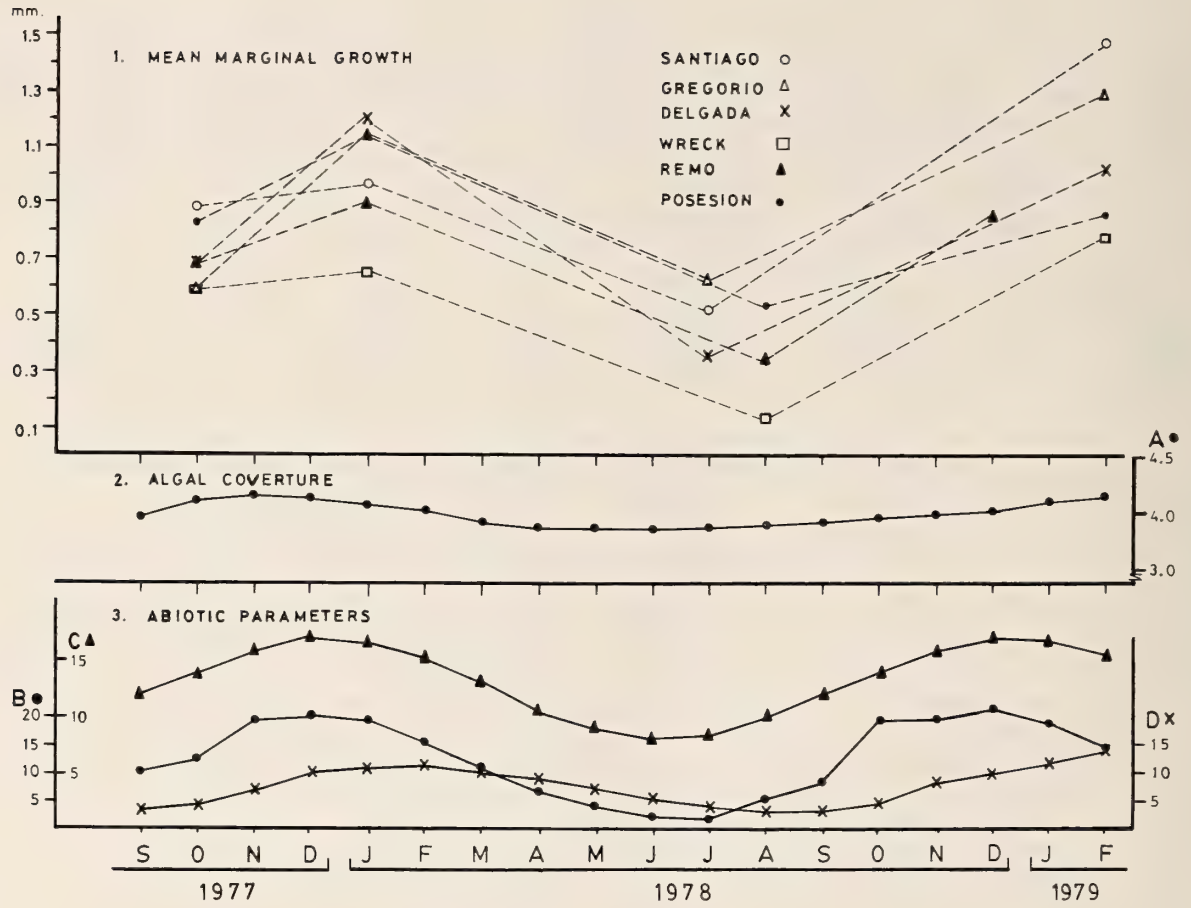


Figure 3

Mean marginal growth of *Nacella (P.) magellanica* at different sites of the Strait of Magellan. The seasonal pattern of some physical and biological growth-related parameters in the study area are included. A●, algal coverage in ln%; B●, solar radiation in Langley/h; C▲, photoperiod in hours with an intensity >10 foot candles (107.6 lux); D×, surface seawater temperature (°C).

exceeds 60 yr (Shabica, 1976, in PICKEN, 1980). This last estimate is similar to the longevity of an intertidal population of *N. (P.) magellanica* from Wollaston Island (62 yr, unpublished data). The studied populations from inner sites, which presented the lowest longevities, showed a clearly higher longevity than that reported by BLANKLEY & BRANCH (1985) for *Nacella delesserti* (8–10 yr) from Marion Island.

Although mortality rate estimates have a predictive value, mortality agents probably exert a relatively low pressure on the studied populations. At least three mortality sources can be mentioned in our case: predation, parasitism, and physical disturbance. Along the studied areas it has been observed that *Anasterias antarctica* (Lutkan, 1856) preys on *Nacella (P.) magellanica,* but the low density and relatively small size of this seastar in the sampling area (personal observations) suggest that predation by this species is unimportant as a regulating factor. Other characteristic limpet predators, the sea gull *Larus dominicanus* (Lichtenstein) and the oystercatchers *Haematopus* spp., have been observed in low density, and restricted to a few sites within the study area (personal observations). A low predation pressure has also been suggested by WALKER (1972) for the Antarctic limpet *Patinigera polaris* (Hombron & Jacquinot) (=*Nacella [P.] concinna*) at the South Orkney Islands, although *L. dominicanus* has been mentioned as the main predator for this species (WALKER, 1972; CASTILLA & ROZBACZYLO, 1985). On the other hand, BRANCH (1985) indicates an important role of *L. dominicanus* preying on a subantarctic limpet, *N. delesserti,* with the predator accounting for about 50% of the known annual mortality of the largest limpets. Parasitism may also contribute to mortality. Limpets at Remo, Baxa, and Tandy showed a variable but unquantified infestation by trematodes of the family Gymnophallidae (M. O. de Nunez, personal communication). As many as 1500 metacercaria have been

found in a single individual (unpublished data). The third major source of mortality is represented by the rolling of cobbles and boulders. Although this aspect has not been evaluated, it likely has a greater influence on the limpet population dynamics, especially during severe storms.

A number of unknown factors induce an ecological gradient along the study area. For example, the population density of the mussel *Mytilus chilensis* (Hupe, 1840) increases substantially from the second narrow toward the eastern entrance of the Strait (Langley *et al.*, 1980), as does the species richness of the infauna and epibenthos (Wendt, 1982; unpublished data). Now we have added the growth trend of *Nacella* (*P.*) *magellanica,* which is correlated with tidal range. However, several physical and biological factors may induce changes in the growth of gastropods (*e.g.,* Branch, 1974; Lewis & Bowman, 1975; Black, 1977; Bretos, 1978; McQuaid, 1981), suggesting that the single tidal range-growth relationship we encountered may not explain all the geographical growth trend reported.

ACKNOWLEDGMENTS

We thank Dr. Marta Bretos of Universidad de la Frontera, Temuco, Chile, for reading and commenting on an early manuscript. Two anonymous reviewers did much to improve a previous version of this paper. We are also grateful to Demetrio Diaz and Mario Donoso for field assistance, and to our colleague Sergio G. Andrade for his cooperation.

LITERATURE CITED

Bartlett, M. S. 1949. Fitting a straight line when both variables are subject to error. Biometric 5:207–211.

Black, R. 1977. Population regulation in the intertidal limpet *Patelloidea alticostata* (Angas, 1865). Oecologia 30:1–22.

Blankley, W. O. & G. M. Branch. 1985. Ecology of the limpet *Nacella delesserti* (Philippi) at Marion Island in the sub-Antarctic southern ocean. Jour. Exp. Mar. Biol. Ecol. 92:259–281.

Branch, G. M. 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 3. Growth rate. Trans. Roy. Soc. S. Africa 41:161–193.

Branch, G. M. 1985. The impact of predation by kelp gulls *Larus dominicanus* on the sub-antarctic limpet *Nacella delesserti.* Polar Biol. 4:171–177.

Bretos, M. 1978. Growth in the keyhole limpet *Fissurella crassa* Lamarck (Mollusca: Archaeogastropoda) in northern Chile. Veliger 21:268–273.

Bretos, M. 1980. Age determination in the keyhole limpet *Fissurella crassa* Lamarck (Archaeogastropoda: Fissurellidae), based on shell growth rings. Biol. Bull. 159:606–612.

Bretos, M. 1982. Biologia de *Fissurella maxima* (Mollusca: Archaeogastropoda) en el norte de Chile. I. Caracteres generales, edad y crecimiento. Cahiers Biol. Mar. 23:159–170.

Carcelles, A. R. & S. Williamson. 1951. Catalogo de los moluscos marinos de la Provincia Magallanica. Mus. Arg. Cs. Nat. Bernardino Rivadavia, Ciencias Zoologicas 2:225–383.

Castilla, J. C. & N. Rozbaczylo. 1985. Rocky intertidal assemblages and predation on the gastropod *Nacella* (*Patinigera*) *concinna* at Robert Island, South Shetland, Antarctica. Ser. Cient. INACH 32:65–73.

Cockcroft, V. G. & A. T. Forbes. 1981. Growth, mortality and longevity of *Cerithidea decollata* Linnaeus (Gastropoda: Prosobranchia) from Bayhead Mangroves, Durban Bay, South Africa. Veliger 23:300–308.

Dell, R. K. 1971. The marine Mollusca of the Royal Society Expedition to southern Chile, 1958–59. Rec. Dom. Museum 7:155–233.

Fisher-Piette, E. 1941. Croissance, taille maxima et longevite possible de quelques animaux intercotidaux en fonction du millieu. Annls. Inst. Oceanog., Monaco 21:1–28.

Francis, C. A. 1972. Duracion del dia para la reaccion fotoperiodica en plantas. Folleto Tecnico No. 2. Centro Internacional de Agricultura Tropical, Cali, Colombia. 32 pp.

Frank, P. W. 1969. Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia 2:232–250.

Gulland, J. A. 1965. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Fish. Tech. Pap. 40, Rev 1. 68 pp.

Guzman, L. 1978. Patron de distribucion espacial y densidad de *Nacella magellanica* (Gmelin, 1791) en el intermareal del sector oriental del Estrecho de Magallanes (Mollusca: Gastropoda). Ans. Inst. Pat., Punta Arenas (Chile) 9:205–219.

Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. Jour. Fish. Res. Bd. Canada 25: 1303–1307.

Langley, S., L. Guzman & C. Rios. 1980. Aspectos dinamicos de *Mytilus chilensis* (Hupe, 1840) en el Estrecho de Magallanes. I. Distribucion, densidad y disposicion espacial en el intermareal. Ans. Inst. Pat., Punta Arenas (Chile) 11:319–332.

Lewis, J. R. & R. S. Bowman. 1975. Local habitat induced variations in the population dynamics of *Patella vulgata* L. Jour. Exp. Mar. Biol. Ecol. 17:165–203.

McLachlan, A. & H. W. Lombard. 1981. Growth and production in exploited and unexploited populations of a rocky shore gastropod, *Turbo sarmaticus.* Veliger 23:221–229.

McQuaid, C. 1981. Population dynamics of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. Jour. Exp. Mar. Biol. Ecol. 54:65–75.

Miranda, O. 1975. Crecimiento y estructura poblacional de *Thais* (*Stromanita*) *chocolata* (Duclos, 1823) en la Bahia de Mejillones del Sur, Chile (Mollusca, Gastropoda, Thaididae). Rev. Biol. Mar. Dep. Oceanol. Univ. Chile 15:263–286.

Otaegui, A. V. 1974. Las especies del genero *Patinigera* Dall 1905 en la Provincia Magallanica (Mollusca, Gastropoda, Prosobranchiata). Physis B. Aires 33:173–184.

Phillips, D. W. 1981. Life-history features of the marine intertidal limpet *Notoacmea scutum* (Gastropoda) in central California. Mar. Biol. 64:95–103.

Picken, G. B. 1979. Growth, reproduction and biomass of the Antarctic gastropod *Laevilacunaria antarctica* Martens 1885. Jour. Exp. Mar. Biol. Ecol. 40:71–79.

Picken, G. B. 1980. The distribution, growth, and reproduction of the Antarctic limpet *Nacella* (*Patinigera*) *concinna* (Strebel, 1908). Jour. Exp. Mar. Biol. Ecol. 4:71–85.

Powell, A. W. B. 1973. The patellid limpets of the world (Patellidae). Indo-Pacific Mollusca 3:75–206.

Powell, E. N. & H. Cummins. 1985. Are molluscan maximum life spans determined by long-term cycles in benthic communities? Oecologia 67:177–182.

Race, M. S. 1981. Field ecology and natural history of *Cer-*

ithidea californica (Gastropoda: Prosobranchia) in San Francisco Bay. Veliger 24:18–27.

SEAPY, R. R. 1966. Reproduction and growth in the file limpet, *Acmaea limatula* Carpenter, 1864 (Mollusca: Gastropoda). Veliger 8:300–310.

SNEDECOR, G. & W. COCHRAN. 1964. Metodos estadisticos aplicados a la investigacion agricola y biologica. Compania Editorial Continental S. A., Mexico. 626 pp.

SOUTHWOOD, T. R. E. 1975. Ecological methods. Chapman and Hall: London. 391 pp.

TAYLOR, C. C. 1959. Cod growth and temperature. Cons. Int. Explor. Mar. 23:366–370.

VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws). II. Human Biology 10: 181–213.

WALFORD, L. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90:141–147.

WALKER, A. J. M. 1972. Introduction to the ecology of the Antarctic limpet *Patinigera polaris* (Hombron & Jacquinot) at Signy Island, South Orkney Islands. Brit. Antarct. Surv. Bull. 28:49–69.

WENDT, A. 1982. Descripcion de comunidades faunisticas intermareales de la costa oriental del Estrecho de Magallanes. Mar. Biol. Tesis, Universidad de Concepcion. 126 pp.

WILBUR, K. M. & G. OWEN. 1964. Growth. Pp. 211–242. *In:* K. M. Wilbur & C. M. Yonge (eds.), Physiology of Mollusca, Vol. I. Academic Press, Inc.

WILLIAMSON, P. & M. A. KENDALL. 1981. Population age structure and growth of the trochid *Monodonta lineata* determined from shell rings. Jour. Mar. Biol. Assoc. U.K. 61: 1011–1026.

The Veliger 30(2):167–172 (October 1, 1987)

THE VELIGER

Herbivory in Juvenile *Ilyanassa obsoleta* (Neogastropoda)

by

GAYLE A. BRENCHLEY

Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717, U.S.A.

Abstract. The mud snail *Ilyanassa obsoleta* (Say, 1822) is unique among the typically carnivorous neogastropods in possessing a crystalline style used to digest plant material. While adults are thought to be obligate omnivores, results of three experiments indicate that juvenile *I. obsoleta* (4–6 mm shell height) are herbivores. Juveniles gained body weight and added shell material when fed monocultures of benthic diatoms (*Acanthes brevipes* and *Nitzschia* sp.). Juveniles of both *I. obsoleta* and the herbivorous mesogastropod *Littorina littorea* (Linneaus) grew on diets of sand microflora and a filamentous green alga (*Pilinia lunatiae*). Furthermore, interspecific effects of density on growth on a sand-microfloral diet were similar to intraspecific effects, indicating that juveniles of the two species similarly exploited the same food items. Because high assimilation efficiency on a plant diet requires style presence, the similarity between the two species' growth patterns suggests that young *I. obsoleta* do not dissolve their styles as adults do. Herbivory may have permitted young *I. obsoleta,* able to compete successfully with herbivorous mesogastropods, to invade upper intertidal marsh habitats and obtain refuge from crustacean predators.

INTRODUCTION

Ilyanassa obsoleta (Say, 1822) is an abundant and widely distributed mud snail on intertidal flats along the east coast of North America. The success of this species is often attributed to its unusually diverse diet (Dimon, 1905; Scheltema, 1964; Crisp, 1969; Curtis, 1980; Curtis & Hurd, 1979, 1981a). The species is unique among the typically carnivorous neogastropods in possessing a crystalline style (Noguchi, 1921; Jenner, 1956; Curtis & Hurd, 1979). The occurrence of this style is apparently unique among the gastropods in general in that it undergoes a cyclic formation and dissolution (Robertson, 1979; Curtis, 1980; Curtis & Hurd, 1981a). The style contains amylase used to digest plant material (Yonge, 1930; Brown, 1969), and during its absence the gut contains proteases. A digestive rhythm allows the organism to utilize both plant and animal tissue.

Although it is well known that *Ilyanassa obsoleta* feeds on benthic algae, Curtis & Hurd (1979) found that one-year old individuals (10.8–14.8 mm shell height) grew only when fed a mixed diet of both meat (shrimp) and vegetable (spinach). They postulated that the cycling of the crystalline style was necessary for the dietary requirements of the species. The inclusion of carrion in the snail's diet is also well known but it is typically a scarce and unreliable resource. This observation led Jenner (1956) to speculate that the snail may obtain most of its nutrition from microorganisms in the sediment. Aptly described as a "biological vacuum cleaner" (Curtis & Hurd, 1981a), the snail consequently needs to swallow large amounts of sediment in order to obtain sufficient quantities of tiny microbes to sustain obligate omnivory.

There are size constraints to bulk deposit feeding, however. Recently settled *Ilyanassa obsoleta* (<7 mm) can apparently swallow particles of mud (<63 μm) but not coarser sand grains (Lopez, 1980). Like other tiny mud snails, young *I. obsoleta* are epistratic grazers, *i.e.,* they scrape microbial bacteria and algae attached to surfaces of sand grains (Lopez, 1980). Epistratic grazing is incompatible with an omnivorous diet requiring the organism to process bulk quantities of sediment.

A hypothesis not previously tested is that juvenile *Ilyanassa obsoleta* may not require animal food for growth, *i.e.,* they are herbivores. Using labeled sediment, Lopez (1980) found that juveniles digested microbial films of algae and bacteria, but stated that most of the label was associated with the bacteria. The present study examines growth of juveniles provided monocultures of benthic diatoms as food. The ability to grow on plant diets does not imply that the snail is normally a strict herbivore in nature,

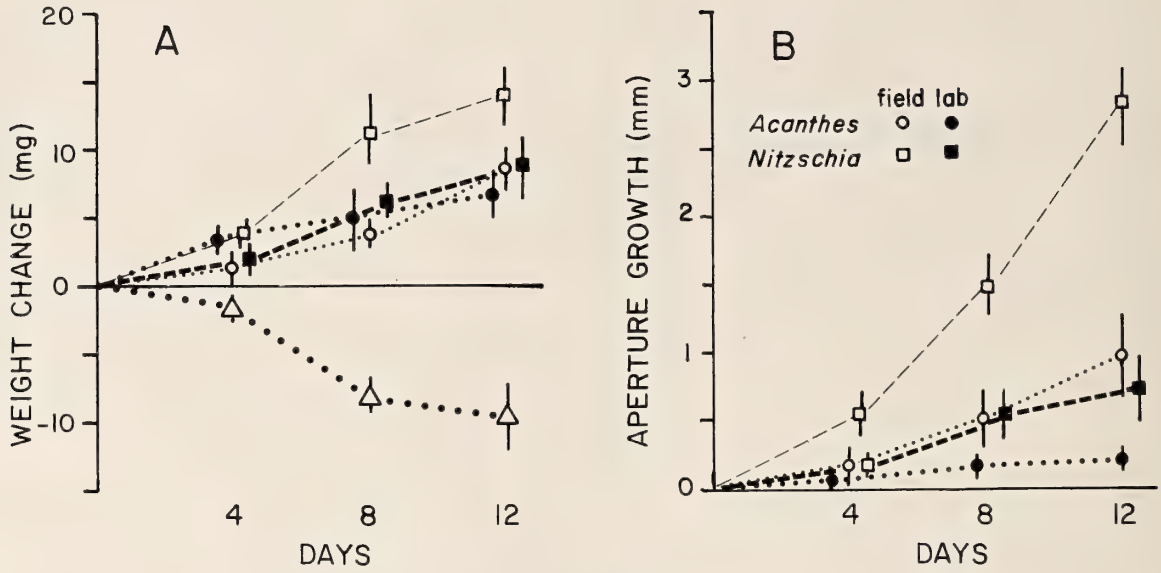


Figure 1

Growth of two groups of juvenile *Ilyanassa obsoleta* fed monocultures of the diatoms *Acanthes brevipes* and *Nitzschia* sp., or starved (triangles) (key to other symbols in insert). The snails were collected fresh from the field or maintained in the laboratory. A. Weight change. B. Growth along the aperture. Symbols show means; bars are ±1 SD.

however. Consequently, additional experiments compared the diet of this neogastropod, which uses a crystalline style to digest plant material, to a mesogastropod, the superorder of typically herbivorous gastropods. Growth of juveniles of *I. obsoleta* was compared to that of juvenile *Littorina littorea* (Linnaeus), a herbivorous mesogastropod (Lubchenco, 1978; Hunter & Russell-Hunter, 1983; Watson & Norton, 1985).

MATERIALS AND METHODS

Juvenile *Ilyanassa obsoleta* and juvenile *Littorina littorea* occur together in sandy marsh habitats in Barnstable Harbor, Massachusetts. All snails used in this study were collected from a marsh tide pool in a sandy habitat (median grain 0.62 mm, 0.8% silt-clay) near the mouth of the bay. Each snail was individually numbered on the spire (total, 144 *I. obsoleta* and 130 *L. littorea*). To measure new shell growth, a line was inked on the outer shell surface along the original aperture edge with a nontoxic ink (Tech-Pen ink, Mark-Tex Corp., Englewood, New Jersey). The secretion of new shell material was measured from the ink line using an ocular micrometer (±0.02 mm). Snails were maintained without food (1) for 36–48 h prior to feeding or (2) for the duration of each study (controls). All studies were conducted at temperatures between 20 and 23°C and at salinities of 31–34‰.

Juvenile *Ilyanassa obsoleta* were fed monocultures of the diatoms *Acanthes brevipes* and *Nitzschia* sp. in the laboratory. Diatoms were grown under fluorescent light on autoclaved dishes (14 cm diameter) containing an enriched seawater medium (Hinegarden & Tuzzi, 1981:229) and washed with filtered seawater. Six snails (4–6 mm shell length) collected fresh from the field in August 1985, or eight snails (also 4–6 mm) maintained without meat or carrion at 8–12°C for a year in the laboratory, were placed into separate dishes. Snails were changed to fresh dishes every 2 days to minimize growth of bacteria on feces. Aperture growth and snail weight (±0.002 g) after blotting the aperture were measured every 4 days for 12 days for individuals on a diet of *Acanthes* and subsequently for 12 days on a *Nitzschia* diet. At the end of the experiment the new shell material was removed and the snails were reweighed. Effects of diet on weight change and aperture growth of snails were determined by analyses of covariance using log-transformed data and initial weight and days lapsed as covariates. Bartlett's test was used to test for homogeneity of variances in these and all other ANOVAs.

Growth of juvenile *Ilyanassa obsoleta* (4–6 mm) and juvenile *Littorina littorea* (5–7 mm) was studied in outdoor seawater tanks in August 1981. Snails were placed into compartments (4 × 4 × 4 cm) of plastic storage boxes perforated with numerous holes, too small for the snails to pass through but adequate for circulation, and maintained on the floor of the empty tanks with seawater constantly flowing over them. The snails were collected 36–48 h prior to the experiments and marked. Twenty control snails (each species) were maintained indoors without food. For single-species treatments, 10 snails of one species were placed into a compartment and provided (1) one living adult *I. obsoleta* with a green alga (*Pilinia lunatiae*) growing on its shell, (2) 1.5 cm^3 of diatomaceous sand freshly collected from the marsh pool, or (3) both a shell and 1.5 cm^3

Table 1

Analysis of covariance tables for aperture growth and weight gain in two groups of juvenile *Ilyanassa obsoleta* on two diatom monocultures. The covariates are initial shell length and days lapsed.

Source	df	Mean square	*F* ratio
Aperture growth[1]			
Group	1	5.808	47.288***
Diet	1	3.411	27.770***
Interaction	1	0.162	1.315
Covariate	2	2.417	19.675***
Error	66	0.123	
Weight gain[2]			
Group	1	1.478	25.363***
Diet	1	0.496	8.507**
Interaction	1	0.256	4.385*
Covariate	2	1.570	26.947***
Error	74	0.583	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[1] Bartlett's test for homogeneity of variances, $\chi^2 = 1.614$, df = 3, $P > 0.05$.

[2] Bartlett's test, $\chi^2 = 2.423$, df = 3, $P > 0.05$.

of sand. Snails were not weighed in this experiment. Comparisons of aperture growth [$\log_{10}(x + 1)$] after 8 days were made between species and diets by analysis of covariance, using shell length as a covariate. The quality and quantity of plant material on the sand and shells (five replicates each) were determined by extracting plant pigments overnight in darkness at 4°C with 10 mL of cold, 90% glass-distilled methanol after the methods of FENCHEL & STRAARUP (1971). Spectral absorbances before and after acidification were converted to mg pigment per shell or 1.5 cm^3 sand using the Parsons-Strickland equations (STRICKLAND & PARSONS, 1972).

Growth was also measured in two-species communities to determine if juveniles grazed the same food items. Fresh sand (1.5 cm^3) was provided in compartments containing (a) 5 (n = 4 compartments), 10 (n = 2), or 20 (n = 1) juveniles of one species, or (b) equal numbers (5 [n = 2], 10 [n = 2], or 20 [n = 1 compartment]) of both species. Growth was measured along the aperture after 8 days. By two-way analyses of covariance, the per capita growth and the sum growth of each microcosm population (both log transformed) were compared between species using total snail density as a covariate.

RESULTS

Juvenile *Ilyanassa obsoleta* gained weight and added shell material when fed diatom monocultures, but lost weight and added no shell material when starved (Figure 1). New shell material accounted for 33% (±11%) of the weight increase. Field-fresh snails grew significantly more than laboratory reared snails but both groups grew faster on

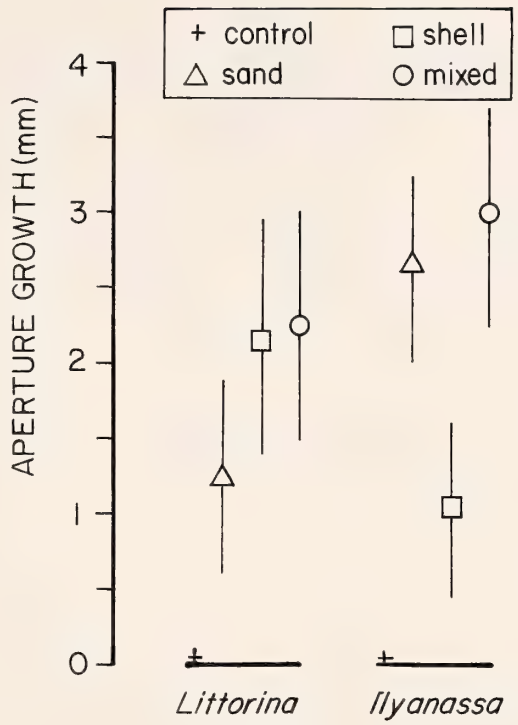


Figure 2

Aperture growth over 8 days of juvenile *Littorina littorea* and juvenile *Ilyanassa obsoleta* on diets of sand, *Pilinia* on mud snail shells, and both sand and shell; control snails were not fed. Symbols show means; bars are ±1 SD. Key to symbols in insert.

Nitzschia than *Acanthes* (Table 1). A significant interaction term was due to the large weight gain of field-fresh snails on the *Nitzschia* diet.

Juveniles of *Ilyanassa obsoleta* and *Littorina littorea* grew on diets of sand microflora and *Pilinia* on mud snail shells (Figure 2). The *Pilinia* diet was richer in all plant pigments studied (Table 2). Differences in growth between species and diets were not significant (Table 3), but the significant interaction term demonstrated that the species responded differently to the diets: *L. littorea* grew slowly on sand but equally fast on *Pilinia* and the mixed diet, whereas juvenile *I. obsoleta* grew best on a mixed diet and better on sand than on *Pilinia*.

In both single and two-species systems, per capita growth of individuals on a diet of sand declined with density (Figure 3A) but total growth of microcosm populations remained constant over density (Figure 3B, Table 4). Species differences were significant: *Ilyanassa obsoleta* grew faster than *Littorina littorea*. For per capita growth, interspecific density effects were not significantly different from intraspecific effects, and the interaction term was not significant (Table 4). Thus, individuals grew at similar rates whether or not neighbors were related. Relative to monocultures, the total growth was about 50% less in mixed cultures

Table 2

Plant pigments (mg) for sand microflora (1.5 cm^3) and shell epiflora (one shell); means and standard deviations of five replicates.

Pigment	Sand microflora	Shell epiflora	Shell/ sand
Chlorophyll a	1.6 ± 0.2	2.8 ± 0.2	1.75
Chlorophyll b	0.19 ± 0.05	0.24 ± 0.05	1.26
Chlorophyll c	0.76 ± 0.12	1.18 ± 0.06	1.55
Carotenoids	0.70 ± 0.05	0.87 ± 0.05	1.24

(with 50% more individuals) (Figure 3B). The total population growth of *I. obsoleta* was more depressed (owing to a faster growth rate) than that of *L. littorea* in the mixed cultures.

DISCUSSION

This study found that juvenile *Ilyanassa obsoleta* added body and shell material when fed only benthic diatoms. Because benthic diatoms trigger the planktonic larvae to settle (SCHELTEMA, 1961), they are likely to be a major component of the juvenile's diet. Juveniles can detach algal and bacterial films from coarse sands (Figure 2; LOPEZ, 1980) and solid surfaces such as rocks (or glass dishes, Figure 1). However, they have difficulty manipulating fine silt particles within the buccal cavity (LOPEZ, 1980) and also do poorly on filamentous algae like *Pilinia* (Figure 2) and *Enteromorpha* (Brenchley, unpublished data) because their radula is unable to purchase flexible surfaces.

Juvenile *Ilyanassa obsoleta* are strikingly similar to juvenile *Littorina littorea* in sandy habitats of Barnstable Harbor (Brenchley, unpublished data). Both species settle into marshes during summer months and attain a similar size by autumn. The young snails graze on decaying marsh grasses and ascend marsh vegetation during high tide. Despite the propensity of *L. littorea* to graze on hard substrata,

Table 3

Analysis of covariance table for aperture growth (log transformed) of juvenile *Ilyanassa obsoleta* and juvenile *Littorina littorea* on single and mixed diets of sand and shell epiflora; the covariate is initial shell length.

Source[1]	df	Mean square	*F* ratio	*P*
Species	1	0.0047	0.18	0.671
Diet	2	0.0650	2.53	0.089
Interaction	2	0.0842	3.28	0.046
Covariate	1	0.0016	0.06	0.803
Error	50	0.0256		

[1] Bartlett's test, $\chi^2 = 5.681$, df = 5, $P > 0.05$.

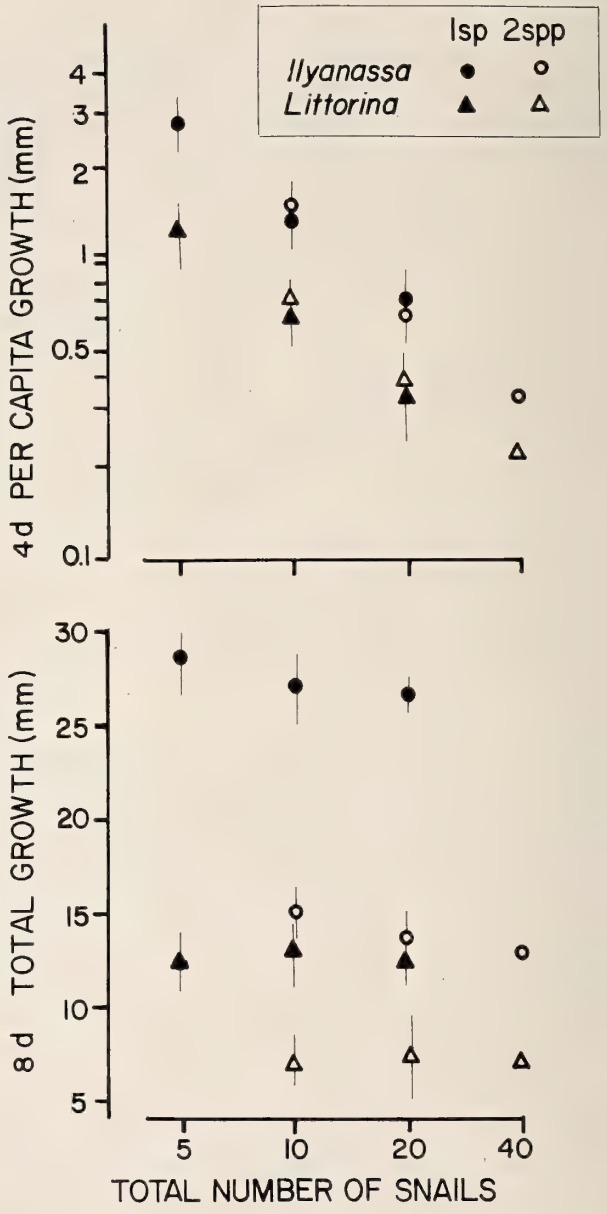


Figure 3

Aperture growth of juvenile *Littorina littorea* and juvenile *Ilyanassa obsoleta* as a function of total snail density in single and two-species systems over 8 days on a diet of diatomaceous sand. A. Per capita growth over 4-day intervals. B. Total growth of microcosm populations in 8 days. Symbols show means; bars are ±1 SD. Key to symbols in insert.

e.g., Pilinia on adult mud snail shells (Figure 2), only 7% of the juveniles compared to 3% of juvenile *I. obsoleta* occur on shell substrata in the tide pool; most juveniles of both species occur on the sandy substrata.

The two taxonomic groups represented here do not nor-

Table 4

Analysis of covariance tables for aperture growth and total microcosm growth of juvenile *Ilyanassa obsoleta* and juvenile *Littorina littorea* on a diet of diatomaceous sand in single and mixed species communities. The covariate is total snail density.

Source	df	Mean square	*F* ratio	Comments
Per capita growth[1]				
Species	1	1.878	27.234***	growth *Ilyanassa* > *Littorina*
1 vs. 2 species	1	0.217	3.147	intra = interspecific effects
Interaction	1	1.415	0.021	
Covariate	1	2.608	37.821***	growth decreases with density
Error	145	0.069		
Total growth[2]				
Species	1	0.105	150.06***	growth *Ilyanassa* > *Littorina*
1 vs. 2 species	1	0.066	94.68***	less growth in mixed cultures
Interaction	1	0.227	32.44***	*Ilyanassa* grows less in mixed system
Covariate	1	<0.001	0.42	total growth independent of density
Error	15	0.0007		

*** $P < 0.0001$.

[1] Bartlett's test, $\chi^2 = 6.015$, df = 3, $P > 0.05$.

[2] Bartlett's test, $\chi^2 = 5.776$, df = 3, $P > 0.05$.

mally compete for food, owing to a divergence in diet that began during the Mesozoic. BROWN (1969) and CURTIS (1980) have speculated that the ancestral stock of *Ilyanassa obsoleta* could not compete with its more specialized, carnivorous neogastropod relatives, nor with the more efficient, microherbivorous mesogastropods. Presumably, digestion of plant foods in the neogastropod stock was dependent upon an innovation, *i.e.,* style acquisition. Results of this study suggest that because of this innovation, young *I. obsoleta* exploit the same foods as the mesogastropod *Littorina littorea.* If the density effects of Figure 3 were due to interference, *e.g.,* stress due to crowding, then the total growth of microcosm populations should have declined with increased density, but such trends were not significant (Table 4). Studies of sympatric gastropods have shown that unrelated species exploit algae differently while congeners often have similar exploitation abilities (reviewed by BRANCH, 1984). The similarities in per capita growth curves in single versus mixed systems of young *I. obsoleta* and *L. littorea* (Figure 3A) imply equal exploitative ability, providing the first example for unrelated species.

The results strongly suggest that the young *Ilyanassa* retain rather than cycle their crystalline style. Because algae cannot be digested when the style is absent, dissolution of the style would greatly reduce assimilation efficiency on a plant diet. However, the similarity in growth patterns (Figure 3A) indicates that the mud snail was as efficient in assimilating plant foods as the littorinid. There is limited evidence that young *Ilyanassa* in marsh habitats may not cycle their styles (CURTIS & HURD, 1981b), in contrast to the cyclic pattern frequently reported for large (16–25 mm), sexually mature snails (*e.g.,* CURTIS & HURD, 1981a, b).

Several workers have speculated that the success of *Ilyanassa* is due to a diverse diet, yet few have suggested how the style innovation could enhance the species' abundance. In addition to possible costs associated with the formation or dissolution of the style, the style cycling is quite costly to adult snails because much ingested material passes undigested. CURTIS & HURD (1981a) relate the species' success to its unique role in the benthic community. Despite a unique niche, the species' broad diet does not eliminate the adults' reproductive need for carrion (HURD, 1985), and the style innovation places the juveniles in competition with herbivorous snails (this study). An explanation not previously suggested is that the innovation allows the snail to invade (new) habitats and thereby avoid predators.

Studies of the snail's ecology in Barnstable Harbor suggest that only as a herbivore can the young *Ilyanassa* occupy a predator refugium in sandy intertidal habitats. The mesogastropods and littorinids in particular are tolerant of desiccation and thus can obtain refuge from most predators by inhabiting the upper tidal zones. The neogastropods are less tolerant of desiccation; most nassariids of temperate sand flats remain near or below mean low water and only the adults move into the intertidal zone (*e.g.,* KUSKINS & MANGUM, 1971; TALLMARK, 1980). Adult *I. obsoleta* are more tolerant of desiccation than the young (SCHAEFER *et al.,* 1968) and immune from attack by the shell-crushing crustaceans of the lower tide zones (BRENCHLEY, 1982, unpublished data). Susceptible to desiccation and particularly to crab predators, young *I. obsoleta* obtain refuge by settling into upper intertidal pools, seeps, and creek beds. Herbivory may be a prerequisite for marsh habitation, as drift carrion is scarce; the snails emigrate to the sand flats upon reaching maturity (Brenchley, unpublished data).

Consequently, the style innovation may permit young snails to enter a predator refugium, which may partly explain the numerical success of this ubiquitous species.

ACKNOWLEDGMENTS

The outdoor seawater tanks were provided by the Woods Hole Oceanographic Institution. I thank Merryl Alber for assisting in the growth studies, Naomi Culp in the pigment analyses, Patrick Leahy for providing diatom cultures, and Peter Dixon for identifying *Pilinia*. Roger Griffis, Larry Curtis, and Lynn Carpenter provided helpful comments on the manuscript. The research was supported in part by a faculty grant from the University of California, Irvine.

LITERATURE CITED

Branch, G. M. 1984. Competition between marine organisms: ecological and evolutionary implications. Oceanogr. Mar. Biol. Ann. Rev. 22:429–593.

Brenchley, G. A. 1982. Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. Mar. Ecol. Prog. Ser. 9:255–262.

Brown, S. C. 1969. The structure and function of the digestive system of the mud snail, *Nassarius obsoletus* (Say). Malacology 9:477–500.

Crisp, M. 1969. Studies on the behavior of *Nassarius obsoletus* (Say) (Mollusca, Gastropoda). Biol. Bull. 136:355–373.

Curtis, L. A. 1980. Daily cycling of the crystalline style in the omnivorous, deposit-feeding estuarine snail *Ilyanassa obsoleta*. Mar. Biol. 59:137–140.

Curtis, L. A. & L. E. Hurd. 1979. On the broad nutritional requirements of the mud snail, *Ilyanassa* (*Nassarius*) *obsoleta* (Say), and its polytrophic role in the food web. Jour. Exp. Mar. Biol. Ecol. 4:1–9.

Curtis, L. A. & L. E. Hurd. 1981a. Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, *Ilyanassa obsoleta*. Estuarine Coast. Shelf Sci. 13:277–285.

Curtis, L. A. & L. E. Hurd. 1981b. Crystalline style cycling in *Ilyanassa obsoleta* (Say) (Mollusca: Neogastropoda): further studies. Veliger 24:91–96.

Dimon, A. C. 1905. The mud snail: *Nassa obsoleta*. Cold Spring Harbor Monogr. 5:1–50.

Fenchel, T. & B. J. Straarup. 1971. Vertical distribution of photosynthetic pigments and the penetration of light in marine sediments. Oikos 22:172–182.

Hinegarden, R. T. & M. M. R. Tuzzi. 1981. Laboratory culture of the sea urchin *Lytechinus pictus*. Pp. 291–302. *In:* National Research Council, Marine Invertebrates. National Academy Press: Washington, D.C.

Hunter, R. D. & W. D. Russell-Hunter. 1983. Bioenergetic and community changes in intertidal Aufwucks grazed by *Littorina littorea*. Ecology 64:761–769.

Hurd, L. E. 1985. On the importance of carrion to reproduction in an omnivorous estuarine neogastropod, *Ilyanassa obsoleta* (Say). Oecologia 65:513–515.

Jenner, C. E. 1956. The occurrence of a crystalline style in the marine snail, *Nassarius obsoletus*. Biol. Bull. 111:304.

Kuskins, L. J. & C. P. Mangum. 1971. Responses to low oxygen conditions in two species of the mud snail *Nassarius*. Comp. Biochem. Physiol. 39A:421–435.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive ability. Amer. Natur. 112:23–39.

Lopez, G. R. 1980. The availability of microorganisms attached to sediment as food for some marine deposit-feeding molluscs, with notes on microbial detachment due to the crystalline style. Pp. 387–405. *In:* K. R. Tenore & B. C. Coull (eds.), Marine benthic dynamics. Univ. South Carolina Press: Columbia.

Noguchi, H. 1921. *Cristispira* in North American shellfish. A note on a spirillum found in oysters. Jour. Exp. Med. 34: 295–315.

Robertson, J. R. 1979. Evidence for tidally correlated feeding rhythm in the eastern mud snail, *Ilyanassa obsoleta*. Nautilus 93:38–40.

Schaefer, C. W., N. L. Levin & P. Milch. 1968. Death from desiccation in the mud-snail, *Nassarius obsoletus*: effects of size. Nautilus 82:28–31.

Scheltema, R. S. 1961. Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. Biol. Bull. 120:92–108.

Scheltema, R. S. 1964. Feeding habits and growth in the mud snail *Nassarius obsoletus*. Chesapeake Sci. 5:161–166.

Strickland, J. D. H. & T. R. Parsons. 1972. A practical handbook of seawater analysis. Fish. Res. Bd. Canada, Bull. 167.

Tallmark, B. 1980. Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. Mar. Ecol. Prog. Ser. 3:51–62.

Watson, D. C. & T. A. Norton. 1985. Dietary preferences of the common periwinkle, *Littorina littorea*. Jour. Exp. Mar. Biol. Ecol. 88:193–211.

Yonge, C. M. 1930. The crystalline style of the Mollusca and a carnivorous habitat cannot normally co-exist. Nature 125: 444–445.

The Veliger 30(2):173–183 (October 1, 1987)

THE VELIGER

Starvation Metabolism in the Cerithiids *Cerithidea (Cerithideopsilla) cingulata* (Gmelin) and *Cerithium coralium* Kiener

by

Y. PRABHAKARA RAO, V. UMA DEVI, AND D. G. V. PRASADA RAO

Department of Zoology, Andhra University, Waltair 530 003, India

Abstract. The effect of starvation has been investigated in two tropical cerithiids, *Cerithidea (Cerithideopsilla) cingulata* (Gmelin, 1790) and *Cerithium coralium* Kiener, 1841. There was no mortality up to 28 days in *Cerithidea cingulata* and 14 days in *Cerithium coralium*; 50% mortality was recorded at 98 and 38 days in *Cerithidea cingulata* and *Cerithium coralium* respectively. Water content did not change significantly ($P > 0.05$) in either species during starvation. The body component indices of both species were found to decrease gradually with the period of starvation. Significant changes ($P < 0.05$) in the level and content of all the biochemical constituents (viz. carbohydrates, glycogen, protein, total ninhydrin positive substances [TNPS] and lipids) were observed in different body components of both the animals during starvation. Among the three tissues examined, the gonad-digestive gland complex contributed greatly to energy needs when the animals were exposed to starvation. "Carbohydrate-oriented" metabolism was noticed in both species. *Cerithidea cingulata* preferred lipids next to carbohydrates while *Cerithium coralium* utilized proteins after carbohydrates in all the body components. During starvation, oxygen consumption exhibited a decreasing tendency ($P < 0.05$) when considered per snail or per tissue weight in both species. Starvation also decreased the intercept values "a" (recalculated) in both species.

INTRODUCTION

Cerithidea (Cerithideopsilla) cingulata (Gmelin, 1790) and *Cerithium coralium* Kiener, 1841, inhabit the backwaters of Bhimilipatnam on the east coast of India (83°28′E, 17°54′N), 35 km north of Visakhapatnam. There is an extensive, shallow backwater region adjoining the coast covering an area of 4.5 km^2. A small river, Gousthani, and three freshwater creeks empty themselves into the backwater system. The backwater is connected to bay waters through a narrow entrance channel. The substratum of the backwater system is composed of medium-sized grains of sand (0.350–0.250 mm diameter). *Cerithidea cingulata* is found in the upper and middle reaches of the backwater system. During the hot weather season (March–June), these areas are partly dried up and stagnation occurs more frequently. *Cerithium coralium* inhabits the lower reaches of the backwaters where there is an abundant supply of algae and diatoms. The hydrographical conditions in the habitat of these two cerithiids also exhibit wide fluctuations and, thus, they come from ecologically distinct regions (PRABHAKARA RAO, 1981). Therefore, several investigations have been carried out to understand the nature of the species' physiological adaptations by exposing them to temperature (PRABHAKARA RAO & PRASADA RAO, 1983a), salinity (PRABHAKARA RAO & PRASADA RAO, 1981, 1984a), oxygen tension (PRABHAKARA RAO & PRASADA RAO, 1983b), and atmospheric oxygen (PRABHAKARA RAO & PRASADA RAO, 1983c, d). In addition, the availability of food needed for growth and reproduction also plays a dominant role in the above system (PRABHAKARA RAO, 1981). Because these snails occur in large numbers in the field, there is a possibility of depletion of food resources. The closure of the operculum during adverse environmental conditions (PRABHAKARA RAO & PRASADA RAO, 1981) may also force these animals to starve for brief periods. Therefore, the present investigation was initiated to study the utilization of body biochemical constituents of *Cerithidea cingulata* and *Cerithium coralium* by subjecting them to starvation.

Table 1

Rates of oxygen consumption and mortality in *Cerithidea cingulata* and *Cerithium coralium* at different intervals of starvation (a: % mortality; b: oxygen consumption μL O_2/h ± SD and % decrease over initial value; c: weight specific oxygen consumption μL O_2/mg/h ± SD and % decrease over initial value; d: log "a" intercept values). n = 10; F-test, * $P <$ 0.05.

No. of days	*Cerithidea cingulata*				*Cerithium coralium*			
	a	b	c	d	a	b	c	d
0	0	111.00 ± 4.77	2.8460 ± 0.1223	1.0011	0	68.00 ± 3.54	1.9714 ± 0.1011	0.6551
7	0	107.62 ± 3.18 3.05	2.8320 ± 0.0837 0.50	0.9877	0	65.56 ± 2.12 4.99	1.9570 ± 0.0633 0.73	0.6328
14	0	76.44 ± 5.12* 31.14	2.1840 ± 0.1463 23.26	0.8391	0	55.04 ± 1.77* 20.23	1.8979 ± 0.0610 0.11	0.5569
21	0	66.52 ± 2.16* 40.07	2.0788 ± 0.0675 26.96	0.7788	13	46.08 ± 2.03* 33.22	1.8808 ± 0.0829 0.13	0.4797
28	0	56.14 ± 3.04* 49.42	2.0050 ± 0.1086 29.55	0.7051	27	32.18 ± 3.64* 53.36	1.7878 ± 0.2022 7.80	0.3238
38	20	46.72 ± 4.01* 57.91	1.7969 ± 0.1542* 36.86	0.6253	50	16.28 ± 4.07* 76.41	1.0853 ± 0.2713* 44.95	0.0279
48	23	38.84 ± 3.77* 65.01	1.6183 ± 0.1571* 43.14	0.5451				
68	35	29.12 ± 2.46* 73.77	1.3236 ± 0.1118* 53.49	0.4200				
98	50	20.10 ± 1.89* 81.89	1.0090 ± 0.0945* 64.55	0.2590				

MATERIALS AND METHODS

Experimental Animals

Animals of both the species, *Cerithidea cingulata* and *Cerithium coralium,* were collected from the backwaters of Bhimilipatnam. Care was taken to select animals of approximately the same size (38 to 42 mg of dry weight of soft parts). They were brought to the laboratory and were cleaned thoroughly before using them for experimental work. Then they were equilibrated to laboratory conditions in an aquarium containing seawater (32‰) at 25 ± 0.5°C for 24 h.

During the first phase of the experiment, the effect of starvation was studied on the mortality rate of both the species. For this study, 100 animals of each species were placed in two different aquaria filled with Whatman-42 filtered seawater. The filtered seawater was aerated continuously and the water was changed daily. At 98 days of starvation 50% mortality was observed for *Cerithidea cingulata* and at 38 days of starvation for *Cerithium coralium.*

Sampling Technique

Changes in the biochemical constituents were studied by taking a set of 175 animals of each species in two different aquaria. Ten animals from each set were sacrificed to serve as controls (0 day). The rest of the animals were exposed to starvation stress as just described. The intervals at which successive samples of 10 each were taken for biochemical analysis were arranged depending on the mortality data of each species.

The experimental animals, after sacrificing at each interval, were dissected into body components, viz., foot, gonad-digestive gland complex (GDG complex) and viscera. The above body components were pooled separately for *Cerithidea cingulata* and *Cerithium coralium.* Because the gonad and digestive gland were found to be closely associated, they were taken together as the GDG complex. The different body components were weighed before and after drying in an oven at 90°C for 48 h to get wet and dry weights respectively. Then they were powdered and preserved in clean, dry glass vials placed in a desiccator. This dry powder was used for the estimation of total carbohydrates, glycogen, proteins, total ninhydrin positive substances (TNPS) and lipids.

Biochemical Analysis

Total carbohydrates and glycogen were estimated by the method of CARROL *et al.* (1956). LOWRY *et al.* (1951) was used for the determination of proteins. Total free amino acids were represented as total ninhydrin positive substances (TNPS) and these were estimated by using the method of MOORE & STEIN (1954). The procedure of chloroform:methanol (2:1) extraction was adopted for quantification of lipids (FOLCH *et al.,* 1957).

Biochemical Level and Content

The level of each biochemical class is presented on a milligram per gram dry weight basis. Nutrient content is calculated by multiplying the level times the body com-

Table 2

Effect of starvation on the water content and body component indices of *Cerithidea cingulata* and *Cerithium coralium* (a: % water content; b: body component index).

No. of days	*Cerithidea cingulata*						*Cerithium coralium*					
	Foot		GDG complex		Viscera		Foot		GDG complex		Viscera	
	a	b	a	b	a	b	a	b	a	b	a	b
0	82 ± 3	0.791	75 ± 2	3.22	78 ± 2	5.61	80 ± 2	0.769	75 ± 4	3.01	77 ± 4	4.69
7	81 ± 2	0.776	74 ± 3	3.12	77 ± 1	5.47	80 ± 3	0.749	75 ± 5	2.87	76 ± 5	4.60
14	80 ± 3	0.761	71 ± 2	3.00	78 ± 2	5.34	80 ± 2	0.728	76 ± 3	2.71	77 ± 4	4.54
21	81 ± 1	0.741	71 ± 3	2.86	77 ± 3	5.22	83 ± 1	0.709	80 ± 2	2.56	81 ± 4	4.43
28	82 ± 3	0.719	70 ± 3	2.74	76 ± 2	5.09	81 ± 3	0.685	79 ± 3	2.36	80 ± 3	4.18
38	79 ± 4	0.699	70 ± 2	2.58	77 ± 2	4.94	80 ± 1	0.653	79 ± 4	2.10	82 ± 2	3.84
48	77 ± 3	0.659	69 ± 2	2.43	76 ± 1	4.76						
68	75 ± 4	0.614	68 ± 4	2.22	75 ± 3	4.55						
98	76 ± 3	0.549	66 ± 5	1.93	74 ± 2	4.20						

ponent index (the relative size of the particular body component on a weight basis for a hypothetical 100-g animal; dry weight of component/weight of the animal × 100) and expressed in grams (STICKLE, 1975).

Respiration

For each species, 10 animals of uniform size (as described earlier) were chosen and numbered serially from 1 to 10. After determining their initial oxygen consumption, they were placed in Whatman-42 filtered seawater (salinity 32‰, pH 8) for starvation. The animals of each species were maintained separately in glass troughs at a temperature of 25 ± 0.5°C with continuous aeration. Respiration of each species was studied individually at the same intervals of starvation at which biochemical samples were taken. Oxygen consumption of the animals was determined every 2 h over a period of 6 h by adopting the same method used by PRABHAKARA RAO & PRASADA RAO (1983c). Dissolved oxygen was estimated by using the Winkler method.

Statistical Evaluation

The values are given as the mean ± 1 SD. One-way analysis of variance (ANOVA) (SNEDECOR & COCHRAN, 1967) was employed to determine the significance of variation in biochemical level and content during starvation. The data were studied further by using Duncan's Multiple Range Test (SNEDECOR & COCHRAN, 1967). The same test was also used for the comparison of respiratory rates at different intervals of starvation.

RESULTS

Table 1 represents the mortality rates of *Cerithidea cingulata* and *Cerithium coralium* at different periods of starvation. In *Cerithidea cingulata,* there was no mortality up to 28 days of starvation, whereas mortality started at 21 days of starvation in *Cerithium coralium.* It is also interesting (Table 1) that the periods at which 50% mortality occurred were different: 98 days of starvation for *Cerithidea cingulata* and 38 days for *Cerithium coralium.* The rest of the experiments were designed based on these results.

The percentage water contents of both species at different intervals of starvation are presented in Table 2. ANOVA reveals no significant difference ($P > 0.05$) in these values in all the body components of both the animals exposed to starvation. However, the percentage water content of all the tissues was found to be slightly higher in *Cerithidea cingulata* than *Cerithium coralium* (Table 2). The body component indices of both the animals are shown in Table 2. In both species there was a gradual decrease in the indices of different body components as starvation progressed and this decrease was high in the GDG complex (40% in *Cerithidea cingulata* and 30% in *Cerithium coralium*) when compared to the foot and viscera.

Biochemical Level

Figures 1–3 depict the changes in the level of biochemical constituents in the foot, GDG complex, and viscera respectively. Significant variations (ANOVA, $P < 0.05$) were found in all the biochemical constituents of different body components, and the data were further subjected to Duncan's analysis.

Foot: A significant decrease ($P < 0.05$) in total carbohydrates started from 28 days of starvation in *Cerithidea cingulata* and 21 days of starvation in *Cerithium coralium* (Figure 1). The glycogen values decreased significantly ($P < 0.05$) from 38 days of starvation in *Cerithidea cingulata* and 14 days of starvation in *Cerithium coralium.* The proteins of both the species followed the same trend as that of carbohydrates. A significant increase ($P < 0.05$) in the TNPS was observed from 14 days of starvation in *Cerithidea cingulata* and *Cerithium coralium.* The lipids started to decrease significantly ($P < 0.05$) from 48 days of starvation in *Cerithidea cingulata.* In *Cerithium coralium,* the significant ($P < 0.05$) decrease in lipids occurred from 21 days of starvation.

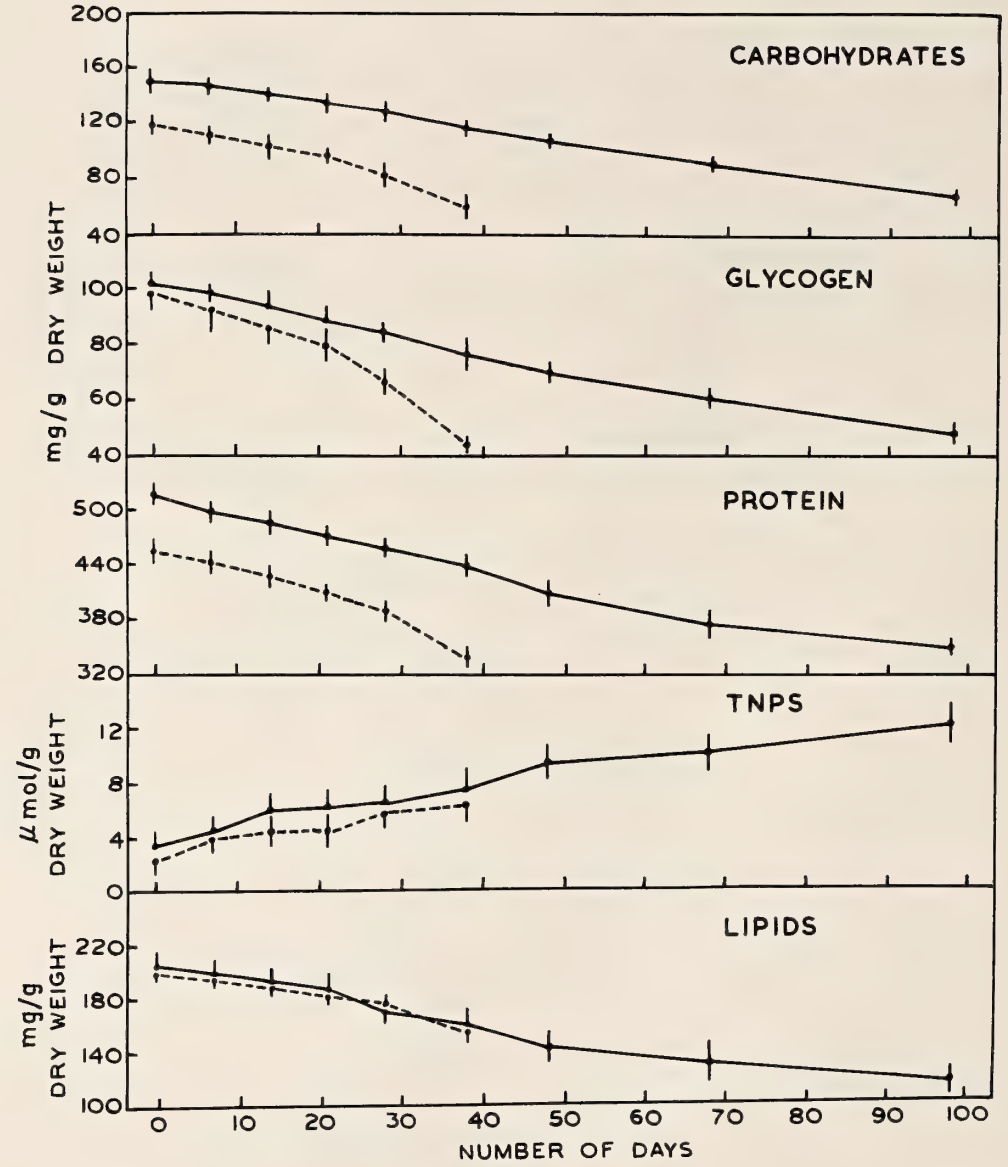


Figure 1

Changes in the levels of different biochemical constituents in the foot of *Cerithidea cingulata* (——) and *Cerithium coralium* (-----). Vertical bars represent 1 SD.

GDG complex: In *Cerithidea cingulata,* the carbohydrates began to decrease significantly ($P < 0.05$) from 7 days of starvation and continued up to 98 days (Figure 2). The carbohydrates of *Cerithium coralium* exhibited a significant decrease ($P < 0.05$) from 14 days of starvation (Figure 2). The glycogen levels of both the species showed a significant fall ($P < 0.05$) from 21 days of starvation. The proteins of *Cerithidea cingulata* decrease little and the significant decrease was observed ($P < 0.05$) from 68 days and 98 days of starvation. TNPS values exhibited a significant increase ($P < 0.05$) from 14 days of starvation in *Cerithidea cingulata* and *Cerithium coralium.* The lipids of *Cerithidea cingulata* started to decrease significantly from 48 days of starvation, but there was a significant decrease ($P < 0.05$) in the lipid content of *Cerithium coralium* from the 7th day onwards.

Viscera: The carbohydrates and glycogen of *Cerithidea cingulata* exhibited a significant decrease from 28 days and 48 days of starvation respectively. In contrast, a significant fall ($P < 0.05$) in the quantities of carbohydrates and glycogen was noticed from 21 days of starvation in *Cerithium coralium.* In *Cerithidea cingulata,* the protein content started to decrease significantly from 21 days of starvation

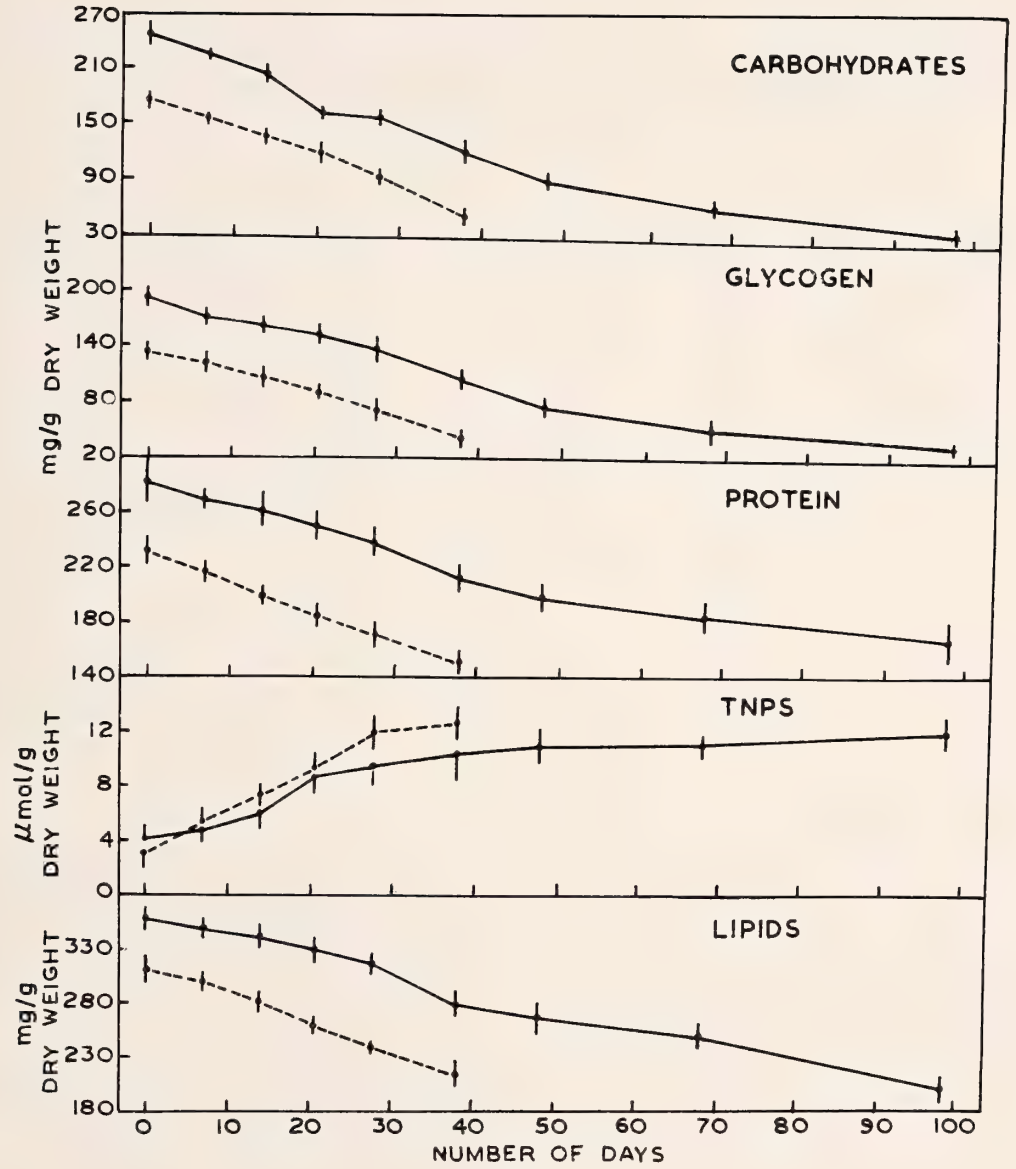


Figure 2

Changes in the levels of different biochemical constituents in the GDG complex of *Cerithidea cingulata* (——) and *Cerithium coralium* (-----). Vertical bars represent 1 SD.

and TNPS quantities increased significantly from 14 days of starvation. A significant fall ($P < 0.05$) in the quantities of protein from 7 days of starvation coincided with the significant increase in TNPS values of *Cerithium coralium*. The lipid values of *Cerithidea cingulata* and *Cerithium coralium* showed a fall in their levels from 38 days and 21 days of starvation respectively.

Biochemical Content

Tables 3–5 present data on the different body biochemical contents of *Cerithidea cingulata* and *Cerithium coralium* at different periods of starvation. ANOVA showed significant variations ($P < 0.05$) in biochemical composition during different periods of starvation. Duncan's analysis further proved (Tables 3–5) that carbohydrates, glycogen, proteins, and lipids decreased significantly ($P < 0.05$) with increasing periods of starvation in different body components of both the species. It is evident from Tables 3–5 that there are differences in the periods from where the significant decrease ($P < 0.05$) starts. There are also differences in these periods not only between levels and contents but also between the two species. However, TNPS content showed an increase in both the species with increasing starvation period (Tables 3–5).

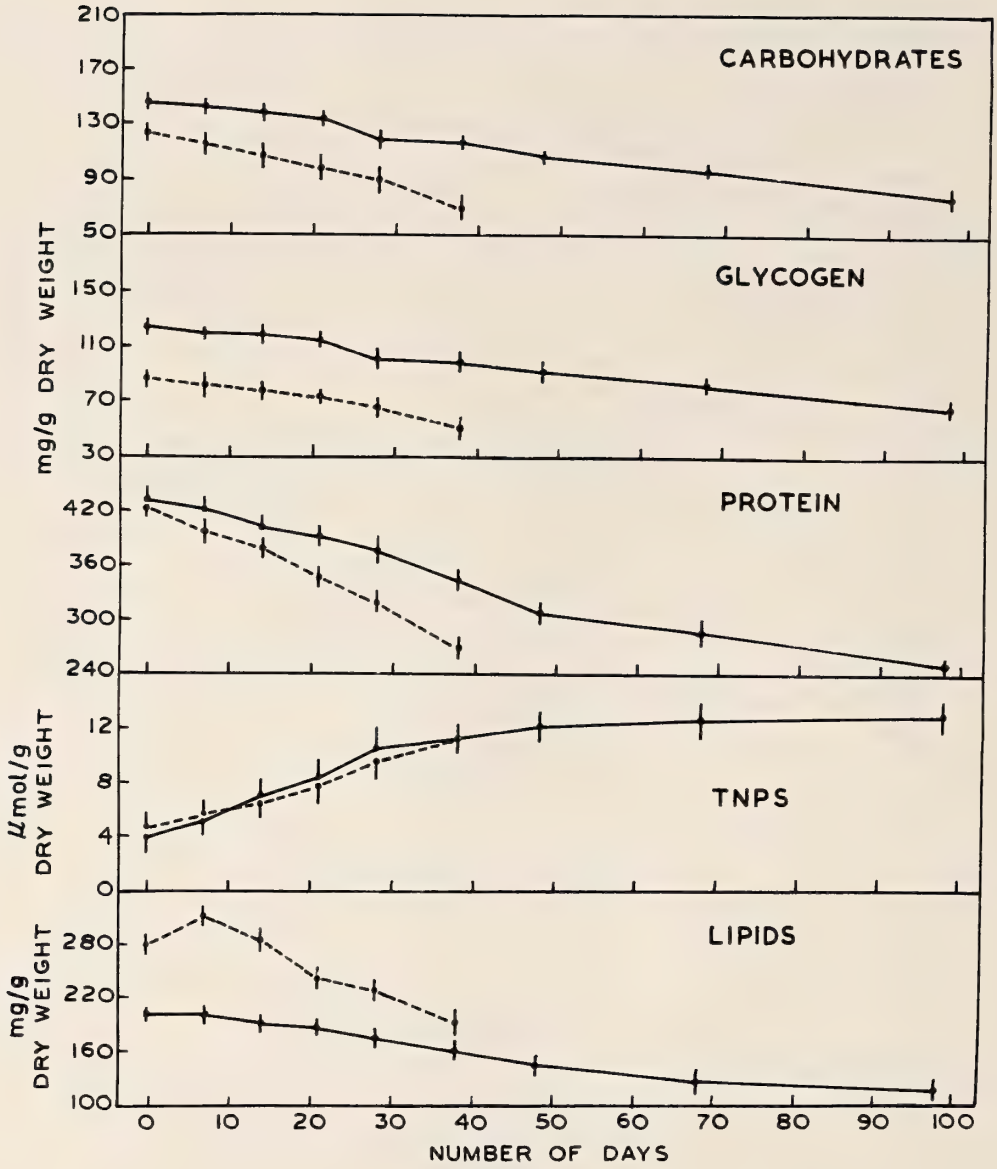


Figure 3

Changes in the levels of different biochemical constituents in the viscera of *Cerithidea cingulata* (——) and *Cerithium coralium* (-----). Vertical bars represent 1 SD.

Respiration

The respiratory rates of *Cerithidea cingulata* and *Cerithium coralium* were studied at different intervals of starvation (Table 1). It is evident from the table that the percentage decreases in oxygen consumption are gradual with increases in the period of starvation in both the animals when calculated on a per animal basis. Duncan's Multiple Range Test revealed significant decreases ($P < 0.05$) in the oxygen consumption rates from day 14 of starvation in both the species (Table 1). When the oxygen consumption values are presented on a tissue weight basis (tissue weight is deduced from the percentage decrease in dry tissue weight during starvation), the decrease, although gradual, is not as much as that of the per animal values in both the species (Table 1). The intercept values of log "a" in both the animals presented in the table are calculated using the exponential equation $Y = aW^b$, in which the regression coefficient "b" is taken from earlier investigations (Prabhakara Rao & Prasada Rao, 1984b). It is clear from the table that there is a gradual decrease in the log "a" values as starvation progresses in both species.

Table 3

Effect of starvation on the content of different biochemical constitutents in the foot of *Cerithidea cingulata* (a) and *Cerithium coralium* (b). All values are expressed as g/100 g dry weight of the tissue ± SD except TNPS (m mol/100 g dry weight of the tissue ± SD). *F*-test, * $P < 0.05$.

No. of days	Carbohydrates		Glycogen		Proteins		TNPS		Lipids	
	a	b	a	b	a	b	a	b	a	b
0	0.120 ±0.005	0.092 ±0.004	0.081 ±0.003	0.076 ±0.005	0.409 ±0.010	0.350 ±0.012	0.0027 ±0.0008	0.0018 ±0.0007	0.161 ±0.010	0.154 ±0.005
7	0.115 ±0.004	0.085 ±0.005	0.077 ±0.002	0.070 ±0.007	0.389* ±0.009	0.332 ±0.010	0.0034* ±0.0009	0.0030 ±0.0010	0.154 ±0.009	0.147* ±0.003
14	0.108 ±0.003	0.076* ±0.007	0.072 ±0.005	0.063 ±0.005	0.372* ±0.008	0.311 ±0.010	0.0046* ±0.0009	0.0032* ±0.0009	0.145 ±0.011	0.138* ±0.005
21	0.101 ±0.005	0.068* ±0.005	0.066 ±0.003	0.057* ±0.003	0.350* ±0.009	0.290* ±0.009	0.0046* ±0.0010	0.0033* ±0.0009	0.139 ±0.010	0.130* ±0.002
28	0.093 ±0.004	0.056* ±0.007	0.061* ±0.003	0.046* ±0.003	0.329* ±0.009	0.267* ±0.009	0.0046* ±0.0010	0.0040* ±0.0008	0.124* ±0.008	0.120* ±0.003
38	0.083 ±0.003	0.039* ±0.006	0.054* ±0.004	0.029* ±0.005	0.308* ±0.009	0.221* ±0.008	0.0052* ±0.0009	0.0042 ±0.0009	0.113* ±0.009	0.101* ±0.005
48	0.070* ±0.005		0.046* ±0.003		0.268* ±0.010		0.0062* ±0.0007		0.094* ±0.007	
68	0.057* ±0.003		0.038* ±0.002		0.230* ±0.009		0.0066* ±0.0009		0.079* ±0.009	
98	0.038* ±0.004		0.027* ±0.002		0.191* ±0.006		0.0066* ±0.0008		0.063* ±0.007	

DISCUSSION

The results clearly indicate that the effect of starvation is not much during the early stages in both species. The differences in the periods at which the mortality started (35 days in *Cerithidea cingulata* and 21 days in *Cerithium coralium*) reveal that the former can better tolerate starvation stress than the latter. This is further evidenced by the data that 50% mortality occurred at 98 days in *Cerithidea cingulata* and 38 days in *Cerithium coralium*. The reason may be their distribution: *Cerithium coralium* occurs towards wave-swept regions where there is abundant supply of food in the form of algae and diatoms while *Cerithidea cingulata* lives in the upper reaches of the estuary where there is less possibility for the growth of algae and other vegetation (Prabhakara Rao, 1981). *Cerithidea cingulata* may have a better inherent capacity for tolerance to starvation than *Cerithium coralium* because the body biochemical constituents were found to be higher in the former than the latter. Several other species of mollusks have been found to survive for various periods when exposed to starvation. In *Nucella lamellosa*, 90% survival was reported during 53 days of starvation (Stickle & Duerr, 1970); *Morula granulata* exhibited 50% mortality in 70 days of starvation (Uma Devi *et al.*, 1986); and 90% survival was observed during 50 days of starvation in *Lamellidens marginalis* (Mastanamma & Ramamurti, 1983).

There is no significant variation ($P > 0.05$) in the percentage water content of different body components in the two species studied. This is possibly due to the higher proportion of bound water in the soft parts of the animal and this may be used for metabolic adjustments during starvation. A similar condition was reported in *Paratelphusa hydrodromus* when exposed to starvation (Kotaiah & Rajabainaidu, 1973). Another reason for this insignificant change in the water content may be the presence of higher quantities of free amino acids in both the cerithiids (Prabhakara Rao & Prasada Rao, 1983b); these free amino acids can retain water and prevent its escape from the soft parts of the animal. In *Morula granulata* also, no changes in the percentage water content were recorded during starvation (Uma Devi *et al.*, 1986).

The present investigation suggests that the GDG complex serves as a storage organ in both species. The GDG complex indices in both species showed tremendous decreases when compared to the foot and viscera. Decreases in body component indices have also been reported in several other mollusks—*Nucella lamellosa* (Stickle, 1971), *Morula granulata* (Uma Devi *et al.*, 1986), *Thais haemastoma* (Belisle & Stickle, 1978), *Katharina tunicata* (Giese & Hart, 1967; Himmelman, 1978), *Chiton iatricus* (Nagabhushanam & Deshpande, 1982) and *Cryptochiton stelleri* (Lawrence *et al.*, 1965)—when food reserves are utilized for energy purposes.

From Figures 1–3 and Tables 3–5, it is clear that the different biochemical constituents (viz., carbohydrates, glycogen, proteins and lipids) which form the reserve food

Table 4

Effect of starvation on the content of different biochemical constituents in the GDG complex of *Cerithidea cingulata* (a) and *Cerithium coralium* (b). All values are expressed as g/100 g dry weight of the tissue ± SD except TNPS (m mol/ 100 g dry weight of the tissue ± SD). *F*-test, * $P < 0.05$.

No. of days	Carbohydrates		Glycogen		Proteins		TNPS		Lipids	
	a	b	a	b	a	b	a	b	a	b
0	0.808 ±0.045	0.533 ±0.024	0.622 ±0.039	0.406 ±0.030	0.911 ±0.052	0.698 ±0.030	0.013 ±0.003	0.009 ±0.003	1.159 ±0.032	0.930 ±0.036
7	0.711 ±0.019	0.456 ±0.017	0.543 ±0.031	0.353 ±0.029	0.855* ±0.037	0.626 ±0.023	0.016* ±0.003	0.015 ±0.004	1.035* ±0.034	0.358 ±0.032
14	0.621 ±0.036	0.371 ±0.022	0.492 ±0.030	0.290 ±0.033	0.786* ±0.045	0.545 ±0.019	0.018* ±0.004	0.020 ±0.003	1.029* ±0.030	0.764 ±0.024
21	0.529 ±0.029	0.312 ±0.028	0.446* ±0.034	0.236 ±0.023	0.724* ±0.037	0.476 ±0.023	0.025* ±0.003	0.024 ±0.003	0.941* ±0.034	0.666 ±0.021
28	0.444* ±0.033	0.229 ±0.021	0.386* ±0.038	0.177 ±0.026	0.655* ±0.030	0.406 ±0.024	0.026* ±0.004	0.028 ±0.003	0.871* ±0.027	0.569 ±0.014
38	0.328* ±0.036	0.118 ±0.021	0.279* ±0.034	0.095 ±0.027	0.552* ±0.031	0.319 ±0.017	0.027* ±0.003	0.027 ±0.003	0.722* ±0.034	0.454 ±0.025
48	0.226* ±0.032		0.185* ±0.027		0.484* ±0.029		0.027* ±0.003		0.649* ±0.034	
68	0.144* ±0.024		0.115* ±0.031		0.413* ±0.024		0.024* ±0.002		0.553* ±0.024	
98	0.083* ±0.019		0.075* ±0.015		0.328* ±0.027		0.023* ±0.002		0.386* ±0.023	

material are stored in different parts of the body in different proportions. When the snails are exposed to starvation, all of these stored food materials exhibit a tendency to decrease with time. During the early periods of starvation, the rate of decrease is slower when compared to the later periods in both species (Figures 1–3; Tables 3–5).

In *Cerithidea cingulata,* the greatest decrease was found for carbohydrates (89.75% for content and 82.87% for level) and glycogen (87.94% for content and 79.79% for level) of the GDG complex. The same trend was noticed in the GDG complex of *Cerithium coralium* (77.86% for content and 68.36% for level of carbohydrates; 76.70% for content and 66.67% for level of glycogen) but the changes were less. This was followed by lipids (66.69% for content and 44.44% for level) in *Cerithidea cingulata,* whereas in *Cerithium coralium* proteins were utilized (54.30% for content and 34.48% for level) next to carbohydrates. The protein utilization in *Cerithidea cingulata* was found to be less (63.99% for content and 39.93% for level) when compared to carbohydrates and lipids. In *Cerithium coralium,* lipids played a minor role (51.18% for content and 25.89% for level).

The biochemical constituents of the foot are utilized next to those of the GDG complex in both species. In the foot also, the carbohydrates (68.33% for content and 53.95% for level in *Cerithidea cingulata* and 57.61% for content and 50.83% for level in *Cerithium coralium*) played the major role as a fuel for energy needs during starvation. The same trend of utilizing lipids (60.87% for content and 44.12% for level) next to carbohydrates was noticed in *Cerithidea cingulata. Cerithium coralium* utilized proteins (36.86% for content and 25.71% for level) next to carbohydrates. In *Cerithidea cingulata,* proteins were least utilized (53.30% for content and 32.88% for level) whereas lipid utilization was found to be less (43.42% for content and 22.50% for level) in *Cerithium coralium.*

The viscera of both animals play almost a minor role during starvation stress. The biochemical constituents were reduced on exposure to starvation but to a lesser extent. In this tissue also, the utilization of carbohydrates (57.70% for content and 43.54% for level in *Cerithidea cingulata* and 52.41% for content and 41.94% for level in *Cerithium coralium*) and glycogen (58.90% for content and 45.16% for level in *Cerithidea cingulata* and 51.36% for content and 40.70% for level in *Cerithium coralium*) was more when compared to proteins and lipids. Lipid utilization, which followed that of carbohydrates in *Cerithidea cingulata* was 57.24% for content and 42.85% for level. In *Cerithium coralium,* protein utilization was high (48.17% for content and 36.17% for level) when compared to lipids. The biochemical constituents that were least affected in *Cerithidea cingulata* and *Cerithium coralium* were proteins (56.35% for content and 41.67% for level) and lipids (43.56% for content and 31.07% for level) respectively.

The levels and contents of different body biochemical constituents suggest that total carbohydrates constitute the major fuel during starvation in both species and that, among all the body components, the GDG complex contributes

Table 5

Effect of starvation on the content of different biochemical constituents in the viscera of *Cerithidea cingulata* (a) and *Cerithium coralium* (b). All values are expressed as g/100 g dry weight of the tissue ± SD except TNPS (m mol/100 g dry weight of the tissue ± SD). *F*-test, * $P < 0.05$.

No. of days	Carbohydrates		Glycogen		Proteins		TNPS		Lipids	
	a	b	a	b	a	b	a	b	a	b
0	0.825 ±0.028	0.582 ±0.038	0.696 ±0.039	0.403 ±0.019	2.424 ±0.084	1.993 ±0.056	0.023 ±0.007	0.021 ±0.007	1.139 ±0.045	1.313 ±0.052
7	0.788 ±0.022	0.538 ±0.032	0.662 ±0.011	0.377 ±0.042	2.308 ±0.071	1.840 ±0.064	0.030* ±0.008	0.026 ±0.005	1.105 ±0.049	1.435 ±0.060
14	0.748 ±0.021	0.495 ±0.036	0.636 ±0.032	0.354 ±0.023	2.163 ±0.059	1.684 ±0.050	0.036* ±0.007	0.030 ±0.006	1.036 ±0.043	1.294 ±0.059
21	0.710 ±0.016	0.443* ±0.044	0.606 ±0.031	0.323* ±0.018	2.057* ±0.052	1.546 ±0.053	0.043* ±0.008	0.035 ±0.006	0.971* ±0.052	1.081* ±0.058
28	0.616* ±0.026	0.385* ±0.038	0.519 ±0.036	0.284* ±0.025	1.929* ±0.076	1.342 ±0.054	0.055* ±0.007	0.040 ±0.006	0.886* ±0.046	0.961* ±0.042
38	0.588* ±0.020	0.277* ±0.042	0.494* ±0.040	0.196* ±0.031	1.699* ±0.059	1.033 ±0.042	0.055* ±0.005	0.043 ±0.005	0.795* ±0.049	0.741* ±0.054
48	0.524* ±0.019		0.443* ±0.038		1.471* ±0.062		0.059* ±0.006		0.695* ±0.057	
68	0.455* ±0.023		0.382* ±0.014		1.306* ±0.064		0.058* ±0.007		0.582* ±0.059	
98	0.349* ±0.038		0.286* ±0.029		1.058* ±0.042		0.055* ±0.006		0.487* ±0.046	

more to meeting energy demands. Thus it is clear from our results on both species that the decrease in the percentage of different biochemical constituents is more when calculated on the basis of content than on the level. Lipids are preferred after carbohydrates by *Cerithidea cingulata* while *Cerithium coralium* takes proteins after carbohydrates. Finally, proteins and lipids are least utilized by *Cerithidea cingulata* and *Cerithium coralium* in all three body components. Therefore, the metabolism of both the cerithiids is "carbohydrate-oriented" when exposed to starvation. Such a condition of carbohydrate-oriented metabolism was reported in the cerithiid *Clypeomorus clypeomorus* (Manmadha Rao, 1977), and several other mollusks were also found to show "polysaccharide-oriented" metabolism. Emerson (1967) suggested that certain terrestrial and freshwater mollusks show carbohydrate-oriented metabolism, whereas marine mollusks exhibit "lipid-oriented" metabolism. Von Brand *et al.* (1957) reported appreciable utilization of polysaccharides in the freshwater snail *Australorbis glabratus*. *Mytilus edulis*, an estuarine and marine bivalve (Bayne, 1973), also exhibited reduced levels of carbohydrates when exposed to starvation. Ramamurti & Subrahmanyam (1976) noticed carbohydrate metabolism in the terrestrial snail *Cryptozona semirugata* during starvation. *Planorbis corneus*, a freshwater snail, also showed a carbohydrate-oriented metabolism when subjected to starvation (Emerson, 1967). In some of marine snails—*Nucella lamellosa* (Stickle & Duerr, 1970), *Thais lapillus* (Bayne & Scullard, 1978), *Littorina keenae* (Emerson & Duerr, 1967), and *Morula granulata* (Uma Devi *et al.*, 1986), lipid-oriented metabolism was reported. The importance of lipids and their utilization in invertebrates was discussed by Giese (1966). Thus, there is a preferential utilization of a particular body reserve during starvation. The estuarine cerithiids of the present investigation belong to the category of carbohydrate-oriented metabolism, and thus tend to resemble freshwater rather than marine mollusks.

Earlier investigations (Prabhakara Rao & Prasada Rao, 1983b) on these cerithiids revealed utilization of glycogen when exposed to oxygen-free seawater. During reproduction, when there is an energy demand for the production of sperm and ova, the cerithiid *Clypeomorus clypeomorus* (Manmadha Rao, 1977) also depends on a carbohydrate reserve food material. Thus, the cerithiids show carbohydrate-oriented metabolism whenever energy is needed for the body. The differences in the utilization of carbohydrates in both species depend on the quantities stored inside the body. *Cerithidea cingulata* stored greater amounts of carbohydrates compared to *Cerithium coralium*. As long as carbohydrate reserves remain, the animals are able to survive. Death occurs due to insufficient amounts of carbohydrates, even though lipids and proteins can substitute to some extent. A similar observation was recorded in *Planorbis corneus* where death occurs due to complete exhaustion of carbohydrates during starvation exceeding 58 days (Emerson, 1967). The preference of lipid utilization next to carbohydrates in *Cerithium coralium* may be

attributed to environmental differences. The storage of body biochemical reserves were found to be higher in *Cerithidea cingulata,* which normally faces this type of stress in the upper reaches of the estuary. As food material is readily available in the habitat of *Cerithium coralium,* storage inside the body of the animal is unnecessary.

The rates of oxygen consumption in both species decreased gradually with increasing periods of starvation. The weight-specific oxygen consumption was also observed to decrease during starvation in both species, but the decrease was not so rapid when compared to the decrease in the rates of oxygen consumption (Table 1). However, similar trends of decreases in the rates of oxygen consumption have been reported in several mollusks when exposed to starvation: *Ancylus fluviatilis* (Berg *et al.,* 1958), *Lymnaea stagnalis* (Duerr, 1965), *Littorina keenae* (Emerson & Duerr, 1967), *Potamopyrgus jenkinsi* (Lumbye & Lumbye, 1965), *Nerita albicilla* and *Nerita chemaeleon* (Prasada Rao & Jaya Sree, 1983), *Thais lapillus* (Stickle & Bayne, 1982) and *Morula granulata* (Uma Devi *et al.,* 1986). The intercept values also showed a decreasing trend with starvation period in both cerithiid species but the decrease was greater in *Cerithidea cingulata* than *Cerithium coralium.* In *M. granulata,* a similar tendency of decreasing intercept values "a" when subjected to starvation was reported (Uma Devi *et al.,* 1986). However, Stickle & Bayne (1982) did not find any change in the intercept values of *Thais lapillus* during starvation, although according to Bayne & Scullard (1978), the intercept values showed a decreasing tendency in *T. lapillus.* Our results of the weight-specific oxygen consumption in both species during starvation corroborates results on *M. granulata.* However, *Nucella lamellosa* exhibited an increased or constant weight-specific oxygen consumption (Stickle & Duerr, 1970; Stickle, 1971). The decreased rates observed in the present investigation may be an adaptation of the animals to conserve stored food.

ACKNOWLEDGMENTS

The authors are thankful to the Head of the Department of Zoology, Andhra University, for providing the necessary facilities. V.U.D. and Y.P.R. are grateful to the authorities of the Council of Scientific & Industrial Research for financial assistance.

LITERATURE CITED

Bayne, B. L. 1973. Aspects of the metabolism of *Mytilus edulis* during starvation. Neth. Jour. Sea Res. 7:339–410.

Bayne, B. L. & C. Scullard. 1978. Rates of oxygen consumption by *Thais* (*Nucella*) *lapillus* (L.). Jour. Exp. Mar. Biol. Ecol. 32(1):97–111.

Belisle, B. W. & W. B. Stickle. 1978. Seasonal patterns in the biochemical constituents and body component indexes of the muricid gastropod *Thais haemastoma.* Biol. Bull. 155: 259–272.

Berg, K., J. Lumbye & K. W. Ocklemann. 1958. Seasonal and experimental variations of oxygen consumption of limpet *Ancylus fluviatilis.* Jour. Exp. Biol. 35:43–73.

Carrol, N. V., R. W. Longley & J. H. Roe. 1956. The determination of glycogen in liver and muscle by use of anthrone reagent. Jour. Biol. Chem. 220:583–593.

Duerr, F. 1965. Some effects of diet on the respiratory rate of freshwater pulmonate snail *Lymnaea palustris.* Proc. So. Dak. Acad. Sci. 44:245.

Emerson, D. N. 1967. Carbohydrate oriented metabolism of *Planorbis corneus* (Mollusca. Planorbidae) during starvation. Comp. Biochem. Physiol. 22:571–579.

Emerson, D. N. & F. Duerr. 1967. Some physiological effects of starvation in the intertidal prosobranch *Littorina planaxis* (Philippi 1847). Comp. Biochem. Physiol. 20:45–53.

Folch, J., Lees, H. & G. H. Sloane Stanely. 1957. A simple method for the isolation and purification of total lipids from animal tissues. Jour. Biol. Chem. 266:497–509.

Giese, A. C. 1966. Lipids in the economy of marine invertebrates. Physiol. Rev. 40:244–298.

Giese, A. C. & M. A. Hart. 1967. Seasonal changes in the component indices and chemical composition in *Katharina tunicata.* Jour. Exp. Mar. Biol. Ecol. 1:34–46.

Himmelman, J. H. 1978. The reproductive cycle of *Katharina tunicata* Wood and its controlling factors. Jour. Exp. Mar. Biol. Ecol. 31:27–41.

Kotaiah, K. & B. S. Rajabainaidu. 1973. Starvation stress on the metabolism of tropical freshwater crab *Paratelphusa hydrodromus* (Herbert). Indian Jour. Exp. Biol. 13:180–184.

Lawrence, A. L., J. M. Lawrence & A. C. Giese. 1965. Cyclic variations in the digestive gland and glandular oviduct of chitons (Mollusca). Science 147:510.

Lowry, O. H., N. J. Rosenbrough, A. L. Farr, & R. J. Randall. 1951. Protein measurement with the Folin Phenol reagent. Jour. Biol. Chem. 193:265–275.

Lumbye, J. & J. Lumbye. 1965. The oxygen consumption of *Potamopyrgus jenkinsi* (Smith). Hydrobiology 25:489–500.

Manmadha Rao, L. 1977. Studies on some aspects of the biology of a littoral snail *Clypeomorus* sp. (Gastropoda: Cerithidae) of the Waltair coast. Doctoral Thesis, Andhra University.

Mastanamma, P. & R. Ramamurti. 1983. Studies on the pattern of utilisation of major organic nutrients during starvation in the freshwater mussel *Lamellidens marginalis* (Lamarck). Indian Science Congress Association. 110 pp.

Moore, S. & W. H. Stein. 1954. A modified ninhydrin reagent for the photometric determination of amino acids and related compounds. Jour. Biol. Chem. 211:907–913.

Nagabhushanam, R. & U. D. Deshpande. 1982. Changes in body component indices in relation to reproductive cycle of chiton *Chiton iatricus.* Indian Jour. Mar. Sci. 11:276–277.

Prabhakara Rao, Y. 1981. Studies on the respiration of cerithiids. Doctoral Thesis, Andhra University.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1981. Survival of *Cerithidea* (*Cerithideopsilla*) *cingulata* (Gmelin 1790) and *Cerithium coralium* Kiener 1841 under anoxia and low salinities. Indian Jour. Zoo. 22:29–34.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1983a. Effect of temperature on the size related metabolism of *Cerithidea* (*Cerithideopsilla*) *cingulata* and *Cerithium coralium.* Indian Jour. Zoo. 24:37–43.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1983b. End products of anaerobic metabolism in *Cerithidea* (*Cerithideopsilla*) *cingulata* (Gmelin 1790) and *Cerithium coralium* Kiener 1841. Can. Jour. Zool. 61:1304–1310.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1983c. Effect

of temperature on aquatic and aerial oxygen consumption of *Cerithidea* (*Cerithideopsilla*) *cingulata* (Gmelin 1790) and *Cerithium coralium* Kiener 1841. Monitre Zool. Ital. 17:113–119.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1983d. Aerial respiration of *Cerithidea* (*Cerithideopsilla*) *cingulata* (Gmelin 1790) and *Cerithium coralium* Kiener 1841 in relation to body weight. Proc. Indian Acad. Sci. 92(5):381–386.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1984a. Oxygen consumption as a function of salinity in *Cerithidea* (*Cerithideopsilla*) *cingulata* (Gmelin 1790) and *Cerithium coralium* Kiener 1841. Geobios 11:179–182.

Prabhakara Rao, Y. & D. G. V. Prasada Rao. 1984b. Effect of body size on the respiration of *Cerithidea* (*Cerithideopsilla*) *cingulata* (Gmelin 1790) and *Cerithium coralium* Kiener 1841. Jour. Moll. Stud. 50:92–95.

Prasada Rao, D. G. V. & P. Jaya Sree. 1983. Effect of starvation on the oxygen consumption of the intertidal gastropods *Nerita albicilla* and *Nerita chamaeleon*. Geobios 10: 276–278.

Ramamurti, R. & D. V. Subrahmanyam. 1976. Organic composition of haemolymph, hepatopancreas and foot muscle of garden snail *Cryptozona semirugata* (Beck) with reference to starvation. Indian Jour. Exp. Biol. 14:492–498.

Snedecor, G. W. & W. G. Cochran. 1967. Statistical methods. The Iowa State University Press: Ames, Iowa. 587 pp.

Stickle, W. B. 1971. The metabolic effects of starving *Thais lamellosa* immediately after spawning. Comp. Biochem. Physiol. 40A:627–634.

Stickle, W. B. 1975. The reproductive physiology of the intertidal prosobranch *Thais lamellosa* Gmelin. II. Seasonal changes in the biochemical composition. Biol. Bull. 148:448–460.

Stickle, W. B. & B. L. Bayne. 1982. Effects of temperature and salinity on oxygen consumption and nitrogen excretion in *Thais lapillus* (L.). Jour. Exp. Mar. Biol. Ecol. 58:1–17.

Stickle, W. B. & F. G. Duerr. 1970. Effect of starvation on the respiration and major stores of *Thais lamellosa*. Comp. Biochem. Physiol. 33:689–695.

Uma Devi, V.,Y. Prabhakara Rao & D. G. V. Prasada Rao. 1986. Starvation as a stress factor influencing the metabolism of a tropical gastropod *Morula granulata* (Duclos). Proc. Indian Acad. Sci. 95:539–547.

von Brand, T., P. McMahon & M. O. Nolan. 1957. Physiological observations on starvation and desiccation of the snail *Australorbis glabratus*. Biol. Bull. 113:99–102.

The Veliger 30(2):184–189 (October 1, 1987)

THE VELIGER

A New and Polytypic Species of *Helminthoglypta* (Gastropoda: Pulmonata) from the Transverse Ranges, California

by

BARRY ROTH

Research Associate, Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara, California 93105, U.S.A.

Abstract. A new species of land snail, *Helminthoglypta* (*Helminthoglypta*) ***salviae,*** is described from the Transverse Ranges in southern Kern and northern Ventura counties, California. Two subspecies, differing in shell sculpture and details of coiling, are recognized, *H.* ***salviae salviae*** from Quatal and Apache canyons, and *H.* ***salviae mina*** from the vicinity of Frazier Park.

INTRODUCTION

The following species was first recognized as new by the late W. O. Gregg in the course of his extensive work on the land snails of southern California. Between 1947 and 1957 he and W. B. Miller collected it at several localities east and west of the town of Frazier Park, Kern County. Still earlier, probably some time in the 1930s, George Willett collected a sample of the same taxon near the head of San Emigdio Canyon, Kern County. In April 1984, T. A. Pearce found similar specimens at lower elevations a short distance to the southwest, in Quatal and Apache canyons, Ventura County.

The species remained undescribed because anatomical material was lacking. Species of *Helminthoglypta* can be assigned to subgenus only on the basis of genital anatomy (Miller, 1985). In April 1986, W. B. Miller, F. G. Hochberg, P. H. Scott, and I secured adequate material for dissection and the species is described below.

Two subspecies are recognized, differing consistently in shell characters but identical in genital anatomy. The basic description below pertains to the species in the broad sense; it is followed by shorter, differential diagnoses and designations of type material for each subspecies and a discussion that again pertains to the species in the broad sense.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, author's collection, San Francisco, California; CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; LACM, Natural History Museum of Los Angeles County; RLR, collection of R. L. Reeder, Tulsa, Oklahoma; SBMNH, Santa Barbara Museum of Natural History; TAP, collection of T. A. Pearce, Berkeley, California; USNM, U.S. National Museum of Natural History; WBM, collection of W. B. Miller, Tucson, Arizona.

SYSTEMATICS

Family Helminthoglyptidae Pilsbry, 1939

Helminthoglypta Ancey, 1887

Type species: *Helix tudiculata* A. Binney, 1843, by original designation.

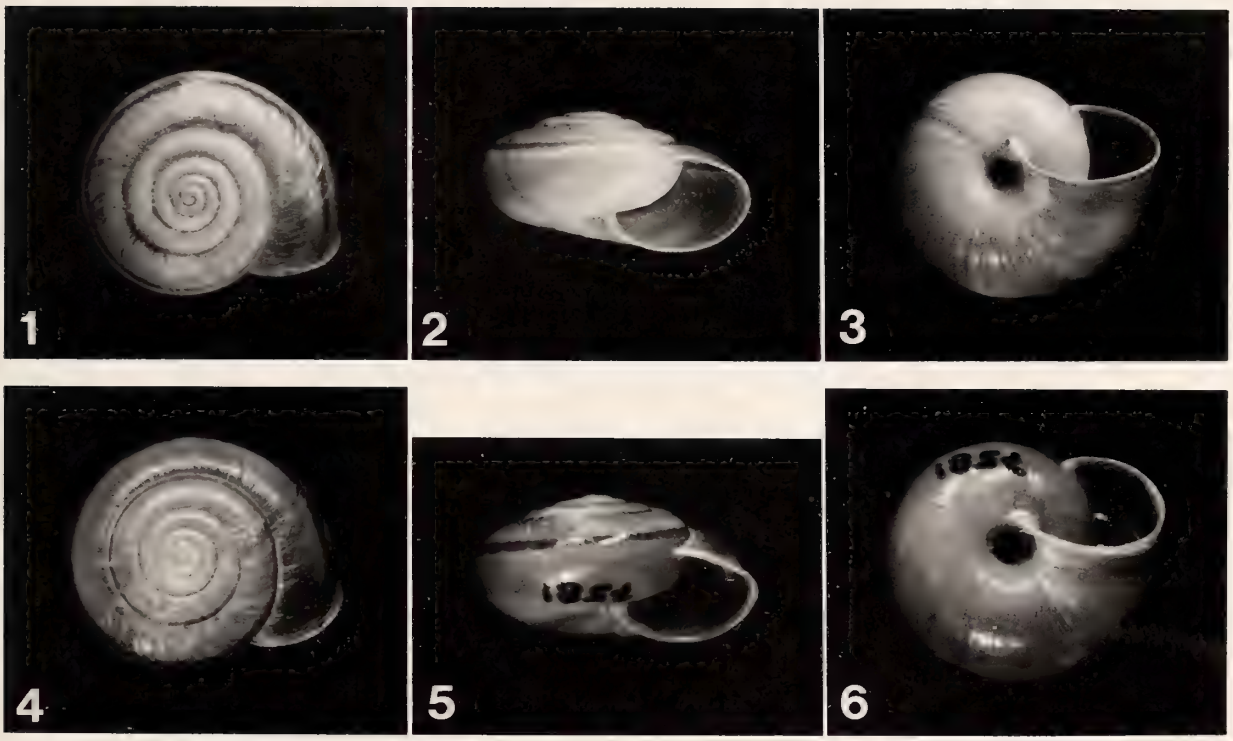
Subgenus *Helminthoglypta s.s.*

Helminthoglypta (*Helminthoglypta*) ***salviae***
Roth, sp. nov.

(Figures 1–8)

Diagnosis of the species: A small *Helminthoglypta* (*Helminthoglypta*) with depressed, matte to glossy, umbilicate, tightly coiled shell, sculptured with minute, slightly wavy, incised spiral striation. Lip thickened but barely turned outward. Dart sac moderately small; common duct of mucus bulbs thick-walled; lower chamber of penis short, conical.

Description of the species: Shell small for the genus, tightly coiled, moderately thin, glossy (in subspecies *H.* ***s. mina***) or matte to silky (in subspecies *H.* ***s. salviae***), depressed, umbilicate, umbilicus contained about 5.3–7.5 (in *H.* ***s. mina***) or 6.8–10.5 (in *H.* ***s. salviae***) times in diameter.



Explanation of Figures 1 to 6

Figures 1–3. *Helminthoglypta* ***salviae salviae***, shell; holotype SBMNH 34872, top, apertural, and basal views. Diameter 16.2 mm.

Figures 4–6. *Helminthoglypta* ***salviae mina***, shell; holotype SBMNH 34876, top, apertural, and basal views. Diameter 15.6 mm.

Spire low to very low-conic, whorl profile low-convex, suture moderately impressed. Embryonic whorls 1.75, set off from teleoconch by a constriction; initially smooth, thereafter with weak, irregular wrinkles radiating from suture, more or less broken up into closely spaced granules on first whorl, and stronger, widely spaced, diagonally arranged, round papillae. Early teleoconch whorls with low, narrow, closely spaced growth rugae (in *H. s. **salviae***, some rugae broken up into rows of axially elongated granules) and, from about middle or end of fourth whorl on, a system of closely but irregularly spaced, minute, slightly wavy, incised spiral striae. Striation strongest on shoulder of whorl behind lip, but also continuing over base into umbilical region. Base glossy (to matte in *H. s. **salviae***), inflated, tumid around umbilicus. Last ¼ whorl gently descending, not constricted behind lip. Aperture broadly auricular, moderately oblique, peristome at angle of 30° to vertical; lip narrowly, crudely thickened and turned outward but barely reflected except at the columellar insertion. Upper limb of peristome produced and slightly downturned. Inner lip barely encroaching on umbilicus. Parietal callus thin, its surface granular. Shell pinkish tan under a yellowish brown periostracum; with a 0.5-mm wide russet spiral band on shoulder (prolonging trajectory of suture), with traces of paler zones of equal width on either side of the band.

Two subspecies are recognized. The holotype of the nominate subspecies, next presented, is of course the holotype of the species as well.

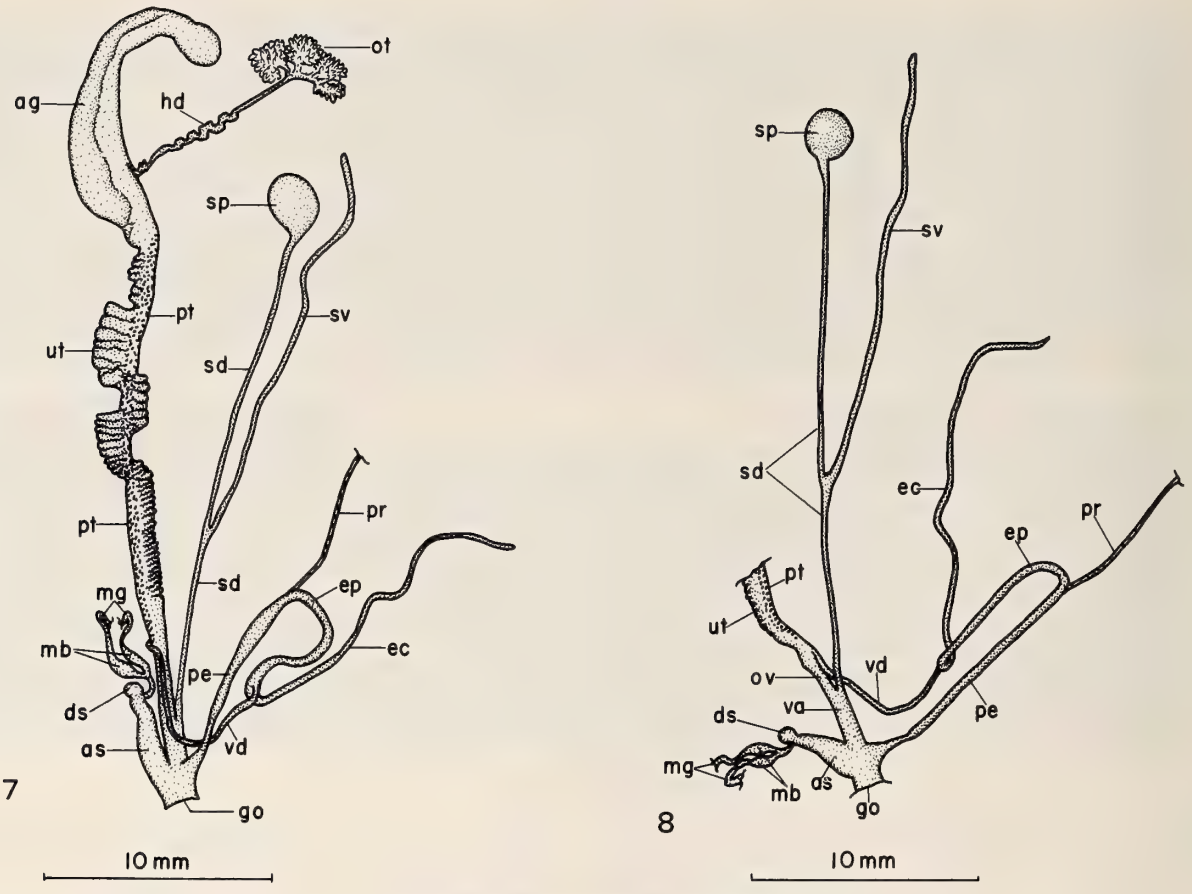
Helminthoglypta (*Helminthoglypta*) ***salviae salviae*** Roth, subsp. nov.

(Figures 1–3, 7)

Diagnosis: Shell matte to silky, umbilicus contained 6.8–10.5 times in diameter. Early teleoconch whorls with coarse growth rugae, some rugae broken up into rows of axially elongated granules. Closely but irregularly spaced, minute, slightly wavy, incised spiral striae present from end of fourth whorl on. Base glossy to matte.

Dimensions of holotype: Diameter (exclusive of expanded lip) 16.2 mm, height 8.6 mm, diameter of umbilicus 2.2 mm; whorls 5.25.

Type material: Holotype: Santa Barbara Museum of Natural History, SBMNH 34872 (shell and dissected soft anatomy), CALIFORNIA: Ventura County: south side of Apache Canyon, 4.0 km west-southwest of Nettle Spring



Explanation of Figures 7 and 8

Helminthoglypta ***salviae***, dissections of reproductive system drawn from projections of stained whole mounts.

Figure 7. *H.* ***salviae salviae***, paratype SBMNH 34874.

Figure 8. *H.* ***salviae mina***, holotype SBMNH 34876; upper part of uterus and prostate removed.

Abbreviations: ag, albumen gland; as, atrial sac; ds, dart sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; hd, hermaphroditic duct; mb, mucus gland bulbs; mg, mucus gland membranes; ot, ovotestis; ov, oviduct; pe, penis; pr, penial retractor muscle; pt, prostate; sd, spermathecal duct; sp, spermatheca; sv, spermathecal diverticulum; ut, uterus; va, vagina; vd, vas deferens.

Campground and 10.4 km east of California State Highway 33 [NE¼ sec. 16, T. 8 N, R. 23 W, San Bernardino Base and Meridian], elevation 1280 m; under pine deadfalls and dead yuccas. W. B. Miller, F. G. Hochberg, P. H. Scott, and B. Roth coll., 22 April 1986.

Paratypes: SBMNH 34873 (10 shells and soft parts), SBMNH 34874 (whole mount of stained genitalia), all from same locality as holotype. Additional paratypes deposited in ANSP, BR, CAS, FMNH, LACM, RLR, USNM, and WBM.

Referred material: Additional specimens have been examined from the following localities (all, California: Ventura County): Gully entering north side of Quatal Canyon [NW¼ sec. 22, T. 9 N, R. 23 W], elevation 1400–1450 m; under dead yuccas and under rocks. T. A. Pearce *et al.* coll., 19 April 1984 (TAP). South side of Quatal Canyon [NE¼ SE¼ sec. 33, T. 9 N, R. 23 W]. T. A. Pearce coll., 19 April 1984 (TAP). North side of Apache Canyon, approximately 4.5 mi [7.2 km] west of Nettle Spring Campground, 0.1 mi from road; under dead yuccas. F. G. Hochberg coll., 22 April 1986 (SBMNH). Approximately 0.8 km east of Nettle Spring, Apache Canyon [NE¼ sec. 11, T. 8 N, R. 23 W], elevation 1400–1450 m; under dead yuccas. T. A. Pearce coll., 20 April 1984 (TAP).

Etymology: From the Latin *salvia*, sage, for the Thistle Sage (*Salvia carduacea* Benth.) prominent around the type locality.

Helminthoglypta (*Helminthoglypta*) ***salviae mina*** Roth, subsp. nov.

(Figures 4–6, 8)

Diagnosis: Shell glossy, umbilicus contained 5.3–7.5 times in diameter. Early teleoconch whorls with fine growth

Table 1

Shell dimensions (in mm) and ratios in *Helminthoglypta* ***salviae***. Statistics are range, with mean ± one SD in parentheses. Only adult shells included.

Subspecies	n	D	H	U	W	H/D	U/D
H. s. salviae	22	14.2–18.9 (15.83 ± 1.18)	8.2–10.5 (9.17 ± 0.66)	1.5–2.5 (1.92 ± 0.26)	5.2–5.6 (5.36 ± 0.13)	0.531–0.620 (0.580 ± 0.024)	0.095–0.146 (0.121 ± 0.013)
H. s. mina	60	12.3–20.1 (15.40 ± 1.93)	6.3–11.0 (8.24 ± 1.06)	1.9–3.0 (2.46 ± 0.25)	4.8–5.8 (5.27 ± 0.24)	0.493–0.570 (0.535 ± 0.018)	0.135–0.186 (0.161 ± 0.013)

rugae, not broken up into rows of axially elongated granules. Closely but irregularly spaced, minute, slightly wavy, incised spiral striae present from about middle of fourth whorl on. Base glossy.

Dimensions of holotype: Diameter (exclusive of expanded lip) 15.6 mm, height 8.6 mm, diameter of umbilicus 2.4 mm; whorls 5.4.

Type material: Holotype: Santa Barbara Museum of Natural History, SBMNH 34876 (shell, whole mount of mantle tissue, and whole mount of stained genitalia), CALIFORNIA: Kern County: 6.1 km west of Frazier Park post office, north side of Frazier Mountain Park Road [NW¼ sec. 33, T. 9 N, R. 20 W, San Bernardino Base and Meridian], elevation 1600 m; under rocks loosely seated in soil on south-facing ridge. W. B. Miller, F. G. Hochberg, P. H. Scott, and B. Roth coll., 21 April 1986.

Paratypes: SBMNH 34877 (5 shells), from same locality as holotype, in abandoned wood rat nest, F. G. Hochberg coll., 21 April 1986. North side of Cuddy Canyon [now Frazier Mountain Park] Road 3.8 mi [6.1 km] west of Frazier Park, elevation 5000 ft [1500 m]; under rocks. W. O. Gregg coll., 26 January 1947 (SBMNH 34878), 23 March 1947 (SBMNH 34879), 19 December 1953 (SBMNH 34880). Additional paratypes deposited in ANSP, BR, CAS, FMNH, LACM, RLR, USNM, and WBM.

Referred material: Additional specimens have been examined from the following localities (all, CALIFORNIA: Kern County). The collectors' original topographic measurements, usually expressed in miles and feet, have been preserved, with metric equivalents added.

Head of San Emigdio Canyon, elev. 6000 ft [1800 m], under logs. G. Willett coll. (CAS). (Willett's original label states "Head of S. Emigdio Can., Mt. Pinos," which is internally inconsistent unless "Mt. Pinos" is construed loosely.) North side of Cuddy Canyon, 4 mi [6.4 km] west of Frazier Park School, elevation 5200 ft [1600 m]. W. B. Miller, W. O. Gregg coll., 2 March 1957 (WBM). North side of highway, 1.9 mi [3.0 km] west of Frazier Park; under dead yuccas. W. O. Gregg coll., 1 January 1947 (WBM). Gully north of Cuddy Canyon Road, 1.8 mi [2.9 km] west of Frazier Park, elevation 5000 ft [1500 m]; under granite rocks and rotten wood debris. W. O. Gregg coll., 23 March 1947 (WBM). North side of Frazier Mountain Park Road 1.5 mi [2.4 km] west of Frazier Park; under dead yuccas. F. G. Hochberg coll., 21 April 1986 (SBMNH). Approximately 1 mi [1.6 km] southeast of Frazier Park, near big rock slide, elevation approximately 5000 ft [1500 m]; under yuccas. W. O. Gregg coll., 15 February 1948 (WBM). North of highway, 1.3 mi [2.1 km] east of Frazier Park; under dead yuccas. W. O. Gregg coll., 19 December 1953 (WBM). 1.5 mi [2.4 km] east of Frazier Park, north of bed of Cuddy Creek; under dead yuccas. W. B. Miller, F. G. Hochberg, P. H. Scott, and B. Roth coll., 21 April 1986 (BR, SBMNH, WBM).

Etymology: From the Latin *mina,* bare, smooth.

DISCUSSION

Shell Variation

On 82 adult specimens from 17 lots, representing most of the localities from which *Helminthoglypta* ***salviae*** is known, the following measurements were taken: maximum diameter (exclusive of the expanded outer lip) (D); height parallel to the axis of coiling (H); breadth of the umbilicus parallel to maximum shell diameter (U); and number of whorls (W), counted by the method of PILSBRY (1939:xi, fig. B). Relative height of shell (H/D) and relative umbilical width (U/D) were calculated. Ranges, means, and standard deviations of these variables were calculated for the two subspecies (Table 1). The complete data are on deposit in the SBMNH. The variation was examined by means of principal components analysis (BLACKITH & REYMENT, 1971) with the BMDP Biomedical Computer Program (FRANE & JENNRICH, 1981) at the University of California, Berkeley.

A bivariate plot of relative height (H/D) against relative umbilical width (U/D) (Figure 9) shows that *Helminthoglypta* ***s. salviae*** tends to have relatively higher shells and relatively smaller umbilical width. Slopes of the regression lines for the two subspecies differ significantly from each other ($P < 0.001$).

Five principal components were computed; the first three cumulatively account for 96% (51, 37, and 8% respectively) of the total variance. Table 2 shows loadings of the entered variables. The first principal component is largely an expression of overall size and whorl number; a high score on this factor indicates a large shell with a high whorl count. The raw measures of size (H and D) and whorl

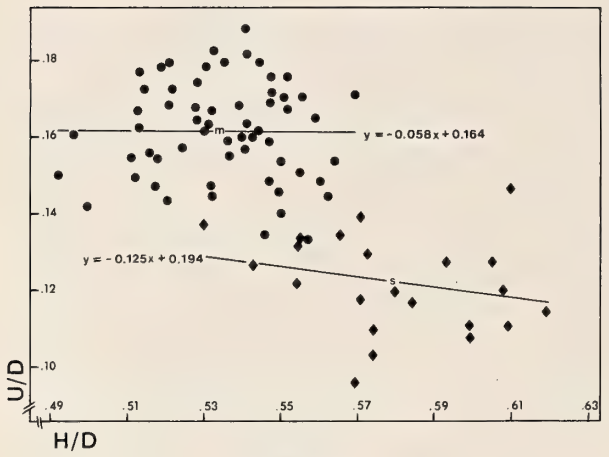


Figure 9

Relation between relative height of shell (H/D) and relative umbilical width (U/D) in 82 adult specimens of *Helminthoglypta* ***salviae***. Diamonds, *H.* ***s. salviae***; circles, *H.* ***s. mina***; s, group mean for *H.* ***s. salviae***; m, group mean for *H.* ***s. mina***.

number are strongly associated (all pairwise correlations 0.808 or greater). The second principal component expresses umbilical size; a high score indicates a shell with a large umbilicus, both in absolute terms and relative to the diameter of the shell. Relative height (H/D) loads negatively on this factor. Both H/D and U/D load positively on the third factor; a high score indicates a relatively high shell with a relatively large umbilicus.

The summary statistics of the scores of the two subspecies on these three factors (Table 3) indicate that specimens of *Helminthoglypta* ***s. salviae*** tend to score higher on Factor 1, lower on Factor 2, and moderately lower on Factor 3 than specimens of *H.* ***s. mina***. The combination of a high score on Factor 1 and a low score on Factor 2 (signifying a large, relatively high shell with a relatively small umbilicus) is especially characteristic of *H.* ***s. salviae***.

On Figure 10 the scores of the measured specimens on the first three principal components are plotted on a triaxial graph. Factor scores were coded by adding the quantity necessary to set the lowest score on each factor to zero; a specimen's score on an axis of the graph is its corresponding coded factor score expressed as a percentage of the sum of its three coded factor scores. The two subspecies are well discriminated, with shells of *Helminthoglypta* ***s. salviae*** tending to score higher on the first axis and lower on the second axis than shells of *H.* ***s. mina***. The spread of both subspecies along the third axis is similar.

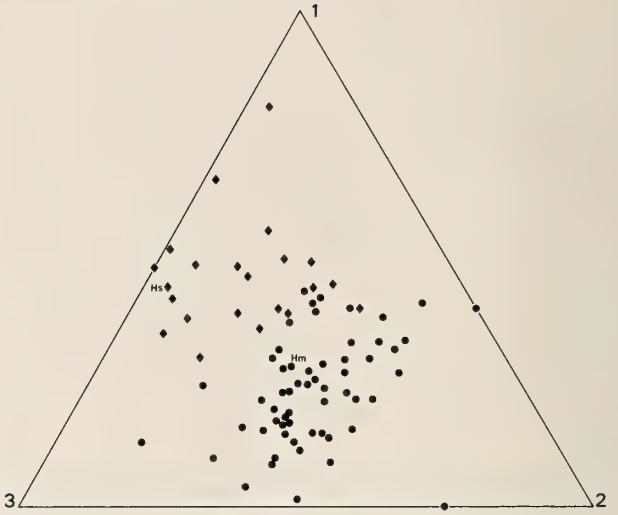


Figure 10

Triaxial plot of scores on first three principal components of 82 adult specimens of *Helminthoglypta* ***salviae***, coded as described in text. Diamonds, *H.* ***s. salviae***; circles, *H.* ***s. mina***; Hs, holotype of *H.* ***s. salviae***; Hm, holotype of *H.* ***s. mina***. Each symbol represents one or more specimens.

Soft Anatomy

Six specimens of *Helminthoglypta* ***s. salviae*** and one of *H.* ***s. mina*** were dissected. The figured reproductive systems are drawn from stained whole mounts.

Table 2

Factor loadings of variables and eigenvalues of factors in principal components analysis of shells of *Helminthoglypta* ***salviae***. Unrotated factors are principal components.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
D	0.909	0.351	−0.126	−0.175	−0.054
H	0.982	0.006	0.068	−0.152	0.087
W	0.879	0.268	0.041	0.391	−0.002
U	0.125	0.962	0.223	−0.087	−0.031
H/D	0.328	−0.755	0.566	−0.030	−0.031
U/D	−0.597	0.725	0.338	0.025	0.035
Eigenvalue	3.045	2.217	0.507	0.216	0.014

Table 3

Summary statistics of factor scores in principal components analysis of shells of *Helminthoglypta* ***salviae***.

Subspecies	Factor 1	Factor 2	Factor 3
H. ***s. salviae***			
Mean	0.6742	−1.2336	−0.1175
Maximum	1.802	0.343	2.391
Minimum	−0.136	−2.233	−1.903
H. ***s. mina***			
Mean	−0.2472	0.4523	0.0431
Maximum	2.101	2.057	3.544
Minimum	−1.952	−1.028	−2.382

The body is slaty gray, the mantle collar light tan. The mantle over the lung is light tan with black spots covering about 30–40% of the surface, mostly discrete but somewhat confluent along the dorsal edge. There is a 1 mm by 3 mm patch of black pigment immediately behind the dorsal end of the mantle collar.

The reproductive system (Figures 7, 8) is typical of the nominate subgenus, with a short atrium. The atrial sac is about ⅔ the length of the vagina and bears a rather small dart sac at its proximal end. The mucus gland bulbs are of moderate size, joined by a thick-walled, Y-shaped common duct that enters the atrial sac at the base of the dart sac. The duct of the spermatheca is fine, somewhat cavernous at its base, and bears a moderately long diverticulum of greater diameter than the duct itself. The penis has a short, conical lower chamber and a long, double-walled upper chamber, leading to an epiphallus of the same diameter as the penis. The epiphallic caecum ("flagellum") is long for the size of the animal.

Remarks

Helminthoglypta ***salviae*** is the only species of *Helminthoglypta* thus far found in its immediate area. *Helminthoglypta* (*Helminthoglypta*) *cuyama* Hanna & Smith, 1937, occurs approximately 80 km to the west, in the valley of the Cuyama River (Pilsbry, 1939) and in Colson Canyon, Santa Barbara County (WBM, LACM). *Helminthoglypta cuyama* is larger (to almost 29 mm diameter), also glossy and depressed, but has malleate sculpture instead of fine spiral striation; its peristome is reflected. The mantle over the lung is very dark, 90% or more covered with black pigment flecks, almost uniform over the last ¼ whorl but breaking up into spots behind that. The epiphallic caecum is shorter than that of *H.* ***salviae*** even though the adult animal is larger, and the dark sac is larger in diameter than the atrial sac.

The enigmatic *Helminthoglypta cuyamacensis venturensis* (Bartsch, 1916), described from Ventura County but never subsequently recognized, differs from *H.* ***salviae*** in being coarsely, densely papillose all over. It seems highly improbable that *H. c. venturensis* is really a subspecies of *Helminthoglypta* (*Rothelix*) *cuyamacensis* (Pilsbry, 1895), but until the species is rediscovered and living material dissected it cannot be firmly allocated.

To the east the geographically nearest taxon is *Helminthoglypta* (*H.*) *traskii tejonis* Berry, 1930, from rockslides in the vicinity of Fort Tejon, Kern County, with a large, tumid, low-conic shell, reaching a maximum diameter of over 30 mm. Also in the vicinity of Fort Tejon have been found specimens resembling *Helminthoglypta* (*H.*) *traskii traskii* (Newcomb, 1861), one of which was figured by Pilsbry (1939:fig. 85f). Shells that I have examined are of about the same shape and size as presumed topotypic *H. traskii traskii* from Point Fermin, Los Angeles County, but the incised spiral sculpture is finer (7 striae/mm on the last ¼ of the body whorl as compared to 4 or 5 striae/mm on *H. traskii traskii*). It is possible that these specimens represent an eastern occurrence of *H.* ***salviae***. If they are *H. traskii,* then dissected material should show the rather large subglobular dart sac found in that species.

The range of *Helmithoglypta* ***salviae*** is within Juniper-Pinyon Woodland (Küchler, 1977), characterized by open, mixed groves of California juniper (*Juniperus californica* Carr.) and singleleaf pinyon (*Pinus monophylla* Torr. & Frém.), both of which here range from large shrubs to small trees. *Yucca whipplei* Torr. is locally common, and the moist interior of its decaying clumps forms prime snail habitat. East of Frazier Park, *H.* ***s. mina*** was found in clumps of *Y. whipplei* in overgrazed pasture. West of Frazier Park, *H.* ***s. mina*** occurs in open areas in an ecotone between Juniper-Pinyon Woodland and Southern Jeffrey Pine (*Pinus jeffreyi* Grev. & Balf.) Forest. We did not find any *Helminthoglypta* in pure stands of Jeffrey pine.

ACKNOWLEDGMENTS

I am grateful for the aid and field companionship of Eric Hochberg and Paul Scott. Tim Pearce kindly put specimens at my disposal. The computer-assisted analysis was performed with the help of David R. Lindberg and Tim Pearce. Dick Reeder read and commented on the manuscript. I especially acknowledge the collaboration of Walter B. Miller, who collected, dissected, and drew many of the specimens and identified the *Salvia* at the type locality of *Helminthoglypta* ***salviae***.

LITERATURE CITED

Blackith, R. E. & R. A. Reyment. 1971. Multivariate morphometics. Academic Press: New York.

Frane, J. & R. Jennrich. 1981. Factor analysis. Pp. 656–684. *In:* W. J. Dixon (ed.), BMDP Biomedical computer programs. University of California Press: Berkeley.

Küchler, A. W. 1977. The map of the natural vegetation of California. Pp. 909–939, map. *In:* M. G. Barbour and J. Major (eds.), Terrestrial vegetation of California. John Wiley and Sons: New York.

Miller, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). Veliger 28(1):94–98 (1 July 1985).

Pilsbry, H. A. 1939. Land Mollusca of North America (north of Mexico). Acad. Natur. Sci. Philadelphia, Monogr. 3, 1(1): 1–573.

The Veliger 30(2):190–195 (October 1, 1987)

THE VELIGER

A New Species of *Naquetia* (Muricidae) from the Gulf of Aqaba

by

ANTHONY D'ATTILIO AND CAROLE M. HERTZ

Department of Marine Invertebrates, San Diego Natural History Museum,
P.O. Box 1390, San Diego, California 92112, U.S.A.

Abstract. *Naquetia* ***fosteri*** D'Attilio & Hertz, sp. nov., is described from the Gulf of Aqaba in the Red Sea; it is compared to *N. trigonula* (Lamarck, 1816) and *N. annandalei* (Preston, 1910).

INTRODUCTION

Eight specimens of a *Naquetia* species were submitted to the senior author for identification. While referable to *Naquetia,* the new species differs from similar species, *N. trigonula* (Lamarck, 1816) and *N. annandalei* (Preston, 1910), in shell characters and distribution. The new species has been reported only from the Red Sea at the Gulf of Aqaba.

TAXONOMIC ACCOUNT

Family MURICIDAE Rafinesque, 1815

Subfamily Muricinae Rafinesque, 1815

Genus *Naquetia* Jousseaume, 1880

Type species: *Murex triqueter* Born, 1778, by original designation.

Naquetia is a genus of non-spinose trivaricate muricids with noded axial costae, deep anal sulcus, and anteriorly webbed varical flanges. Both radula and operculum are as in Muricinae.

Although *Naquetia* has been considered a subgenus of *Pterynotus* Swainson, 1833 (CERNOHORSKY, 1967, 1971; VOKES, 1968) and *Chicoreus* Montfort, 1810 (VOKES, 1974, 1978; HOUART, 1985), it differs from those genera based on shell morphology (RADWIN & D'ATTILIO, 1976). While *Naquetia* has the trivaricate nature of the heavier *Chicoreus* (type species: *Murex ramosus* Linné, 1758), it lacks the foliaceous varical spines of *Chicoreus.* In *Naquetia* the varical extensions are sparse, appearing on the anterior end of the body whorl and canal. In *Pterynotus* (type species: *Murex pinnatus* Swainson, 1822) the three varical extensions are bladelike flanges that continue over the entire body whorl and spire.

Naquetia ***fosteri*** D'Attilio & Hertz, sp. nov.

(Figures 1–6)

Type material and locality: SDNHM 91996: Holotype (Figures 1, 2). 92.2 × 37.0 mm. Gulf of Aqaba, off Eilat, Red Sea.

SDNHM 91997: Paratype (Figures 3, 4). 71.5 × 26.2 mm. Gulf of Aqaba, off Eilat, Red Sea.

SDNHM 91998: Paratype. 75 × 29 mm. Gulf of Aqaba, off Eilat, Red Sea.

Donald Pisor Collection: Paratype (*ex* Aryeh Hadar and A. D'Attilio Collections). 77.5 × 30.5 mm. Eilat, Israel. [Figured in RADWIN & D'ATTILIO, 1976: pl. 15, fig. 10, as *N. annandalei*.]

Kay Vaught Collection No. 4583: Paratype. 75.7 × 26.5 mm. Off Eilat, Israel. 40–45 m. Dani Bloome, *leg.*

Glass and Foster Collection No. 86-037: Paratype. 94.5 × 36 mm. Eilat, Israel, Dec. 1985.

→

Explanation of Figures 1 to 4

Figures 1, 2. *Naquetia* ***fosteri*** sp. nov., holotype (SDNHM 91996), 92.2 × 37.0 mm (protoconch missing). Type locality: Gulf of Aqaba, off Eilat, Israel. Apertural (Figure 1) and dorsal (Figure 2) views.

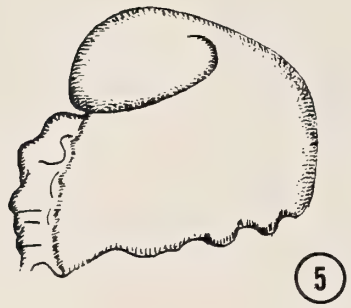
Figures 3, 4. *Naquetia* ***fosteri***, paratype (SDNHM 91997), 71.5 × 26.2 mm. Gulf of Aqaba, off Eilat, Israel in 40 m. Apertural (Figure 3) and dorsal (Figure 4) views.

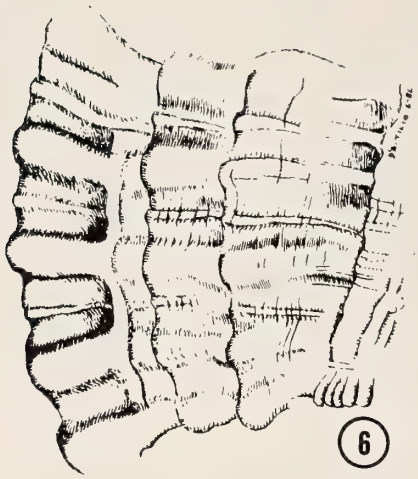

1


2


3


4





Explanation of Figures 5 and 6

Figure 5. *Naquetia **fosteri***, paratype (Glass and Foster Collection). Camera lucida drawing of protoconch, ×20.4.

Figure 6. *Naquetia **fosteri***, detail of sculpture at edge of apertural flange, ×2.5.

Glass and Foster Collection No. 85-1045: Paratype. 93 × 37 mm. Eilat, Israel.

Glass and Foster Collection: Paratype. 81 × 30 mm. Gulf of Aqaba, Red Sea.

Etymology: It is with great pleasure that we name this species for Robert Foster, who with Charles Glass has been generous in making specimens from their collections available both for study and as additions to the malacology collection of the San Diego Natural History Museum.

Description: Shell (Figures 1–4) large (to 94.5 × 36 mm), moderately fusiform with 7–8 convex postnuclear whorls and protoconch of 1½ convex nuclear whorls (Figure 5). Spire relatively low, less than one-half shell length. Suture impressed; aperture narrow, lenticular–ovate; outer lip edge strongly erect and recurved, with 14 denticles becoming lirae extending into aperture; anal sulcus well defined, narrow, deep, V-shaped; inner lip mostly appressed; canal long, sinuous, narrowly open, weakly recurved distally; siphonal fasciole retaining two prior canal terminations.

Three prominent rounded varices extending to and abutting previous whorls; varices appearing with first postnuclear whorl; receding side of varix weakly concave; 3–5 intervarical costae, irregularly distributed. Fluted varical flanges on lower portion of body whorl extend to canal.

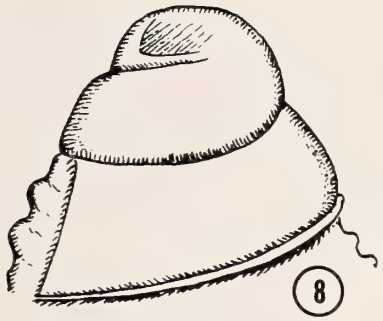
Figure 7

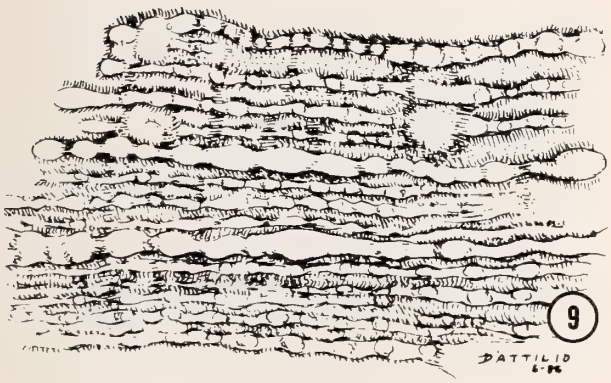
Naquetia annandalei (Preston, 1910), apertural view of holotype (ZSI Reg'd. nom. 4708/1), 76.5 mm long (per Preston). Type locality: "Off Gopalpore," Bay of Bengal.

Body-whorl sculpture of 10 primary spiral cords, 2 of which are above shoulder, with 3 additional, widely spaced cords on canal. Transverse cords with minor interstitial cords throughout, most defined on canal portion of flange. Raised nodes formed where transverse cords cross costae; growth striae very weakly defined (Figure 6). First 5 teleoconch whorls vary from bright pink to pale light orange, with cream-colored varices; remaining 3 whorls rich pink, cream, and brown; sometimes with faint indications of 3 darker brownish bands on body whorl. (In the holotype the color has faded to pale orange.) Aperture white.

Distribution: *Naquetia **fosteri*** is known only from the area off Eilat, Israel, in the northern end of the Gulf of Aqaba.

Remarks: Although *Naquetia **fosteri*** is related morphologically to its congeners *N. annandalei* (Preston, 1910) (Figure 7) and *N. trigonula* (Lamarck, 1816), material examined confirms that *N. **fosteri*** is a distinct taxon (see Table 1). Thirteen specimens of *N. annandalei* from 48.2 to 104.9 mm in height and 8 specimens of *N. **fosteri*** from 71.5 to 94.5 in height were examined. *Naquetia annandalei* is broader than *N. **fosteri***. The protoconch of *N. annandalei* consists of 3½ rounded (Figure 8) rather than 1½ rounded whorls as in *N. **fosteri*** (Figure 5). The outer lip of *N. annandalei* is crenulate lacking lirae within, whereas that of *N. **fosteri*** bears 14 denticles which become lirate inte-





riorly. *Naquetia annandalei* has 8 moderately convex postnuclear whorls and the body whorl is encircled by 14 extremely fine nodose spiral cords which form knobs as they cross the costae. The entire shell is transversely, microscopically sculptured, giving the shell a sandpaper-like texture (Figure 9). *Naquetia* ***fosteri,*** with 7 to 8 postnuclear whorls, has 10 strong primary cords with minor interstitial cords and no microsculpture.

Naquetia trigonula (Figure 10) is a smaller species, attaining a height of 55.5 mm compared to 94.5 mm for *N.* ***fosteri***. *Naquetia trigonula* has a protoconch of 2¼–2½ tabulate whorls (Figure 11) contrasted to the 1½ rounded whorls in *N.* ***fosteri***. In the 30 specimens of *N. trigonula* studied, the teleoconch is of 5 to 6 rapidly expanding whorls with 1 or 2 strongly noded intervarical costae and a body whorl of 10 rows of knobby spiral cords with fine interstitial cords and extremely fine granular microsculpture.

←

Explanation of Figures 8 and 9

Figure 8. *Naquetia annandalei* (Preston, 1910). Camera lucida drawing of protoconch of specimen (SDNHM 81673), 65.0 mm long, showing three rounded whorls. Shaded area designates missing portion, ×20.4.

Figure 9. *Naquetia annandalei,* detail of spiral sculpture on body whorl, ×7.7.

Table 1

Comparison of shell morphology in *Naquetia* ***fosteri*** sp. nov., *N. annandalei* and *N. trigonula.*

	N. ***fosteri***	*N. annandalei*	*N. trigonula*
Protoconch	1½ convex whorls	3½ rounded whorls	2¼–2½ tabulate whorls
Teleoconch	7–8 whorls	8 whorls	5–6 whorls
Maximum height	94.5 mm	104.9 mm	55.5 mm
Spire-height-to-total-height ratio, mean*	0.385	0.322	0.385
Maximum width on body whorl	35 mm	46 mm	19.5 mm
Width-height ratio (W/H), mean	0.384	0.419	0.434
Aperture	lenticular–ovate; deep, narrow anal sulcus with one node on columellar side of sulcus	ovate with deep V-shaped anal sulcus; two nodes on apertural side of sulcus with thickened ridge on columellar side	lenticular with V-shaped anal sulcus; one node on columellar side of sulcus
Outer lip	14 denticles becoming lirate within	crenulate, no lirae within	13 or 14 denticles becoming lirate within
Spiral sculpture	10 strong primary cords on body whorl and canal with minor interstitial cords; no microsculpture	14 nodose cords on body whorl and canal, with fine nodose interstitial cords; extremely fine granular microsculpture	10 nodose cords on body whorl with fine nodose interstitial cords; extremely fine granular microsculpture
Axial sculpture	trivaricate, 3 or 4 noded intervarical costae	trivaricate, 3 or 4 intervarical costae, often only distinguished by nodes at the shoulder	trivaricate, 1 or 2 strongly noded intervarical costae

* Measured from receding side of apertural varix to tip of spire.

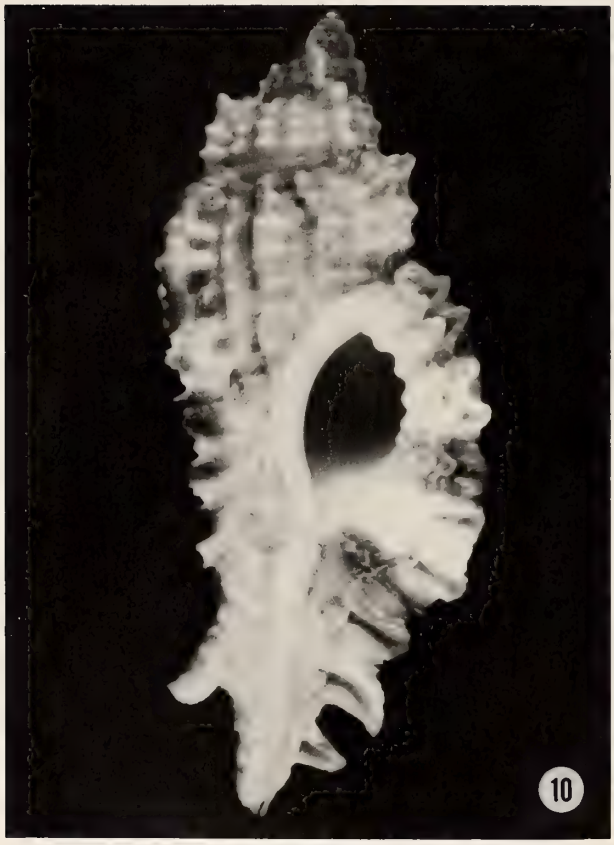


Figure 10

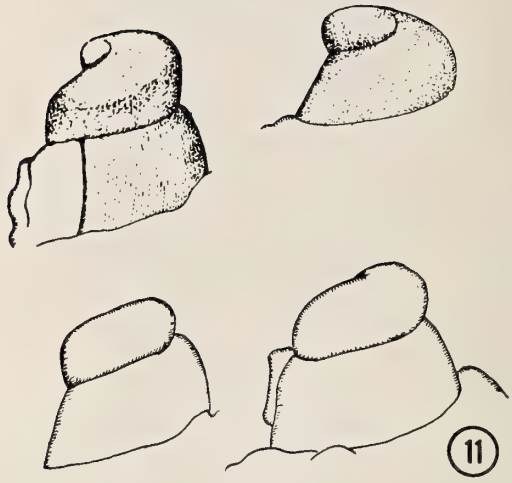
Naquetia trigonula (Lamarck, 1816) (SDNHM 87737), 49.3 mm long, apertural view.

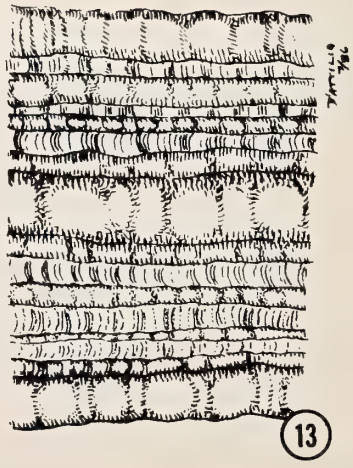
Naquetia ***fosteri***, with 7 to 8 postnuclear whorls, lacks microsculpture and bears 3 or 4 noded intervarical costae.

Naquetia trigonula occurs throughout the Indo-Pacific and *N. annandalei* is found from the Bay of Bengal to the Philippine Islands and southeastern Japan; *N.* ***fosteri*** is known only in the northern end of the Gulf of Aqaba.

ACKNOWLEDGMENTS

The following friends and colleagues have placed specimens at our disposal: Charles Glass and Robert Foster,





→

Explanation of Figures 11 to 13

Figure 11. *Naquetia trigonula* (Lamarck, 1816), 55.5 mm long (SDNHM 85974). Camera lucida drawings showing four views of the protoconch, ×20.4.

Figures 12, 13. *Naquetia trigonula,* 55.5 mm long (SDNHM 80840). Camera lucida drawings of transverse sculpture of spiral cords with depressed areas containing microsculpture. Figure 12. Spiral cords, ×2.5. Figure 13. Detail of microsculpture in interspaces, ×7.7.

both of Santa Barbara, California, donated the holotype (SDNHM 91996) and one paratype (SDNHM 91998) and specimens of other *Naquetia* species. Marion Magee of Speedway, Indiana, donated a paratype (SDNHM 91997). Donald Pisor of San Diego, California, Kay Vaught of Scottsdale, Arizona, and Eugenia Wright of Phoenix, Arizona, lent paratype specimens. N. V. Subba Rao of the Zoological Survey of India kindly provided photographs of the type of *N. annandalei*. William K. Emerson and Emily H. Vokes gave helpful suggestions, and Eugene Coan critically reviewed the manuscript. Theo Fusby typed the preliminary and final drafts.

Unless otherwise noted, the photography is by David K. Mulliner.

LITERATURE CITED

Born, I. [Edler von]. 1778. Index rerum naturalium Musei Caesarei Vindobonensis, pars I. Testacea. [Verzeichniss der natürlichen Seltenheiten des k. k. naturalien Kabinets zu Wien, erster Theil. Schalthiere.]. Pp. [xlii] + 458 + [80] + [2]; 1 pl. [not seen] Vindobonae (Krausiana).

Cernohorsky, W. O. 1967. The Muricidae of Fiji (Mollusca: Gastropoda). Pt. 1. Subfamilies Muricinae and Tritonalinae. Veliger 10(2):111–132, pls. 14 and 15 (Oct. 1).

Cernohorsky, W. O. 1971. Contribution to the taxonomy of the Muricidae (Gastropoda: Prosobranchia). Veliger 14(2): 187–191 (Jan. 1).

Houart, R. 1985. Gros plan sur les *Naquetia* (Gastropoda: Muricidae). Xenophora 29:8–14 (Sept.–Oct.).

Jousseaume, F. P. 1880. Divison méthodique de la famille de *Purpurides*. Le Naturaliste, yr. 2(42):335–336 (Dec. 15).

Lamarck, J. B. P. A. de M. de. 1816. Tableau encyclopédique et méthodique detrois règnes de la nature (vers. testaces). Pls. 315–448. Paris.

Montfort, P. D. de. 1810. Conchyliologie systematic, et classification méthodique des coquilles 2:676 pp. Paris.

Preston, H. B. 1910. Descriptions of new shells. Rec. Indian Mus., Calcutta 5:118–119, fig. 3.

Radwin, G. E. & A. D'Attilio. 1976. Murex shells of the world. Stanford Univ. Press: Stanford, California. 284 pp., 32 pls., 192+ text figs.

Rafinesque, C. S. 1815. Analyse de la nature ou tableau de universe et des corps organisés. Pp. 5–6, 136–149, 218–223. Varravecchea: Palermo.

Swainson, W. 1833. Zool. Illus. 2(3):22, pl. 100. Mollusca. London.

Vokes, E. H. 1968. On the identity of *Murex trigonulus* of authors (Gastropoda: Muricidae). Jour. Conchol. 26(5):300–304, pl. 13. (Oct.).

Vokes, E. H. 1974. On the identity of *Murex triqueter* Born (Gastropoda: Muricidae). Veliger 16(3):258–264, 1 pl. (Jan. 1).

Vokes, E. H. 1978. Muricidae (Mollusca: Gastropoda) from the eastern coast of Africa. Ann. Natal Mus. 23(2):375–418, pl. 5 (Oct.).

The Veliger 30(2):196–205 (October 1, 1987)

THE VELIGER

Pyropeltidae, a New Family of Cocculiniform Limpets from Hydrothermal Vents

by

JAMES H. McLEAN

Los Angeles County Museum of Natural History,
Los Angeles, California 90007, U.S.A.

AND

GERHARD HASZPRUNAR

Institut für Zoologie, Universität Innsbruck,
Technikerstr. 25, A-6020 Innsbruck, Austria

Abstract. A new genus, ***Pyropelta***, is proposed for two new species from hydrothermal vents: the types species, ***P. musaica***, from the Juan de Fuca Ridge off Washington, and ***P. corymba***, from the Guaymas Basin in the Gulf of California. Shells resemble some genera of Pseudococculinidae in having a similar pattern of erosion. Absence of cephalic lappets, differences in the excretory system, presence of an osphradium, and major differences in the radula warrant recognition of the new family Pyropeltidae for the genus. Relationships of the Pyropeltidae among the Lepetellacea are discussed, with comparisons to those families with a similar radula (Pseudococculinidae, Osteopeltidae). The two species live directly on sulfide crust, unlike all other Lepetellacea, which are usually associated with biogenic substrata.

INTRODUCTION

The hydrothermal-event environment has yielded a number of remarkable discoveries among mollusks. Although limpets of a number of families are well represented (McLean, 1985b), the presence of cocculiniform limpets in the hydrothermal-vent habitat had not been recognized until now. In a preliminary report on limpets of the hydrothermal vents, McLean (1985b) noted the absence of members of this group, a generalization that is here emended. Large numbers of one new species described here were first collected at the Juan de Fuca Ridge by the submersible *Pisces IV* in July 1986. A single specimen of a species from the Guaymas Basin had been collected in January 1982, but its radula was not examined and its affinity not ascertained until now.

The cocculiniform limpets include the families Cocculinidae Dall, 1881; Lepetellidae Dall, 1882; Addisoniidae Dall, 1882; Bathysciadiidae Dautzenberg & Fischer, 1900; Cocculinellidae Moskalev, 1971; Bethyphytophilidae Moskalev, 1978; Pseudococculinidae Hickman, 1983; and Osteopeltidae Marshall, in press. One family with coiled shells has been recognized, the Choristellidae Bouchet & Warén, 1979. These families have recently received new attention, starting with papers by Moskalev (1971, 1973, 1976, 1978) and followed by Hickman (1983) who gave the first SEM illustrations of radulae, and papers by Marshall (1983, 1986) and McLean (1985a). Haszprunar (1987, in press a, b, c, d) has anatomical studies underway relating to these families.

In this paper another cocculiniform family is described. It has a distinctive radular plan and unique combinations of anatomical characters, and it does not require a substrate of biological origin. Other families of cocculiniform limpets occur and feed upon a variety of substrates including wood or other plant material, polychaete tubes, bone, cephalopod beaks, crab exoskeletons, and elasmobranch egg cases.

Type material is placed in the Los Angeles County Museum of Natural History (LACM), the Museum National d'Histoire Naturelle, Paris (NMNH), the National Museum of Natural History, Washington, D.C. (USNM), and the National Museum of New Zealand, Wellington (NMNZ).

TAXONOMY

Superfamily Lepetellacea

Limpets with horseshoe-shaped muscle, lacking juvenile coiling, or coiled with a single (left) shell muscle (Choristellidae only). With or without oral lappets and epipodial tentacles. Several secondary gill-leaflets (pallial and/or subpallial). Heart monotocardian. Two kidneys, the left one small or vestigial and usually connected with the pericardium, the right one larger and isolated. Limpet families hermaphroditic with separated, ventral testis, and dorsal ovary; right cephalic tentacle often serving as copulatory organ, never with copulatory verge proper; open or closed seminal groove at right neck; gonoduct(s) without glands. Statocysts with several or many cones. Rachidian tooth of radula well developed.

Pyropeltidae McLean & Haszprunar, fam. nov.

Because a single genus in this new family is presently known, the generic description and discussion serve for that of the family.

Pyropelta McLean & Haszprunar, gen. nov.

Type species: ***Pyropelta musaica*** sp. nov.

Diagnosis: Shell small for superfamily (maximum length 4.6 mm), white, periostracum unknown (probably worn off). Apex central, at highest elevation of shell. Protoconch and exterior sculpture eroded. Exterior surface of shell etched with irregular concentric lines reflecting uneven erosional pattern. Shell margin thin, fragile. Shell interior with pattern of concentric, wavy, alternating light and dark reflective areas, a pattern not corresponding to the exterior pattern of irregular concentric lines. Muscle scar closer to mid-point of shell than to margin; anterior tips of scar broadly inflated, tips projecting inward. Muscle scar continuous anteriorly with pallial attachment scar, which together with muscle scar makes a continuous oval scar. Surface central to scar areas thickened, opaque white. Interior muscle scar pattern visible externally through translucent shell.

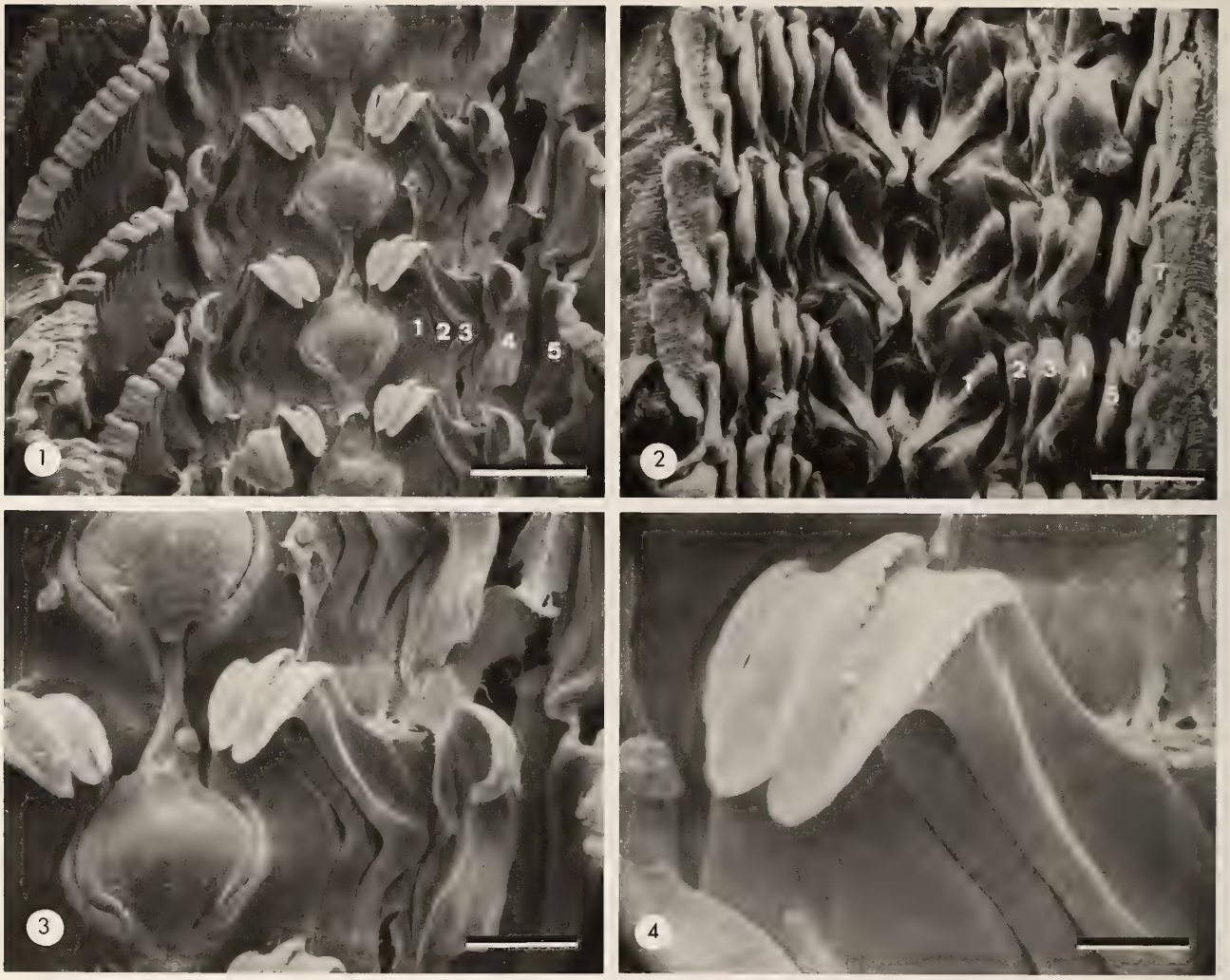
Radula. Rachidian tooth broad, with rounded lateral extremities, tapered base, and long, tapered neck, with small overhanging tip. Shaft and base of first lateral broad, inner edge excavated to accommodate base of rachidian, upper portion of shaft tapering to long overhanging cutting area. Second and third laterals largest, similar, each with pronounced elbow on outer side and deeply grooved upper arm of shaft for accommodation of adjacent teeth; cutting area long, serrated, tip rounded. Fourth lateral unlike first three, shaft broad, lacking elbow, its cutting area concavely arched and serrate on inner side. Fifth lateral similar to fourth in having broad shaft and undulating cutting edge, its tip with projecting cusps. Lateromarginal plate elongate (visible from basal side of ribbon), positioned between tooth rows. Marginal basal plate present; marginals numerous, not separated at base, first and second marginal not enlarged.

External anatomy. Oral disc broad, circular, lappets lacking; cephalic tentacles equal, like the mantle devoid of papillae. No subpallial glands. Foot with deeply contracted central area. Posterior pair of epipodial tentacles present. Gill tips especially prominent on right side; mantle skirt above neck thin. Right cephalic tentacle (copulatory organ) simple and solid; from its base an open seminal groove leads to the genital opening along right neck.

Internal anatomy. Two uninterrupted shell muscles forming a horseshoe-shaped organ, the left muscle slightly larger than right. Pedal gland small but distinct. Mantle cavity shallow, from left (in dorsal view) a distinct osphradium, pericardium, left kidney, anus, right excretory/genital opening, and genital gland. No hypobranchial gland. Secondary gill leaflets up to 18, at central and/or right pallial roof, continuing into right subpallial cavity. Gill leaflets respiratory and provided with sensory pockets. Heart monotocardian, pericardium large, ventricle posterior to auricle. Left kidney extremely small and vestigial (max. dimension 100 × 60 × 30 μm), isolated. Right kidney forms large coelomic system; fused with single and simply ciliated gonoduct immediately at common opening. Testis ventral, ovary dorsal, more posterior, separated, no accessory glands or vesicles along common gonoduct. Eggs large and yolk-rich, no allosperm observed. From excretory/genital opening a glandular open duct runs forwards to anterior end of right shell muscle, further continued by seminal groove. Jaws paired, consisting of toothlike elements. Sublingual cavity shallow, no subradular organ. Two pairs of cartilages, posterior pair smaller, radular diverticulum present. Salivary glands paired, pouchlike. Anterior oesophagus broad, with dorsal food channel and pouches. Folds of channel posteriorly fused during oesophageal torsion. Stomach with gastric shield and tooth, lacking protostyle, with paired mid-gut glands, the right enlarged anteriorly. Several intestinal loops, rectum penetrating ventricle. Nervous system streptoneurous, hypoathroid, with pedal ganglia (two commissures), visceral ganglia indistinct; a single (left) osphradial ganglion. No eyes or optic nerve; osphradial epithelium well developed; statocysts with several statocones.

Remarks: Two species are known, the type species from hydrothermal vents on the Juan de Fuca Ridge off Washington, and ***Pyropelta corymba*** from hydrothermal vents in the Guaymas Basin, Gulf of California. ***Pyropelta*** is the only hydrothermal vent limpet not known from either of the two sites on the East Pacific Rise (near 21 N and 13 N), where 14 limpet species are known from each site (McLean, 1985b).

Exterior surfaces of both species are eroded, but this is probably normal for the genus. It is compensated by thickening of the shell from within. Such erosion also takes place in other deep-sea habitats and is usual in many pseudococculinid species.



Explanation of Figures 1 to 4

Figures 1 to 4. SEM views of radula of ***Pyropelta musaica*** sp. nov. Lateral teeth numbered 1 through 5; 6 = lateromarginal plate; 7 = marginal basal plate.

Figure 1. Rachidian, laterals, and marginals. Bar = 20 μm.

Figure 2. Basal view, showing rachidian, laterals, lateromarginal plate, and marginal basal plate. Bar = 20 μm.

Figure 3. Rachidian and laterals. Bar = 10 μm.

Figure 4. Laterals 1, 2, and 3. Bar = 4 μm.

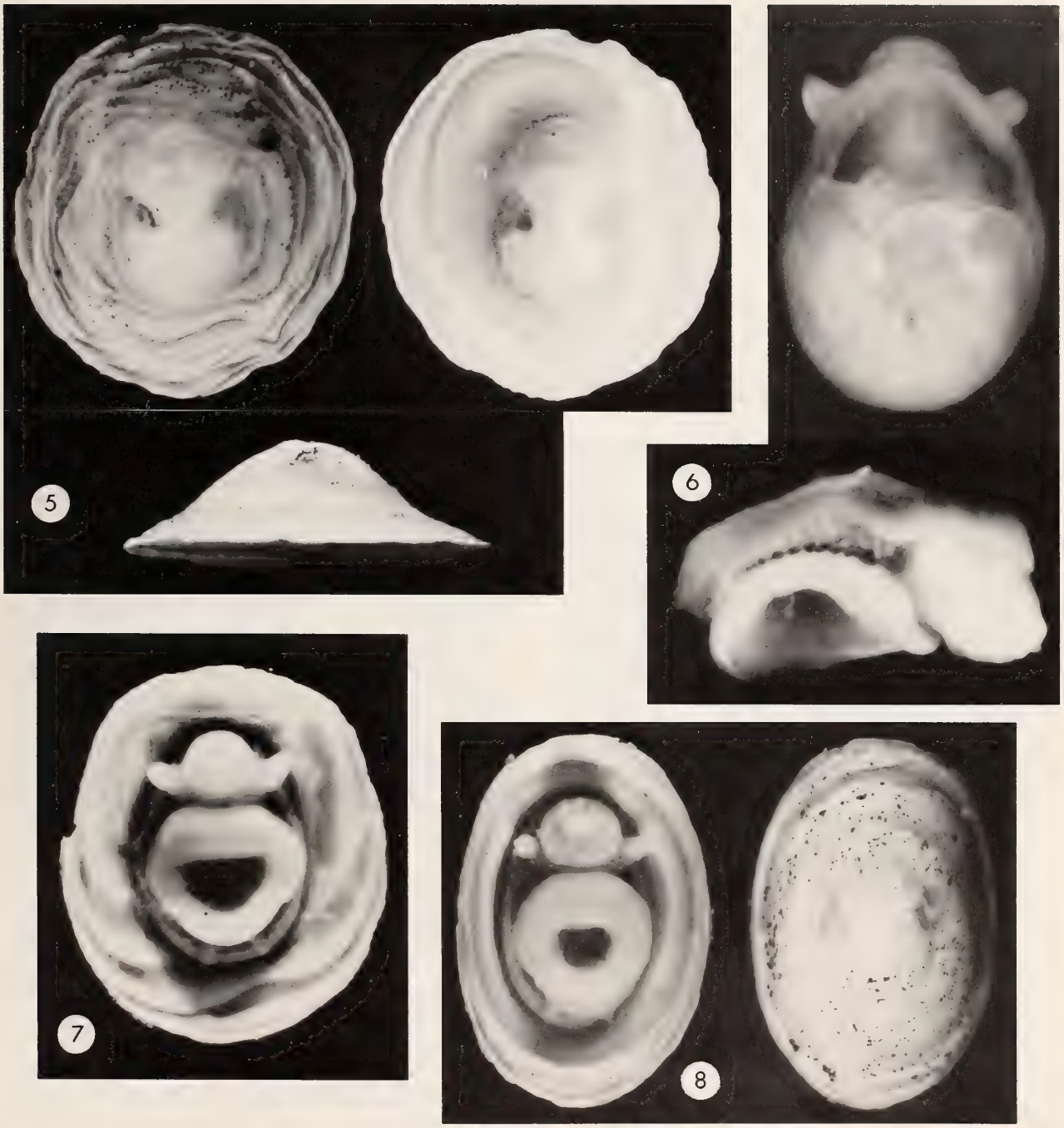
Pyropelta musaica McLean & Haszprunar, sp. nov.

(Figures 1–8, 9A)

Description: Shell (Figures 5, 7, 8) small (maximum length 4.6 mm), white, periostracum unknown (probably eroded). Height low to moderate, that of holotype 0.26 times length. Apex central, at highest elevation of shell. Protoconch and exterior sculpture entirely eroded. Exterior surface of shell etched with irregular concentric lines reflecting uneven erosional pattern. Shell margin thin, fragile; plane of aperture nearly flat in shells of oval outline; laterally compressed forms have ends raised relative to sides. Muscle scar pattern visible from exterior through translucent shell; muscle closer to mid-point of shell than to margin; anterior tips of scar broadly inflated, tips projecting inward. Shell interior with pattern of concentric, wavy, light and dark reflective areas, not corresponding to exterior pattern of irregular concentric lines. Shell thin and transparent enough to reveal the exterior pattern from inner side. Muscle scar of interior as described above, continuous anteriorly with pallial attachment scar, which together with muscle scar makes a continuous oval scar. Surface central to scar areas thickened, opaque white.

Dimensions. Length 3.0, width 2.7, height 1.0 mm (holotype).

Radula (Figures 1–4) described above under generic heading.



Explanation of Figures 5 to 8

Figures 5 to 8. ***Pyropelta musaica***.

Figure 5. Holotype. Exterior, interior (anterior at top), and lateral (left side) views of shell. Length 3.0 mm.

Figure 6. Holotype body out of shell, dorsal and lateral (right side) views, showing gill lamellae projecting on right. For orientation see Figure 9A. Length 1.9 mm.

Figure 7. Ventral view of paratype showing light and dark reflective areas of shell interior. Length 3.2 mm.

Figure 8. Ventral and dorsal views of paratype (laterally compressed form). Length 3.1 mm.

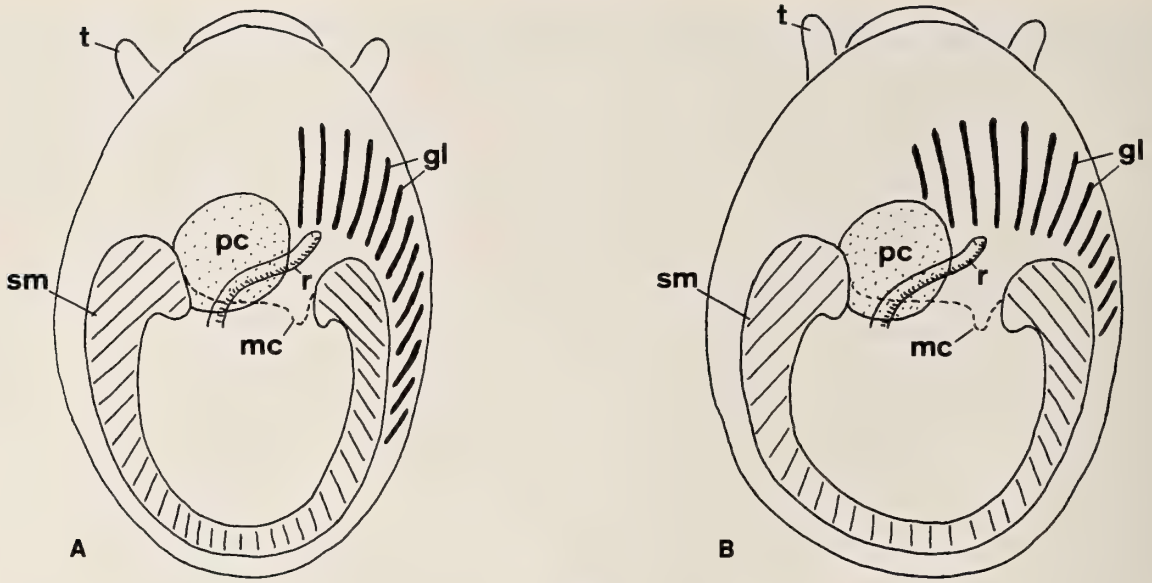


Figure 9

Comparison of arrangement of gill-leaflets in ***Pyropelta*** species. Dorsal view, schematic. A. ***P. musaica***. B. ***P. corymba***. Abbreviations: gl, gill leaflets; mc, posterior end of mantle cavity; pc, pericardium; r, rectum; sm, shell muscle.

External anatomy (Figures 6–8, 9A) described under generic heading.

Internal anatomy described under generic heading. For purposes of comparison with ***Pyropelta corymba***, the left kidney of ***P. musaica*** is extremely small (30 × 50 × 30 μm). Gill leaflets up to 25 μm long at right pallial roof, reaching posteriorly in right subpallial cavity up to two-thirds of body length (Figure 9A). Anterior edge of shell muscles not specialized.

Type locality: Axial Seamount, Juan de Fuca Ridge, off Washington (45°59.5′N, 130°03.5′W), 1575 m.

Type material: Holotype and paratypes from 6 *Pisces IV* dives, July–August 1986, depth and coordinates as above. Holotype from dive 1733, paratypes from following dives: 6 specimens, dive 1723, Hammond's Hell Vent, 19 July; 10 specimens, dive 1728, Southern Axial Vent, 29 July; 16 specimens, dive 1729, Anemone Ridge, 30 July; 8 specimens, dive 1730, Eastern Axial, 31 July; 1 specimen, dive 1731, Post Taylor's Vent, 1 August; 50 specimens, dive 1733, Not-so-miserable Vent, 3 August. Holotype, LACM 2275 (dive 1733); 65 paratypes LACM 2276; 10 paratypes USNM 784760, 10 paratypes MNHN; 5 paratypes NMNZ. Specimens from dive 1733 were sectioned.

Etymology: The name is Latin for *mosaic*, with reference to both the exterior erosional pattern and the interior banding pattern.

Remarks: In addition to radular differences, ***Pyropelta musaica*** may be distinguished from pseudococculinid species on its generic characters—the pattern of light and dark banding on the shell interior, and the lack of oral lappets. Although the shell is variable in height, the most elevated specimens are not as high as the single specimen of ***P. corymba*** sp. nov.

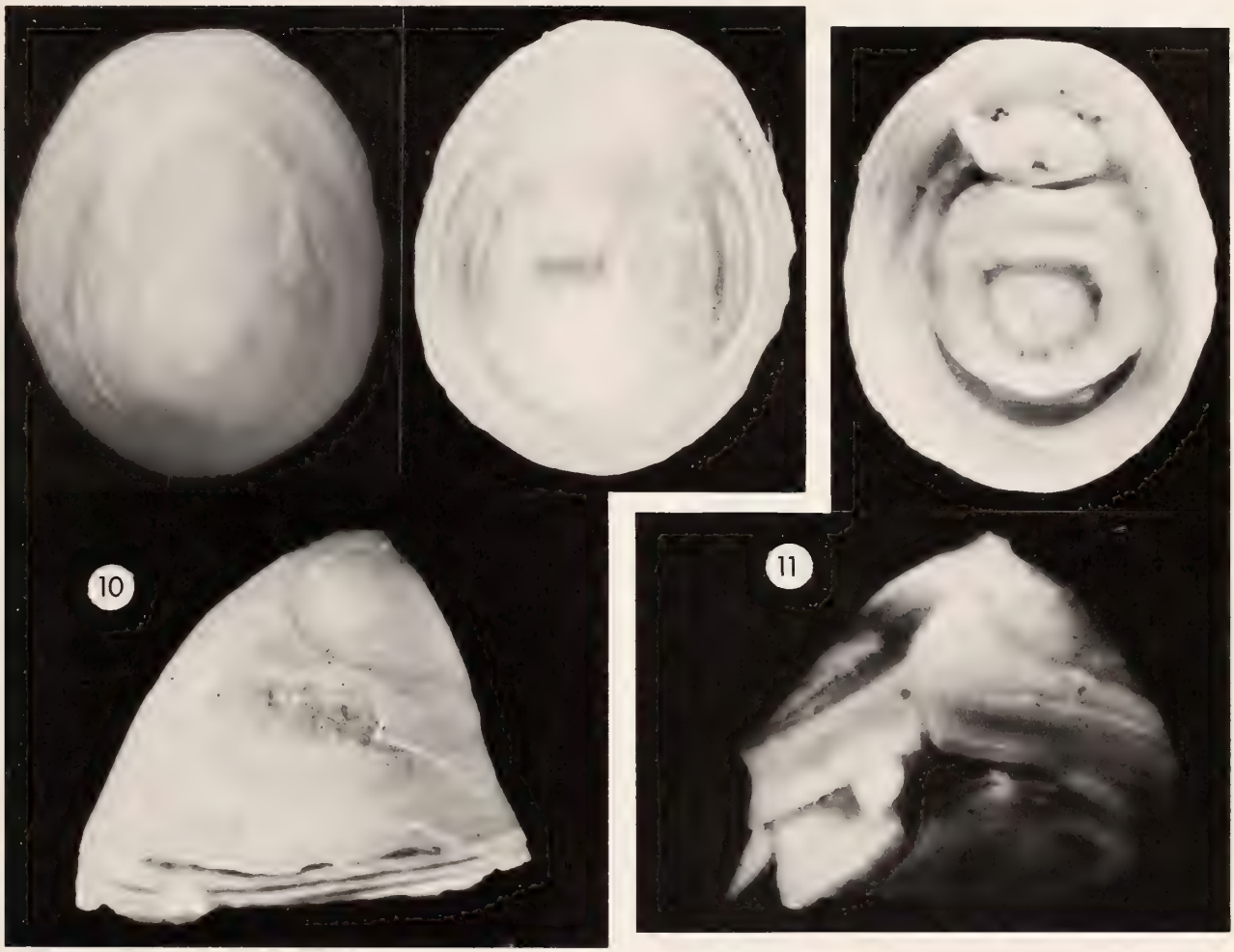
There is a considerable range of expression in apertural shape, ranging from broadly oval (Figure 5) to laterally compressed, with more elevated ends (Figure 8). Some shells, as for example the holotype (Figure 5), change during growth from somewhat compressed to lower and more oval. This range of variation in apertural shape suggests that individuals are adapted to a habitual site of attachment, which they may leave in foraging for food.

General descriptions of the biota at Axial Seamount (the type locality) are given by CHASE *et al.* (1985) and TUNNICLIFFE *et al.* (1985), although the existence of ***Pyropelta musaica*** is not mentioned, as it had not been collected prior to 1986. According to V. Tunnicliffe (personal communication), these limpets live "in the warm water vents and on surrounding rocks." They were apparently not collected directly from washings of the vestimentiferan tubes. The species has not been found at the Explorer Ridge farther to the north. One other much larger limpet (description by MCLEAN, in press) is common at all sites on the Juan de Fuca and Explorer ridges.

Pyropelta corymba McLean & Haszprunar, sp. nov.

(Figures 9B, 10, 11)

Description: Shell (Figure 10) small (maximum length 3.0 mm), white, periostracum lacking. Elevation extremely high, that of holotype 0.83 times length. Apex posterior,



Explanation of Figures 10 and 11

Figures 10 and 11. ***Pyropelta corymba*** sp. nov. Holotype.

Figure 10. Exterior, interior (anterior at top), and lateral (left side) views of shell. Length 3.0 mm.

Figure 11. Ventral (in shell) and lateral views of body (left side) prior to sectioning. For orientation see Figure 9B.

at highest point of shell, two-thirds shell length from anterior margin. Protoconch and exterior sculpture eroded, no evidence of sculpture on exterior surface. Exterior surface of shell etched with irregular concentric lines reflecting uneven erosional pattern. Shell margin thin, easily broken; plane of aperture with ends raised relative to sides. Shell interior with pattern of concentric, wavy alternating light and dark reflective areas, not corresponding to the exterior pattern of irregular concentric lines. Shell thin and transparent enough to reveal the exterior pattern from inner side. Muscle scar closer to mid-point of shell than to margin; anterior tips of scar broadly inflated, tips projecting inward, continuous anteriorly with pallial attachment scar, which together with muscle scar makes a continuous oval scar. Surface central to scar areas thickened, opaque white. Muscle scar pattern apparent on exterior of shell.

Dimensions. Length 3.0, width 2.5, height 2.5 mm (holotype).

Radula not available (specimen sectioned).

External anatomy (Figure 11) as described for the genus.

Internal anatomy as described for the genus. For comparison with ***Pyropelta musaica,*** the left kidney of ***P. corymba*** is larger (100 × 60 × 40 μm). Gill leaflets up to 60 μm long, extending from central pallial roof to the right, reaching posteriorly in right subpallial cavity up to one-half body length (Figure 9B). Anterior edge of shell muscles bordered by a strongly ciliated epithelial ridge.

Type locality: Southern trough of Guaymas Basin, Gulf of California, off Guaymas, Sonora, Mexico (27°01.0′N, 111°25.0′W), 2022 m.

Type material: 1 specimen from type locality, *Alvin* dive

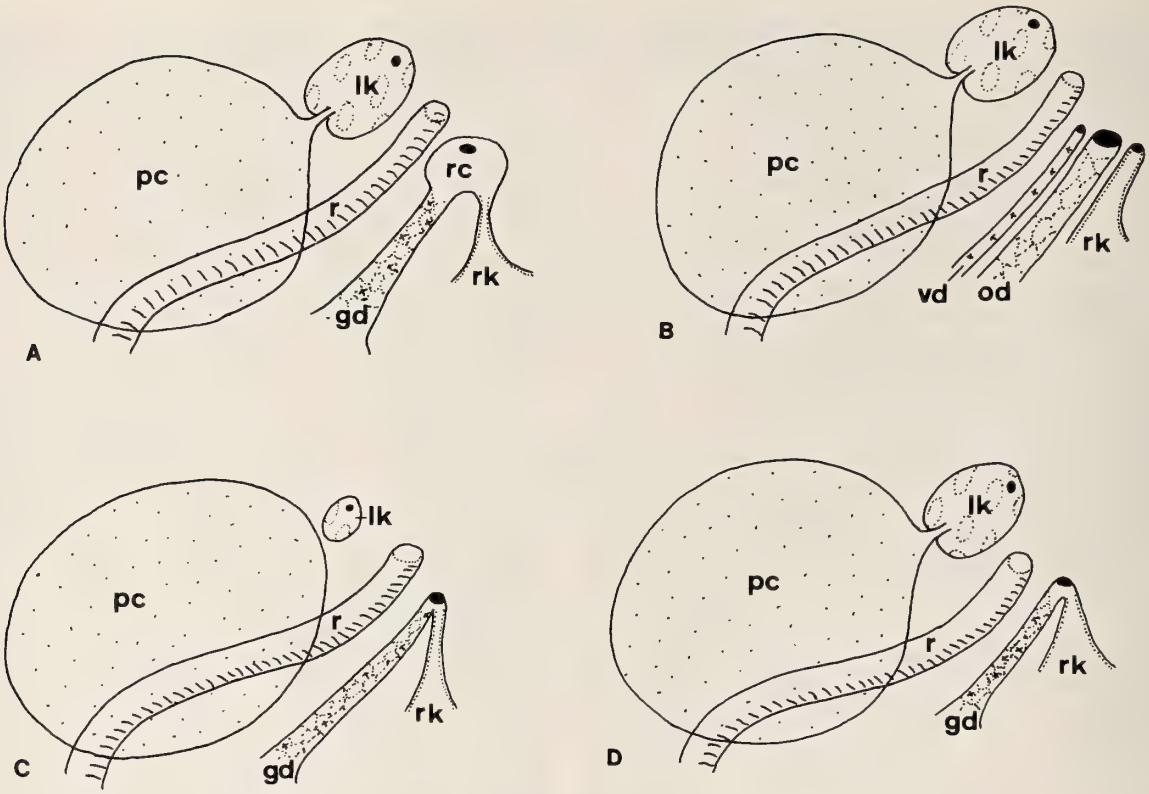


Figure 12

Comparison of coelomic systems of lepetellacean families. A. Lepetellidae. B. Osteopeltidae, Cocculinellidae, and Addisoniidae. C. Pyropeltidae. D. Pseudococculinidae. Abbreviations: gd, gonoduct; lk, left kidney; od, oviduct; pc, pericardium; r, rectum; rc, releasing chamber; rk, right kidney; vd, vas deferens.

1176, 19 January 1982. Holotype, LACM 2277. No other specimens are known. The body of the holotype has been sectioned.

Etymology: The name is derived from Greek, *corymbos,* peak, with reference to the high profile of the shell.

Remarks: The shell meets the generic criteria for ***Pyropelta*** in being relatively small, with exterior erosion as well as the interior pattern of alternating light and dark reflective areas. It differs from ***P. musaica*** in having a much higher profile and a more posterior apex. The left kidney is larger, the gill leaflets are longer, and the anterior edge of the shell muscle is bordered by a strongly ciliated epithelial ridge (unspecialized in ***P. musaica***).

Although the height of the single specimen places it well outside the range of variation noted in ***Pyropelta musaica***, it is impossible to tell in the absence of additional material whether this specimen represents the extreme or the norm.

One other limpet (described by McLean, in press) is known from the Guaymas Basin site. A general description of the hydrothermal site and its biota was given by Lonsdale (1984).

This species has previously been cited (McLean 1985b: 160, 162) under the vernacular name "Group-C, high-conical." There is no affinity to other Group-C limpets (terminology of Hickman, 1983) for which the descriptions are now in preparation by McLean, the anatomy under study by V. Fretter. The lack of cephalic lappets led to that assignment, but the radula and anatomy were not examined at that time.

DISCUSSION

Systematic Position

The shell and anatomy of ***Pyropelta*** fall well within the lepetellacean "bauplan" (see above definition of superfamily). Affinity is closest to the Pseudococculinidae and Osteopeltidae on the basis of similarities in the shell, radula, and gill leaflets. The erosional pattern of the shell and corresponding prominence of the muscle scar occurs in typical species of the Pseudococculinidae. Except for the lack of cephalic lappets and the lack of papillae on the cephalic tentacles and mantle margin (both also absent in *Osteopelta* Marshall, in press), the features of the external anatomy also agree with what is known of pseudococculinids.

The internal anatomy of ***Pyropelta*** also resembles that of the Pseudococculinidae. However, all characters in common are regarded as primitive (plesiomorphic) for the Lepetellacea (HASZPRUNAR, in press d), including the presence of sensory pockets at the efferent axes of the gill-leaflets (such pockets also occur in the Lepetellidae; unpublished observation of G.H. on three species in two genera).

Differences from the Pseudococculinidae are found especially in the excretory system. The Pseudococculinidae, as well as other lepetellacean families so far investigated, have a small, but distinct left kidney, which communicates with the pericardium (Figure 12D). In contrast, the left kidney of ***Pyropelta*** is extremely small, vestigial, and isolated (Figure 12C). This reduction resembles that of the Fissurellacea (ANDREWS, 1981, 1985). The reasons for these reductions are unknown in either family.

In contrast, the relation between the right kidney and the genital system is the same in ***Pyropelta*** and in the Pseudococculinidae. In both families the right kidney is fused with the genital duct immediately at the common opening (Figures 12C, D). The condition is more derived than that in the Lepetellidae, in which the distal portions of the right kidney and the distal genital duct form a releasing chamber that differs in histology from both organs (Figure 12A). The final condition among the Lepetellacea is represented by *Osteopelta* Marshall, in press, *Cocculinella* Thiele, 1909, and *Addisonia* Dall, 1882 (HASZPRUNAR, 1987, in press b, d). There the common gonoduct is separated into vas deferens and oviduct, and three independent openings exist (Figure 12B). Thus, ***Pyropelta*** and the Pseudococculinidae represent an intermediate state with respect to coelomic conditions. Similar trends (common distal releasing chamber or duct—common opening—separate openings, male and female ducts) also occur among the Bivalvia (MACKIE, 1984).

There are major differences between the radula of ***Pyropelta*** and that of pseudococculinids. ***Pyropelta*** agrees with the pseudococculinid plan in having a broadly inflated rachidian and the first lateral has the broad shaft and elbow characteristic of pseudococculinids. As in the Pseudococculinidae (and unlike the Cocculinidae), the lateromarginal plate and marginal basal plate are present. It differs from the general plan in having long overhanging cutting areas on the first three pairs of laterals. The fourth lateral of ***Pyropelta*** is an independent element that more closely resembles the fifth, outer lateral; in pseudococculinids the fourth lateral is similar to the second and third laterals and has a pronounced elbow. Marginal teeth of ***Pyropelta*** also differ; inner marginals, particularly the second pair, are not enlarged as in some pseudococculinids. In some pseudococculinid genera, the enlarged cusps of the second pair of marginals make them the largest and most potentially functional teeth; in ***Pyropelta,*** the three inner laterals are the most effective teeth in the row.

The osteopeltid radula differs from both the pseudococculinid and pyropeltid radula in lacking marginal basal plates (see MARSHALL, in press). As in the Pseudococculinidae, the osteopeltid radula has a massive fifth lateral. It is unique in having a massive first lateral.

The alimentary tract of ***Pyropelta*** strongly resembles that of the Pseudococculinidae, being primitive for the superfamily (HASZPRUNAR, in press c). The only difference is the presence of two mid-gut glands, whereas only one exists in the Pseudococculinidae. *Osteopelta* differs in its specialized buccal apparatus (a single pair of cartilages only) and in having distinct oesophageal glands instead of pouches.

Most features of the nervous system of ***Pyropelta,*** as well as the Pseudococculinidae, reflect primitive lepetellacean conditions, whereas *Osteopelta* has a concentrated cerebropedal ring (HASZPRUNAR, in press a). Like *Cocculinella* the pedal cords of ***Pyropelta*** are concentrated and represent true ganglia with only two commissures. As is typical for lepetellacean limpets, there is a single (left) osphradial ganglion. However, ***Pyropelta*** still has retained an osphradial epithelium, whereas the Pseudococculinidae generally lack it. Otherwise the sense organs (lack of eyes, a single posterior pair of epipodial tentacles, lack of subradular organ, statocysts with several statoconia) are typical for the Lepetellacea. The presence of oral lappets is regarded as primitive for cocculiniform limpets and for archaeogastropods in general (HASZPRUNAR, in press d). Among the Lepetellacea, these lappets are lost in certain Lepetellidae (MOSKALEV, 1978) and in the derived lepetellacean families Osteopeltidae, Cocculinellidae, and Addisoniidae (HASZPRUNAR, 1987, in press b, d).

Summing up, ***Pyropelta*** is obviously closely related to the Pseudococculinidae. However, the lack of cephalic lappets, and the absence of sensory papillae on the cephalic tentacles and mantle margin, the major differences in the radula, the vestigial left kidney, the existence of pedal ganglia, and a distinct osphradial epithelium warrant the recognition of the new family Pyropeltidae. Moreover, the condition of the right excretory/genital system places the family closest to the Pseudococculinidae (shell muscles solid, right kidney forming a large coelomic system), but at present it cannot be decided which family first split off. The Lepetellidae (still with muscle bundles, releasing chamber, small and compact right kidney) are clearly more primitive than both, whereas the remaining lepetellacean families Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae, with distinct oesophageal glands and completely separated gonoducts, are more highly derived than ***Pyropelta*** and the Pseudococculinidae (HASZPRUNAR, in press d). Thus, the sequential (*sensu* WILEY, 1981) arrangement of lepetellacean families is now as follows: Lepetellidae, Pseudococculinidae, Pyropeltidae, Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae; the poorly known Bathyphytophilidae may belong here. The Cocculinidae and Bathysciadiidae together comprise the Cocculinacea (HASZPRUNAR, in press a).

Biology and Evolutionary History

Pyropelta appears to be unique among cocculiniform limpets in living directly on a non-biological substrate—the sulfide crust deposits of deep-sea hydrothermal vents. Other cocculiniform limpets live and feed on such substrates as wood, cephalopod beaks, whale or fish bone, and elasmobranch egg cases. The hydrothermal-vent habitat has an abundant food source in the chemoautotrophic bacteria that proliferate on surfaces exposed to vent water. This food source would not require the specialization necessary for feeding on the harder substrates utilized by other members of the suborder, although such substrates may be weakened by bacterial activity.

It could be argued that the unspecialized feeding of ***Pyropelta*** reflects the basal biology of the Lepetellacea and Cocculinacea. This view is supported by the pyropeltid radula, which seems more primitive than that of the pseudococculinids in having functional lateral teeth (the long overhanging cutting edges, contrasting with the small, hook-shaped cutting edges of pseudococculinids) and unspecialized marginal teeth. Also, the remaining alimentary tract of ***Pyropelta*** is primitive for lepetellaceans, but this is less significant, considering that certain pseudococculinids with specialized feeding (*e.g., Tentaoculus neolithodicola* on carapaces of deep-sea stone crabs, MARSHALL, 1986) also have a primitive alimentary tract (HASZPRUNAR, in press c).

However, considering that Pseudococculinidae, the most primitive family of Lepetellacea, and Cocculinidae, the most primitive family of Cocculinacea, feed predominantly on wood, wood-feeding was probably basic to cocculiniform evolution (HASZPRUNAR, in press d). Moreover, the lack of oral lappets, a derived condition, favors the secondary nature of the feeding biology of ***Pyropelta***. Thus, it seems more likely that the hydrothermal-vent habitat and nourishment of ***Pyropelta*** are secondary for the Lepetellacea.

Although most other hydrothermal-vent limpets are probably descendents of shallow-water ancestors (MCLEAN, 1981, 1985b, in press), ***Pyropelta*** has its closest relatives, the Pseudococculinidae, among typically deep-water to abyssal forms. Of the other mollusks in this habitat, the turrid gastropods and most of the bivalves also are related to deep-water genera (TURNER *et al.*, 1985). The hydrothermal-vent habitat has evidently been invaded by different groups from different habitats at different times.

ACKNOWLEDGMENTS

We are grateful to those who entrusted the material of the new species to us for description: Verena Tunnicliffe of the University of Victoria, British Columbia, and Fred Grassle of Woods Hole Oceanographic Institution. Histologic sections were prepared by B. Ruthensteiner (Vienna). Photographs of the limpet bodies were made by LACM museum volunteer Bertram C. Draper. SEM micrographs of radulae were made at the Center for Electron Microscopy and Microanalysis at the University of Southern California, with the help of Clif Coney. Bruce Marshall of the National Museum of New Zealand made helpful comments on the manuscript.

LITERATURE CITED

ANDREWS, E. B. 1981. Osmoregulation and excretion in prosobranch gastropods. Part 2: Structure in relation to function. Jour. Moll. Studies 42:199–216.

ANDREWS, E. B. 1985. Structure and function in the excretory system of archaeogastropods and their significance in the evolution of gastropods. Phil. Trans. Royal Soc. Lond., ser. B, 310:383–406.

BOUCHET, P. & A. WARÉN. 1979. The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. Sarsia 64:212–243.

CHASE, R. L., J. R. DELANEY, J. L. KARSTEN, H. P. JOHNSON, S. K. JUNIPER, J. E. LUPTON, S. D. SCOTT, V. TUNNICLIFFE, S. R. HAMMOND & R. E. MCDUFF. 1985. Hydrothermal vents on an axis seamount of the Juan de Fuca Ridge. Nature 331:212–214.

HASZPRUNAR, G. 1987. The anatomy of *Addisonia* (Mollusca, Gastropoda). Zoomorphology 106:269–278.

HASZPRUNAR, G. In press a. Anatomy and affinities of cocculinid limpets (Mollusca, Archaeogastropoda). Zool. Scripta.

HASZPRUNAR, G. In press b. Anatomy and systematic position of the bone-feeding limpets, *Cocculinella minutissima* (Smith) and *Osteopelta mirabilis* Marshall, 1987. Jour. Moll. Stud.

HASZPRUNAR, G. In press c. Anatomy and affinities of pseudococculinid limpets (Mollusca, Archaeogastropoda). Zool. Scripta.

HASZPRUNAR, G. In press d. Comparative anatomy of cocculiniform gastropods and its bearing on archaeogastropod systematics. Proc. 9th Int. Malacol. Congr. Edinburgh 1986.

HICKMAN, C. S. 1983. Radular patterns, systematics, diversity, and ecology of deep-sea limpets. Veliger 26:73–92.

LONSDALE, P. 1984. Hot vents and hydrocarbon seeps in the Sea of Cortez. Pp. 21–24. *In:* P. R. Ryan (ed.), Deep-sea hot springs and cold seeps. Oceanus 7.

MACKIE, G. L. 1984. Bivalves. Pp. 351–418. *In:* A. S. Tompa, N. H. Verdonk & J. A. M. Van Den Biggelaar (eds.), The Mollusca. Vol. 7. Reproduction. Academic Press: New York.

MARSHALL, B. A. 1983. The family Cocculinellidae (Mollusca: Gastropoda) in New Zealand. Rec. Natl. Mus. New Zeal. 2(12):139–143.

MARSHALL, B. A. 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. New Zealand Jour. Zool. 12: 505–546.

MARSHALL, B. A. In press. Osteopeltidae (Mollusca: Gastropoda): a new family of limpets associated with whale bone in the deep-sea. Jour. Moll. Stud.

MCLEAN, J. H. 1981. The Galapagos Rift limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. Malacologia 21:291–336.

MCLEAN, J. H. 1985a. The archaeogastropod family Addisoniidae Dall, 1882: life habit and review of species. Veliger 28(1):99–108.

MCLEAN, J. H. 1985b. Preliminary report on the limpets at hydrothermal vents. Pp. 159–160. *In:* M. L. Jones (ed.),

The hydrothermal vents of the eastern Pacific: an overview. Bull. Biol. Soc. Wash. 6:159–166.

McLean, J. H. In press. New archaeogastropod limpets from hydrothermal vents, superfamily Lepetodrilacea. Part 1: Systematic descriptions. Phil. Trans. Royal Soc. Lond., ser. B.

Moskalev, L. I. 1971. New data on the systematic position of the gastropod molluscs of the order Cocculinida Thiele, 1908. Pp. 59–60. *In:* Molluscs, ways, methods and results of their investigation. Abstracts, Fourth Conference on the Investigation of Molluscs. Academy of Sciences of the USSR, Zoological Institute. Nauka, Leningrad [in Russian].

Moskalev, L. I. 1973. Pacific Ocean Bathysciadiiae (Gastropoda) and related forms. Zoological Journal 52(9):1279–1303 [in Russian].

Moskalev, L. I. 1976. On the generic classification in Cocculinidae (Gastropoda, Prosobranchia). Pp. 59–70. *In:* Z. A. Filatova (ed.), Deep water bottom fauna of the Pacific Ocean. Works of the P. P. Shirshov Institute of Oceanology, The Academy of Sciences of the USSR 99 [in Russian].

Moskalev, L. I. 1978. Lepetellidae (Gastropoda, Prosobranchia) and related forms. Pp. 132–146. *In:* The deep-sea bottom fauna of the subantarctic part of the Pacific Ocean. Akademiya Nauk SSSR, Trudy Instituta Okeanologii P. P. Shirshov 113 [in Russian].

Tunnicliffe, V., S. K. Juniper & M. E. De Burgh. 1985. The hydrothermal vent community on Axial Seamount, Juan de Fuca Ridge. Pp. 453–464. *In:* M. L. Jones (ed.), The hydrothermal vents of the eastern Pacific: an overview. Bull. Biol. Soc. Wash. 6.

Turner, R. D., R. A. Lutz & D. Jablonski. 1985. Modes of molluscan larval development at deep-sea hydrothermal vents. Pp. 167–184. *In:* M. L. Jones (ed.), The hydrothermal vents of the eastern Pacific: an overview. Bull. Biol. Soc. Wash. 6.

Wiley, E. O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. John Wiley: New York. xv + 439 pp.

The Veliger 30(2):206–210 (October 1, 1987)

THE VELIGER

NOTES, INFORMATION & NEWS

Fact or Artifact?

by
S. van der Spoel
Institute for Taxonomic Zoology,
University of Amsterdam,
Plantage Middenlaan 53,
Amsterdam, The Netherlands

The conclusion by GILMER (1986) that the minute, skinny, and aberrant developmental stages in pteropods described by the present author are artifacts is rejected. Though the function of the developmental stages in the life cycle of pteropods, their ecology, and phylogenetic development are not fully understood, such stages exist and can be distinguished on the basis of published data (see literature in GILMER, 1986). Furthermore, living aberrant stages have already been described (PAFORT-VAN IERSEL, 1985), all of which induces me to comment on Gilmer's conclusions (referring throughout to the 1986 paper). For most literature references I also refer to GILMER (1986).

In the abstract, Gilmer states (p. 48) that "inaccurate anatomical observations" were made with regard to developmental stages, but nowhere in his paper is an accurate anatomical observation given. The paper deals only with the external morphology and body weight of complete living or preserved animals.

The term "aberrant" is considered by Gilmer to cover also skinny and minute stages. However, I have always used these three as different terms: all forms that are aberrant are not aberrant "stages." Lumping the terms is enormously confusing, the more so because the skinny and minute stages are more related to each other than to the aberrant stage.

Gilmer states (p. 48) that aberrants are unknown from living specimens. However, they have been described from living specimens (PAFORT-VAN IERSEL, 1985; PAFORT-VAN IERSEL & VAN DER SPOEL, 1986), and the skinny or minute stages are even known as fossils (JANSSEN, 1985).

Gilmer states (p. 51) that I described in 1962 and 1967 food particles from the gut of aberrants; I did not. VAN DER SPOEL (1967) described food particles from juveniles and minute stages, but for the aberrant stages it is described (1962, 1967) that the gut is not completely developed and without food.

Gilmer states (p. 51) that predation or parasites may be responsible for the aberrant forms, but I have indicated that this is not the case (VAN DER SPOEL, 1967:183, 1973: 209).

More importantly, Gilmer studied the external morphology of living and preserved specimens, but nothing is said about their anatomy and histology. The anatomy and histology of minute, skinny, and aberrant stages was, however, fully described (literature in Gilmer) and they differ from the histology and anatomy of normal specimens. Gilmer gives no attention to this difference. Although fixation and preservation may alter external morphology and even the (always artificial) histological picture of tissues, they never alter anatomy, number of cells, types of organs, or configuration of muscles and ducts. I based the skinny, minute, and aberrant developmental stages on such structures.

Preservation affects normal and developmental stages in a probably comparable way, so it is sometimes impossible to tell from the external morphology of a specimen in which stage it is. Aberrants, skinnies, and minutes were originally described from preserved material and it is evident that they will have another appearance when alive (*cf.* GILMER, 1986:fig. 1c; PAFORT-VAN IERSEL & VAN DER SPOEL, 1986). Only thorough histological and anatomical study, not provided by Gilmer, can give an answer. Gilmer's criticisms made with regard to growth and shell formation in skinny and minute stages are correct. The mantle indeed has to be in contact with the shell to secrete it, and some preservation artifacts were probably misinterpreted by me; in living minute and skinny stages the mantle can reach the shell margin.

Gilmer's fig. 1a pictures a fully developed and living *Clio pyramidata,* whereas his fig. 1b shows a normal, preserved *C. pyramidata* not showing the glove-shaped body form of an aberrant stage. The specimen in fig. 1b is not, however, the same specimen as that in fig. 1a, although this is stated. The shell in 1b is broader than in 1a, which suggests that the two specimens may even have originated from different populations. Furthermore, the protoconch is preserved in the fig. 1b specimen after fixation, whereas it appears missing in the living specimens of fig. 1a. Thus it seems impossible that 1a and 1b are of the same specimen. These two pictures prove only that fixation alters body shape, a well known fact.

Gilmer's fig. 1c shows a young *Cuvierina columnella* with the caudal spine intact but without the closing septum below the teleoconch (this specimen should for this reason already be considered a skinny specimen). The body, except for the mantle gland, is extremely slender further indicating that this is a skinny stage. Fig. 1d represents a skinny specimen of *C. columnella* with all the characters of this stage; it is probably the same as that in fig. 1c. These two figures do not support Gilmer's ideas but rather my published data. With animals like those photographed more about shell formation in the skinny stage could have been studied.

Gilmer's fig. 1e shows a not yet full grown *Cavolinia tridentata.* Fig. 1f also shows a *C. tridentata* but not, as is stated, the same specimen as fig. 1e, judging from the

differences in the shape of the upper lip and lateral spines and the shell parameters. The specimen in fig. 1e is likely in a growth phase between the minute and adult stages, judging from shell development. However, only a histological study can prove if it is a minute or not; an external investigation is not sufficient here.

Finally, that a SCUBA diver does not easily encounter the skinny, minute and, especially, the aberrant stages in the relative small volume of water investigated is not astonishing. Such forms are only rarely found in museum material collected from millions of cubic meters of water.

Literature Cited

GILMER, R. W. 1986. Preservation artifacts and their effects on the study of euthecosomatous pteropod mollusks. Veliger 29(1):48–52.

JANSSEN, A. W. 1985. Evidence for the occurrence of a "skinny" or "minute stage" in the ontogenetical development of Miocene *Vaginella* (Gastropoda, Euthecosomata) from the North Sea and Aquitaine basins. Meded. Werkgr. Tert. Kwart. Geol. 21(4):193–204.

PAFORT-VAN IERSEL, T. 1985. A contribution to pelagic zoogeography of the mid North Atlantic Ocean. Doctoral Thesis, Univ. of Amsterdam. 185 pp.

PAFORT-VAN IERSEL & S. VAN DER SPOEL. 1986. Schizogamy in the planktonic opisthobranch *Clio*—a previously undescribed mode of reproduction in the molluscs. Intern. Jour. Reprod. Develop. 10:43–50.

VAN DER SPOEL, S. 1962. Aberrant forms of the genus *Clio* Linnaeus, 1767 with a review of the genus *Proclio* Hubendick, 1951. Beaufortia 9(107):173–200.

VAN DER SPOEL, S. 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda). J. Noorduyn & Zn: Gorinchem. 375 pp.

VAN DER SPOEL, S. 1973. Strobilation in a mollusc; the development of aberrant stages in *Clio pyramidata* Linnaeus, 1767 (Gastropoda, Pteropoda). Bijdr. Dierkunde 43(2):202–215, pls. 1, 2.

Response to "Fact or Artifact?" by S. van der Spoel

by
Ronald W. Gilmer
Department of Biology,
Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543, U.S.A.

In GILMER (1986) I presented results from a simple experiment using live thecosome pteropods, regardless of the collection method. Van der Spoel's objections that the fig. 1 photographs are not of the same individuals are not only wrong but beside the point, as the figures merely show results that are easily repeatable. For clarification, all photographs in fig. 1 of GILMER (1986) are as labeled. The animal in fig. 1a was swimming when photographed—it is a ventral view and is slightly tilted; fig. 1b (after preservation) is a dorsal view in a flat plane so that the protoconch is now apparent.

I consider van der Spoel's statement (in "Fact or Artifact?") that the mantle can reach the shell aperture in his "minute" and "skinny" stages an admission that he misrepresented in his published descriptions what he considers to be their live morphology. This is not a trivial admission as van der Spoel relied heavily on external morphology in establishing these stages. The contracted, contorted body and mantle are supposed to be major characteristics of live individuals. Indeed, the "skinny" and "minute" names of the stages are obviously taken from the external morphology of preserved specimens. I find no histological or anatomical evidence from van der Spoel's descriptions of these two stages that could not be due to fixation artifacts.

Recent studies on the aberrant stages of *Clio*, primarily by Pafort-van Iersel (cited in "Fact or Artifact?"), correctly show the need to separate this phenomenon from the "minute and skinny" controversy. The apparent morphological changes that occur in some specimens of this genus may represent the first documented case of molluscan reproduction via segmentation and splitting of the body. Further work is necessary to demonstrate clearly whether this remarkable phenomenon is not a collection artifact caused by trauma in the plankton net or not due to parasitic infection, to which this particular genus is often subjected (*e.g.*, PERKINS, 1983; GOTTO, 1986).

Literature Cited

GILMER, R. W. 1986. Preservation artifacts and their effects on the study of euthecosomatous pteropod mollusks. Veliger 29:49–52.

GOTTO, R. V. 1986. A new parasitic copepod crustacean of uncertain affinities: *Megallecto thirioti n. gen., n. sp.* Bull. Zool. Mus. Amsterdam 10:185–189.

PERKINS, P. S. 1983. The life history of *Cardiodectes medusaeus* (Wilson), a copepod parasite of lanternfishes (Myctophidae). Jour. Crust. Biol. 3:70–87.

California Malacozoological Society

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed 6 January 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger*. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); or Endowment Fund (the income from which is available; the principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C.M.S., Inc., are deductible by donors as provided in section 170 of the Internal Revenue

Code (for Federal income tax purposes). Bequests, legacies, gifts, and devises are deductible for Federal estate and gift tax purposes under sections 2055, 2106, and 2522 of the Code. Upon request, the Treasurer of the C.M.S., Inc., will issue suitable receipts which may be used by donors to substantiate their tax deductions.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on 23 September 1986, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 30 of *The Veliger*. For affiliate members of the Society, the subscription rate for Volume 30 will be US$25.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will be US$50.00, also now with postage to domestic addresses included. An additional US$3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. There is a one-time membership fee of US$2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription.

Send all business correspondence, including subscription orders, membership applications, payments for them, and changes of address to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Page Charges

Although we would like to publish papers without charge, high costs of publication require that we ask authors to defray a portion of the cost of publishing their papers in *The Veliger*. We wish, however, to avoid possible financial handicap to younger contributors, or others without financial means, and to have charges fall most heavily on those who can best afford them. Therefore, the following voluntary charges have been adopted by the Executive Board of the California Malacozoological Society: $30 per *printed* page for authors with grant or institutional support and $10 per page for authors who must pay from personal funds (2.5 manuscript pages produce about 1 printed page). In addition to page charges, authors of papers containing an extraordinary number of tables and figures should expect to be billed for these excess tables and figures at cost. It should be noted that even at the highest rate of $30 per page the Society is subsidizing well over half of the publication cost of a paper. However, authors for whom the regular page charges would present a financial handicap should so state in a letter accompanying the original manuscript. The letter will be considered an application to the Society for a grant to cover necessary publication costs.

We emphasize that these are *voluntary* page charges and that they are unrelated to acceptance or rejection of manuscripts for *The Veliger*. Acceptance is entirely on the basis of merit of the manuscript, and charges are to be paid *after* publication of the manuscript, if at all. Because these contributions are voluntary, they may be considered by authors as tax deductible donations to the Society. Such contributions are necessary, however, for the continued good financial health of the Society, and thus the continued publication of *The Veliger*.

Reprints

While it was hoped at the "*birth*" of *The Veliger* that a modest number of reprints could be supplied to authors free of charge, this has not yet become possible. Reprints are supplied to authors at cost, and requests for reprints should be addressed directly to the authors concerned. The Society does not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

Patronage Groups

Since the inception of *The Veliger* in 1958, many generous people, organizations, and institutions have given our journal substantial support in the form of monetary donations, either to *The Veliger* Endowment Fund, *The Veliger* Operating Fund, or to be used at our discretion. This help has been instrumental in maintaining the high quality of the journal, especially in view of the rapidly rising costs of production.

At a recent Executive Board Meeting, we felt we should find a way to give much-deserved recognition to those past and future donors who so evidently have our best interests at heart. At the same time, we wish to broaden the basis of financial support for *The Veliger,* and thus to serve our purpose of fostering malacological research and publication. Accordingly, it was decided to publicly honor our friends and donors. Henceforth, donors of $1000.00 or more will automatically become known as **Patrons** of *The Veliger,* donors of $500.00 or more will be known as **Sponsors** of *The Veliger,* and those giving $100.00 or more will become **Benefactors** of *The Veliger*. Lesser donations are also sincerely encouraged, and those donors will be known as **Friends** of *The Veliger*. To recognize continuing support from our benefactors, membership in a patronage category is cumulative, and donors will be listed at the highest applicable category. As a partial expression of our gratitude, the names only of donors in these different categories will be listed in a regular issue of the journal. Of course, we will honor the wishes of any donor who would like to remain anonymous. The Treasurer of the California Malacozoological Society will provide each donor of $10.00 or more with a receipt that may be used for tax purposes.

We thank all past and future donors for their truly helpful support and interest in the Society and *The Veliger*. Through that support, donors participate directly and im-

portantly in producing a journal of high quality, one of which we all can be proud.

Donations during 1986–1987

Friends

Dr. Mark Mitchell
Dr. Teuo Miyauti
Dr. J. T. Smith
Dr. Kikutaro Baba
Dr. Alan Bebbington
Dr. K. Ekawa
Mrs. Heidi Petersons
Dr. K. Masuda
Dr. Ellen Moore
Mrs. Gordon Neiswanger
Mr. George R. Plummer
Dr. Ralph T. Smith
Dr. Sakae O'Hara
Mr. Allan Fukuyama
Dr. Carol N. Hopper
A. & S. Miller
Dr. J. J. Landye
Dr. Art L. Metcalf
Dr. Seigoro Takahashi
Dr. Toshiaki Fuse
Dr. R. Tucker Abbott
Dr. E. A. Kay
Anonymous
Mr. John P. McQueen
Dr. Louella R. Saul
Dr. Earl Segal
Mr. Dale V. Stingley
Dr. David R. Lindberg

Benefactors—$100 or more

Mrs. Richard H. Hagemeyer
Dr. Cadet Hand
Dr. Druid Wilson
Dr. A. Richard Palmer
Dr. Frank A. Pitelka
Mr. William Pitt
Dr. Carole S. Hickman
Dr. Howard A. Bern
Dr. John S. Hensill
Dr. Joan Emily Steinberg

Patrons—$1000 or more

Dr. Harold W. Harry
Mrs. Jean M. Cate

Notes to Prospective Authors

The increasing use of computers to prepare manuscript copy prompts the following notes. We request that the right margin of submitted papers be prepared "ragged," that is, *not* justified. Although right-justified margins on printed copy sometimes look "neater," the irregular spacing that results between words makes the reviewer's, editor's, and printer's tasks more difficult and subject to error. Similarly, the automatic hyphenation capability of many machines makes for additional editorial work and potential confusion; it is best not to hyphenate words at the end of a line. Above all, manuscripts should be printed with a printer that yields unambiguous, high-quality copy. With some printers, especially some of the dot-matrix kinds, copy is generally difficult to read and, specifically, the letters "a, p, g, and q" are difficult to distinguish, especially when underlined as for scientific names; again, errors may result.

Other reminders are (1) that three copies of everything (figures, tables, and text) should be submitted to speed the review process, and (2) absolutely everything should be double-spaced, including tables, references, and figure legends.

Because *The Veliger* is an international journal, we occasionally receive inquiries as to whether papers in languages other than English are acceptable. Our policy is that manuscripts must be in English. In addition, authors whose first language is other than English should seek the assistance of a colleague who is fluent in English *before* submitting a manuscript.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date and not less than *six weeks* before our regular mailing dates. Send notification to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges:

change of address and re-mailing of a returned issue—$5.00.

Sale of C.M.S. Publications

All back *volumes* still in print, both paper-covered and cloth-bound, are available only through "The Shell Cabinet," 12991 Bristow Road, Nokesville, VA 22123. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Morgan Breeden at the above address.

Volumes 1 through 13, 24, 26, and 27 are out of print.

Supplements still available are: part 1 and part 2, supplement to Volume 3, and supplements to Volumes 7, 11, 14, 15, and 16; these can be purchased from "The Shell Cabinet" only. Copies of the supplement to Volume 17 ("Growth rates, depth preference and ecological succession

of some sessile marine invertebrates in Monterey Harbor" by E. C. Haderlie) may be obtained by applying to Dr. E. C. Haderlie, U.S. Naval Post-Graduate School, Monterey, CA 93940.

Some out-of-print editions of the publications of C.M.S. prior to Volume 26 are available as microfiche reproductions through Mr. Steven J. Long. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm, and can be supplied immediately. The following is a list of items now ready:

Volumes 1–6: $9.95 each.

Volumes 7–12: $12.95 each.

Supplement to Volume 6: $3.95; to Volume 18, $6.95. Send orders to Mr. Steven J. Long, Shells and Sea Life, 1701 Hyland, Bayside, CA 95524.

Single copies of back issues of *The Veliger* still in print are available *exclusively* from:

Conchylien Cabinet,
Grillparzerstrasse 22,
D-6200 Wiesbaden, BRD (West Germany).

The Veliger 30(2):211–212 (October 1, 1987)

THE VELIGER

BOOKS, PERIODICALS & PAMPHLETS

Living Terebras of the World

by Twila Bratcher & Walter Cernohorsky, edited by R. Tucker Abbott. 1987. American Malacologists, Inc.: Melbourne. 240 pp.; 68 pls. + 6 color pls. $54.00.

The systematics of the Terebridae (Neogastropoda) have been neglected far too long. The evolutionary relationships within the family remain mysterious; the last comprehensive review is nearly a century old. Terebrid ecology is also poorly known, despite excellent contributions by B. A. Miller (1975, *Pacific Science* 29:227–241; 1979, *Pacific Science* 33:289–306) and a few others. Bratcher & Cernohorsky's volume, although flawed, goes a long way toward summarizing our knowledge of the Terebridae and correcting two centuries of taxonomic miscues. They have collaborated to produce a valuable contribution to malacology, worthy of notice by collectors everywhere.

Bratcher & Cernohorsky's monograph opens with a brief review of the ecology and life history of terebrid gastropods. While not comprehensive, the authors do provide a useful layman's guide to these ubiquitous marine tropical snails. There is a brief, and unsatisfying, discussion of the status of the terebrid genera followed by the centerpiece of their efforts: a detailed review of each species. Every known terebrid species (268) is described and illustrated. Complete synonymies are provided for each species and, in most cases, type specimens are illustrated. The synonymies appear to be carefully compiled and should go a long way toward eliminating confusion surrounding terebrid nomenclature. The geographical range of each species together with available ecological information is included. The volume does not include a key to the identification of species, but species are grouped together by faunal province and with similar forms to allow quick comparisons. Also, the authors take reasonable care to identify characteristics useful for distinguishing similar species.

There is a brief discussion of the fossil record of the family but the taxonomy of forms known only as fossils is outside the scope of the present volume. Bratcher & Cernohorsky state that the earliest known terebrid is Eocene in age, a conclusion at variance with J. D. Taylor *et al.* (1980, *Palaeontology* 23:375–409) who indicate a Late Cretaceous (Maastrichtian) origin for the family. Bratcher & Cernohorsky make no reference to this work, leaving me to wonder whether they simply overlooked the earlier report or discount it for some unknown reason.

The most serious problem in this volume is the inadequate treatment of evolutionary relationships among terebrid species. The volume is arguably pre-darwinian. There is no discussion of, or reference to, evolution within the family. This might be acceptable in a guide for shell collectors, but not in a taxonomic monograph of an important clade of prosobranch gastropods. The terebrid genera (and the authors recognize four: *Terebra* Bruguière, 1789, *Hastula* H. & A. Adams, 1853 [including the subgenera *Hastula s.s.* and *Impagnes* E. A. Smith, 1873], *Duplicaria* Dall, 1908, and *Terenolla,* Iredale, 1929) are avowedly form genera, without evolutionary significance. The classification is entirely conchological. The genus *Terebra* is employed explicitly as a taxon of convenience for species lacking features characteristic of the other genera. These shortcomings are certainly not of the authors' making, and it is one that the authors certainly recognize, but one would hope to see this longstanding situation resolved or at least improved. The authors make no attempt to remedy the inadequacies in terebrid classification. They fail to introduce new information to establish meaningful evolutionary relationships. But these shortcomings might be one student's treasure trove: Bratcher & Cernohorsky have laid the groundwork for a excellent study of the evolutionary relationships of this diverse modern clade. The status of countless conchological species has been clarified and the next contribution can move on to include molecular, anatomical, shell microstructure or other evidence in a thorough phylogenetic analysis.

The authors are prone to pronouncing judgement without explanation or even acknowledging that different opinions might exist. For example, Rudman (1969, *Veliger* 12: 53–64) argued that fundamental anatomical differences exist between species of the genus *Pervicacia* and the Terebridae. He concluded that the differences indicated the genus was independently derived from a primitive toxoglossan ancestor. Rudman therefore proposed the family Pervicaciidae as a separate clade of the Toxoglossa. Bratcher & Cernohorsky list Rudman's family as a synonym of the Terebridae and synonymize *Pervicacia* with *Terebra* but offer no comment, discussion, or justification for these actions. From the text one would not surmise the existence of any doubt. In effect, they have casually rejected a legitimate (though not necessarily valid) hypothesis of phylogenetic relationships.

Another unfortunate problem with the book is that more than a few errors have crept into the text. Some are trivial and can be overlooked, such as occasional failures to italicize binomial names or depths given in odd units (the depth range of *Terebra albida* is given as "to 275 mm" [page 80]: either that depth range is *very* precisely established or else the range extends to 257 m). Others are more annoying, such as mixing up the numerical sequence of species' reference numbers for 11 species, so that the reader is referred to a particular species number for comparison but finds that number occupied by a different species. One wonders how many similar careless errors are to be found in the synonymies.

A separate shortcoming is the disappointing quality of the black and white plates. Too many illustrations are fuzzy, lack contrast, or are amateurishly prepared. The plates are not up to the standards set by other fine publications of American Malacologists. Nevertheless, collectors will certainly find the numerous illustrations useful in identifying their shells.

As with most books, one's estimation of the volume will follow from one's expectations. Bratcher & Cernohorsky have compiled a thorough review of the known terebrid species, together with detailed summaries of the nomenclatural histories of those species. Collectors and malacologists seeking to identify terebrids or to resolve synonymies will find the book to be of inestimable value. Others, who might seek the evolutionary relationships among the species of Terebridae or between the Terebridae and other toxoglossans (assuming the family is a true clade), will find the volume sadly wanting. The volume is a long overdue consolidation of our conchological knowledge of the Terebridae. We are now poised to move forward, using modern techniques and methods of phylogenetic analysis, to advance and test hypotheses about the taxonomic relationships of terebrid gastropods.

P. W. Signor

A Faunal Study of the Bivalves of San Felipe and Environs, Gulf of California, from the Gemmell Collection (1965 to 1976)

by Joyce Gemmell, Barbara W. Myers & Carole M. Hertz. 1987. San Diego Shell Club, *The Festivus* 18(Suppl.):72 pp., 79 text figs. (26 Feb. 1987). Available for $8.75 domestic postpaid, $9.25 overseas (surface mail) from the San Diego Shell Club, 3883 Mt. Blackburn Ave., San Diego, CA 92111.

This substantial paper is the culmination of several years of effort by these workers. This, like their earlier papers, is well illustrated by excellent line drawings, and their identifications are often based on study of type material. This is a significant work in the study of the marine bivalves of the eastern Pacific, continuing the long tradition of professional-level contributions by amateurs on the Pacific coast.

Gene Coan

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

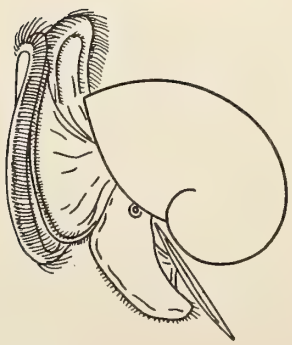
It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

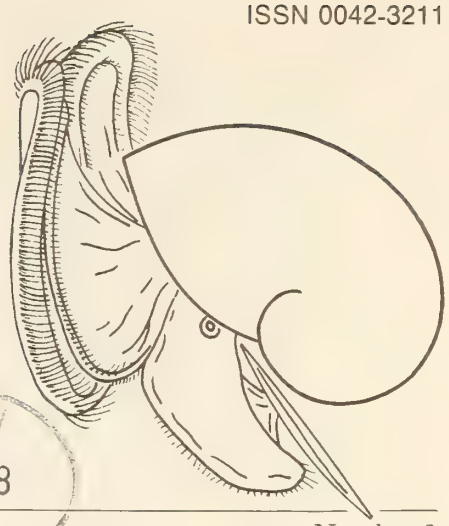
An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.



ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 30 January 4, 1988 Number 3

Contents

Contents — *Continued*

The Veliger (ISSN 0042-3211) is published quarterly on the first day of July, October, January and April. Rates for Volume 30 are $25.00 for affiliate members (*including* domestic mailing charges) and $50.00 for libraries and nonmembers (*including* domestic mailing charges). An additional $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Department of Zoology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Scope of the journal
The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

Membership and Subscription
Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. As an affiliate member, a person may subscribe to The Veliger for US $25.00 (Volume 30), which now *includes* mailing charges to domestic addresses. There is a one-time membership fee of US $2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription; a reinstatement fee of US $3.00 will be required if membership renewals do not reach the Society on or before April 1 preceding the start of the new Volume. If a receipt is required, a self-addressed, stamped envelope (or in the case of foreign members, the envelope and two International Postal Reply coupons) should be included with the membership or subscription request.

The annual subscription rate to The Veliger for libraries and nonmembers is US $50.00 (Volume 30), which now *includes* mailing charges to domestic addresses.

An additional US $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Memberships and subscriptions are by Volume only (July 1 to April 1) and are payable in advance to California Malacozoological Society, Inc. Single copies of an issue are US $25.00 plus postage.

Send all business correspondence, including subscription orders, membership applications, payments for them, changes of address, to: C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709, USA.

Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616, USA.

The Veliger 30(3):213–221 (January 4, 1988)

THE VELIGER

The Functional Morphology of Scaphopod Captacula

by

RONALD L. SHIMEK[1]

Bamfield Marine Station, Bamfield, British Columbia, Canada V0R 1B0

Abstract. Captacular functional morphology was examined in *Dentalium rectius, Cadulus aberrans,* and *Pulsellum salishorum* by examination of histological sections, scanning electron microscopy, and observation of living individuals. Subsidiary information was obtained from scanning electron microscopy of *C. tolmiei* and *D. pretiosum.* The captacular morphology of all these species is similar except for the ciliation and internal musculature of the captacular stalk. *Dentalium* species have a complete ciliated band running the length of the captacular stalk. *Cadulus* species have a sequence of ciliated tufts, and *Pulsellum* species have no stalk ciliation. *Dentalium* has 8–10 longitudinal captacular retractor muscles in the stalk, while the other genera have only six.

A captaculum is extended by the bulb cilia, which pull the captaculum out of the mantle cavity and through the sediment. The captacula likely adhere to prey by the action of a dual-gland adhesive system. At least two glandular secretions are released into the area of the pit that adheres to the prey. Contraction of the stalk longitudinal muscles pulls the captaculum within the mantle cavity.

Dentalium uses the complete stalk ciliation to collect small particulate matter in a manner analogous to terebellid polychaete tentacles. *Cadulus* can also do this, but only in some circumstances, while *Pulsellum* cannot feed in this manner.

These differences in captacular stalk ciliation are reflected in the variety of prey consumed, and lead directly to differential prey utilization and indirectly to differential habitat utilization by these species.

INTRODUCTION

Although widespread, scaphopods are poorly known. While common in deep water, shallow water representatives are seldom abundant enough for reliable collection and observation (Morton, 1959; Jones, 1964; Coan, 1964; Davis, 1968; Gainey, 1972; McFadien, 1973; Bilyard, 1974; Rokop, 1977; Scarabino, 1979; Carter, 1983). At least six species in three nominal genera are found in the shallow waters of Barkley Sound on the southwest side of Vancouver Island, British Columbia, and three species are common enough to be collected consistently, sometimes in great abundance.

Scaphopods have been called "the most homogeneous class of mollusks" (Morton, 1959). Within any sympatric assemblage of closely related organisms, behavioral or structural modifications resulting in differential resource utilization are likely to have arisen. In the course of an investigation of the ecological interactions of this particular scaphopod assemblage (Shimek, in preparation), I examined the functional morphology of scaphopod prey capture, manipulation, and feeding. Dietary resources are commonly partitioned in marine mollusks, particularly among benthic predators (Kohn, 1959; Kohn & Nybakken, 1975; Shimek, 1983a, b). Thus, differences in the means of prey capture and feeding are important, and fundamental, to the success and diversity of these groups.

Captacula, characteristic of scaphopods, are small, elongate, retractile tentacles originating lateral to the base of the buccal pouch or proboscis. Typically several hundred tentacles are found, but in smaller individuals, less than a hundred may be present (Morton, 1959) (Figure 1). Although they clearly function in prey capture and manipulation, the full range of captacular action in a normal situation has never been clearly documented (Morton, 1959; Dinamani, 1964; Gainey, 1972; Bilyard, 1974; Poon, 1987). This is due to the infaunal habitat of the animals, and the fact that, if disturbed, they may take several hours or days to resume normal behavior.

Captacula have been observed adherent to potential prey items (Morton, 1959; Gainey, 1972; Bilyard, 1974) and it has been presumed that they function to pull larger prey into the mantle cavity. Dinamani (1964) and Gainey (1972) have observed particulate transfer up the captacular stalk in *Dentalium,* and Poon (1987) documented a similar

[1] Present mailing address: P.O. Box 69793, Seattle, Washington 98168, U.S.A.

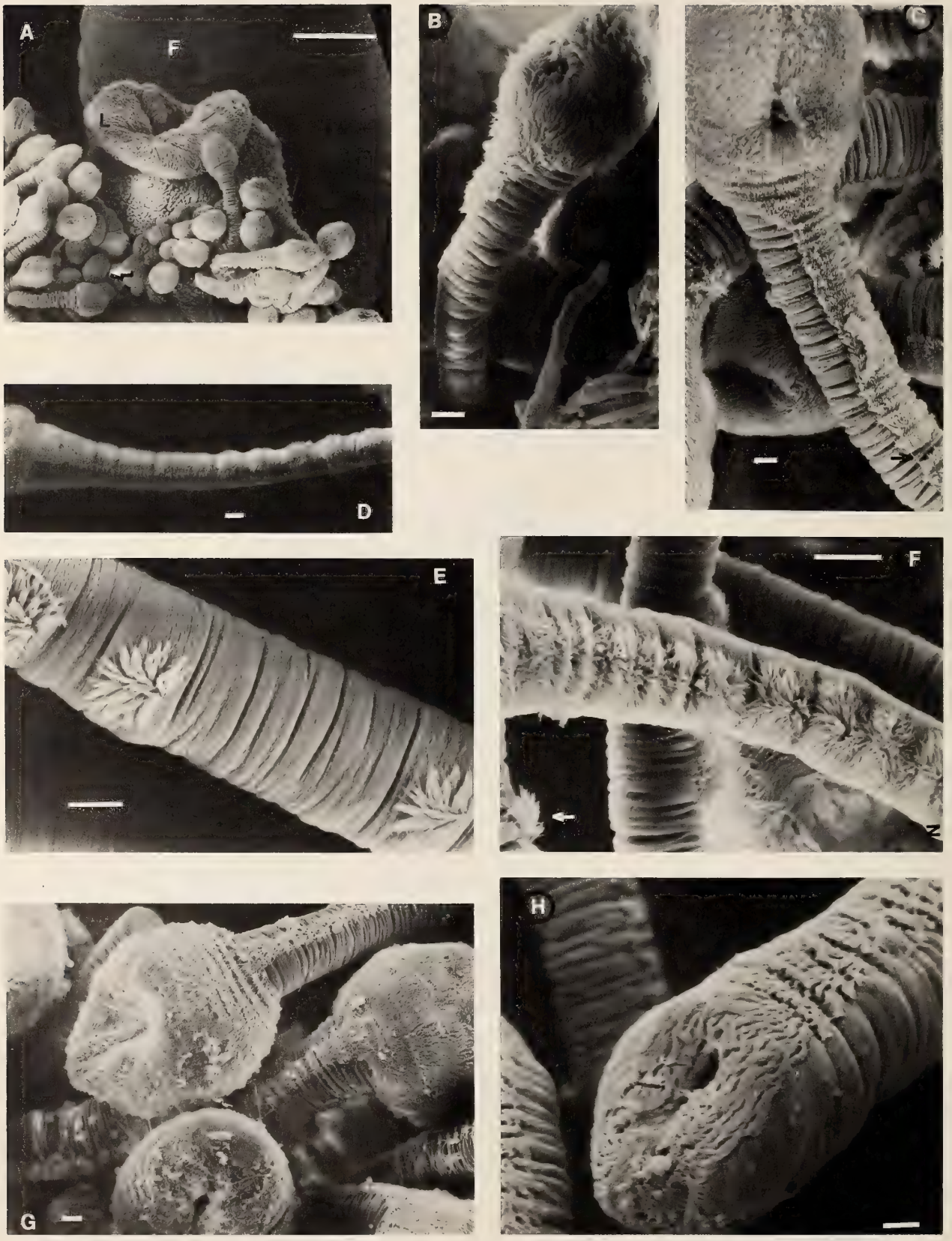

A
F
L
B
C
D
E
F
G
H

Table 1

Scaphopod collection sites, with depth, substrate type, and species collected.

Sites	Mayne Bay (48°58.7′N, 125°19.5′W)	Imperial Eagle Channel (48°52.7′N, 125°11.4′W)	Trevor Channel (48°49.7′N, 125°11.0′W)	Sarita Bay (48°53.5′N, 125°03.0′W)
Depth	35–40 m	75–80 m	30–110 m	120–200 m
Substrate type	silt	silt	sand	silt
Species collected	*Dentalium rectius*	*Dentalium rectius*	*Dentalium rectius*	*Dentalium rectius**
			*Dentalium pretiosum**	
	Pulsellum salishorum	*Pulsellum salishorum*	*Pulsellum salishorum*	*Pulsellum salishorum*
		*Cadulus aberrans**	*Cadulus aberrans*	
		*Cadulus tolmiei**	*Cadulus tolmiei**	*Cadulus tolmiei*

* Rare at this site.

process in *Cadulus tolmiei*. Although the anatomy of *Dentalium* captacula has been described (Morton, 1959; Fisher-Piette & Franc, 1968), the mechanism for either adherence to large particles or small particulate transfer has not been thoroughly investigated.

In the present study, I examined fixed captacula from individuals of *Dentalium rectius* Carpenter, 1864; *D. pretiosum* Sowerby, 1860; *Cadulus aberrans* Whiteaves, 1887; *C. tolmiei* Dall, 1897; *C. californicus* Pilsbry & Sharp, 1898; and *Pulsellum salishorum* Marshall, 1980. Furthermore, I examined captacular action in living specimens of *C. aberrans, D. rectius,* and *P. salishorum* with the objective of determining the mode of captacular function, and the variation in function and morphology between these species.

MATERIALS AND METHODS

Specimens were dredged from Barkley Sound (Table 1) and maintained in cooled seawater (≤5°C) until they were brought to the laboratory. Individuals to be examined alive were rinsed clean of sediment from the shell apertures and placed in a container of fresh sediment from their habitat. Failure to clean the apertures of sediment generally resulted in death, as the animals seemed incapable of removing the impacted sediment. Specimen containers had been modified with screens in the bottom to allow water circulation through the sediment; thus no anaerobic sediment developed. The containers were placed in sea tables in a flow-through seawater system. The ambient seawater temperature never exceeded 15°C.

Animals treated in this manner remained healthy, and could be maintained in the laboratory longer than three months. Allowing the animals to get warmer than 15°C, failure to clean the sediment out of the shell, or placing the animals in bowls with no water circulation resulted in high mortality or aberrant behavior.

Live animals were observed in a refrigerated room, at 10°C, using a Wild M-5 Stereo Microscope. These animals were placed in thin layers of sediment from their natural habitat or in transparent sediments. If the sediment depth was insufficient to allow the animals to maintain their normal "concave-side up" orientation, they were braced in that position by gluing them to glass microscope slides with a drop of cyanoacrylic glue. There was no mortality associated with this procedure and the animals could be subsequently detached from the slide. Animals observed at higher temperatures shed captacula, refused to feed or burrow, and became moribund.

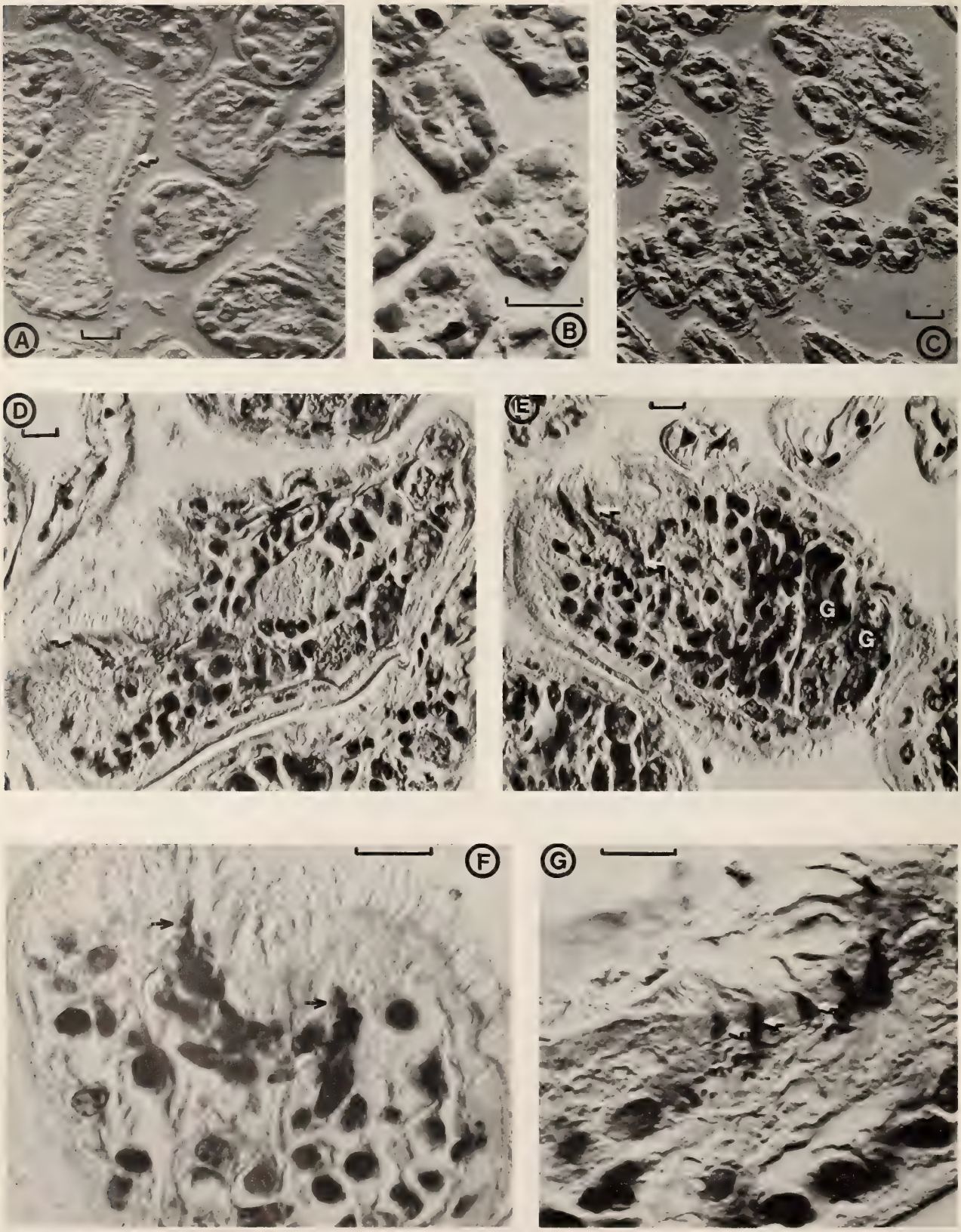
Transparent sediment was made using two methods. The first used sieved crystalline cryolite (Na_3AlF_6). Although this method initially appeared to be satisfactory, subsequent observations indicated cryolite was toxic, and caused captacular shedding, prolonged retraction, and death. Captacula were seldom shed when observed in a substrate of transparent seawater agar.

Transparent agar, made by boiling a 1% (by weight)

←

Figure 1

Scale bar = 100 μm in 1A, 10 μm in all others. A. *Pulsellum salishorum*. Dorsal view, shell and mantle removed. F, foot; L, proboscis lips. Arrow indicates an immature captaculum. B. *Pulsellum salishorum*. Single captaculum. Note ciliated bulb and, except for a small distal fringe, the lack of ciliation on the captacular stalk. C. *Cadulus tolmiei*. Single captaculum. Arrow indicates gap in ciliated band. Note the ciliated bulb and that the ciliated tract is completed distally. Compare with Figure 1F. D. *Cadulus aberrans*. Single captaculum. Note how the ciliated band on the stalk becomes incomplete and tufted proximally. E. *Cadulus aberrans*. Proximal captacular stalk. Note that the ciliary tufts are distinct. F. *Cadulus tolmiei*. Captacular stalks. Foreground stalk is distal and contracted; note how the ciliated tufts act to form a band. Arrow indicates an isolated ciliary tuft on an elongated captacular stalk. G. *Dentalium rectius*. Captacula. Note the complete band of cilia on the stalks. Metachronal ciliary beating is evident on the captacular bulbs. H. *Dentalium pretiosum*. Captaculum. Note the complete ciliary bands visible in the foreground and in the background.


A
B
C
D
E
G
G
F
G

suspension of agar in seawater for 1 h with distilled water added periodically to maintain the water level, was cooled, forced through a 250-μm screen, and allowed to settle to a depth of 1–3 cm in transparent containers. After these containers were carefully submerged in a sea table and a bacterial growth had developed, *Dentalium rectius* could be maintained in them for at least two months. If live foraminiferans were added to the vessels subsequent to the bacterial film development, *Cadulus aberrans* or *Pulsellum salishorum* could also be maintained, although for shorter periods.

Scaphopod behavior and captacular action could be observed in these containers if they were handled gently. When the animal was close to the substrate surface, captacular and foot movements in prey manipulation and capture were clearly visible.

Animals to be sectioned were brought to the laboratory, cleaned of sediment, placed in bowls of fresh seawater, and maintained at ≤10°C overnight. They were fixed and concurrently decalcified in Bouin's fluid made with seawater, dehydrated, imbedded in synthetic paraffin, and sectioned at either 8 or 15 μm. Various sections were stained either with a modification of Masson's triple stain (SHIMEK, 1975), or with hematoxylin and eosin.

For scanning electron microscopy, the animals were fixed for 1 h in phosphate-buffered 2.5% glutaraldehyde and post-fixed for 1 h in 2% osmium tetroxide buffered in sodium bicarbonate. The specimens were rinsed, dehydrated, and stored in 100% ethanol. The specimens were critical point dried, mounted on stubs, gold coated, and observed on a JEOL JSM-35 scanning electron microscope.

Voucher specimens of the following species have been deposited as the indicated lots in the Los Angeles County Museum of Natural History: *Dentalium rectius* no. 124485; *Pulsellum salishorum* no. 124486; and *Cadulus aberrans* no. 124487. Voucher specimens of *C. tolmiei* have been deposited in the mollusk collection of the U.S. National Museum of Natural History as lot no. 859073.

Buccal contents were obtained by dissection of the buccal pouches (proboscides) of animals fixed immediately upon collection, and stained with Rose Bengal, which allowed the determination of which prey had been alive when fixed (BILYARD, 1974). The buccal pouch contents were examined, and live organisms, or organism remains, were identified to the lowest possible systematic category. All other ingested items were identified as precisely as possible.

RESULTS

External Captacular Morphology

The basic captacular anatomy was similar in all the scaphopods examined. Although there were some differences in the relative dimensions of the captacula examined, they were small, and were likely due to the relative sizes of the animals examined, with larger animals having larger captacula. The captacula arose as slender stalks from a proliferative region on either side of the buccal pouch. Each mature captaculum terminated in a ciliated bulb, containing a pit, the alveolus of MORTON (1959), on one surface (Figure 1). The alveolus enlarges as the captaculum grows and lengthens. The terminal bulb was ovoid and ciliated on all surfaces, including the pit. These cilia, which beat metachronally and continuously (Figure 1G), extended the captacula out of the mantle cavity and through the substrate.

As the captacula extended, the captacular stalk muscles were relaxed and the stalk was stretched passively. In large (aperture width ≥ 2.0 mm) *Dentalium rectius*, the captacula often extended 6 mm, and occasionally I was able to measure them extended as far as 10 mm from the aperture.

The captacular stalk ciliation varied between the genera examined (Figure 1). The *Dentalium* species had a narrow, but complete ciliated tract running from the terminal bulb down the stalk to the base. Species of *Cadulus* lacked the complete tract, but had regularly spaced ciliated tufts, while *Pulsellum salishorum* lacked any stalk ciliation (Figure 1).

Internal Captacular Morphology

The captacular stalk was covered with a thin squamous epithelium. Below a narrow basement membrane were longitudinal muscles that shorten the stalk, retracting the captaculum. In *Dentalium* there were usually eight or more

←

Figure 2

Scale bar = 10 μm. All sections are 8 μm in thickness, and all have been photographed using Nomarski differential interference microscopy. A. *Dentalium rectius*. Captacular stalks. Arrow indicates a glancing longitudinal section; note helically arranged muscles in the captacular stalk. In the transverse sections of captacular stalk, note the thin squamous epithelium (the ciliary band is visible on most sections) and the 8–10 captacular stalk retractor muscles just below the epithelium. B. *Cadulus aberrans*. Captacular stalks. Transverse sections. Note only 6 longitudinal captacular stalk retractor muscles. C. *Pulsellum salishorum*. Captacular stalks. Transverse sections. Note only 6 longitudinal captacular stalk retractor muscles. D. *Dentalium rectius*. Captacular bulb. Near mid-sagittal section. Arrow indicates opening of basal glands. E. *Dentalium rectius*. Captacular bulb. Oblique frontal section. G, basal glands. Arrows indicate duct of basal glands. F. *Dentalium rectius*. Captacular bulb. Distal transverse section. Arrows indicate pit glandular areas not associated with the basal glands. G. *Dentalium rectius*. Captacular bulb. Lateral sagittal section in area of ciliary pit. Arrows indicate pit glands not associated with the basal glands.

muscle cells; in *Cadulus* and *Pulsellum* there were six (Figures 2A–C). Occasionally small cellular processes were seen in the stalk; these were likely nerves.

The captacular bulb contained at least two types of secretory cells. Typically two large globular cells, found near the proximal end of the bulb, contained a diffuse granular secretion. Careful examination of serial sections showed these cells emptied their products into the captacular pit through long ducts that terminated in the distal lateral margins of the pit (Figures 2D, E). Smaller, narrow cells adjacent to the pit also contained similar, although more intensely staining, secretory products. These cells also discharged into the pit lumen through ducts terminating in the bottom or sides of the pit (Figures 2F, G).

The longitudinal muscles of the captacular stalk were lacking in the bulb; however, oblique muscles were found just below the ciliated squamous epithelium. The musculature around the ciliated pit was diffuse; although muscle fibers did attach to the basement membrane in that region, they were few and slender (Figures 2D–F). Several other cell types were found in the bulb, and a faintly staining region corresponding to the ganglion described by Plate (1892, in Fisher-Piette & Franc, 1968) was present (Figure 2D).

Observed Captacular Function

The basic captacular functions were similar in the three genera. Active muscular contraction did not cause extension of the captacula. The captacula were extended by the action of cilia on the bulb, and retracted by muscular contraction in the stalk. When the bulb was about to adhere to some item, the bulb moved over it until the pit was positioned on the surface. The bulb flattened slightly bringing the pit into contact with the surface of the item. In most cases the pit was moved from place to place over the item until the captaculum stopped moving and abruptly fastened to it. Shortly thereafter the captaculum stalk contracted and the bulb was obviously adherent. There was no appreciable deformation of the bulb when adhesion occurred. Similarly, there was no noticeable change in shape if the bulb detached from the item.

The connection between the bulb and the object was strong; the active contraction of less than five captacula pulled a foraminiferan that was 100 μm in diameter free of the sediment, through the feeding cavity, and into the mantle cavity.

Captacula were often sloughed, particularly in stressed animals. Autotomized captacula were never seen to become adherent. Conversely, if they were autotomized after adhering to an object, they were not seen to release. Captacula appear to be regenerated easily, and in many sections and some scanning electron micrographs, immature captacula are recognizable (Figure 1A).

Captacula also manipulated food inside the mantle cavity. Small specimens of *Dentalium rectius, Cadulus aberrans,* and *Pulsellum salishorum* have transparent shells and mantles, and captacular action was easily observed within the mantle cavity. Food items were brought into the mantle cavity by contraction of adherent captacula, or by the action of the foot. In the latter cases, the foot would scoop the food item and some sediment into the mantle cavity using the dorsal depression (*Dentalium*), or sediment would adhere to the side of the foot (*Cadulus* or *Pulsellum*). In any event, no food item was taken directly to the mouth. Instead the item was manipulated and moved vigorously around within the mantle cavity. Most items brought into the mantle cavity were subsequently released by all captacula, and settled to the floor of the mantle cavity. These items were regularly ejected from the mantle cavity by a contraction of the foot, which expelled fluid and particulate matter from the mantle cavity.

Acceptable items were brought, by captacula, to the densely ciliated lips (Figure 1A) which engulfed them. Food was held within the buccal pouch for some time prior to being masticated by the radula. Although the amount of time food was held varied with the species and the animal's condition, most food items were ground up within 30 h (Shimek, in preparation).

Very fine sediment particles were also eaten (Table 2). *Dentalium rectius* commonly collected sediment by moving fine particles up the ciliated captacular stalk. Sediment composed a substantially smaller dietary component of the other genera (Table 2). Once sediment was moved into the mantle cavity, it was collected and manipulated by the captacular bulbs in a manner similar to the manipulation of larger particulate material. Eventually a sediment bolus was formed, passed to the mouth, and ingested.

Sediment was also collected by adhesion to the captacular bulb ciliated pit in *Pulsellum* and *Cadulus,* although I never saw this mode of collection used by *Dentalium.* When sediment was collected this way, it was drawn within the mantle cavity by captacular contraction.

Captacula moved freely through all parts of the mantle cavity, and were even seen extending from the dorsal aperture. They appeared to collect mucus and perhaps adherent particulate material from the ciliated ridges on the lateral mantle wall. The fate of this collected material was unclear.

DISCUSSION

The captacula are the major food-collection organs of scaphopods. Although particulate food may sometimes be brought into the mantle cavity by direct action of the foot, particularly in the dentalioids, this is a relatively rare event (Shimek, in preparation).

Morton's (1959) hypothesis of hydrostatic extension of the captacula is clearly incorrect. The extension is entirely due to the ciliated bulb, which moves in a manner not unlike that of a ciliated protozoan. Captacula are slender and their haemocoelic cavities are narrow; thus, the fluid resistance within the stalk would be correspondingly high. It is quite unlikely that muscular contractions around

Table 2

Summary of buccal content information on three species of scaphopods at three sites.

Species:	*Dentalium rectius*	*Dentalium rectius*	*Dentalium rectius*	*Cadulus aberrans*	*Pulsellum salishorum*	*Pulsellum salishorum*	*Pulsellum salishorum*
Collection site:	Mayne Bay	Imperial Eagle Ch.	Trevor Channel	Trevor Channel	Mayne Bay	Imperial Eagle Ch.	Trevor Channel
Total number examined	84	68	76	87	43	38	68
Number with buccal contents	55	47	44	86	25	24	53
Proportion feeding	0.655	0.691	0.579	0.989	0.581	0.632	0.779
Buccal contents proportion							
Sediment bolus	0.163	0.145	0.203	<0.001	0.054	0.037	0.008
Mineral grains	0.027	0.073	0.093	0.012	0.027	0.085	0.065
Fecal pellets	0.076	0.081	0.027		0.027		
Arthropod eggs	0.120	0.097	0.050		0.027		
Other	0.079	0.144	0.051	0.005		0.012	
Total non-foram.	0.465	0.540	0.424	0.017	0.135	0.134	0.073
Foraminiferans							
Live	0.394	0.290	0.429	0.761	0.595	0.561	0.674
Dead (tests only)	0.095	0.089	0.066	0.087	0.072	0.061	0.065
Test fragments	0.046	0.081	0.082	0.139	0.225	0.244	0.181
Number of items	368	124	182	2500	111	82	368

any portion of the haemocoel could result in appreciable or even noticeable extension of a captaculum.

Captacular bulb adhesion in scaphopods was proposed to occur as a muscular suction cup (MORTON, 1959). Active muscular suction is unlikely for several reasons. First, when adhesion of a bulb to a prey item occurs, and then that captaculum is shed, the bulb remains adherent to the item. Secondly, during adhesion no bulb deformation occurs. The muscular contraction necessary for active suction adhesion would certainly deform the bulb's opposite side as well as the pit, and would relax, causing detachment upon shedding of the captaculum. Thirdly, the bulb, including the pit, is covered with a dense ciliary layer. An active ciliary covering would seem to preclude the necessary seal for suction to occur unless substantial mucous secretions are involved. There are no indications of any such secretions (Figure 1). Finally, sections of the bulb indicate relatively few muscles. It seems unlikely these few muscles could maintain the suction necessary to pull the relatively bulky prey through sediment.

A more plausible hypothesis involves the action of a dual-gland adhesive system (HERMANS, 1983). The large glands at the base of the bulbs with their relatively diffuse secretions, and the small glands with dense secretory granules near the pit, both empty into the bulb pit or its edges. These two glands correspond well, in gross structure, to descriptions of the dual-gland adhesive systems now seen in several invertebrate taxa (HERMANS, 1983). If these secretions were under neural control, it would explain why shed captacula do not detach from adherent items or tightly adhere to any item. Furthermore, the lack of captacular deformation is explained by this hypothesis. Finally, while some muscularity of the bulb is necessary to allow deformation and ease of movement through sediment interstices, the large active muscles needed to form an active suction cup are lacking. The lack of such a muscular component is easily explained by the hypothesis of a dual-gland adhesive system.

The pit in the captacular bulb is the place of adhesion, and is likely the major sensory area of the captacular bulb as well. It appears as if, prior to adhesion, the pit area is the site of prey item assessment.

In my histological sections a pale, faintly staining region corresponding in location to the described nerve ganglion can be demonstrated, and these cells may be neural in origin. Ultrastructural examination should confirm the presence of such a ganglion, and the associated sensory neurons.

Although the muscular component of the captacular bulb is weak and diffuse, that of the captacular stalk is large and evident. Either 6, in *Cadulus* or *Pulsellum*, or 8–10, in *Dentalium rectius*, longitudinal smooth muscle cells were found surrounding the captacular stalk lumen. *Dentalium entalis* is described as having 10 longitudinal muscles (MORTON, 1959). The cells are staggered along the length of the stalk, and are helically arranged (Figure 1A). Muscular contraction results in the shortening of the extended stalk and rapid retraction of the unattached captacula. The presence of six longitudinal muscles in the representatives of the Siphodentalioidea and more than six in the Dentalioidea may be of use as a systematic character; however, more representatives in both orders should be examined. The functional significance of such a difference is unclear.

Sediment has been seen moving on the captacular stalk in both *Dentalium* and *Cadulus* (DINAMANI, 1964; GAINEY, 1972; POON, 1987; Shimek, present study); however, the mechanism for this movement was not previously clearly described. In *D. rectius* the ciliated captacular stalk allows a substantial amount of sediment to be collected. A similar ciliated tract has been reported for *D. entalis* by Fol (1889, in MORTON, 1959), although Morton could not demonstrate it. In light of the presence of such a band on the captacula of the two *Dentalium* species examined here, the lack of noticeable ciliation in Morton's sections is likely due to a fixation artifact. This feeding mode is common in *D. rectius* from Barkley Sound. Sediment is a major dietary component, particularly in small animals (total length $\leq$ 10 mm), where more than 75% of the hindgut contents is sediment. *Dentalium rectius* seldom grinds foraminiferan or other particulate prey beyond recognition, and consequently the amount of sediment ingested can easily be assessed. Most, if not all, of this sediment is collected by the captacular stalk ciliation.

Although the captacular stalk ciliation has been seen to move particles into the mantle cavity in one *Cadulus* species (POON, 1987), it is unclear under what conditions this is an important process. The tufted stalk ciliation found in *Cadulus* may be unable to move much sediment if the stalk is maximally extended. POON (1987) examined *C. tolmiei*, which lives in silty habitats. My data indicate that while *C. aberrans*, which lives in relatively clean sand, does occasionally eat sediment, it is much more realistically termed a foraminiferan dietary specialist. Perhaps the tufted stalk ciliation pattern is important for sediment collection only in those species common in fine sediment.

Pulsellum salishorum is unable to move any particulate matter in this manner, as it lacks stalk ciliation altogether. This species specializes upon foraminiferans, although sediment is also occasionally found in the diet. This sediment is likely collected only in the captacular pit or by the foot.

The differences in the captacular structure are reflected in the diets of the species examined, and serve to explain some of the dietary differences. *Dentalium rectius* can collect sediment regardless of its habitat owing to the possession of a complete ciliated tract on the stalk of the captacula. *Cadulus* species appear to be able to transport some sediment into the mantle cavity using their tufted stalk ciliation, but this feeding mode is important only in *C. tolmiei*, which lives in sediment dominated by silt-clay; *C. aberrans*, found in sand, eats virtually no sediment. Finally, *Pulsellum salishorum*, which has no ciliation on the captacular stalk, ingests small quantities of sediment in all habitats. This sediment is brought into the mantle cavity either by adhesion to the bulb pit or the foot.

Thus, the specialization of *Cadulus aberrans* upon fo-

raminiferan prey is due, at least in part, to captacular structure. In the habitat where this species is common, foraminiferan prey can be collected by the captacula. Mineral grains in this habitat are too large to be transported by tufted ciliation, and fine sediment particles may be too infrequent to be effectively collected by pit adhesion. *Pulsellum salishorum,* from the same habitat as *C. aberrans,* collects substantially less fine sediment to be formed into boluses than it does in either of its other habitats (Table 2). All sediment collected by this species must be collected by bulb adhesion or by the foot. Fine sediment may be too uncommon in the well-sorted sand of the Trevor Channel site to be efficiently collected by any but the completely ciliated tract of *Dentalium rectius.* Thus, although all scaphopods appear to be able to utilize their captacula for the collection of relatively large particulate prey such as foraminiferans, small bivalves, or kinorhynchs, only one genus has the ability to efficiently collect large amounts of small, silt-clay sized, sediment particles. This ability appears to give *D. rectius* a functionally defined competitive advantage over the foraminiferan predators such as *C. aberrans* in habitats with a large silt-clay fraction and small numbers of foraminiferans, and undoubtedly contributes to the widespread distribution of this common species.

ACKNOWLEDGMENTS

This study was supported in large part by the Bamfield Marine Station. Additional financial support came from the Pacific Northwest Shell Club, and the University of Washington Friday Harbor Laboratories. The scanning electron microscopy was done at the Biology Department, University of Victoria, Victoria, B.C. I thank the Directors of the Bamfield Marine Station and the University of Washington Friday Harbor Laboratories for the permission to use those facilities. Dr. D. A. Thomson of the University of Arizona generously allowed the use of his laboratory during a portion of this study. I thank the following individuals for assistance: A. Bergey, J. Dietrich, J. Elliott, R. Fredrickson, J. Glazier, S. Leader, S. Rumrill, C. Singla, S. Tveit, and R. Warren.

LITERATURE CITED

Bilyard, G. R. 1974. The feeding habits and ecology of *Dentalium entale stimpsoni* Henderson (Mollusca: Scaphopoda). Veliger 17:126–138.

Carter, M. S. 1983. Interrelation of shell form, soft part anatomy and ecology in the Siphonodentalioida (Mollusca, Scaphopoda) of the northwest Atlantic continental shelf and slope. Ph.D. Thesis, University of Delaware, Lewes, Delaware. xvi + 214 pp.

Coan, E. 1964. The Mollusca of the Santa Barbara County area. Part I. Pelecypoda and Scaphopoda. Veliger 7:29–33.

Davis, J. D. 1968. A note on the behavior of the scaphopod, *Cadulus quadridentatus* (Dall) 1881. Proc. Malacol. Soc. Lond. 38:135–138.

Dinamani, P. 1964. Feeding in *Dentalium conspicuum.* Proc. Malacol. Soc. Lond. 36:1–5.

Fisher-Piette, E. & A. Franc. 1968. Classe des Scaphopodes. *In:* P. P. Grasse (ed.), Traite de zoologie: anatomie, systematique, biologie. Mollusques, Gasteropodes et Scaphopodes. Tome 5:Fasc. III:987–1017.

Gainey, L. F., Jr. 1972. The use of the foot and the captacula in the feeding in *Dentalium.* Veliger 15:29–34.

Hermans, C. O. 1983. The duo-gland adhesive system. Oceanogr. Mar. Biol. Ann. Rev. 21:283–339.

Jones, G. F. 1964. The distribution and abundance of subtidal benthic Mollusca on the mainland shelf of southern California. Malacologia 2:43–68.

Kohn, A. J. 1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. 29:47–90.

Kohn, A. J. & J. W. Nybakken. 1975. Ecology of *Conus* on eastern Indian Ocean fringing reefs: diversity of species and resource utilization. Mar. Biol. 29:211–234.

McFadien, M. S. 1973. Zoogeography and ecology of seven species of Panamic-Pacific scaphopods. Veliger 15:340–347.

Morton, J. E. 1959. The habits and feeding organs of *Dentalium entalis.* Jour. Mar. Biol. Assoc. U.K. 38:225–238.

Poon, P. 1987. The diet and feeding behavior of *Cadulus tolmiei* Dall, 1897 (Scaphopoda, Siphonodentalioida). Nautilus 101: 88–92.

Rokop, F. J. 1977. Seasonal reproduction of the brachiopod *Frieleia halli* and the scaphopod *Cadulus californicus* at bathyl depths in the deep sea. Mar. Biol. 43:237–246.

Scarabino, V. 1979. Les scaphopodes bathaux et abyssayx de l'Atlantique occidental (Systematique, distributions, adaptations). Nouvelle classification pour l'ensemble de la classe. Doctoral Thesis, Universite d'Aix-Marseille II. U. E. R. des Sciences de la Mer et de l'Enveronment. 154 pp.

Shimek, R. L. 1975. The morphology of the buccal apparatus of *Oenopota levidensis* (Gastropoda, Turridae). Z. Morph. Tiere. 80:59–96.

Shimek, R. L. 1983a. Biology of the northeastern Pacific Turridae. I. *Ophiodermella.* Malacologia 23:281–312.

Shimek, R. L. 1983b. The biology of the northeastern Pacific Turridae. II. *Oenopota.* Jour. Moll. Stud. 49:146–163.

The Veliger 30(3):222–229 (January 4, 1988)

THE VELIGER

Ontogenetic Change in the Radula of the Gastropod *Epitonium billeeana* (Prosobranchia: Epitoniidae)

by

ANDREW J. PAGE AND RICHARD C. WILLAN

Department of Zoology, University of Queensland, St. Lucia,
Brisbane, Queensland 4067, Australia

Abstract. *Epitonium billeeana* (DuShane & Bratcher, 1965) is identified and described from the Great Barrier Reef, Australia. Like other epitoniids, *E. billeeana* was found to be a protandric hermaphrodite, changing sex between 8.6 and 12.7 mm shell length. Middle lateral radular teeth change within a particular row with growth, from a relatively small denticulate structure to a larger smooth structure. Transitional radulae are identified. We suggest the radula change is mediated or instigated by the change from the male to the female reproductive state.

INTRODUCTION

One of us (A.J.P.) is currently investigating the ecology of coral eating gastropods on Australia's Great Barrier Reef. A thin-shelled wentletrap is moderately abundant on middle- and outer-shelf coral reefs where it is obligately associated with scleractinian corals belonging to the family Dendrophylliidae. Not only does this epitoniid feed exclusively on two particular species of dendrophylliid coral, but the animal also resembles these host corals by being vivid golden-yellow in color; such pigmentation is an outstanding exception for a family whose other members are all generally white. This distinctive epitoniid has been known from Australia as the "golden wentletrap" for a decade and figured in color in several publications (MACLEISH, 1973; COLEMAN, 1978, 1981; ENDEAN, 1982; RUDMAN, 1984) but no specific name has been attached to it. We show here it is referable to an eastern Pacific taxon, *Epitonium billeeana* (DuShane & Bratcher, 1965). The species' full range extends, in tropical waters, throughout the Pacific and across the Indian Ocean to the Maldive Islands.

In the course of studying the gut of *Epitonium billeeana,* we made the unexpected discovery that an ontogenetic change takes place in the shape of teeth within rows of its radula. The purpose of this paper is to document this significant change, which has not been hitherto suspected in the Epitoniidae.

The ptenoglossan radula of epitoniids bears similar, elongate teeth with or without denticles on the blade (THIELE, 1928). As with most other gastropods possessing a multiseriate radula, numbers of teeth and tooth size increase with an individual's growth (THOMPSON, 1958; BERTSCH, 1976). Most species of epitoniids whose radulae have been studied possess denticles (THIELE, 1928; CLENCH & TURNER, 1952; TAKI, 1956, 1957; DUSHANE & BRATCHER, 1965; DUSHANE, 1974, 1979). None of these authors reports any alteration in the presence of denticles with growth in any species, so tooth shape has been assumed to be invariable and hence specifically diagnostic, as for most other gastropods (FRETTER & GRAHAM, 1962). Here we report one clear instance where this is not the case. We show that the teeth of *Epitonium billeeana* change in shape within an individual as it grows.

MATERIALS AND METHODS

Epitonium billeeana was collected from its host corals, *Dendrophyllia gracilis* Milne Edwards & Haime and *Tubastrea faulkneri* Wells in 6 to 16 m on Heron and Wistari reefs (23°27'S, 151°55'E) at the southern end of the Great Barrier Reef in Queensland, Australia, in September 1984 and September 1985. Twenty-six specimens from 4.8 to 23.6 mm shell length were collected specifically to examine their radulae. All were fixed in Bouin's solution, which decalcified the thin shells in three days. The gonad was sectioned (6 μm) to determine sex and sections were stained using Mayer's hematoxylin and 0.3% alcoholic eosin (LUNA, 1968).

Two methods were used to prepare radulae for light microscopy. In one, the pharyngeal mass was excised and heated in 10% KOH at 100°C for 20 min. The isolated radula was then rinsed in distilled water, blotted dry, stained in acidic fuchsin (1 h), rinsed briefly (30 sec), and mounted

Figure 1

Epitonium billeeana, SEMs of shell. A. Whole shell (length = 4.9 mm). B. Protoconch (bar = 0.5 mm). C. Detail of sculpture (bar = 100 μm).

in polyvinyl-alcohol-lactophenol (PVA). The second method followed MIKKELSEN (1985). The excised pharyngeal mass was placed in a marked well of a multi-well Boener slide in 10% KOH at room temperature (20–27°C) for 24 h. The isolated radula was then stained briefly (approximately 5 min) in acidic fuchsin before mounting in carboxymethyl-cellulose (CMC). For light microscopy, best results were obtained following the techniques outlined by MIKKELSEN (1985), except for larger radulae, which were mounted in PVA which necessitated longer staining (1 h) in acidic fuchsin. The more viscous PVA medium gave greater control in manipulating radulae while they were being mounted.

Radulae to be examined by the scanning electron microscope (SEM) were placed individually in small vials of distilled water and ultrasonicated for 20 sec. Some were attached to the flat surface of pin-type SEM stubs with double-sided adhesive tape. In other preparations, copper paint was dabbed onto the stub (to create an elevation on the surface) and allowed to dry. Then glue from adhesive tape, which had been obtained by brushing the tape with a fine-tipped paint brush dipped in chloroform, was used to attach the radulae to the paint spots. This latter technique produced better results in that relatively more radular teeth were available for examination.

All measurements of teeth were made with a calibrated

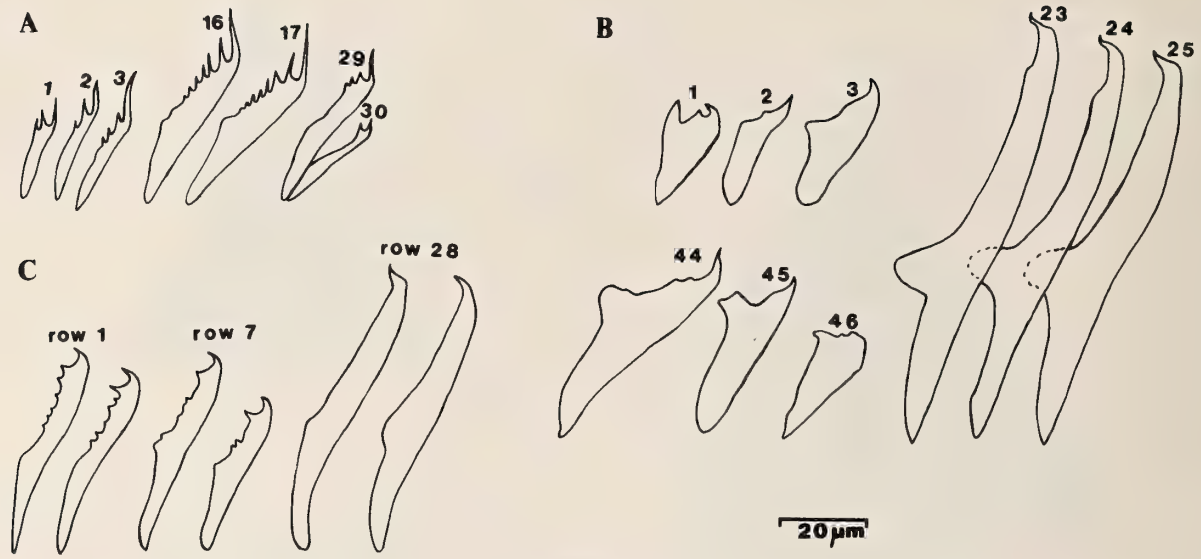


Figure 2

Epitonium billeeana, radular teeth. A. Inner laterals (tooth numbers 1–3 counting outwards from the midline), middle laterals (16, 17), outer laterals (29, 30), shell length = 6.4 mm. B. Inner laterals (1–3), middle laterals (23–25), outer laterals (44–46), shell length = 23.6 mm. C. Middle lateral teeth from anterior (row 1) to posterior (row 28) tooth rows, shell length = 9.9 mm.

eye piece and drawings made with the use of a camera lucida.

TAXONOMY

Epitonium billeeana (DuShane & Bratcher) is a distinctive epitoniid because of its shell sculpture, animal pigmentation, and habit of living obligately with dendrophylliid corals. It was first described from the Gulf of California (DuShane & Bratcher, 1965) and is currently recognized as being widespread in the Panamic Province of the eastern Pacific Ocean (DuShane, 1967, 1974; Keen, 1971). Specimens from the eastern Pacific are identical with western Pacific and eastern Indian Ocean material, and we have no hesitation in identifying them as *E. billeeana.* Robertson & Schutt (1984) provisionally applied this name to Indo-Pacific populations of the "golden wentletrap."

It is desirable to give a full synonymy so researchers can consult literature on this species without being confused by the different names that have been applied in different countries.

Synonymy

Scalina (*Ferminoscala*) *billeeana* DuShane & Bratcher, 1965: 160–161, pl. 24, figs. 1–4; DuShane & Poorman, 1967: 424.

Epitonium (*Asperiscala*) *billeeana* (DuShane & Bratcher): DuShane, 1967:87; DuShane & McLean, 1968:1, 2, fig. 1.

Epitonium billeeana (DuShane & Bratcher): Robertson, 1970:45.

Epitonium (*Asperiscala*) *billeeanum* [*sic*] (DuShane & Bratcher): Keen, 1971:424, fig. 612; DuShane, 1974:9, 10, figs. 13, 15, 155a, 155b; Robertson & Schutt, 1984: 1, 4.

Epitonium sp.: MacLeish, 1973:755 (photograph by V. Taylor); Coleman, 1978:116; Coleman, 1981:13, 44; Endean, 1982:138, fig. 137; Rudman, 1984:172.

Epitonium sp. 5: Loch, 1982:5, illust.

We share DuShane & Bratcher's (1965) and Robertson & Schutt's (1984) uncertainty that *Epitonium* is really the most appropriate genus-level taxon to accommodate *Scalina billeeana.* The species does seem incongruous in that genus, but is more suitable there than in *Amaea* or *Cirsotrema.* Proper generic allocation must await a phylogenetic analysis of the entire family. The specific name, *billeeana,* is a patronym honoring Ms. Billee Dilworth. As such it is a non-Latin noun in apposition and hence indeclinable, *i.e.,* its termination cannot be changed to agree in gender with the generic name ("*billeeanum*" is thus incorrect in the combination *Epitonium billeeanum,* even though the gender of the Latin genus *Epitonium* is neuter).

Description

The following brief description distinguishes *Epitonium billeeana* from other, sympatric, Indo-Pacific congeners.

Shell (Figure 1A) to 25 mm in height. Protoconch (Figure 1B) high and conical, multispiral (3–4 whorled),

Figure 3

Epitonium billeeana, SEMs of radular teeth and coral spirocyst tubes. A. Denticulate middle lateral teeth, shell length = 6.0 mm, bar = 10 μm. B. Smooth middle lateral teeth, shell length = 21.3 mm, bar = 10 μm. C. Teeth with undischarged coral spirocyst tubes, shell length = 12 mm, bar = 10 μm. D. Detail of spirocyst tube from C, bar = 1 μm.

possessing faint, opisthocline axial ridges, dull purple in color. Teleoconch elongate, possessing 7 or 8, thin, globose, strongly convex whorls when full grown; sutures deeply impressed; sculpture reticulate, consisting of equal, low, rounded, spiral cords (12–15 on body whorl) that are overridden by numerous (60–130 on body whorl), sharp, axial ridges (Figure 1C) each ridge elevated into a lamella where it crosses a spiral cord; sculpture weaker on body whorl of adults, spiral cords predominating; color white, with a purplish hue extending to 4th teleoconch whorl as a thin median stripe; overlain by a thin, adherent, pale buff periostracum. Aperture circular, peristome vertical with a moderate anterior expansion. Shell umbilicate. Head-foot, mantle and visceral mass of animal chrome-yellow; showing everywhere through the shell in life.

SEXUALITY

Like other wentletraps (Robertson, 1981; Boss, 1982; Melone, 1986), *Epitonium billeeana* is a protandric her-

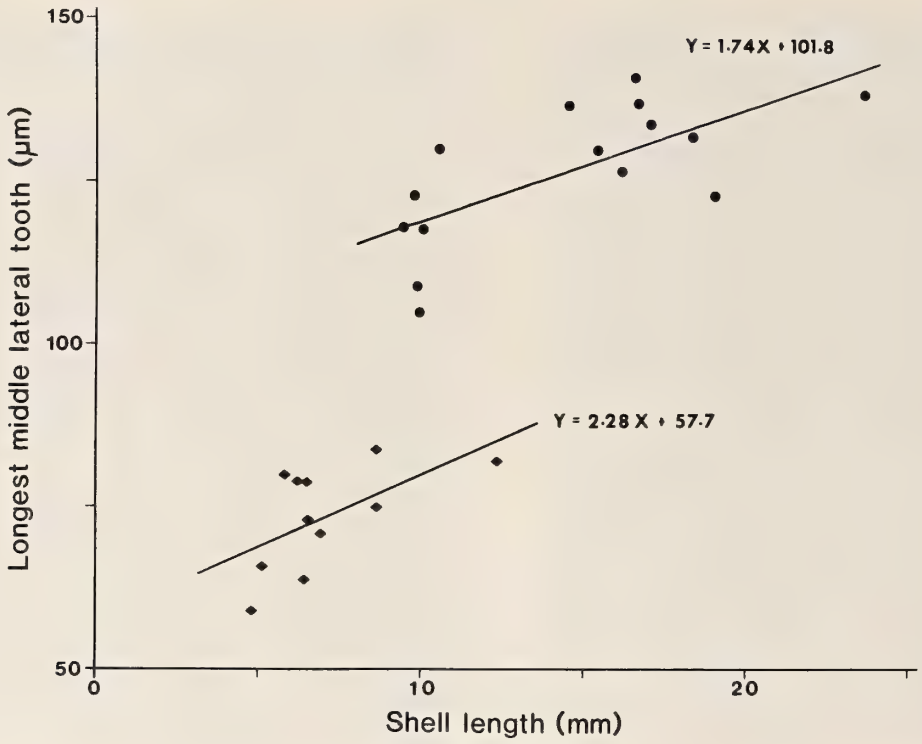


Figure 4

Epitonium billeeana, relationships between shell length and the length of the longest middle lateral tooth. (◆) Denticulate teeth, regression line Y = 2.28X + 57.7, $r = 0.596$, $P < 0.1$. (●) Smooth teeth, regression line Y = 1.74X + 101.8, $r = 0.698$, $P < 0.05$.

maphrodite. Based on our own observations on the state of the gonad, males (with shell lengths from 4.8 to 12.3 mm) are generally smaller than females (8.6 to 23.6 mm). Mature and developing spermatozeugmata and spermatozoa (as figured by NISHIWAKI [1964], TOCHIMOTO [1967], and NISHIWAKI & TOCHIMOTO [1969]) were observed in the testes of males and mature and developing ova were present in the ovaries of females. When sampled, all females were identifiable by the presence of strings of egg capsules.

RADULA DESCRIPTION

Epitoniids have a ptenoglossan radula, a broad structure that possesses many lateral teeth but lacks a rachidian (GRAHAM, 1965; BOSS, 1982). Within the radula, each row consists of two symmetrical halves. In that of *Epitonium billeeana,* the inner laterals of every half row (*i.e.,* those teeth nearest the midline) are smallest. Moving outwards, tooth size gradually increases to a maximum about halfway along each half row. Beyond this point, tooth size gradually decreases to the point where the outer laterals are only slightly longer than the inner ones. Teeth of every half row can thus be divided into three groups—inner, middle, and outer laterals (Figures 2A, B). Similar changes in relative tooth size across a half row have been noted in some of the epitoniids examined by CLENCH & TURNER (1952) and TAKI (1956, 1957). TAKI (1956) even segregated the teeth of *E. latifasciatum* (Sowerby) into three regions—inner, middle, and outer. All the teeth of *E. billeeana* terminate with a single, pointed cusp and below the cusp there may be up to seven prominent denticles along the blade. The cusp is always larger than any of the denticles. When a tooth possesses more than one denticle, that immediately below the cusp exceeds all the others in length (Figure 3A).

The radula of epitoniids covers the entire surface of the odontophore, which is divided into halves by a deep, middorsal, longitudinal groove (GRAHAM, 1965). Consequently radulae are extremely difficult to mount flat and radular formulae are often difficult to determine precisely. For this reason, it was only possible to count the numbers of lateral teeth accurately in three radular preparations of *Epitonium billeeana.* These, together with the length of each specimen's shell in parentheses, are as follows: 30 × 30.0.30 (6.4 mm); 39 × 40.0.40 (8.6 mm); 57 × 62.0.62 (15.9 mm).

ONTOGENETIC CHANGE

The large middle lateral teeth exhibit the greatest degree of change with growth of an individual. The middle lateral teeth of small *Epitonium billeeana* differ from those of large *E. billeeana* in size and the presence or absence of denticles

(Figure 4). Small specimens of *E. billeeana* (<8.6 mm) were found to have comparatively small (average length of longest middle lateral tooth 71 μm), denticulate (3–7 denticles), middle lateral teeth (Figures 3A, C). Large *E. billeeana* (>12.3 mm) were found to have longer (average length of longest middle lateral tooth 133 μm), smooth, middle lateral teeth (Figure 3B). Wentletraps of intermediate size (8.6–12.3 mm) were found to have middle lateral teeth of intermediate size (average length of longest middle lateral tooth 105 μm) which were either denticulate (1–7 denticles) or smooth. *Epitonium billeeana* of intermediate size with smooth middle lateral teeth also possess at least some denticulate middle laterals at the anterior end of their radula. In these cases (six examined) the oldest middle lateral teeth are always denticulate and smaller than the smooth, more recently formed middle lateral ones nearer the germinal epithelium (Figure 2C). These radulae are in transition between possessing relatively small, denticulate and longer, smooth middle lateral teeth. The occurrence of transitional radulae in *E. billeeana* of intermediate size demonstrates the change in tooth morphology with ontogeny. Table 1 correlates the ontogenetic changes of tooth morphology with sex in *E. billeeana.*

Through the courtesy of Mr. I. Loch of The Australian Museum, Sydney, we were able to examine SEMs of radular teeth and the protoconch of a specimen from Christmas Island, eastern Indian Ocean. These characters are in agreement (in size and shape) with those described here for *Epitonium billeeana.* Some of the teeth even have what appear to be atrophied denticles indicating that they may have come from a transitional radula. Unfortunately the shell length of this Christmas Island specimen is not available.

The results presented here are at odds with DuShane & Bratcher's (1965) description of the radular teeth of *Epitonium billeeana.* Many of the radular teeth of their 7-mm specimen were figured as smooth or possessing only a single denticle (DuShane & Bratcher, 1965:pl. 24). From our results (Figure 4), we would predict that all the teeth of such a small individual should be denticulate. This contradiction can perhaps be resolved by ontogenetic studies of the radulae of eastern Pacific material.

Table 1

Epitonium billeeana. Changes in sex and radular tooth morphology with growth of 26 specimens.

Shell length (mm)	Sex	Number of specimens	Radula description
<8.6	male	8	All teeth denticulate; 1–3 denticles on inner laterals, 3–7 on middle laterals, 1–5 on outer laterals.
8.6–12.3	male or female	9	As above, or with smooth middle lateral teeth posteriorly and at least some denticulate middle laterals anteriorly.
>12.3	female	9	Middle lateral teeth smooth; inner and outer laterals may be denticulate (1 or 2 denticles).

DISCUSSION

Reports of ontogenetic change in tooth morphology between rows in gastropod radulae are appearing more and more frequently. Several authors have demonstrated that the number of teeth within a half row increases as the individual grows (*e.g.,* Sterki, 1893; Bertsch, 1976; Robertson, 1985). Beyond this simple allometric increase, there are a few reports like this one of ours of alteration in tooth morphology within a particular row with growth. Sterki (1893) first described such changes in the shape of teeth in some pulmonates, and Carriker (1943) and Hollister (1954) observed that the pattern of denticulation of some prosobranchs' teeth depended on the size of the snail. McLean & Nybakken (1979) and Nybakken (1970, 1981) reported that several species of *Conus* changed their radula morphology with growth. Hickman (1980) discovered ontogenetic change within rows in the radula of *Hipponix conicus* (Schumacher). Thompson & Brown (1984:11–17) described a "dental metamorphosis" in the opisthobranchs *Tritonia hombergi* Cuvier and *T. plebeia* Johnston wherein juveniles have denticulate lateral teeth and adults have completely smooth laterals. The rachidian teeth of several muricids alter with growth (Fujioka, 1982, 1984a, b, 1985); for example, those of *Morula margariticola* (Broderip) change from pentacuspidate to tricuspidate (Fujioka, 1984b). Most recently has come the finding that denticulation of the "pseudocentral" tooth in the radula of *Tricolia variabilis* (Pease) also changes with growth (Robertson, 1985). All these reports indicate that the phenomenon of ontogenetic change in tooth morphology within particular rows may be more widespread in the Gastropoda than previously suspected.

The most vexing question—what causes this alteration—remains. Dietary change or sexual dimorphism seem to be the two most probable explanations, yet neither appears, at the present time, to offer a satisfactory answer for the observations. Our data on *Epitonium billeeana* present some challenges to both these hypotheses. Hickman (1980) and Nybakken (1981) attributed changes in tooth morphology to differing juvenile and adult diets. In the case of *E. billeeana,* small and large individuals occur, often side by side, on exactly the same coral and they apparently exhibit the same feeding behavior. Other evidence correlates differing radular morphologies with the sex of an individual; for example, the radula of male *Drupella* species and *Tricolia variabilis* changes from a female-like state in juveniles to the male state with sexual maturity (Fujioka, 1982; Robertson, 1985 respectively). Our observations on *E. billeeana* indicate the radular change may be sexually

mediated, or at least instigated, but individuals apparently switch sex from male to female before the radular change is completed. The reason for the divergence of radular tooth morphology between sexes, in both dioecious and protandric hermaphrodite gastropods, may ultimately be shown to be related to feeding efficiency and, hence, the energy requirements of the sexually reproducing female individual.

ACKNOWLEDGMENTS

The Director and staff of the Heron Island Research Station are thanked for providing facilities for, and advice on, research. The Hawaiian Malacological Society and the Great Barrier Reef Marine Park Authority generously provided financial support for field work (for A.J.P.). Mr. I. Loch of The Australian Museum, Sydney, freely supplied information on Christmas Island material. Ms. L. J. Newman provided the scanning micrographs and Ms. J. F. Rifkin identified coral spirocyst tubes. Drs. R. Robertson, T. S. Hailstone, and K. Warburton, Ms. L. J. Newman, and Mr. R. H. M. Eertman are thanked for reading the manuscript and offering criticisms. This study was supported from funds from the Australian Universities Grants Commission (to R.C.W.).

LITERATURE CITED

Bertsch, H. 1976. Intraspecific and ontogenetic radular variation in opisthobranch systematics (Mollusca: Gastropoda). Syst. Zool. 25:117–122.

Boss, K. J. 1982. Mollusca. Pp. 945–1116. *In:* S. P. Parker (ed.), Synopsis and classification of living organisms. Vol. 1. McGraw-Hill Book Co.: New York.

Carriker, M. R. 1943. Variability, developmental changes, and denticle replacement in the radula of *Lymnaea stagnalis appressa* Say. Nautilus 57:52–59.

Clench, W. J. & R. D. Turner. 1952. The genera *Epitonium* (part II), *Depressiscala, Cylindriscala, Nystiella* and *Solutiscala* in the western Atlantic. Johnsonia 2:289–356.

Coleman, N. 1978. A look at the wildlife of the Great Barrier Reef. Bay Books: Sydney. 128 pp.

Coleman, N. 1981. Shells alive. Rigby: Sydney. 94 pp.

DuShane, H. 1967. *Epitonium* (*Asperiscala*) *billeeana* (DuShane & Bratcher, 1965) non *Scalina billeeana* DuShane & Bratcher, 1965. Veliger 10:87–88.

DuShane, H. 1974. The Panamic–Galapagan Epitoniidae. Veliger 16(Suppl.):1–84.

DuShane, H. 1979. The family Epitoniidae (Mollusca: Gastropoda) in the northeastern Pacific. Veliger 22:91–134.

DuShane, H. & T. Bratcher. 1965. A new *Scalina* from the Gulf of California. Veliger 8:160–161.

DuShane, H. & J. H. McLean. 1968. Three new epitoniid gastropods from the Panamic province. Contrib. Sci. (Los Angeles) 145:1–6.

DuShane, H. & R. Poorman. 1967. A checklist of mollusks for Guaymas, Sonora, Mexico. Veliger 9:413–440.

Endean, R. 1982. Australia's Great Barrier Reef. University of Queensland Press: St. Lucia; London; New York. 348 pp.

Fretter, V. & A. Graham. 1962. British prosobranch molluscs: their functional anatomy and ecology. Ray Society: London. 755 pp.

Fujioka, Y. 1982. On the secondary sexual characteristics found in the dimorphic radula of *Drupella* (Gastropoda: Muricidae) with reference to its taxonomic revision. Venus 40:203–223.

Fujioka, Y. 1984a. Remarks on two species of the genus *Drupella* (Muricidae). Venus 43:44–54.

Fujioka, Y. 1984b. Sexually dimorphic radulae in *Cronia margariticola* and *Morula musiva* (Gastropoda: Muricidae). Venus 43:315–330.

Fujioka, Y. 1985. Seasonal aberrant radular formation in *Thais bronni* (Dunker) and *T. clavigera* (Küster) (Gastropoda: Muricidae). Jour. Exp. Mar. Biol. Ecol. 90:43–54.

Graham, A. 1965. The buccal mass of ianthinid prosobranchs. Proc. Malacol. Soc. Lond. 36:323–338.

Hickman, C. S. 1980. Gastropod radulae and the assessment of form in evolutionary paleontology. Paleobiology 6:276–294.

Hollister, S. C. 1954. Some notes on the radula. Nautilus 68:44–46.

Keen, A. M. 1971. Sea shells of tropical west America. 2nd ed. Stanford Univ. Press: Stanford, California. 1064 pp.

Loch, I. 1982. Queensland epitoniids. Aust. Shell News 39: 3–6.

Luna, L. G. 1968. Manual of histologic staining of the armed forces institute of pathology. 3rd ed. McGraw-Hill Book Co.: New York. 258 pp.

MacLeish, K. 1973. Exploring Australia's coral jungle. Natl. Geogr. Mag. 143:743–778.

McLean, J. H. & J. Nybakken. 1979. On the growth stages of *Conus fergusoni* Sowerby, 1873, the reinstatement of *Conus xanthicus* Dall, 1910, and a new species of *Conus* from the Galapagos Islands. Veliger 22:135–144.

Melone, G. 1986. Sex changes in *Opalia crenata* (L.) (Gastropoda: Epitoniidae). Abstracts, Ninth Int. Malacol. Congress, Edinburgh, 1986: 54 (abstract only).

Mikkelsen, P. S. 1985. A rapid method for slide mounting of minute radulae, with a bibliography of radula mounting techniques. Nautilus 99:62–65.

Nishiwaki, S. 1964. Phylogenetical study on the type of the dimorphic spermatozoa in Prosobranchia. Sci. Rept. Tokyo Kyoiku Daigaku Sect. B. 11:237–275.

Nishiwaki, S. & T. Tochimoto. 1969. Dimorphism in typical and atypical spermatozoa forming two types of spermatozeugmata in two epitoniid prosobranchs. Venus 28:37–46, 2 pls.

Nybakken, J. 1970. Radular anatomy and systematics of the west American Conidae (Mollusca, Gastropoda). Amer. Mus. Novit. 2414:1–29.

Nybakken, J. 1981. Ontogenetic change in the molluscan radula, some cases from the genus *Conus*. Bull. Amer. Malacol. Union 1981:28 (abstract only).

Robertson, R. 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. Pacific Sci. 24:43–54.

Robertson, R. 1981. Protandry with only one sex change in an *Epitonium* (Ptenoglossa). Nautilus 95:184–186.

Robertson, R. 1985. Archaeogastropod biology and the systematics of the genus *Tricolia* (Trochacea: Tricoliidae) in the Indo-West-Pacific. Monogr. Mar. Mollusca 3:1–103.

Robertson, R. & P. L. Schutt. 1984. Golden wentletraps on golden corals. Hawaiian Shell News 32:1, 4.

Rudman, W. B. 1984. Molluscs. Pp. 172–197. *In:* Reader's Digest book of the Great Barrier Reef. Reader's Digest: Sydney.

Sterki, V. 1893. Growth changes of the radula in land-mollusks. Proc. Acad. Natur. Sci. Phila. 1893:388–400, pls. 10, 11.

Taki, I. 1956. Anatomical study on Japanese Epitoniidae (1) *Epitonium, Amaea* and *Papyriscala.* Bull. Natur. Sci. Mus. (Tokyo) 3:71–79, pls. 13–17.

Taki, I. 1957. Anatomical study on Japanese Epitoniidae (2) *Gyroscala* and *Acutiscala.* Bull. Natur. Sci. Mus. (Tokyo) 3: 176–182, pls. 34–38.

Thiele, J. 1928. Über ptenoglosse Schnecken. Z. Wiss. Zool. 132:73–94.

Thompson, T. E. 1958. Observations on the radula of *Adalaria proxima* (A. & H.) (Gastropoda, Opisthobranchia). Proc. Malacol. Soc. Lond. 33:49–56.

Thompson, T. E. & G. Brown. 1984. Biology of opisthobranch molluscs. Vol. II. The Ray Society: London. 229 pp.

Tochimoto, T. 1967. Comparative histochemical study on the dimorphic spermatozoa of the Prosobranchia with special reference to polysaccharides. Sci. Rept. Tokyo Kyoiku Daigaku Sect. B. 13:75–109.

The Veliger 30(3):230–243 (January 4, 1988)

THE VELIGER

Illustrated Embryonic Stages of the Eastern Atlantic Squid *Loligo forbesi*

by

S. SEGAWA,[1] W. T. YANG, H.-J. MARTHY,[2] AND R. T. HANLON

The Marine Biomedical Institute, The University of Texas Medical Branch,
200 University Boulevard, Galveston, Texas 77550, U.S.A.
[1] Tokyo University of Fisheries, Minato-Ku, Konan-cho, Tokyo 108, Japan
[2] Universite Pierre et Marie Curie, Biologie Marine, Laboratoire Arago,
66650 Banyuls-sur-Mer, France

Abstract. The embryonic development of *Loligo forbesi* was observed from 14-day-old eggs to natural hatching. Egg strands were spawned in floating cages by wild-caught females in the Azores Islands, air-shipped to Galveston, and incubated in a closed seawater system. The period from spawning to hatching ranged from 68 to 75 days at a mean temperature of 12.5°C (SD 0.5°C). The diameters of individual eggs ranged from 3.0 to 3.1 mm and the dorsal mantle lengths of hatchlings ranged from 4.3 to 4.9 mm. The major developmental patterns were nearly identical to those of *L. vulgaris* (eastern Atlantic Ocean) and *L. pealei* (western Atlantic Ocean), except that *L. forbesi* took longer to hatch because of the larger embryos and hatchlings. The most noticeable differences in development involved the number and distribution of chromatophores. The chromatophore pattern was one of the best criteria for staging *L. forbesi* in late development.

INTRODUCTION

Loligo forbesi Steenstrup, 1856, is an eastern Atlantic Ocean species distributed from about 60°N on the coast of Norway to 20°N on the coast of northwest Africa (ROPER *et al.*, 1984) and throughout the Mediterranean Sea (MANGOLD-WIRZ, 1963). It is one of the economically important species in the English Channel (HOLME, 1974), in Scottish waters (THOMAS, 1973), in the Azores Islands (MARTINS, 1982), and off Spain and France (WORMS, 1983a). Studies to date on this species have been primarily of a taxonomic nature (ADAM, 1955) or works concerned mainly with aspects of fisheries biology (HOLME, 1974; MARTINS, 1982). Embryological observations are limited to a short note by NAEF (1928) comparing *L. forbesi* to *L. vulgaris*.

This embryological study was undertaken primarily to help predict the onset of hatching in laboratory growth studies (*e.g.*, YANG *et al.*, 1980; BOLETZKY & HANLON, 1983; HANLON *et al.*, 1985). Loliginid squids are important for biomedical experimentation (*e.g.*, NIXON & MESSENGER, 1977; TANSEY, 1979), especially the giant fibers of the peripheral nervous system (ADAMS *et al.*, 1983). *Loligo forbesi* is a particularly promising species to culture because of its large hatchling size (HANLON *et al.*, 1985).

The present paper illustrates the morphological form of post-cleavage stages in the embryonic development of *Loligo forbesi*. Criteria established by NAEF (1928) for *L. vulgaris* and ARNOLD (1965) for *L. pealei* have been used in conjunction with our observations of several additional characters, namely chromatophore pattern development (*cf.* FIORONI, 1965) and internal organ formation.

MATERIALS AND METHODS

Egg capsules were laid 28 January 1986 by captive adult female *Loligo forbesi* caught with squid jigs at a depth of 200 m near the island of Faial in the Azores Islands. The females laid their eggs in a large floating cage (2 × 3 × 2 m) in Horta harbor on Faial where the local water temperature was 14 to 16°C and the salinity 36‰. Live embryos were transported by air freight from the Azores to the Marine Biomedical Institute 11 days after spawning. Twenty-two strands of eggs were shipped in two plastic bags containing about 5 L of seawater and an equal volume of oxygen at temperatures of 12 to 15°C. Upon arrival the eggs were acclimated gradually to the conditions of the closed recirculating tank system. The egg capsules were suspended in the water column and incubated at a salinity of 34 to 35‰ and a mean temperature of 12.5°C (SD 0.5°C).

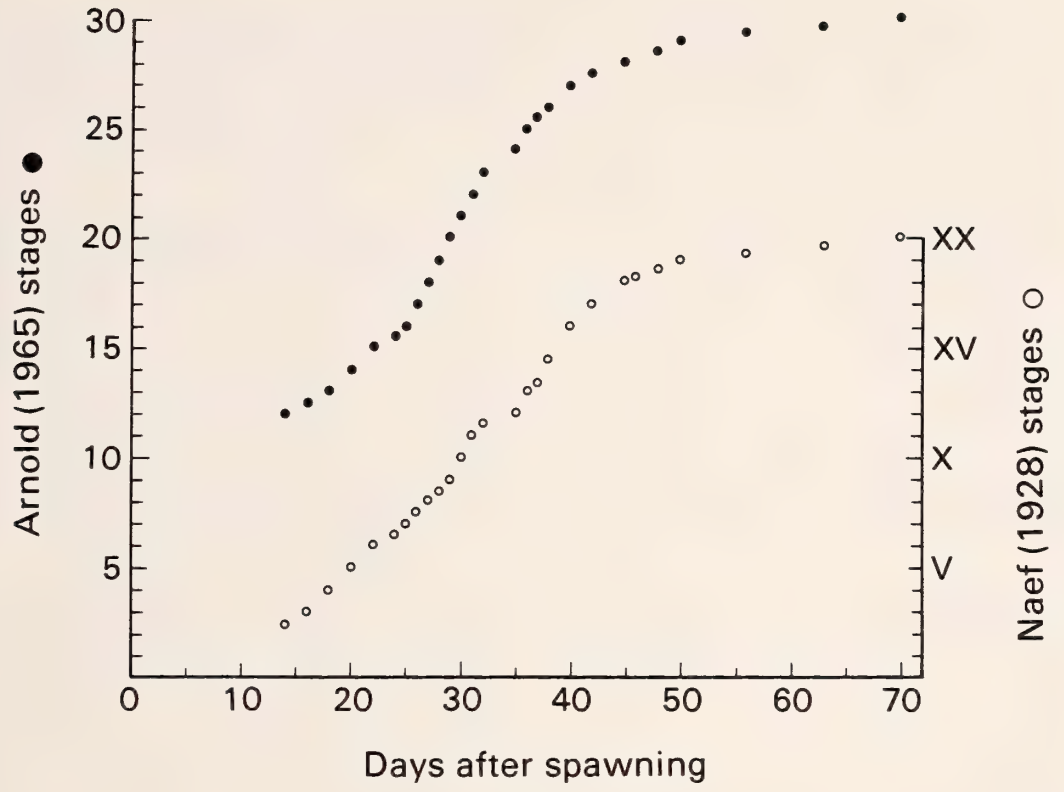


Figure 1

Embryonic development of *Loligo forbesi* in comparison to the stages proposed by ARNOLD (1965) and NAEF (1928) during the period from 14-day-old embryo to hatching. (Mean incubation temperature 12.5°C; SD 0.5°C.)

Regular observations were made from 14-day-old eggs throughout the remainder of embryonic development on four egg strings with embryos of uniform age. Representative embryos were observed carefully and drawn to scale under a dissecting microscope. All drawings were made from living embryos. In the early stages before organogenesis, embryos were observed through the chorion after careful removal of the tunic, and in older ones observations were made after removal of the chorion. The arabic stage represents the stage proposed by ARNOLD (1965) and the Roman numeral stage represents the stage proposed by NAEF (1928). Both ventral and dorsal views are given after stage 26 (XIV) (Figure 19); before that the dorsal view did not add substantially more information. Chromatophores on the fins were included in the "dorsal mantle" counts.

RESULTS

The egg capsules were transparent, soft, gelatinous, and fingerlike in shape. At the beginning of our observations (14 days after spawning), the eggs were stage 12 according to ARNOLD's (1965) scheme and stage II+ by NAEF's (1928) scheme, and each egg capsule was approximately 18 cm long and contained about 85 to 100 eggs arranged in a spiral. The diameters of the embryos ranged from 3.0 to 3.1 mm. From egg laying to day 14 in the Azores Islands, the environmental conditions were only moderately constant in the harbor for 11 days and during the 36 h of transportation to the U.S.A. The embryos took 68 to 75 days to hatch at 12.5 ± 0.5°C, with the main hatch on days 69 and 70. Figure 1 shows the developmental time of *Loligo forbesi* from day 14 to hatching according to the developmental stages of both ARNOLD (1965) and NAEF (1928).

Pre-organogenesis: Germ Layer Formation

Figure 2: Stage 12, Arnold (1965); (Stage II+), Naef (1928): Formation of the germ layer, or "gastrulation," is a complex process that begins when the margin of the blastoderm becomes two-layered as described in *Loligo pealei* (SINGLEY, 1977) and *L. vulgaris* (MARTHY, 1982), and the radial arrangement of blastocones becomes streaked. The definite separation of the blastoderm into an ectodermal and a mesendodermal germ layer is accomplished during stages 12–13 (III).

Pre-organogenesis: Germ Layer Proliferation (Blastoderm Growing)

Figure 3: Stage 13− (III–IV): Blastoderm covers 10 to 20% of the egg length, and border of blastoderm becomes sharply distinct.

Figure 4: Stage 13 (IV): Blastoderm covers about one-third of the egg surface.

Figure 5: Stage 14 (V): Blastoderm covers about one-half of the egg.

Figures 6 and 28: Stage 15 (VI): Blastoderm covers three-fifths to two-thirds of the egg.

Figure 7: Stage 15+ (VI–VII): Blastoderm covers about four-fifths of the egg. A shallow girdling depression appears around the equator forming a boundary between the future external yolk sac and the future embryonic body. The chorion is not illustrated in this and following figures.

Organogenesis

Figure 8: Stage 16 (VII), lateral view: Outer yolk sac envelope nearly closed. Primordia of optic vesicles are rudimentary and visible as disc-like elevations. Primordium of shell gland now visible.

Figure 9: Stage 17 (VII–VIII), lateral view: Outer yolk sac envelope closed. A ridge of the disc-like elevation transforms into a fold in the ventral area and forms a ridge in the dorsal part that becomes the optic vesicle. Border of the shell gland elevated slightly. Primordia of arms and tentacles first visible.

Figure 10: Stage 18 (VIII), lateral view: The disc-like fold entirely surrounds prospective retina and starts growing over it. Primordia of statocysts appear. Arms and tentacles grow and begin to project.

Figure 11: Stage 19 (VIII–IX), ventral view: Closure of the optic vesicle is progressing. Other organ primordia become prominent, such as gills and anal knoll.

Figure 12: Stage 20 (IX), ventral view: Opening of the optic vesicle closes. Shell gland invagination is progressing. Posterior and anterior funnel folds extend towards the midline.

Figure 13: Stage 21 (X), ventral view: Shell gland completely closes and transverse fin folds develop upon the broadening mantle. Anterior and posterior funnel folds fuse together. Funnel folds on each side elevate clearly but fusion in midline has not begun. First suckers appear on tentacles.

Figure 14: Stage 22 (XI), ventral view: Anterior part of funnel fold comes together at the margin. Lens primordia first visible. Mantle covers one-half to two-thirds of gills. Suckers appear on arms III. Retina pigmentation begins.

Figures 15 and 29: Stage 23 (XI–XII), ventral view: Funnel fold fuses anteriorly. Statocysts completely formed. Lenses are evident as refractive rods. Gills segmented clearly, showing six pairs of leaflets.

Figure 16: Stage 24 (XII), ventral view: Funnel tube closed. Mantle covers the anal papilla and gills but funnel retractor muscle is still visible.

Figure 17: Stage 25 (XIII), ventral view: Mantle covers the posterior portion of the funnel but triangular opening is still evident. Systemic heart clearly visible. Bases of arms IV and tentacles start to extend. Posterior lobes of internal yolk sac increase in size. First yellow chromatophores appear on the ventral mantle.

Figure 18: Stage 25+ (XIII+), ventral view: Mantle completely covers the posterior margin of the funnel. Ventral mantle chromatophores increase in number. First chromatophores are visible on tentacles; these appear to be dark reddish from the beginning.

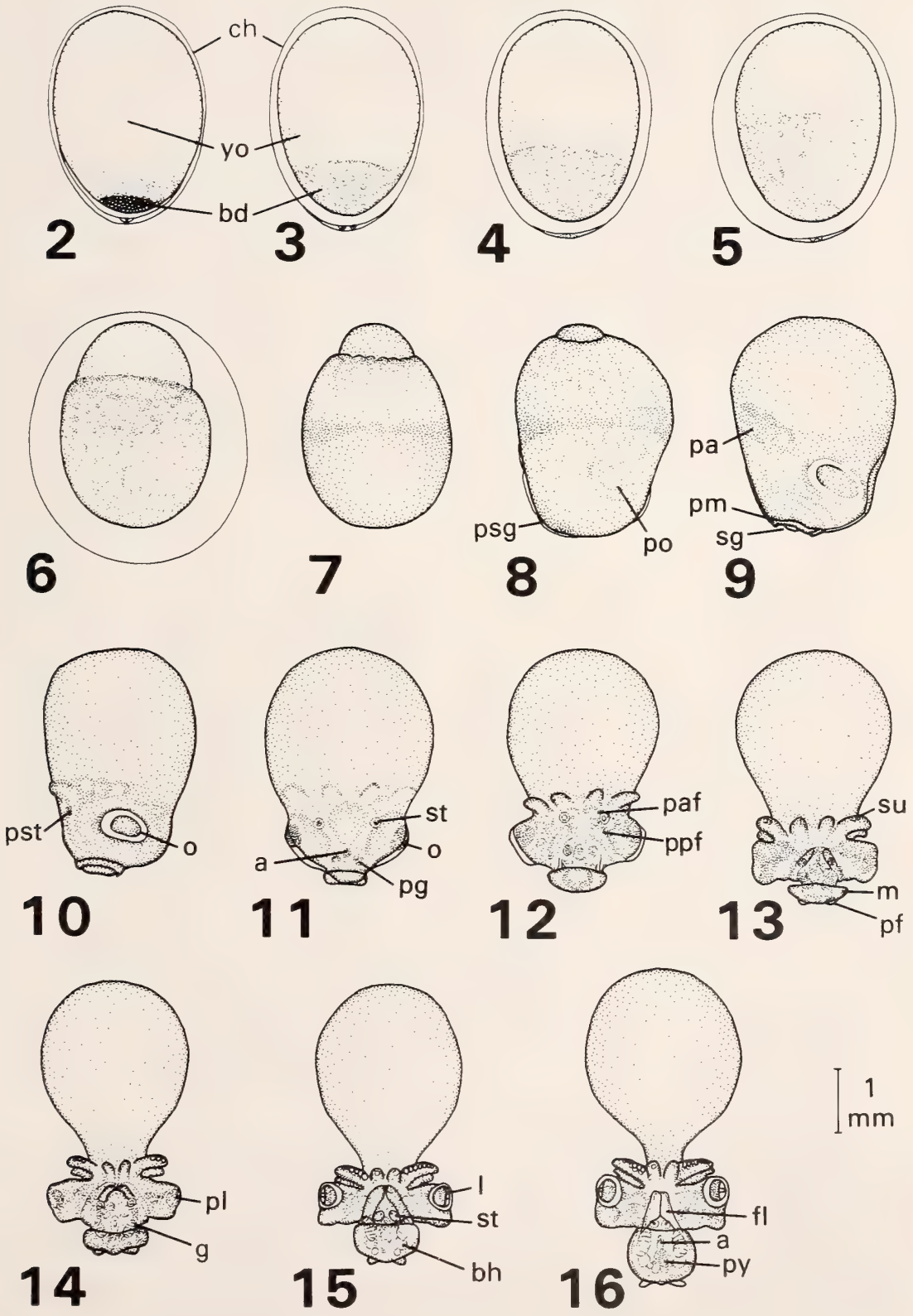
Figure 19: Stage 26 (XIV), dorsal (left) and ventral (right) views: Ventral arm bases (the ventral component of the future primary lid) cover about one-half of the optic ganglia. Ink sac is first visible but no ink is present. Retina color is brilliant reddish. Chromatophores are first visible on the ventral and dorsal sides of head, the dorsal mantle and fins, and the fourth arms.

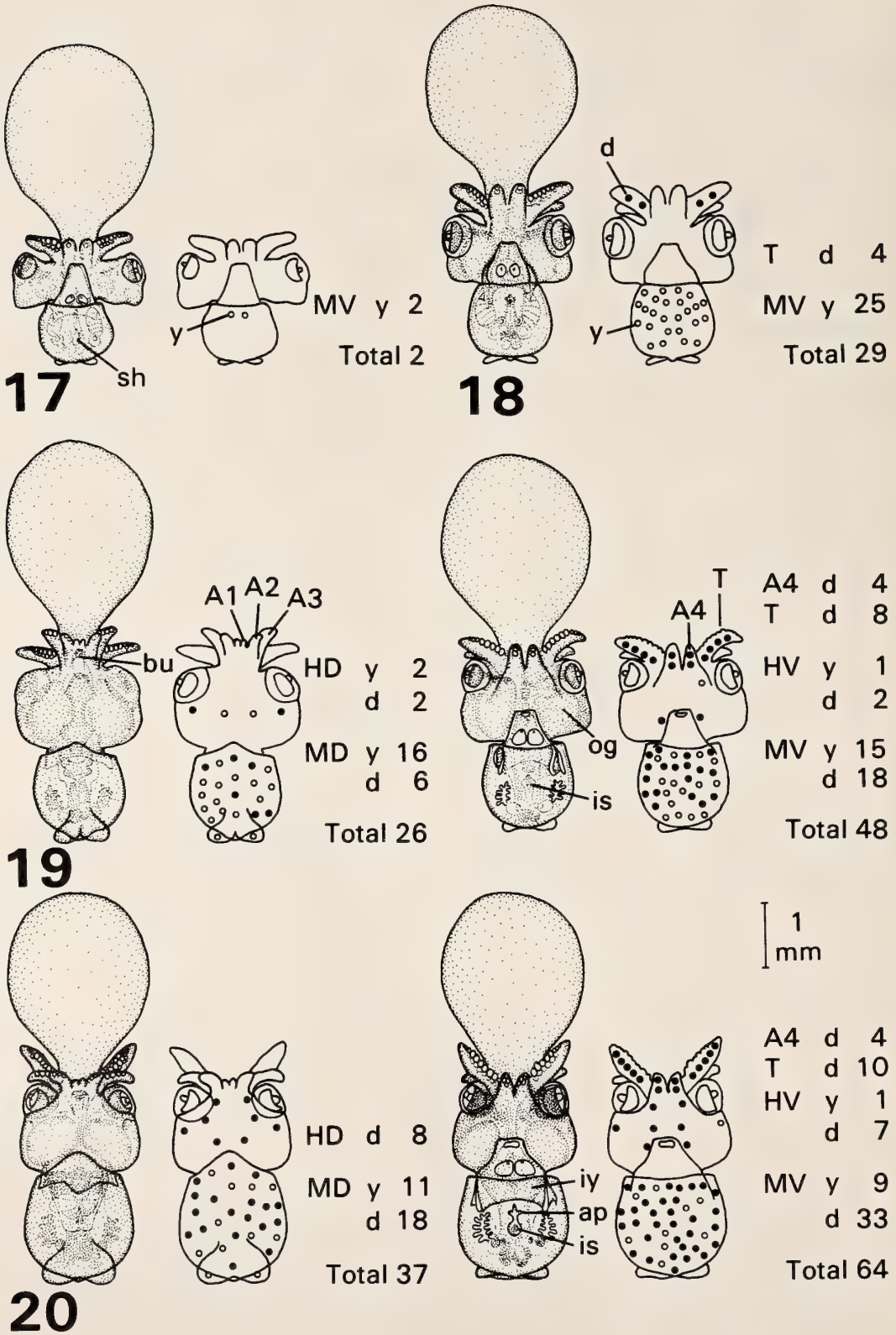
Figure 20: Stage 27 (XVI), dorsal (left) and ventral (right) views: Ventral arm bases extend into a primary lid and the edge reaches posterior end of eye vesicle. Ink sac fills with ink. Anus structure clearly visible with conspicuous anal papillae or flaps.

→

Explanation of Figures 2 to 27

Embryonic development of *Loligo forbesi,* from germ layer formation to newly hatched squid. See Results for details of each Figure. Key to abbreviations: a, anal knoll; ap, anal papilla or flaps; bd, blastoderm; bh, branchial heart; bu, buccal mass; c, caecum; ch, chorion; co, cornea; d, dark reddish chromatophore; ft, funnel tube; g, gill; h, Hoyle's Organ; is, ink sac; iy, internal yolk; l, lens; m, mantle; mg, mid-gut gland; o, optic vesicle; og, optic ganglion; op, olfactory plate; pa, primordia of arms; paf, primordium of anterior funnel fold; pf, primordium of fin; pg, primordium of gill; pl, primordium of lens; pm, primordium of mantle; po, primordium of optic vesicle; ppf, primordium of posterior funnel fold; psg, primordium of shell gland; pst, primordium of statocyst; py, posterior lobes of internal yolk sac; sg, shell gland; sh, systemic heart; sm, stomach; st, statocyst; su, sucker; y, yellow chromatophore; yo, yolk; A1, arm I; A2, arm II; A3, arm III; A4, arm IV; T, tentacle; HD, dorsal side of head; HV, ventral side of head; MD, dorsal side of mantle; MV, ventral side of mantle.


ch
yo
bd
2
3
4
5
6
7
psg
po
8
pa
pm
sg
9
pst
o
10
st
o
a
pg
11
paf
ppf
12
su
m
pf
13
pl
g
14
l
st
bh
15
fl
a
py
16
1
mm


sh
y
MV y 2
Total 2
17
d
y
T d 4
MV y 25
Total 29
18
bu
A1 A2 A3
HD y 2
d 2
MD y 16
d 6
Total 26
19
T
A4
og
is
A4 d 4
T d 8
HV y 1
d 2
MV y 15
d 18
Total 48
1 mm
HD d 8
MD y 11
d 18
Total 37
20
iy
ap
is
A4 d 4
T d 10
HV y 1
d 7
MV y 9
d 33
Total 64

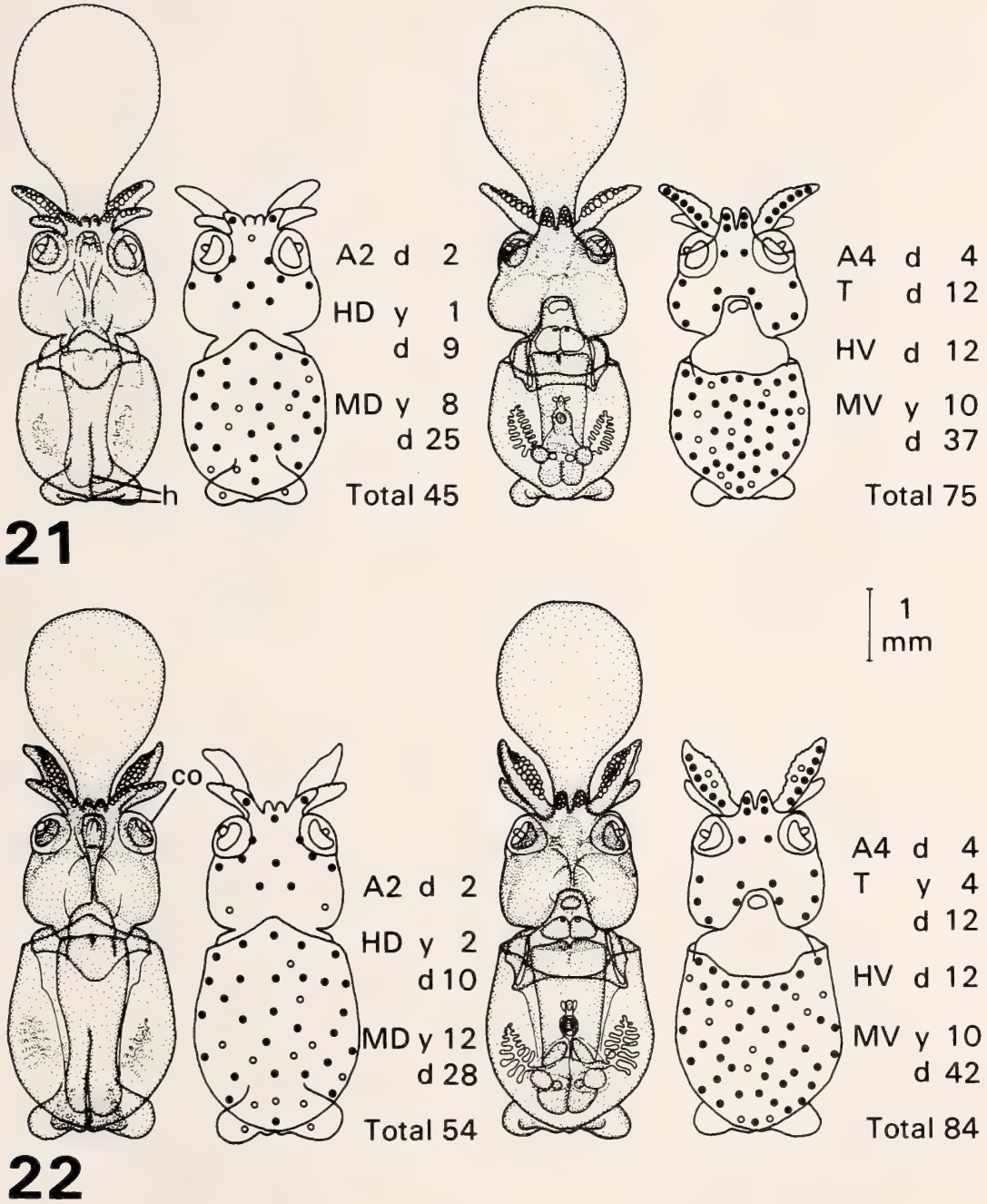
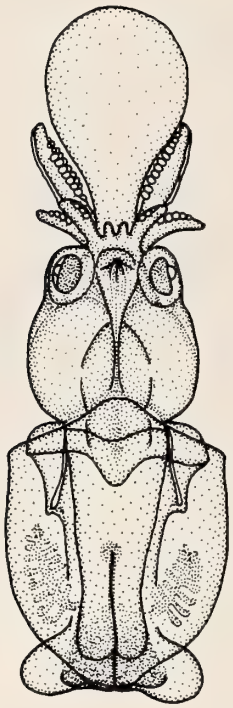


Figure 21: Stage 27+ (XVII), dorsal (left) and ventral (right) views: The edge of the primary lid covers about one-half of eye vesicle. Hoyle's organ is first visible on dorsal mantle. Chromatophores on arms II first appear. External yolk sac approximately same size as mantle length. Second row of chromatophores appears on the tentacles; these begin as yellows.

Figure 22: Stage 28 (XVIII), dorsal (left) and ventral (right) views: Primary lid completely covers the optic vesicle and part of it transforms into a transparent cornea.

Figure 23: Stage 28+ (XVIII–XIX), dorsal (top) and ventral (bottom) views: Mid-gut gland first visible around the internal yolk sac. Stomach and caecum first visible.



A2 d 2

HD y 4
d 10

MD y 11
d 30

Total 57

1 mm

A4 y 2
d 4

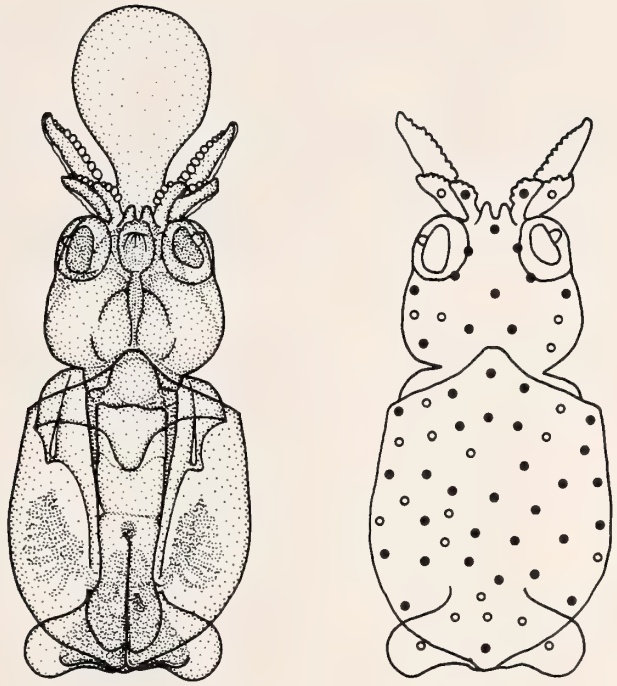
T y 8
d 12

HV y 2
d 12

MV y 10
d 44

Total 94

23



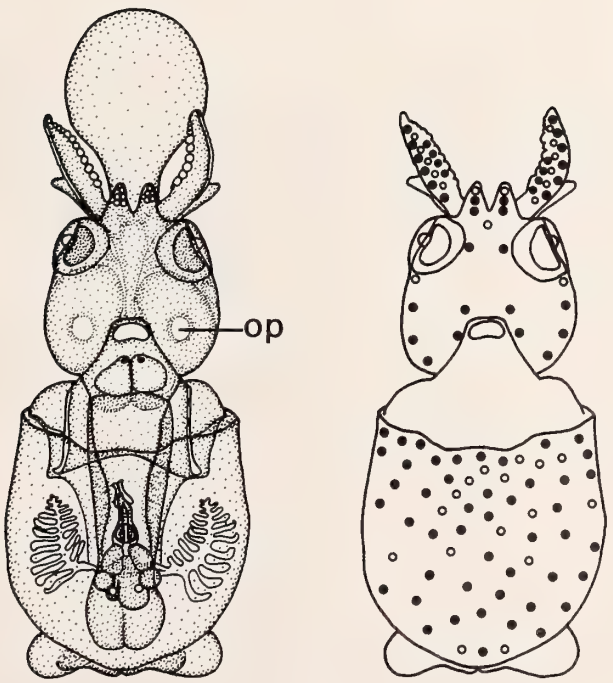
A2 d 2
A3 y 2

HD y 4
d 11

MD y 17
d 30

Total 66

1 mm



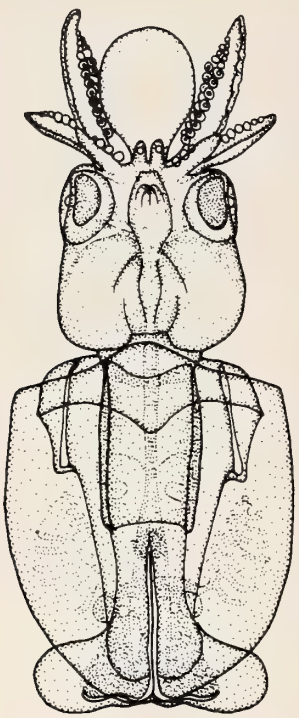
A4 y 2
d 4
T y 11
d 20

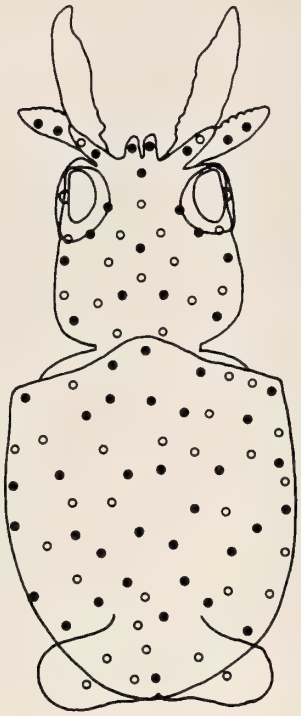
HV y 3
d 12

MV y 16
d 47

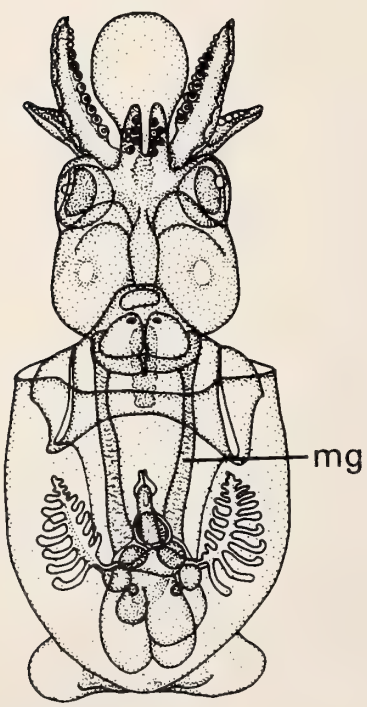
Total 115

24





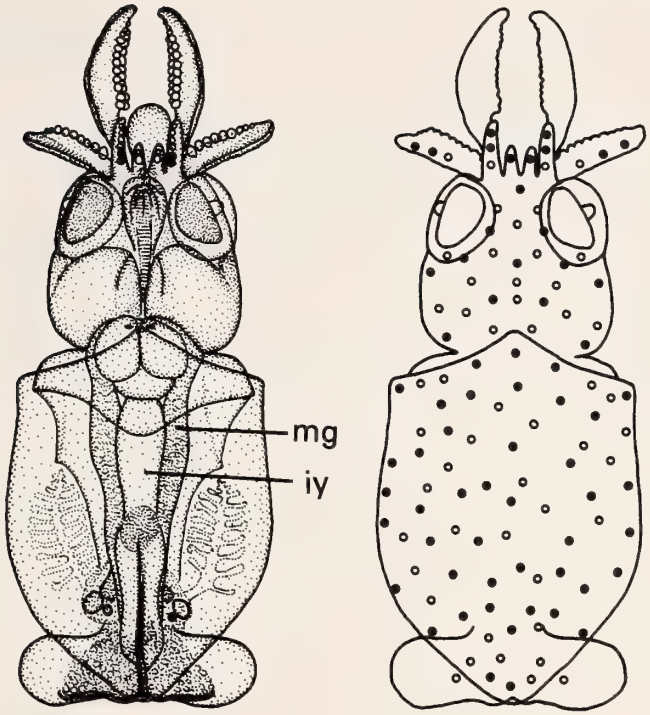
A1	d	2
A2	y	2
	d	2
A3	d	4
HD	y	14
	d	12
MD	y	28
	d	34
Total		98



1 mm

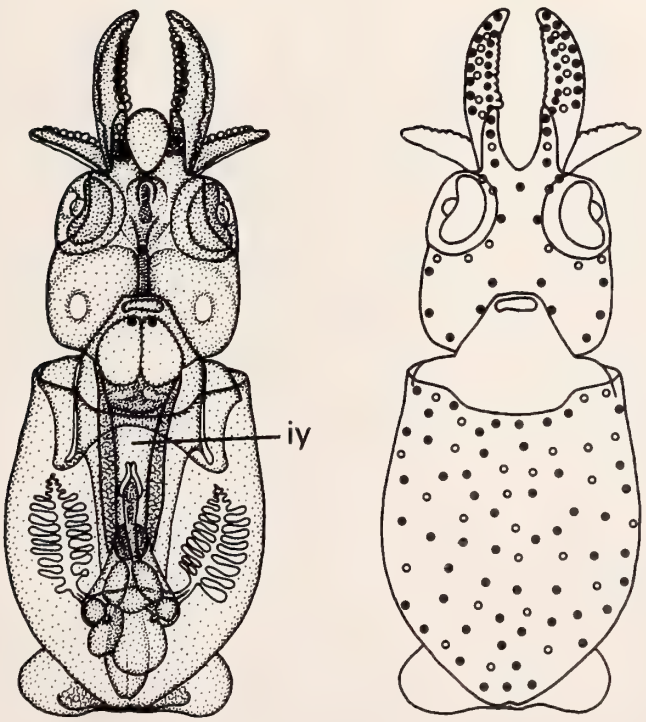
A4	d	6
T	y	14
	d	28
HV	y	7
	d	12
MV	y	26
	d	50
Total		143

25



A1	d	2
A2	y	2
	d	4
A3	y	2
	d	4
HD	y	17
	d	12
MD	y	30
	d	43

Total 116

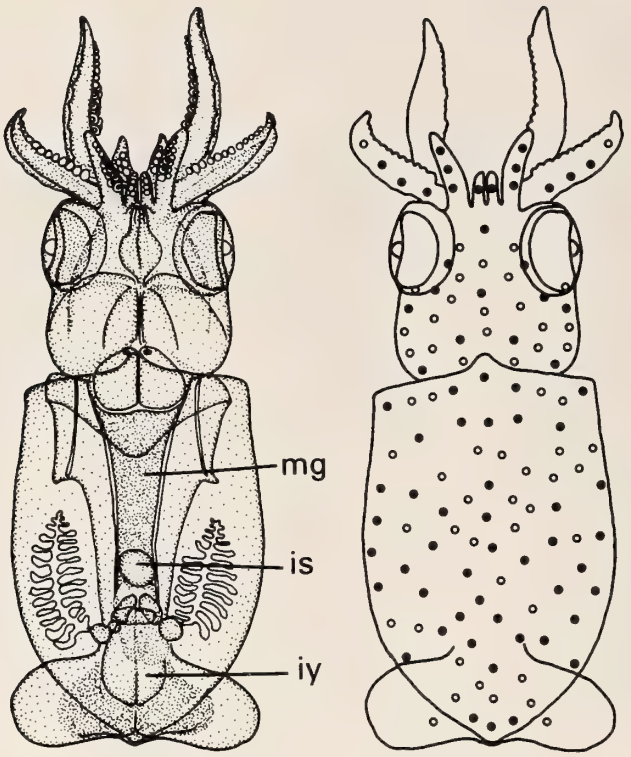


1 mm

A4	y	2
	d	6
T	y	12
	d	32
HV	y	10
	d	13
MV	y	26
	d	53

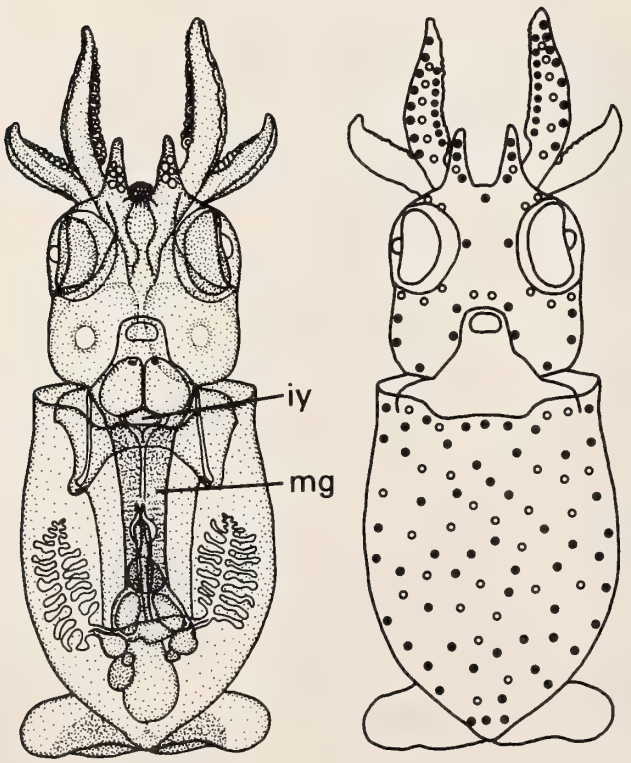
Total 154

26



A1	d	2
A2	d	6
A3	y	2
	d	6
HD	y	21
	d	12
MD	y	33
	d	45

Total 127

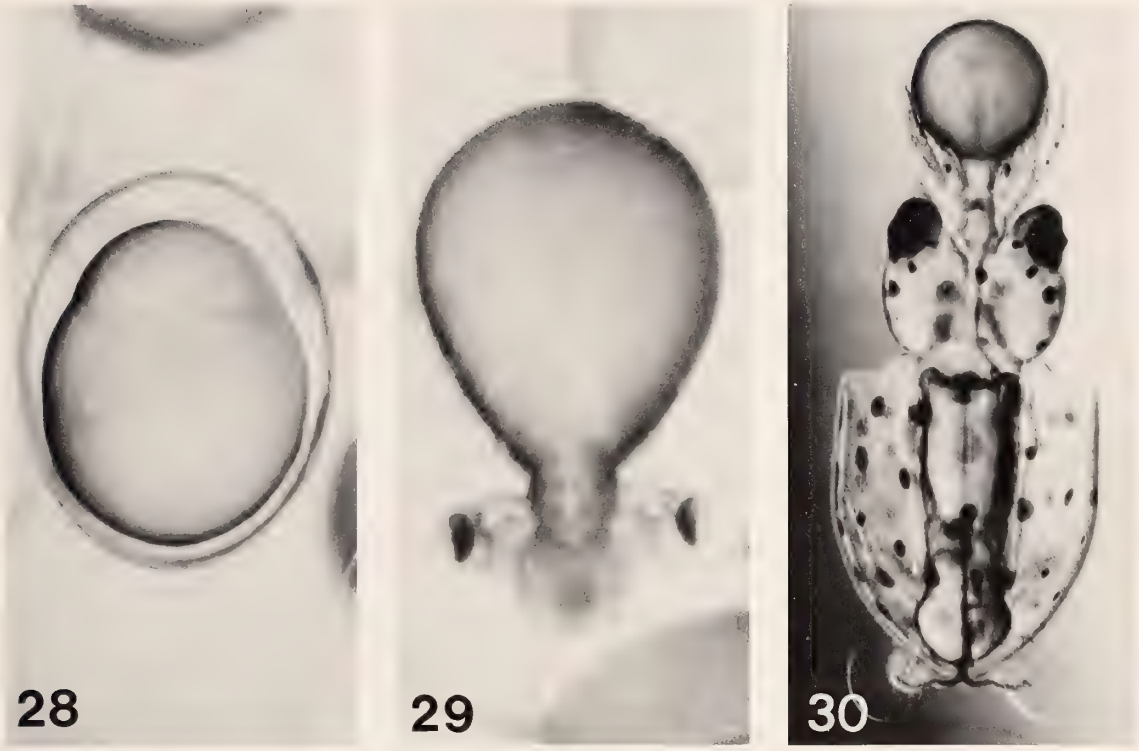


1 mm

A4	y	2
	d	6
T	y	12
	d	33
HV	y	12
	d	13
MV	y	27
	d	54

Total 159

27



Explanation of Figures 28 to 30

Figure 28. Photograph of embryo at stage 15 (VI). Compare Figure 6.

Figure 29. Photograph of embryo at stage 23 (XI–XII). Compare Figure 15.

Figure 30. Photograph of embryo at stage 29 (XIX). Compare Figure 24.

Figures 24 and 30: Stage 29 (XIX), dorsal (top) and ventral (bottom & Figure 30) views: Third row of chromatophores appears on tentacles; these are small and red from the start. First chromatophores appear on arms III. The primordia of the olfactory organ are clearly visible on the ventral head as thickenings of the epidermis.

Figure 25: Stage 29+ (XIX+), dorsal (top) and ventral (bottom) views: Internal yolk sac begins to be absorbed and decreases in size. Mid-gut gland develops around the internal yolk sac. The external yolk sac approximately equal in length to tentacle length. First chromatophores and suckers appear on arms II.

Figure 26: Stage 29++ (XIX–XX), dorsal (top) and ventral (bottom) views: The external yolk sac is approximately equal to length of arms II. Internal yolk sac reduced in size. Caecum and stomach increase in size. In some embryos, the external yolk sac may be lost and premature hatching may occur. Dark chromatophore patterns on both dorsal and ventral head remain the same until hatching.

Figure 27: Stage 30 (XX), dorsal (top) and ventral (bottom) views: Newly hatched squid. Hoyle's organ depleted. Internal yolk sac visible dorsally and reduced to a small triangular body. External yolk almost absorbed and only yolk sac envelope remains. External yolk sac sometimes lost just after hatching. Hatching size ranged from 4.3 to 4.9 mm ML, with a mean of 4.6 mm ML (SD 0.1 mm).

DISCUSSION

The life history of *Loligo forbesi* is known only in general terms (*e.g.*, HOLME, 1974; MARTINS, 1982) and this study plus our laboratory culture experiments (*e.g.*, HANLON *et al.*, 1985) are meant to fill some of the gaps. Details of development may also help distinguish *L. forbesi* from the closely related *L. vulgaris*, with which it shares many morphological features and also overlaps in distribution (ROPER *et al.*, 1984).

For embryological study, among the best-known cephalopods are *Loligo vulgaris* and *L. pealei*, for which detailed staging schemes were established by NAEF (1928) and ARNOLD (1965) respectively. Although there are some dif-

ferences in developmental processes between these two species and *L. forbesi,* Arnold's and Naef's schemes could be transferred directly to the developmental sequence of *L. forbesi.*

The sigmoid developmental pattern of *Loligo forbesi* (Figure 1) was very similar to other species of *Loligo* (Boletzky, 1974:fig. 1) but a little different from that reported for *L. pealei* (Arnold, 1965), whose development after stage 12 was approximately linear. *Loligo forbesi* has large eggs that are deposited in cold water. Individual eggs of *L. forbesi* spawned in the Azores were 3.0–3.1 mm in diameter and represent the largest known egg of *Loligo* spp.: *L. opalescens* 2.0–2.5 mm (Fields, 1965), *L. vulgaris* 2.3–2.7 mm (Worms, 1983b), and *L. pealei* 1.0–1.6 mm (Summers, 1983). As a result, the eggs develop more slowly than other *Loligo* species. It took 68–75 days at 12.5°C for *L. forbesi* compared to 10–27 days at 12–23°C for *L. pealei* (McMahon & Summers, 1971), 30–35 days at 13.6°C for *L. opalescens* (McGowan, 1954), and 45–70 days at 12–14°C for *L. vulgaris* (Mangold-Wirz, 1963; Boletzky, 1974).

Development is a continual process, but the developmental "stages" have been determined arbitrarily. Thus, identification of a particular stage is sometimes difficult. In each case several stages are divisible into two or more steps. The "ideal" staging criteria suggested by Naef (1928), and partially reconsidered by Arnold (1965, 1974), follow morphological events throughout embryogenesis (*e.g.,* easily recognizable steps in eye and shell gland closure, funnel formation, eye lid growth, *etc.*) and are useful in *Loligo forbesi* as well. Progressive closure of the optic vesicle, as described for *L. vulgaris* (Marthy, 1973) and *L. pealei* (Arnold & Williams-Arnold, 1978), is a good indicator for stages 16–20 (VII–IX). The process of funnel folding (Arnold *et al.,* 1978) and of formation of the primary lid over the eye (Naef, 1928; Arnold, 1984) are excellent criteria for stages 20–24 (IX–XII) and stages 25–28 (XIII–XVIII) respectively. The proportions among some internal organs such as internal yolk sac, mid-gut gland, stomach, caecum, and ink sac change rapidly from stages 28 to 30 (XVIII to XX), but their size and position are good staging criteria.

We distinguish yellow from dark chromatophores because nearly all chromatophores in the embryo begin as yellows and transform into a darker (red-brown) pigment with time (*e.g.,* Fioroni, 1965; Forsythe & Hanlon, 1985; Packard, 1985). This progression can be seen in the figures and is useful in staging. The third (inner) row of chromatophores to form on the tentacles at stage 29 (XIX) (Figure 24) are an exception; they start as dark reddish and are conspicuously smaller chromatophore organs, and this appears to be characteristic of *Loligo* spp. hatchlings (*e.g.,* Fioroni, 1965; McConathy *et al.,* 1979). There appears to be no "standard color" of the dark chromatophores at hatching; unpublished data of Hanlon and Boletzky show that some year-classes of *L. forbesi* have red, and some have brown, dark chromatophores. Thus, color alone is not useful in characterizing the species; furthermore, in preservation the colors are not usually distinguishable.

In *Loligo forbesi,* chromatophores on the ventral surface appear at stage 25 (XIII) (Figure 17) and on the dorsal surface at stage 26 (XIV) (Figure 19). These are earlier than those of *L. pealei* (Arnold, 1965) and later than those of *L. vulgaris* (Fioroni & Meister, 1974). After first appearance, chromatophores increase in number and distribution on the head, mantle, fins, arms, and tentacles. The chromatophores (especially the dark reddish ones that are easier to see) on the head, tentacles, and arms are one of the best criteria for determining later developmental stages in *L. forbesi.* There is considerable variation in the pattern of chromatophores on the mantle; thus the use of mantle chromatophores in distinguishing this species from the sympatric *L. vulgaris* will be minimal.

Size of *Loligo forbesi* at hatching ranges from 4.3 to 4.9 mm ML and is larger than other species such as *L. pealei* (about 1.8 mm ML; McConathy *et al.,* 1979), *L. vulgaris* (about 3 mm ML; Boletzky, 1979), and *L. opalescens* (2.5–3.2 mm ML; Fields, 1965; McConathy *et al.,* 1979). Size of hatchlings depends largely upon the size of eggs spawned. In laboratory experiments (unpublished observations), larger hatchlings of squids like *L. forbesi* usually have more successful attacks on food organisms and have better survival rates than smaller hatchlings like *L. pealei.* This suggests that *L. forbesi* has a different way of optimizing survival during its initial life-history stages: the large hatchlings are already a size that takes other *Loligo* hatchlings several weeks to attain, and they can feed immediately on a wide size range and diversity of food organisms (from approximately 0.8 mm to 3.5 mm long; Hanlon *et al.,* submitted). Thus, it should be relatively easier to rear *L. forbesi* in captivity during the first critical month (*e.g.,* Yang *et al.,* 1986) when mortality is generally very high.

ACKNOWLEDGMENTS

S. Segawa thanks the Ministry of Education, Science and Culture of Japan and The Marine Biomedical Institute for funding during his postdoctoral study at The University of Texas Medical Branch in Galveston. We gratefully acknowledge funding for work in the Azores and Galveston on DHHS grant RR 01024 to R.T.H. and W.T.Y. John W. Forsythe did a superb job of acquiring the eggs in the Azores and transporting them, and we thank Dr. Jose Martins, Dr. Helen Rost Martins, and Ricardo de Santis of the University of the Azores for hospitality and assistance with squid work in the Azores. We thank Dr. John Arnold for reviewing a late draft and especially Dr. Sigurd Boletzky for many detailed suggestions on the final draft. Laura A. Koppe kindly typed the drafts and final manuscript.

LITERATURE CITED

Adam, W. 1955. Résultats scientifiques des campangnes de la "Calypso." I. Campagne en Mer Rouge. VI. Cephalopodes. Annales Institut Oceanographique 30:185–195.

ADAMS, D. J., K. TAKEDA & J. A. UMBACH. 1983. Metabolic inhibitors and lithium depress synaptic transmission at the squid giant synapse. Jour. Physiol. 345:147 pp.

ARNOLD, J. M. 1965. Normal embryonic stages of the squid, *Loligo pealii* (Lesueur). Biol. Bull. 128:23–32.

ARNOLD, J. M. 1974. Embryonic development. Pp. 24–49. *In:* J. M. Arnold, W. C. Summers, D. L. Gilbert, R. S. Manalis, N. W. Daw & R. J. Lasek (eds.), A guide to laboratory use of the squid *Loligo pealei.* Marine Biological Laboratory: Woods Hole, Massachusetts.

ARNOLD, J. M. 1984. Closure of the squid cornea: a muscular basis for embryonic tissue movement. Jour. Exper. Zool. 232:187–195.

ARNOLD, J. M. & L. D. WILLIAMS-ARNOLD. 1978. Preliminary studies on the closure of the optic vesicle of *Loligo pealei* embryos. Biol. Bull. 155:426 (abstract).

ARNOLD, J. M., L. D. WILLIAMS-ARNOLD & V. PETERS. 1978. Fusion of tissue masses in embryogenesis—a scanning electron microscope and transmission electron microscope study of funnel development in the squid *Loligo pealei.* Develop. Biol. 65:155–170.

BOLETZKY, S. v. 1974. The larvae of Cephalopoda: a review. Thalassia Jugosl. 10(1/2):45–76.

BOLETZKY, S. v. 1979. Observations on the early post-embryonic development of *Loligo vulgaris* (Mollusca, Cephalopoda). Rapport de la Commission Internationale Pour la Mer Mediterranee 25/26(10):155–158.

BOLETZKY, S. v. & R. T. HANLON. 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. Mem. Natl. Mus. Victoria 44:147–187.

FIELDS, W. G. 1965. The structure, development, food relations, reproduction and life history of the squid *Loligo opalescens* Berry. Calif. Dept. Fish & Game, Fish. Bull. 131: 1–108.

FIORONI, P. 1965. Die embryonale Musterentwicklung bei einigen Mediterranean Tintenfischarten. Vie et Milieu, Serie A: Biologie Marine 16:654–756.

FIORONI, P. & G. MEISTER. 1974. Embryologie von *Loligo vulgaris* Lam. Gemeiner Kalmar. Gustav Fischer Verlag: Stuttgart. Grosses Zoologisches Praktikum, Heft 16 c/2. 69 pp.

FORSYTHE, J. W. & R. T. HANLON. 1985. Aspects of egg development, post-hatching behavior, growth and reproductive biology of *Octopus burryi* Voss, 1950 (Mollusca, Cephalopoda). Vie et Milieu 35(3/4):273–282.

HANLON, R. T., R. F. HIXON, P. E. TURK, P. G. LEE & W. T. YANG. 1985. Behavior, feeding and growth of young *Loligo forbesi* (Cephalopoda: Myopsida) reared in the laboratory. Vie et Milieu 35(3/4):247 (abstract).

HANLON, R. T., W. T. YANG, P. E. TURK, P. G. LEE & R. F. HIXON. Submitted. Laboratory culture of the eastern Atlantic squid *Loligo forbesi.* Aquaculture and Fisheries Management.

HOLME, N. A. 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. Jour. Mar. Biol. Assoc. U.K. 54:481–503.

MANGOLD-WIRZ, K. 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. Vie et Milieu, Suppl. No. 13:285 pp.

MARTHY, H.-J. 1973. An experimental study of eye development in the cephalopod *Loligo vulgaris*: determination and regulation during formation of the primary optic vesicle. Jour. Embryol. Exper. Morphol. 29:347–361.

MARTHY, H.-J. 1982. The cephalopod egg, a suitable material for cell and tissue interaction studies. Pp. 223–233. *In:* M. M. Burger & R. Weber (eds.), Progress in clinical biological research. Vol. 85. Allan R. Liss Publishers: New York.

MARTINS, H. R. 1982. Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. Jour. Mar. Biol. Assoc. U.K. 62:799–808.

MCCONATHY, D. A., R. T. HANLON & R. F. HIXON. 1979. Chromatophore arrangements of hatchling loliginid squids (Cephalopoda, Myopsida). Malacologia 19(2):279–288.

MCGOWAN, J. A. 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens,* at La Jolla, California. Calif. Dept. Fish & Game 40:47–54.

MCMAHON, J. & W. C. SUMMERS. 1971. Temperature effects on the developmental rate of squid (*Loligo pealei*) embryos. Biol. Bull. 141:561–567.

NAEF, A. 1928. Die Cephalopoden. Fauna Flora Golf Neapal 35(II):357 pp.

NIXON, M. & J. B. MESSENGER. 1977. The biology of cephalopods. Symposia of the Zoological Society of London, No. 38. Academic Press: London. 615 pp.

PACKARD, A. 1985. Sizes and distribution of chromatophores during post-embryonic development in cephalopods. Vie et Milieu 35(3/4):285–298.

ROPER, C. F. E., M. J. SWEENEY & C. E. NAUEN. 1984. Cephalopods of the world: an annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis 3(125):277 pp.

SINGLEY, C. T. 1977. An analysis of gastrulation in *Loligo pealei.* Ph.D. Thesis, University of Hawaii, Honolulu.

SUMMERS, W. C. 1983. *Loligo pealei.* Pp. 115–142. *In:* P. R. Boyle (ed.), Cephalopod life cycles. Vol. I: Species accounts. Academic Press: London.

TANSEY, E. M. 1979. Neurotransmitters in the cephalopod brain. Comp. Biochem. Physiol. 64C:173–182.

THOMAS, H. J. 1973. Squid. Scottish Fisheries Bulletin 39: 35–39.

WORMS, J. 1983a. World fisheries for cephalopods: a synoptic overview. FAO Fisheries Technical Papers (231):1–20.

WORMS, J. 1983b. *Loligo vulgaris.* Pp. 143–157. *In:* P. R. Boyle (ed.), Cephalopod life cycles. Vol. I: Species account. Academic Press: London.

YANG, W. T., R. T. HANLON, R. F. HIXON & W. H. HULET. 1980. First success in rearing hatchlings of the squid *Loligo pealei* Lesueur, 1821. Malacol. Rev. 13:79–80.

YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, W. H. HULET & R. T. HANLON. 1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens,* cultured through the life cycle. Fish. Bull. 84(4):771–798.

The Veliger 30(3):244–247 (January 4, 1988)

THE VELIGER

The Red Foot of a Lepidopleurid Chiton: Evidence for Tissue Hemoglobins

by

DOUGLAS J. EERNISSE[1]

Friday Harbor Laboratories, University of Washington,
Friday Harbor, Washington 98250, U.S.A.

AND

NORA B. TERWILLIGER AND ROBERT C. TERWILLIGER

Department of Biology, University of Oregon, Eugene, Oregon 97403, U.S.A. and
Oregon Institute of Marine Biology, Charleston, Oregon 97420, U.S.A.

Abstract. Shallow-water specimens of *Leptochiton rugatus,* a member of an ancient, mostly deep-water, suborder of chitons (Lepidopleurina), have a striking red coloration of the foot and soft tissues. The possibility that the red color of various tissues of *L. rugatus* is caused by a circulating or noncirculating respiratory heme protein was investigated. A hemoglobin was identified in tissue from foot, mantle wall, gills, and surrounding the mouth. No heme protein was found in circulating hemolymph; rather a hemocyanin is likely present. It is hypothesized that the presence of this tissue hemoglobin might somehow facilitate O_2 transport in the shallow, hypoxic habitat of this animal.

INTRODUCTION

Among the diverse chiton fauna on the shores of western North America, a single species of the suborder (or order) Lepidopleurina Thiele, 1910, *Leptochiton rugatus* (Carpenter in Pilsbry, 1892), is occasionally encountered in fair numbers living in shallow water, usually on the underside of large submerged rocks at low tide. Members of the Lepidopleurina, referred to collectively here as "lepidopleurid" chitons, are generally considered the most primitive of our living chitons based on their general lack of well developed and slitted insertion plates (usually in all eight valves), their gills which are few in number and placed posteriorly, and their unspecialized tegmentum and girdle features (Kaas & Van Belle, 1985). Fossil data also support this conclusion. Over 50 fossil lepidopleurid species are known from the Paleozoic and Mesozoic eras (Van Belle, 1981) and, of these, one is possibly a *Leptochiton, L. deshayesi* (Terquem, 1852) reported from the lower Jurassic period of the Mesozoic. In contrast, species assigned to other extant families are unknown from the Paleozoic and number fewer than 10 species from the Mesozoic (Van Belle, 1981; Hoare & Smith, 1984).

As in other groups with some ancient members, the primitive lepidopleurids seem to have persisted primarily in deep waters and have been collected from depths exceeding 7000 m (review by Ferreira, 1979). The absence of lepidopleurids in exposed intertidal habitats may reflect a fundamentally different functional arrangement of gills. Based on observations of actively respiring animals, Yonge (1939) argued that the posterior gill arrangement in the lepidopleurid species *Leptochiton asellus* was less efficient for aerial respiration than the more anterior gill placement of three modern chiton species he examined. Although Yonge based his conclusions on relatively few species, his generalities concerning the morphological and habitat differences between lepidopleurids and modern chitons are probably valid, judging from reviews of gill arrangements and collection depths of more than 200 chiton species by Eernisse (1984, 1985) and Kaas & Van Belle (1985, 1986). Yonge proposed that the innovation in gill arrangement by modern chitons led to the replacement of lepidopleurids in the intertidal. As discussed by Eernisse

[1] Send reprint requests to D.J.E. at Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

(1984), it is equally plausible that lepidopleurids never were able to colonize intertidal habitats, given their posterior gill placement. It is interesting, therefore, that *L. rugatus* can occur in shallow depths as well as in deeper waters (specimens identified as *L. rugatus* have been dredged from a depth of about 458 m). If most lepidopleurids are to some extent limited to deeper water by their gill morphology, the shallow habitat of *L. rugatus* may indicate a special adaptation to shallow water conditions.

It was with the unusual shallow-water habitat in mind that we noted the distinctive red coloration of the foot, gills, and other soft parts on the underside of *Leptochiton rugatus*. As far as we know, this condition is peculiar to *L. rugatus*, and may be peculiar to only shallow-water specimens of *L. rugatus* (R. N. Clark, personal communication). It is also our experience that *L. rugatus* tends to occur in locally dense populations on the bottoms of large rocks submerged in oxygen-poor mud. This study investigates the possibility that the red coloration of the soft parts of *L. rugatus* is caused by a circulating or noncirculating respiratory heme protein which might somehow facilitate respiration in shallow, oxygen-poor habitats.

MATERIALS AND METHODS

Leptochiton rugatus was collected intertidally in May 1986 on the western shores of San Juan Island, Washington, U.S.A. (48°03′N, 123°05′W), and animals were identified according to FERREIRA (1979). The animals studied measured about 6.5–8.0 mm in length.

Ten animals were dissected. An incision was made in the mantle cavity near the gills and a very small amount of hemolymph was collected from each animal. The foot and surrounding mantle tissue were then removed and homogenized in cold phosphate buffer (0.5 M NaCl, 0.05 M sodium phosphate buffer, pH 7.5) in a scintered glass micro-homogenizer. Radular muscles were extracted in the same manner. Animal hardparts were flattened and preserved in 70% ethanol as voucher specimens (DJE coll.). Homogenates and blood samples were centrifuged at 13,000 g for 2 min and supernatants were used in the following studies.

Samples were electrophoresed on a 7.5% polyacrylamide slab gel, pH 8.9, in the absence of denaturants or reducing agents. Samples were also treated with sodium dodecyl sulfate (SDS) and dithiothreitol and electrophoresed on a 12.5% polyacrylamide SDS slab gel (for hemoglobin) or a 4% polyacrylamide SDS slab gel (for hemocyanin) (RYAN *et al.*, 1985).

The extract of foot tissue was examined spectrophotometrically using a dual beam Gibson spectrophotometer. The foot tissue extract was also chromatographed on a calibrated column (1.7 × 24 cm) of Sephadex G-75 superfine in equilibrium with the extraction buffer.

RESULTS

When *Leptochiton rugatus* was bled, the hemolymph did not appear red nor did the red color of the animal's tissues become lighter. When the foot was removed from the animal, the foot tissue retained its red color.

Figure 1

SDS PAGE of *Leptochiton rugatus* hemolymph, 4% polyacrylamide. A, *Helix aspersa* hemocyanin; B, *Leptochiton rugatus* hemolymph; C, *Katharina tunicata* hemocyanin; D, *Octopus dofleini* hemocyanin; E, calibrants (myosin, B-galactosidase, phosphorylase B).

Examination by SDS gel electrophoresis of the very small sample of hemolymph obtained from 10 animals showed no hemoglobin-like subunits. Rather, a strongly staining protein that electrophoresed to the same position as the hemocyanin subunit of *Katharina tunicata* was observed (RYAN *et al.*, 1985) (Figure 1).

The extract of tissues of foot, gills, and surrounding mantle shows absorption maxima of 414,540, and 570 nm, similar to other myoglobins and hemoglobins. The α peak is shifted slightly to the violet and is lower in absorbance than the β peak; an absorbance ratio of α/β peaks of about 0.85 suggests that the protein is susceptible to oxidation and that some met-hemoglobin is present. Attempts to chemically deoxygenate the protein with sodium dithionite resulted in a typical loss of α and β peaks and the appearance of a smooth peak at about 555 nm. However, the Soret maximum was shifted to 422–423 nm and not to 432 nm as seen for other myoglobins and hemoglobins (LEMBERG & LEGGE, 1949). The most likely interpretation of these data is that either some of the hemoglobin was not deoxygenated, some remained in the oxidized met-state (or as some other derivative) or both.

Chromatography of the sample on a column of Sephadex G-75 superfine showed a broad peak with a molecular

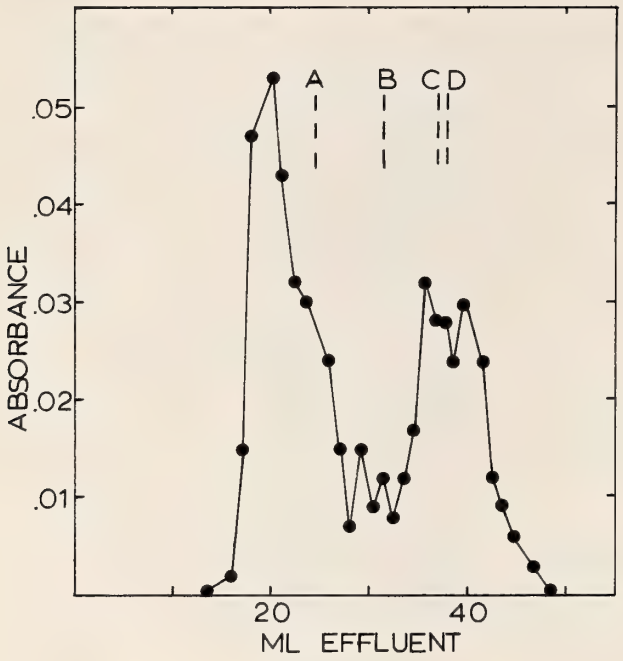


Figure 2

Chromatography of *Leptochiton rugatus* foot and mantle tissue extract on Sephadex G-75 superfine. Column buffer, 0.05 M sodium phosphate, pH 7.5, 0.5 M in NaCl. Calibrants: A, bovine serum albumen; B, *Katharina tunicata* dimeric myoglobin; C, sperm whale myoglobin; D, *Katharina tunicata* monomeric myoglobin. Absorbance at 416 nm.

weight slightly less than that of sperm whale myoglobin (Figure 2) and similar to radular muscle myoglobin of *Katharina tunicata* (Terwilliger & Read, 1970). Absorbance in the void volume was due to turbidity. SDS polyacrylamide gel electrophoresis of the foot and mantle tissue homogenate indicated a strong protein staining band with a molecular weight of about 15–16,000 (Figure 3D), similar to radular myoglobin of *K. tunicata* under the same gel conditions (Figure 3B). The radular muscles of *Leptochiton rugatus* are bright red, with an intensity similar to the redness of other chiton radular muscles (Terwilliger & Read, 1970). A prominent protein band from the radular muscles of *L. rugatus* (Figure 3C) migrated to the same distance upon SDS gel electrophoresis as myoglobins of *K. tunicata* (Figure 3B). Identification of the 15–16,000 molecular weight proteins of both foot and radular tissues as hemoglobin subunits was verified by cross-electrophoresing on SDS the red bands obtained by electrophoresis on a pH 8.9 gel in the absence of denaturants and reducing agents. Owing to very little tissue in both *L. rugatus* foot and radular muscle preparations and difficulty in collecting animals, more detailed studies were not undertaken.

DISCUSSION

Hemoglobins and myoglobins are widespread in mollusks, where they are found as circulating intra- and extracellular proteins and in tissues such as buccal muscles, heart, stomach, and nerves (Read, 1966; Terwilliger & Terwilliger, 1985). There have been no reports of hemoglobin or myoglobin in the Polyplacophora (chitons) except for myoglobins found in the bright red buccal musculature, where both monomeric and dimeric myoglobins are present (Terwilliger & Read, 1970). Furthermore, only hemocyanin has been reported as a circulating respiratory protein in chitons (Manwell, 1960; Van Holde & Miller, 1982; Ryan *et al.*, 1985). We find that *Leptochiton rugatus* resembles other chitons in having myoglobin in its radular muscles and having hemocyanin as its circulating respiratory protein. However, this is the first report of a more widespread presence of hemoglobin in other tissues of the chiton. We base our conclusion that the red color is due to a hemoglobin-like protein on (1) the protein's apparent molecular weight of 15–16,000 by gel chromatography and SDS gel electrophoresis and (2) its hemoglobin-like spectral absorption maxima which change upon deoxygenation with dithionite. Not enough hemoglobin was available for O_2-binding experiments. Experience with other tissue hemoglobins, however, suggests that because the protein is monomeric and not easily deoxygenated with dithionite, it likely has a high oxygen affinity. We are referring to this protein as a hemoglobin rather than a myoglobin because we do not know whether it is found in

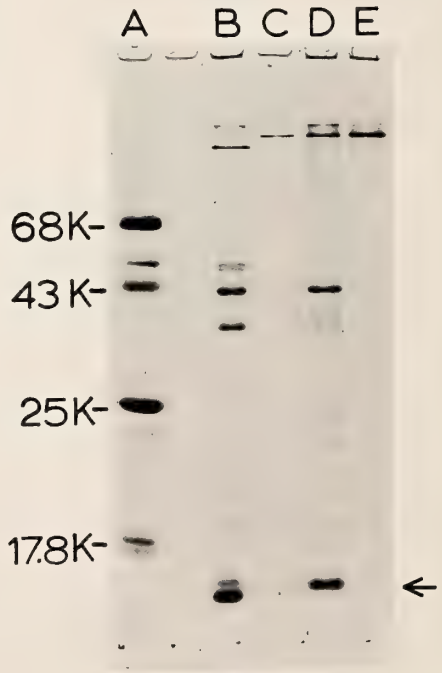


Figure 3

SDS PAGE of *Leptochiton rugatus* hemoglobin-containing tissues, 12.5% polyacrylamide. A, calibrants; B, *K. tunicata* radular muscle; C, *L. rugatus* radular muscle; D, *L. rugatus* foot and mantle tissue; E, *L. rugatus* hemolymph. Arrow indicates the position of tissue hemoglobin.

muscle fibers in all tissues in which it is present. The unusual shallow-water habitat for these chitons, under rocks that are submerged in mud, may point to a reason for the hemoglobin-rich tissue, in contrast to the presumed hemoglobin-poor tissue of lepidopleurids that occupy deep water. The presence of a high-affinity hemoglobin in *L. rugatus* might facilitate diffusion of oxygen to respiring tissues of this organism under hypoxic conditions.

Whatever the connection is between the previously mentioned posterior placement and fewer numbers of gill pairs typical of lepidopleurid chitons and their normal deep-water habitat, it remains a striking observation that, in contrast to modern chitons, there are few reported collections of lepidopleurid chitons from substrates exposed at low tide. This suggests to us that lepidopleurid chitons depend on aquatic, rather than aerial, respiration. Yet *Leptochiton rugatus* is found in a shallow-water habitat that appears oxygen poor; in fact, no modern chitons or other mollusks were observed on the same substrates heavily populated by *L. rugatus*. Moreover, at least two other lepidopleurid species have been reported from similar habitats. Iredale & Hull (1929) report *Terenochiton subtropicalis* (=*Leptochiton norfolcensis* [Hedley & Hull, 1912]) from the Sunday Islands, Kemadec Group (also known from New Zealand), collected living on the underside of embedded dirty stones below low water mark. Iredale & Hull (1929) also report collecting 60 to 80 specimens of the Australian species *Leptochiton badius* (Hedley & Hull, 1909) in one afternoon from under deeply buried stones between tide marks. A prediction consistent with our hypothesis, that the presence of tissue hemoglobins is related to the unusual habitat of *L. rugatus*, would be that the foot and other tissues of *L. subtropicalis* and *L. badius*, like those of *L. rugatus*, should be red as well.

ACKNOWLEDGMENTS

This work was supported by NSF grant OCE-8415258 to R. R. Strathmann and D. J. Eernisse and by NSF grant DMB-8511150 to N. B. Terwilliger and R. C. Terwilliger. We thank Dr. A. O. D. Willows for use of facilities at Friday Harbor Laboratories, University of Washington.

LITERATURE CITED

Eernisse, D. J. 1984. *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora), from the Pacific Coast of the United States: systematics and reproduction. Ph.D. Thesis, University of California, Santa Cruz. 358 pp.

Eernisse, D. J. 1985. The significance of gill placement in chitons. West. Soc. Malacol. Ann. Rept. 17 (for 1984):8–9 (abstract).

Ferreira, A. J. 1979. The family Lepidopleuridae (Mollusca: Polyplacophora) in the eastern Pacific. Veliger 22:145–165.

Hoare, R. D. & A. G. Smith. 1984. Permian Polyplacophora (Mollusca) from west Texas. Jour. Paleontol. 58:82–103.

Iredale, T. & A. F. B. Hull. 1929. The loricates of the Neozelanic region (1). Austral. Zool. 6:75–95.

Kaas, P. & R. A. Van Belle. 1985. Monograph of living chitons (Mollusca: Polyplacophora). Vol. 1. Order Neoloricata: Lepidopleurina. E. J. Brill/Dr. W. Backhuys: Leiden. 240 pp.

Kaas, P. & R. A. Van Belle. 1986. Monograph of living chitons (Mollusca: Polyplacophora). Vol. 2. Suborder Ischnochitonina, Ischnochitonidae: Schizoplacinae, Callochitoninae, & Lepidochitoninae. E. J. Brill/Dr. W. Backhuys: Leiden. 198 pp.

Lemberg, R. & J. W. Legge. 1949. Hematin compounds and bile pigments. Interscience: New York. 749 pp.

Manwell, C. 1960. Comparative physiology: blood pigments. Ann. Rev. Physiol. 22:191–244.

Read, K. R. H. 1966. Molluscan hemoglobin and myoglobin. Pp. 209–232. *In:* K. M. Wilbur & C. M. Yonge (eds.), Physiology of Mollusca. Vol. 2. Academic Press: New York. 645 pp.

Ryan, M., N. B. Terwilliger, R. C. Terwilliger & E. Schabtach. 1985. Chiton hemocyanin structure. Comp. Biochem. Physiol. 80B:647–656.

Terwilliger, R. C. & K. R. H. Read. 1970. The radular muscle myoglobins of the amphineuran molluscs, *Katharina tunicata* Wood, *Cryptochiton stelleri* Middendorf, and *Mopalia muscosa* Gould. Int. Jour. Biochem. 1:281–291.

Terwilliger, R. C. & N. B. Terwilliger. 1985. Molluscan hemoglobins. Comp. Biochem. Physiol. 81B:255–261.

Van Belle, R. A. 1981. Catalogue of fossil chitons. Dr. W. Backhuys, Publisher: Rotterdam. 84 pp.

Van Holde, K. E. & K. I. Miller. 1982. Haemocyanins. Quart. Rev. Biophys. 15:1–129.

Yonge, C. M. 1939. On the mantle cavity and its contained organs in the Loricata (Placophora). Quart. Jour. Microsc. Sci. 81:367–390.

The Veliger 30(3):248–256 (January 4, 1988)

THE VELIGER

Chromosomes of Some Subantarctic Brooding Bivalve Species

by

CATHERINE THIRIOT-QUIEVREUX

Université P. et M. Curie, Station Zoologique, 06230 Villefranche-sur-Mer, France

JACQUES SOYER AND MARC BOUVY

Université P. et M. Curie, Laboratoire Arago, UA 117, 66650 Banyuls-sur-Mer, France

AND

JOHN A. ALLEN

University Marine Biological Station Millport, Isle of Cumbrae, Scotland KA28 0EG

Abstract. Chromosomes of three subantarctic brooding bivalve species have been studied in relation to their type of development and the evolutionary distance between their taxonomic categories. *Gaimardia trapesina* (Gaimardiidae) has a diploid chromosome number of 2n = 38, with 8 chromosome pairs of metacentrics, 7 pairs of submetacentrics, and 4 pairs of subtelocentrics. *Kidderia bisulcata* (Cyamiidae) has 2n = 38, with 3 pairs of metacentrics, 4 pairs of submetacentrics, 7 pairs of subtelocentrics, and 5 pairs of telocentrics. *Kidderia minuta,* another species of Cyamiidae, has 2n = 36, with 3 pairs of metacentrics, 2 pairs of submetacentrics, 8 pairs of subtelocentrics, and 5 pairs of telocentrics. The karyological features of these species are not related to direct development and the brooding of the developing eggs. Evolutionary considerations based on comparison of the chromosomes of the families investigated (the Gaimardiidae and the Cyamiidae) suggest that they are phylogenetically primitive. The recent transfer of *Kidderia bisulcata* (=*Hiatella bisulcata*) from the Hiatellidae (Myoida) to the Cyamiidae (Veneroida) is questioned, and further morphological study is required to determine its true taxonomic position. It is also clear that the evolutionary pattern of karyological features remains unsatisfactory without further investigations of eulamellibranch species.

INTRODUCTION

Cytogenetic studies of chromosome number and morphology might not only show genetic variation between species and populations, but also evolutionary relationships within different taxonomic groups. The knowledge of the chromosomes in the Bivalvia has increased over the last 15 years. NAKAMURA (1985) reviewed recent investigations on chromosomes of 125 bivalve species belonging to 22 of the 102 Recent families. Of these 125 species, 73 belong to the Mytilidae, Pectinidae, Ostreidae, and Unionacea; the other species are scattered mostly within the Pteriomorpha, with fewer within the Heterodonta. Thus, evolutionary interpretation of karyological characteristics remains hazardous without further investigations, especially as the chromosomes of the primitive groups of bivalves have rarely been investigated. Exceptions are two species of Solemyidae (IEYAMA, 1982) and seven species of Arcidae (IEYAMA, 1975, 1983, 1984a, b). A further point of interest concerning primitive bivalves is that non-planktotrophic development appears to be the rule for primitive groups, such as the Protobranchia, Septibranchia, and the eulamellibranch superfamilies Lucinacea and Crassatellacea (JABLONSKI & LUTZ, 1983). Most other bivalve species have planktotrophic development.

Non-planktotrophic development combined with brood protection constitutes a specialized type of development that occurs among some primitive superfamilies (Arcacea,

Leptonacea, and Cyamiacea). Antarctic Bivalvia have a relatively large percentage of species within these superfamilies (DELL, 1972; ARNAUD, 1974; RICHARDSON, 1979).

In a research program on the evolutionary genetics of benthic species from the subantarctic Kerguelen Islands, we selected four species (with direct development and brooding of young) in order to study their chromosomes and to appreciate whether their karyological features may reflect a development type or a phylogenetic trend.

The present paper gives karyological data on three of these species, namely: *Gaimardia trapesina* (Lamarck, 1819) (Heterodonta, Veneroida, Gaimardiacea, Gaimardiidae); *Kidderia bisulcata* (Smith, 1879); and *Kidderia minuta* (Dall, 1876) (Heterodonta, Veneroida, Cyamiacea, Cyamiidae). Because of their peculiar characteristics, the chromosomes of the fourth species investigated, *Lasaea consanguinea* (Smith, 1877) (Heterodonta, Veneroida, Leptonacea, Lasaeidae), are to be described in a separate paper.

Classification follows NEWELL, 1969 (see also, OLDFIELD, 1964; PONDER, 1967; SIMPSON, 1977; MORTON, 1979; RICHARDSON, 1979; BOSS, 1982; O'FOIGHIL, 1986). Detailed comparisons have been made with Antarctic material housed in the British Museum (Natural History).

MATERIALS AND METHODS

Sampling

Populations of *Kidderia minuta* were collected by hand at low tide in the intertidal zone under rocks in a well sheltered area "Halage des Swains," in the southwest part of the Gulf of Morbihan, Kerguelen Islands.

Specimens of *Kidderia bisulcata* and *Gaimardia trapesina* were collected among algae in minute pools of a small reef, exposed only at low tide at Ratmanoff, on the east coast of the Kerguelen Islands.

Chromosome Preparations

Whole animals were treated 2–4 h with 0.005% colchicine in seawater. Then the bodies were removed from their shells under the dissecting microscope and treated 40 min in 0.9% sodium citrate. The material was then fixed in a freshly prepared mixture of absolute alcohol and acetic acid (3:1) with three changes of 20 min duration. Each slide preparation was made from three to five bodies following an air-drying technique (THIRIOT-QUIÉVREUX & AYRAUD, 1982). The preparations were stained with Giemsa (4%, pH 6.8) and photographs of suitable metaphases were taken with a Zeiss II photomicroscope. Cell divisions were mainly observed in gonadic tissue.

Data Analysis

The number of chromosomes seen in the photomicrographs of at least 30 spread metaphases were counted for each species. Then the photographs of individual chromosomes from the better spreads were cut out and arranged in pairs on the basis of size and centromere position for the karyotypes.

Measurements of chromosomes were made with a digitizer (Bit Pad 10, Summa graphic), interfaced with a Victor S1 microcomputer (THIRIOT-QUIÉVREUX, 1984). Relative length or percent total complement length was expressed as 100 times the absolute chromosome pair length divided by the total length of the haploid complement. Centromeric indexes (Ci) were calculated by dividing 100 times the length of the short arm by the total chromosome length. Terminology relating to centromeric position follows that of Levan *et al.* (1964). A chromosome is metacentric (m) if Ci falls in the range 37.5–50.0, submetacentric (sm) if Ci is 25.0–37.5, subtelocentric (st) if Ci is 12.5–25.0, and telocentric (t) if Ci is 0.0–12.5. When a centromere position was found to be on the borderline between two different categories the confidene limit of the means was calculated as $P = 0.05$ and two chromosome categories are listed. The arm ratio is calculated as length of short arm divided by the length of the long arm. The centromeric index and the arm ratio are given, as both express centromeric position and allow comparison with previous studies.

RESULTS

Gaimardia trapesina

The chromosomes of 31 mitotic metaphase spreads were counted. Seventeen cells showed $2n = 38$, 14 cells had an aneuploid number of 33 to 37. A haploid number of 19 was counted in three meiotic metaphases. Thus the diploid chromosome number for this species is $2n = 38$.

Means and standard deviations of relative length, arm ratio, and centromeric index for seven well-spread metaphases from different animals are given in Table 1.

From data on relative length, we recognize five groups of chromosome pairs of decreasing size and, from the centromeric index, we characterize the morphological type of each chromosome pair. Thus, the karyotype (Figure 1) of *Gaimardia trapesina* consists of:

- Group I: pair 1 metacentric, obviously larger than the remainder.
- Group II: pairs 2, 3, 4, 5, 7 submetacentric; pair 6 subtelocentric.
- Group III: pairs 8 and 9 submetacentric; pair 10 subtelocentric to submetacentric, pair 11 subtelocentric.
- Group IV: pairs 12 to 15 metacentric.
- Group V: pairs 16 to 18 metacentric and pair 19 subtelocentric.

In order to visualize better the different types of chromosome pairs, we have constructed an ideogram from centromeric indexes and relative length values. The ideogram for *Gaimardia trapesina* (Figure 2) shows a conspicuous

Table 1

Chromosome measurements and classification in seven cells for *Gaimardia trapesina*.

Group	Chromosome pair number	Relative length		Arm ratio		Centromeric index		Classification
		Mean	SD	Mean	SD	Mean	SD	
I	1	11.92	0.914	0.811	0.058	44.61	1.858	m
II	2	6.69	0.307	0.464	0.043	31.53	1.979	sm
II	3	6.23	0.308	0.413	0.054	29.00	2.800	sm
II	4	6.11	0.258	0.448	0.043	30.66	2.153	sm
II	5	5.87	0.269	0.490	0.051	32.73	2.379	sm
II	6	5.61	0.523	0.306	0.059	23.19	3.567	st
II	7	5.51	0.494	0.428	0.120	28.43	4.166	sm
III	8	5.21	0.438	0.506	0.050	33.34	2.264	sm
III	9	5.11	0.501	0.478	0.051	32.11	2.357	sm
III	10	5.06	0.614	0.335	0.088	24.70	4.834	st–sm
III	11	4.75	0.726	0.296	0.061	22.57	3.577	st
IV	12	4.49	0.433	0.810	0.115	44.38	3.569	m
IV	13	4.33	0.279	0.873	0.077	46.23	2.131	m
IV	14	4.19	0.383	0.848	0.150	45.40	4.219	m
IV	15	4.11	0.541	0.819	0.173	44.28	6.271	m
V	16	3.91	0.304	0.937	0.698	48.08	1.794	m
V	17	3.80	0.223	0.893	0.158	46.44	4.536	m
V	18	3.66	0.318	0.861	0.061	45.90	1.745	m
V	19	3.37	0.456	0.295	0.110	22.14	6.862	st

disparity of size between the pair 1 and the other pairs. Three different types of chromosomes are present: metacentric, submetacentric, and subtelocentric.

We summarize karyological data for this species with the formula: 2n = 38 = 8m, 7sm, 4st = 15m–sm/4st.

Kidderia bisulcata

The chromosome of 35 mitotic metaphases were counted. Twenty-eight cells had 2n = 38, 7 cells had 2n = 36 or 37. Meiotic metaphases were abundant and we scored 36 cells, of which 32 showed a haploid number of 19 and

Figure 1

Karyotype of *Gaimardia trapesina*.

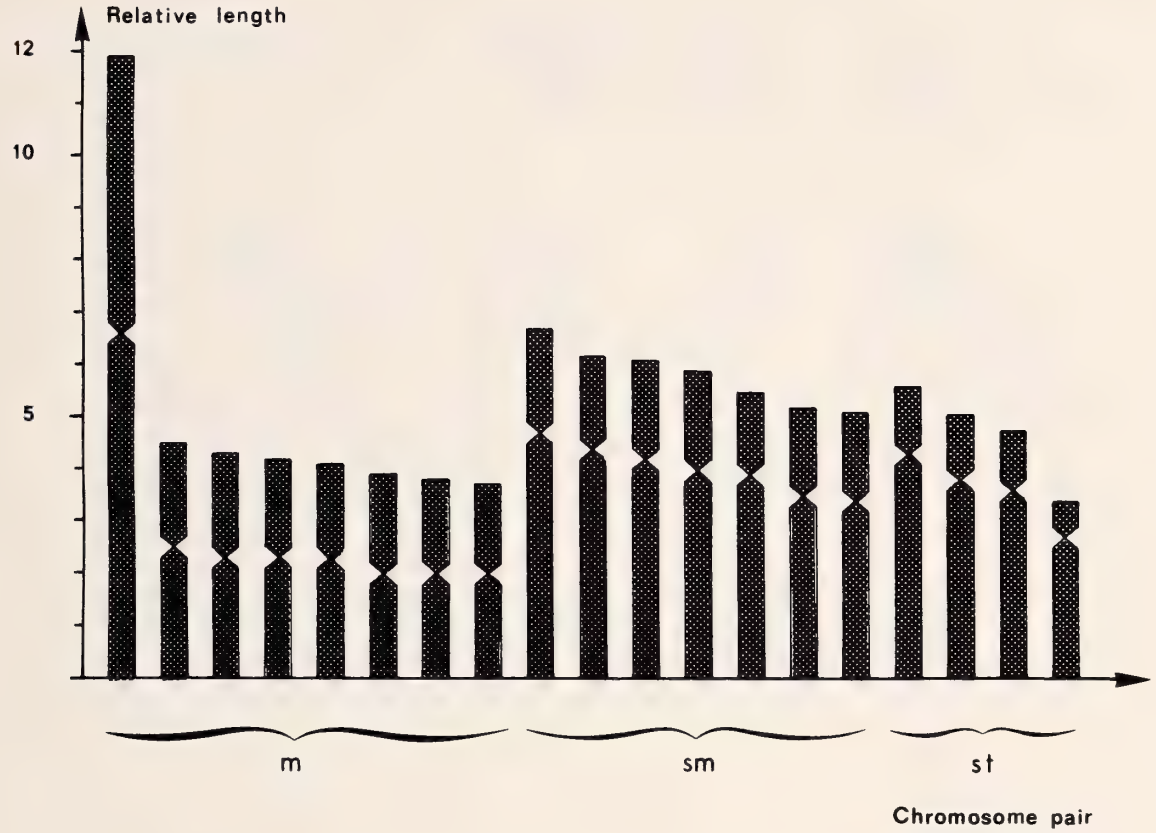


Figure 2

Ideogram of the different types of chromosomes for *Gaimardia trapesina.*

Table 2

Chromosome measurements and classification in eight cells for *Kidderia bisulcata.*

Group	Chromosome pair number	Relative length		Arm ratio		Centromeric index		Classification
		Mean	SD	Mean	SD	Mean	SD	
I	1	8.24	1.075	0.685	0.180	39.76	6.603	m
I	2	7.27	0.535	0.102	0.015	9.24	1.294	t
I	3	6.65	0.272	0.425	0.163	28.49	6.714	sm
II	4	6.39	0.522	0.107	0.034	9.55	2.783	t
II	5	6.38	0.437	0.309	0.107	23.01	5.987	st
II	6	6.05	0.370	0.288	0.118	21.78	6.193	st
II	7	5.69	0.534	0.129	0.028	11.40	2.216	t–st
II	8	5.66	0.282	0.213	0.172	15.71	6.901	st
III	9	5.36	0.155	0.127	0.027	11.15	2.114	t–st
III	10	5.33	0.469	0.139	0.028	12.11	2.138	t–st
III	11	5.32	0.356	0.695	0.105	39.68	5.743	m
III	12	4.99	0.343	0.435	0.076	29.76	3.106	sm
III	13	4.95	0.323	0.343	0.081	25.03	4.591	sm–st
IV	14	4.13	0.593	0.180	0.041	15.09	2.968	st
IV	15	3.91	0.350	0.199	0.083	16.01	4.778	st
IV	16	3.85	0.449	0.455	0.092	30.80	4.600	sm
IV	17	3.54	0.564	0.196	0.055	16.10	3.773	st
IV	18	3.35	0.470	0.203	0.045	16.56	2.944	st
V	19	2.86	0.324	0.709	0.180	40.51	6.382	m

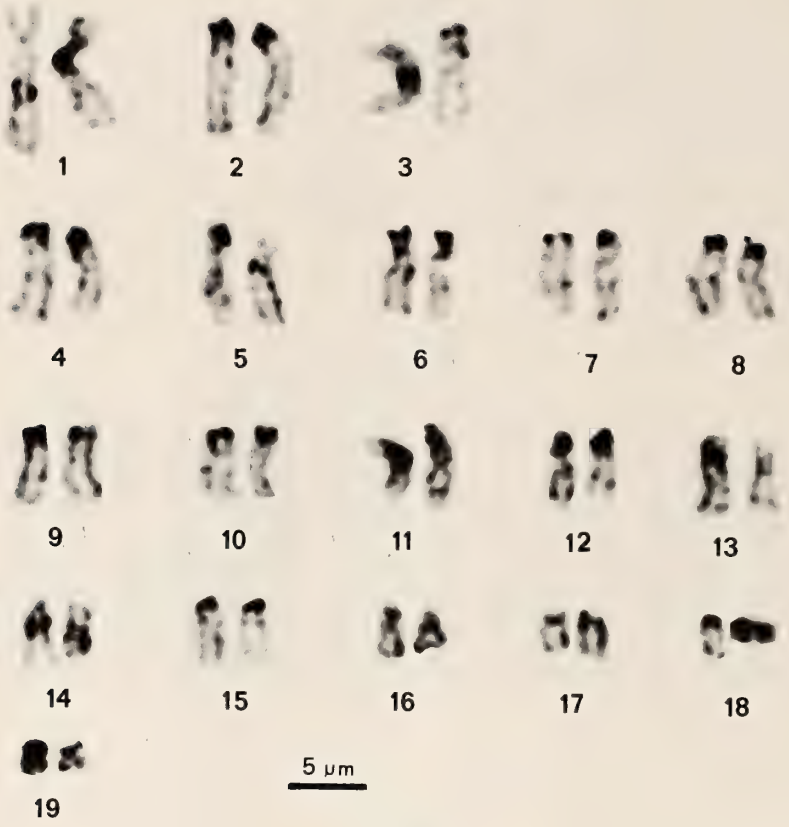


Figure 3

Karyotype of *Kidderia bisulcata*.

2 with 18. Thus, the diploid chromosome number for this species is 2n = 38.

For karyotyping, eight well-spread metaphases from different animals were analyzed (Table 2). The karyotype (Figure 3) of *Kidderia bisulcata* consists of five groups of chromosome pairs with a regular decrease in size:

Group I: pair 1 metacentric, pair 2 telocentric, pair 3 submetacentric.

Group II: pairs 4–8 subtelocentric or telocentric. The pairs 4 and 5, 7 and 8 are very close in relative length and it is difficult to identify them with rigor; however, the position of the centromere is always telocentric in pair 4 and telocentric to subtelocentric in pair 7.

Group III: pairs 9 and 10 are very similar, telocentric to subtelocentric, pair 11 metacentric, pair 12 submetacentric, pair 13 submetacentric–subtelocentric. The last two pairs are also very similar and can be confused.

Group IV: pairs 14 and 15 subtelocentric, pair 16 submetacentric, pairs 17 and 18 subtelocentric.

Group V: pair 19 metacentric and obviously the smallest.

The ideogram (Figure 4) shows the distribution of the four chromosome types. We summarize karyological data for this species with the formula: 2n = 38 = 3m, 4sm, 7st, 5t = 7m–sm/12st–t.

Kidderia minuta

The chromosomes of 36 mitotic metaphases were counted. Twenty-nine cells had 2n = 36, 7 cells had an aneuploid diploid number varying from 32 to 36. Ten meiotic metaphases were also counted, 9 with n = 18, 1 with n = 19. The diploid chromosome number for this species is 2n = 36.

The chromosome measurements and classification were analyzed for seven examples of well-spread metaphases, each from a different animal (Table 3).

The karyotype (Figure 5) consists of six groups of chromosome pairs of decreasing size, the first group being much larger than the other groups, for the latter rank order of decreasing size is relatively regular:

Group I: pair 1 metacentric.

Group II: pair 2 telocentric, pair 3 metacentric, pairs 4 and 5 telocentric.

Group III: pair 6 submetacentric–subtelocentric, pair 7 telocentric, pair 8 metacentric, pair 9 telocentric.

Group IV: pairs 10 to 12 subtelocentric.

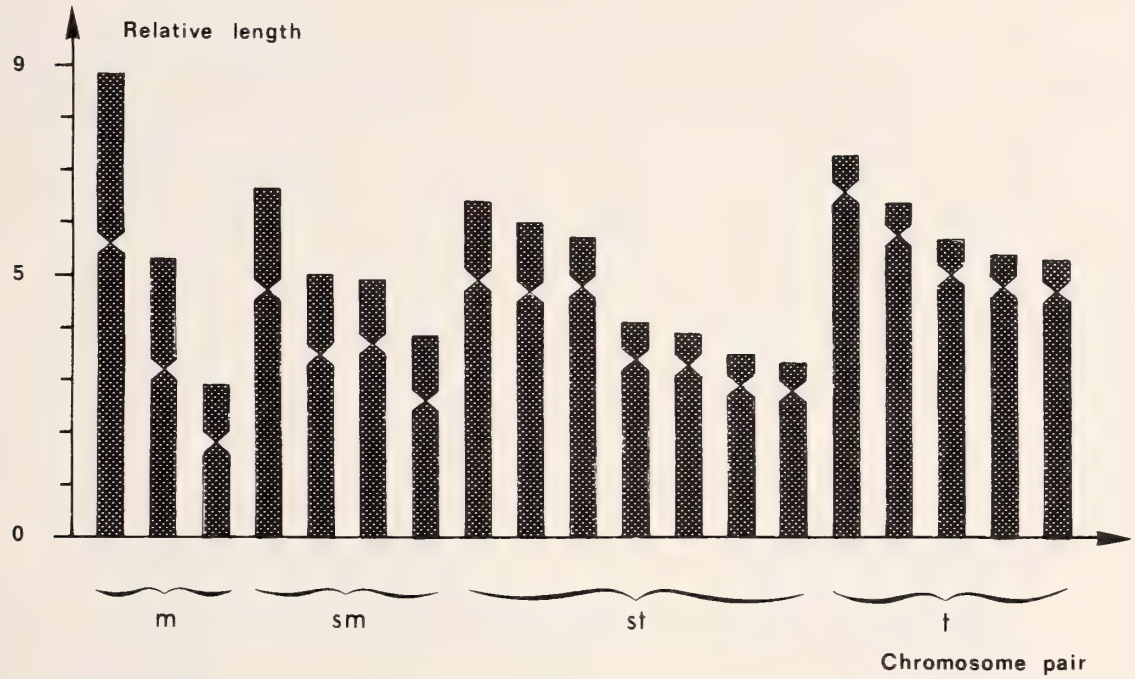


Figure 4

Ideogram of the different types of chromosomes for *Kidderia bisulcata.*

Group V: pairs 13 to 15 subtelocentric.
Group VI: pairs 16 and 17 subtelocentric, pair 18 submetacentric–metacentric.

The ideogram (Figure 6) clearly shows the disparity of size between pair 1 and the other pairs. Four morphological types of chromosomes are present but subtelocentric and telocentric types are dominant in this species.

We summarize karyological data for this species with the formula: 2n = 36 = 3m, 2sm, 8st, 5t = 5m–sm/13st–t.

DISCUSSION

There is considerable debate in the literature as to the exact relationships of the Gaimardiacea and the Cyamiacea (MORTON, 1979). Until recently, both superfamilies were included in the Veneroidea although widely separated in the classification of the order (NEWELL, 1969). MORTON (1979) in his study on *Neogaimardia finlayi* questioned this and concluded that the gaimardiids were closely related to the cyamiids, however, admitting that more comprehensive studies were necessary to be certain. PONDER (1971) included the Gaimardiinae as a subfamily in the Cyamiacea. Furthermore, BOSS (1982) transferred the genus *Kidderia* from the subfamily Gaimardiinae to the family Cyamiidae and, following PONDER (1971), he reinstated the Gaimardiidae to family rank.

The problem is further complicated by the fact that *Kidderia bisulcata* was originally described as a species of *Saxicava* (=*Hiatella*) by SMITH (1879). It was still regarded as such by POWELL (1957) but later considered to be a species of *Kidderia* by DELL (1969). The shell features, including radial grooves, elongate opisthodetic ligament, and hinge structure, would lead one to conclude that it is a hiatellacean species. In contrast, *K. minuta* has no radial grooves and a much thinner hinge plate with cardinal teeth of a different form, although the opisthodetic ligament (more internal in position) is massive and elongate.

Although detailed morphological comparisons need to be carried out, comparison of the karyological data of these three brooding bivalve species does not show close relationship. Moreover, a fourth brooding species investigated, *Lasaea consanguinea,* is totally different, in showing an unusually high number of chromosomes (THIRIOT-QUIÉVREUX *et al.*, in press).

Karyological features are generally species specific and consequently could be related to the evolutionary distance between taxonomic categories. Chromosome data for veneroid bivalves are only recorded for more recent families, such as the Cardiidae, Mactridae, Donacidae, Corbiculidae, Pisididae, and Veneridae (NAKAMURA, 1985) and the diploid chromosome complement is 2n = 36 or 2n = 38 (except for the Pisididae). Three species of Veneridae have been karyologically investigated and show 2n = 38 = 19m–sm (IEYAMA, 1980). We have found the same karyological data for *Ruditapes philippinarum,* another venerid species (personal observations). Nevertheless, within the Cardiidae, a family with a more primitive phylogenetic position, one species, *Cerastoderma edule,* shows karyological data

Table 3

Chromosome measurements and classification in seven cells for *Kidderia minuta*.

Group	Chromosome pair number	Relative length		Arm ratio		Centromeric index		Classification
		Mean	SD	Mean	SD	Mean	SD	
I	1	14.64	0.836	0.783	0.070	43.55	2.393	m
II	2	8.04	0.734	0.094	0.022	8.57	1.842	t
II	3	6.87	0.697	0.851	0.108	45.73	3.134	m
II	4	6.75	0.709	0.102	0.024	9.18	2.059	t
II	5	6.17	0.577	0.106	0.014	9.57	1.168	t
III	6	5.75	0.599	0.374	0.075	26.89	3.999	sm–st
III	7	5.61	0.367	0.123	0.019	10.91	1.541	t
III	8	5.38	0.591	0.751	0.148	42.31	4.657	m
III	9	5.24	0.348	0.124	0.028	10.89	2.215	t
IV	10	4.68	0.366	0.311	0.122	21.84	5.232	st
IV	11	4.57	0.211	0.155	0.045	13.31	3.176	st
IV	12	4.49	0.245	0.154	0.022	13.23	1.627	st
V	13	4.24	0.227	0.173	0.043	14.60	3.160	st
V	14	3.98	0.201	0.153	0.022	13.23	1.732	st
V	15	3.86	0.332	0.327	0.130	22.68	5.947	st
VI	16	3.39	0.441	0.166	0.046	14.01	3.476	st
VI	17	3.28	0.308	0.186	0.050	15.41	3.542	st
VI	18	2.99	0.415	0.643	0.336	36.40	14.695	sm–m

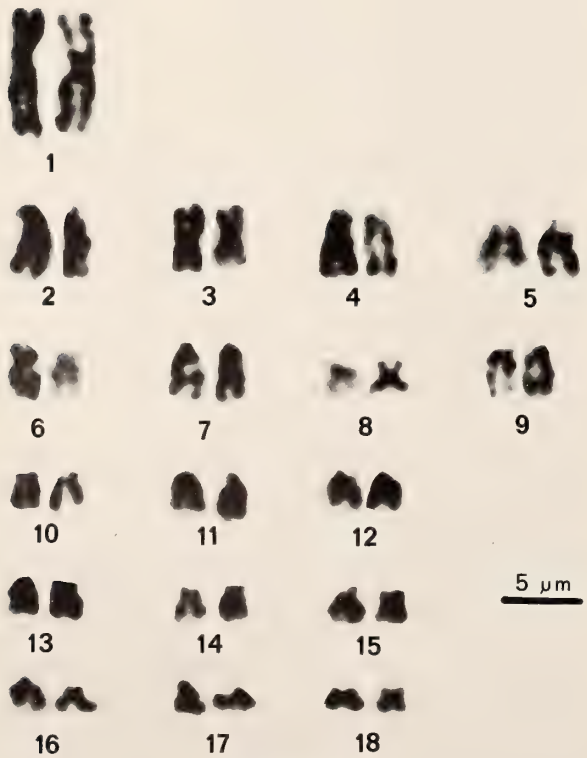


Figure 5

Karyotype of *Kidderia minuta*.

of 2n = 38 = 7sm/12st-t (KOULMAN & WOLFF, 1977). The two species of the family Cyamiidae studied here, *Kidderia bisulcata* with 2n = 38 = 7m-sm/12st-t and *K. minuta* with 2n = 36 = 5m-sm/13st-t are karyologically closer to the Cardiidae than to the Veneridae so far investigated. As reported above there is some doubt as to whether *K. bisulcata* is a cyamiid, but both species are characterized by a variable diploid complement and the presence of the four chromosomal types, the majority being st-t.

A variable number of chromosomes combined with the presence of st-t chromosomes reflects variable karyotypes (WHITE, 1973). In contrast, a majority of m-sm chromosomes suggests a stable karyotype (NAKAMURA, 1985). Thus, the karyotypes of two species of Cyamiidae and one species of Cardiidae seem less stable than those of karyologically known species of the family Veneridae. *Gaimardia trapesina,* with a majority of metacentrics, submetacentrics, and a few subtelocentrics, could tentatively be considered to show a more stable karyotype and therefore have an intermediate position between the Cyamiidae and the Veneridae. But without further investigation of other species of the Veneroida, the evolutionary pattern of karyological features remains incomplete and unsatisfactory.

All the evidence points to the fact that the three species studied here are phylogenetically separated and supports the earlier determinations that the Cyamiacea and Gaimardiacea are distinct from each other. So-called *Kidderia bisulcata* may indeed be a species of *Hiatella* (=*Saxicava*). The issue is made more complex by convergence of form

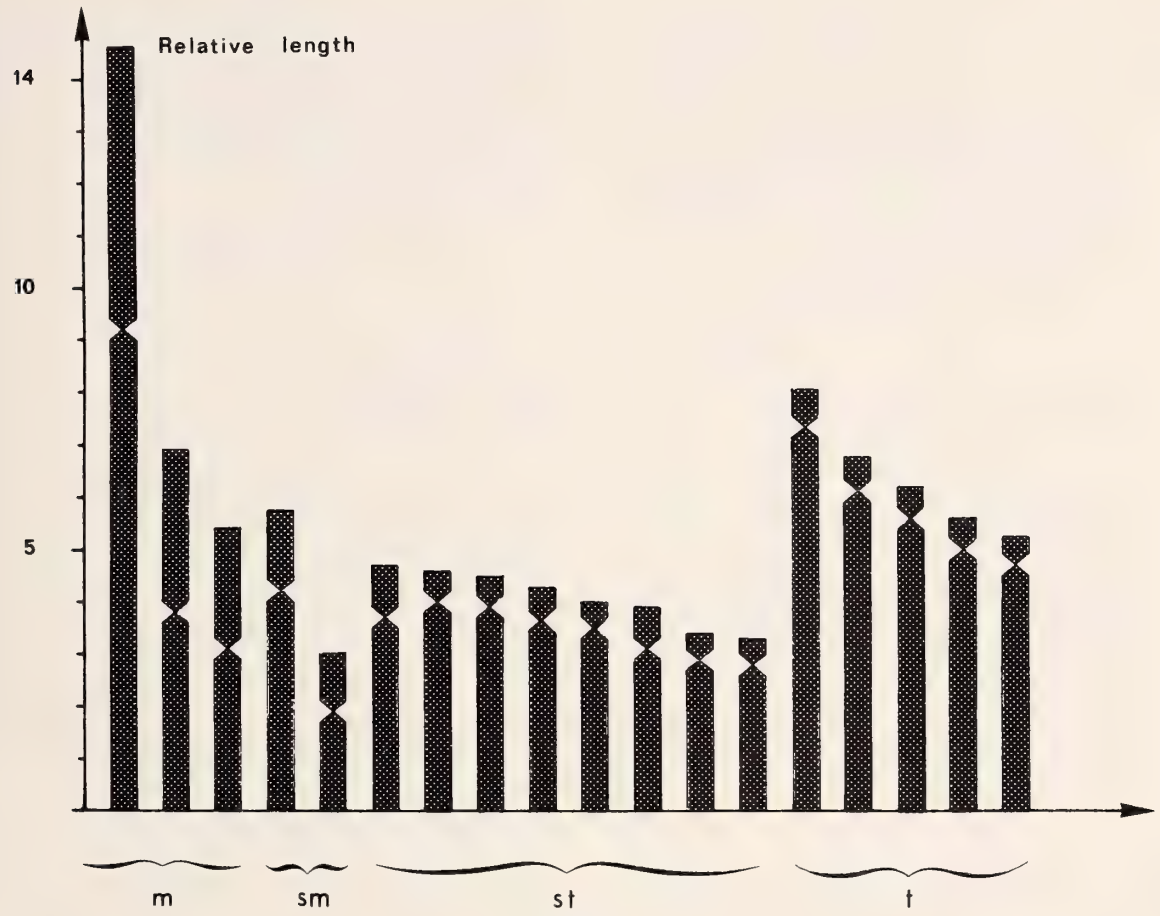


Figure 6

Ideogram of the different types of chromosomes for *Kidderia minuta*.

and reproduction in bivalves of southern high latitudes, which will be the object of further studies.

ACKNOWLEDGMENTS

This work is part of a research program on the evolutionary genetics of benthic species from the Kerguelen region sponsored by the T.A.A.F. (Terres Australes et Antarctiques Françaises). We are especially grateful to the staff of the "Mission de la Recherche," T.A.A.F. for assistance in obtaining specimens in the field at Kerguelen. We also thank P. Albert and G. Quelard for their excellent technical assistance.

LITERATURE CITED

ARNAUD, P. M. 1974. Contribution à la bionomie benthique des régions antarctiques et subantarctiques. Tethys 6:465–653.

BOSS, R. T. 1982. Mollusca. Pp. 945–1166. *In:* S. Q. Parker (ed.), Synopsis and organization of living organisms. McGraw-Hill: New York.

DELL, R. K. 1969. Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. Disc. Rept. 33:93–250.

DELL, R. K. 1972. Antarctic benthos. Adv. Mar. Biol. 10:1–216.

IEYAMA, H. 1975. Chromosome numbers of three species in three families of Pteriomorphia (Bivalvia). Venus 34:26–32.

IEYAMA, H. 1980. Studies on the chromosomes in three species of the Veneridae (Bivalvia). Venus 39:49–55.

IEYAMA, H. 1982. Karyotypes in two species of the Solemyidae (Bivalvia, Cryptodonta). Venus 40:232–236.

IEYAMA, H. 1983. Somatic chromosomes of the arcid *Arca boucardi* (Bivalvia, Pteriomorphia). Chromosome Inf. Serv. 35: 3–4.

IEYAMA, H. 1984a. Chromosomes of six species in three families of Pteriomorphia (Bivalvia). Venus 43:106–111.

IEYAMA, H. 1984b. Chromosome numbers in three species of bivalves (Pteriomorpha: Mollusca). Chromosome Inf. Serv. 36:15–16.

JABLONSKI, D. & R. A. LUTZ. 1983. Larval ecology of marine invertebrates: paleobiological implications. Biol. Rev. 58:21–89.

KOULMAN, J. G. & W. S. WOLFF. 1977. The Mollusca of the estuarine region of the rivers Rhin, Meuse and Scheldt in relation to the hydrography of the area. V. The Cardidae. Basteria 41:21–32.

LEVAN, A., K. FREDGA & A. A. SANDBERG. 1964. Nomenclature for centromere position in chromosomes. Hereditas 52: 101–220.

MORTON, B. 1979. The biology, functional morphology and taxonomic status of *Gaimardia* (*Neogaimardia*) *finlayi* (Bivalvia Gaimardiidae). Jour. Zool. 188:123–142.

NAKAMURA, H. K. 1985. A review of molluscan cytogenetic information based on the CISMOCH-computerized system for molluscan chromosomes. Bivalvia, Polyplacophora and Cephalopoda. Venus 44:193–225.

NEWELL, N. D. 1969. Outline of classification. Pp. 218–224. *In:* R. C. Moore (ed.), Treatise on invertebrate palaeontology, Part N 1: Mollusca 6. Bivalvia. Univ. Kansas Press: Lawrence.

O'FOIGHIL, D. 1986. Prodissoconch morphology is environmentally modified in the brooding bivalve *Lasaea subviridis*. Mar. Biol. 92:517–524.

OLDFIELD, E. 1964. The reproduction and development of some members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchia). Proc. Malacol. Soc. Lond. 36:79–120.

PONDER, W. F. 1967. Observations on the living animals and mode of life of some New Zealand erynacean bivalves. Trans. Roy. Soc. N.Z. Zool. 10:21–32.

PONDER, W. F. 1971. Some New Zealand and subantarctic bivalves of the Cyamiacea and Leptonacea with descriptions of new taxa. Rec. Dom. Mus. Wellington 7:119–141.

POWELL, A. W. B. 1957. Antarctic and subantarctic Mollusca. Rec. Auckland Inst. Mus. 5:117–193.

RICHARDSON, M. G. 1979. The ecology and reproduction of the brooding Antarctic bivalve *Lissarca miliaris*. Brit. Ant. Surv. Bull. 44:125–142.

SIMPSON, R. D. 1977. The reproduction of some littoral molluscs from Macquaries Island (sub-Antarctic). Mar. Biol. 44:125–142.

SMITH, E. A. 1879. An account of petrological, botanical and zoological collections made in Kerguelen's land and Rodriguez during the years 1874–75. Phil. Trans. Roy. Soc. Lond. 168:167–192.

THIRIOT-QUIEVREUX, C. 1984. Chromosome analysis of three species of *Mytilus* (Bivalvia: Mytilidae). Mar. Biol. Lett. 5: 265–273.

THIRIOT-QUIEVREUX, C. & N. AYRAUD. 1982. Les caryotypes de quelques espèces de bivalves et de gastéropodes marins. Mar. Biol. 70:165–172.

THIRIOT-QUIEVREUX, C., J. SOYER, F. DE BOVEE & P. ALBERT. In press. Unusual chromosome complement in the brooding bivalve *Lasaea consanguinea*. Genetica.

WHITE, H. S. D. 1973. Animal cytology and evolution. 3rd ed. Cambridge University Press. 961 pp.

The Veliger 30(3):257–266 (January 4, 1988)

THE VELIGER

Reproduction and Growth of the Brooding Bivalve *Transennella tantilla*

by

MARY ANN ASSON-BATRES[1]

University of Oregon, Institute of Marine Biology,
Charleston, Oregon 97420, U.S.A.

Abstract. *Transennella tantilla* from the South Slough of Coos Bay, Oregon, grow and reproduce year-around. Fecundity and release of young are seasonally variable. Males are smaller than females, and the transition from male to female is progressive over a broad size range, supporting histologic studies that indicate the species is protandric. Mortality is primarily focused on the largest size classes (>2.0 mm, shell length) and appears to be caused by intense seasonal predation. Individuals of *T. tantilla* are larger and appear to be more abundant in False Bay on San Juan Island, Washington, than in the South Slough of Coos Bay. Because these differences are so striking, several life-history traits of animals from the two areas were compared. In False Bay, males reach larger sizes and females begin brooding when larger; egg size is similar, but False Bay females have smaller broods and release young at a larger size than females in South Slough. The fecundity of female *T. tantilla* from both geographic locations is a linear function of body size.

INTRODUCTION

The venerid bivalve *Transennella tantilla* (Gould, 1852) inhabits intertidal soft-substrate communities from Alaska to Lower California (Keen, 1937). Its maximal size varies with geographic location; the reported range is 5.30–7.00 mm in shell length (Gray, 1978; Asson-Batres, 1982). It has been described as a protandrous hermaphrodite (Hansen, 1953). It is ovoviviparous, and mature females are found with broods of embryos and young in all stages of development during every season.

The associations of (1) small size and brooding and (2) small size and protandry have been observed so often that they have prompted investigators to suggest these pairs of traits may be coadapted (Sellmer, 1967; Menge, 1975; Christiansen & Fenchel, 1979; Charnov, 1982). Because of its life-history traits (small size relative to other venerids, brooding behavior, and protandry), *Transennella tantilla* is an appropriate model for tests of coadaptation.

The purpose of this study was to provide a detailed description of the reproductive traits of *Transennella tantilla* from the South Slough of Coos Bay in Oregon. Fecundity was also monitored in females collected from False Bay on San Juan Island, Washington, where the species grows larger and appears to be more numerous. A comparison of latitudinal differences in the reproductive behavior of *T. tantilla* was of interest because differences in the size of females, brood size, or juvenile release size at the two locations could be important determinants of the increased size and apparent abundance of *T. tantilla* at False Bay.

SAMPLING DESIGN

Data collections were designed to obtain information on protandry, fecundity, egg size, juvenile release size, seasonality of reproduction and growth, and size frequencies of *Transennella tantilla* in the South Slough of Coos Bay, Oregon. The purpose of the sampling protocol was to obtain representative data to describe these life-history parameters; it was not intended to provide data on absolute population densities within given areas.

The distribution of *Transennella tantilla* within the community is patchy (Obrebski, 1968). In Coos Bay, adults and juveniles occupy the upper 1–2 cm of sediment and are generally not evident until one perturbs the sediment surface. The clam secretes a byssal thread that anchors it to the grains of sediment, offering some resistence to dispersal by wave action (Narchi, 1970). In areas of strong wave action (boat swells around the base of piers) or in

[1] Current address: Oregon Health Sciences University, Heart Research Lab L464, 3181 S.W. Sam Jackson Park Road, Portland, Oregon 97201, U.S.A.

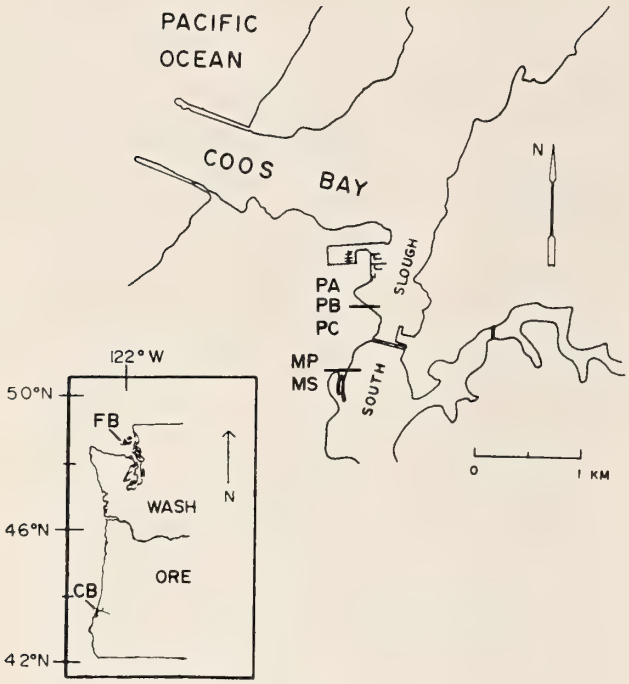


Figure 1

Map of the South Slough of Coos Bay, Oregon, indicating the location of the five study sites: PA, PB, PC, MP, and MS. Offset indicates the geographic location of Coos Bay (CB), Oregon, and False Bay (FB) on San Juan Island, Washington.

areas of fast water runoff during low tide, the clams (particularly those in the largest size classes) are swept along and deposited on the slopes of troughs sculptured by the current. In Coos Bay, the clams are subject to (1) anoxia and (2) burial by shifting sediments during seasonal storms and dredging operations.

The sampling strategy that was adopted for this study took into consideration the distribution of *Transennella tantilla* in the mudflat community and the potential for environmental factors to disrupt established populations. Time was a consideration because sieves that retain *T. tantilla* also retain a considerable amount of sediment which must be microscopically examined for removal of clams.

Size frequencies and protandry were monitored at Coos Bay by collecting a single monthly sample at each of five separated sites on the South Slough mudflat (see Study Sites section below). Given the patchy distribution of *Transennella tantilla* and the potential for a catastrophe (such as storm waves, sediment deposition, or human activity) to wipe out the population at a particular site, it was preferable to regard the mudflat as a single large site and to collect samples at five discrete locations. To allow tests of within sample disparity at each mudflat location, each sample was divided into three equal subsamples in the field, and each subsample was collected and analyzed separately.

A caging experiment was designed to provide qualitative, rather than quantitative, information on the time of growth and release of juvenile *Transennella tantilla* at Coos Bay.

For geographic comparison of female fecundity, samples of *Transennella tantilla* were periodically hand collected from Coos Bay and False Bay. Details and schedules specific to this sampling procedure and those discussed above are described in the Materials and Methods section below.

STUDY SITES

Field studies were conducted at five defined sites (PA, PB, PC, MP, and MS) on the South Slough mudflat of Coos Bay, Oregon (43.8°N). The South Slough empties into the main channel of Coos Bay, approximately 1.3 km from the mouth of the bay (Figure 1). The sites were picked because they were representative of areas where *Transennella tantilla* is commonly found on the South Slough mudflat. All sites were accessible on most low tides and were relatively free of human disturbance. The tidal heights were similar at each location: +0.58 m, +0.34 m, +0.73 m, +0.76 m, and +1.13 m above mean lower low water at sites PA, PB, PC, MP, and MS respectively.

Transennella tantilla was also collected bimonthly at False Bay on San Juan Island, Washington (48.5°N, Figure 1).

MATERIALS AND METHODS

Monthly samples were collected from each of the five sites on the South Slough mudflat from February to December 1981. *Transennella confusa* also occurs in the South Slough of Coos Bay (GRAY, 1982), but only *T. tantilla* was used in this study. Each month, the sites were searched to determine if major changes in clam densities had occurred. Areas where obvious changes were noted (*i.e.*, areas that were anoxic, traversed by streams, or where clams were absent) were excluded, and a sample was selected by randomly tossing a circular sampler (diameter = 35.7 cm, area = 0.1 m^2) onto the substrate in another area within the site. Sediment to a depth of 4 cm was removed from each subsample and sieved with a 500-μm mesh screen. This mesh size was chosen because it retained animals greater than or equal to 800 μm in shell length and an amount of sediment that could be microscopically sorted in a reasonable amount of time. Sieved subsamples were preserved in 70% isopropyl alcohol.

Shell lengths of all clams in the preserved subsamples were measured with an ocular micrometer and the results were grouped into 16 size classes by site and by month. A total of 2099 *Transennella tantilla* were removed from the subsamples collected at sites PA, PB, MP, and MS during the months of March, April, May, July, August, October, and December, and were dissected to determine the size range of males and females. When brooded embryos were not present, sex was determined by examining gonads. Testes in preserved specimens were white, translucent, branching structures; ovaries were globular and contained white or light yellow eggs that were irregular in shape.

Because of the difficulty of dissecting smaller specimens, only individuals greater than or equal to 1.85 mm in shell length were sexed. It was possible to identify the sex of over 98% of the clams examined. The other 2% were either sexually undeveloped or were infected with gonad parasites that obscured identification. Questionable specimens were not included in the sex ratio analysis. Clams from samples collected at site PC were not sexed because fewer than 25 animals were 1.85 mm or longer in the entire 0.1-m^2 sample (data for all subsamples combined) for five of the seven months considered.

To assess directly the time of growth and release of offspring in Coos Bay, *Transennella tantilla* individuals were retained in the field in cages made of plastic tubes, 3.0 cm in diameter × 4.0 cm in height, with fabric affixed to each end (approximate mesh size = 0.35 mm, the height of newly released juveniles). A detailed description of cage construction is available in Asson-Batres (1982). Each cage was half-filled with supratidal bay sand, and one measured clam, 1.0–4.4 mm in shell length, was added. The cages were brought to the laboratory for examination on a monthly or bimonthly schedule. They were held for less than 24 h in outdoor, running seawater aquaria before and after examination. The lengths of all survivors were recorded. Because time was a factor and females cannot be identified externally, only the sediment in cages with survivors greater than 2.67 mm in shell length was microscopically examined for the presence of offspring. Survivors (with the exception of offspring) were returned to their cages with fresh sand and dead clams were replaced. Eight trays of 28 cages each were followed on the South Slough mudflat from December 1980 to June 1981; five trays of 28 cages each were followed from June to December 1981.

To determine female size at maturity, brood size, and the relationship between fecundity and female size or season, specimens of *Transennella tantilla* were collected by hand from the South Slough mudflat in July 1980 and monthly from October 1980 to December 1981. The organisms were retained at 4°C in glass culture dishes filled with fresh seawater. Female lengths were measured, and embryos were removed from the gills and counted. Egg diameters and embryo lengths were measured to the nearest 0.01 mm under 200× magnification. Whole animal (shell included) weights of *T. tantilla* collected during October, November, and December 1980 were determined. Wet weights were recorded to the nearest 0.1 mg.

Samples of *Transennella tantilla* were hand collected from False Bay in May 1980, and bimonthly from November 1980 to October 1981. Living clams were retained and analyzed as described above.

RESULTS

Subsample Analysis

A single classification analysis of variance with repeated measures (Phillips, 1978) was carried out to compare subsample densities. Data from each site were analyzed independently. For a given month, at a given site, subsample densities were always comparable ($P > 0.60$). As a result, subsample data were combined for further analyses.

Table 1

Sex structure of the *Transennella tantilla* population at sites PA, PB, MP, and MS on the South Slough of Coos Bay, Oregon, sampled from March to December 1981.

Size class (mm)*	n†	% male
1.85–2.07	758	89
2.15–2.37	592	70
2.44–2.66	326	36
2.74–2.96	187	12
>2.96	236	1

* Shell lengths were measured in divisions with an ocular micrometer. Conversion of divisions into mm (×100, one division = 0.074 mm) results in discontinuous size-class groupings.

† n indicates the number of animals examined.

Size Range of Males and Females

The wet tissue weight (WTW, mg) of *Transennella tantilla* was related to shell length (SL, mm) by the regression, $\log_{10}WTW = 3.04 \log_{10}SL - 0.54$ ($SD_{regr} = 0.06$; $r^2 = 0.98$; $n = 42$). Because there was a good correlation, the anteroposterior dimension (length) was used as an indicator of clam weight.

Shell lengths of *Transennella tantilla* ranged from 0.55 to 5.33 mm. The largest male found during the study was 3.48 mm (dissected live, January 1981); the smallest female found was 1.70 mm long (dissected live, July 1981: the specimen had ripe ovaries, but no brood). The transition from male to female occurred over a broad size range, with the majority of males less than 2.37 mm long (Table 1).

Seasonal Effects on Fecundity

An average (±SD) of 36 (±13) broods were counted monthly (range = 15–56). Broods ranged in size from one egg in each of three clams, 2.07, 2.29, and 2.37 mm in length, to 327 embryos in a specimen 5.10 mm in length. The smallest brooding female was 1.92 mm, and the largest was 5.33 mm.

Females of all sizes were found with broods throughout the year (Figure 2, Table 6). Broods contained uncleaved eggs and embryos with and without shells. Uncleaved eggs and the smallest embryos were held tightly together in packets in the gills; older embryos were more loosely connected to the rest of the brood. Eggs ranged from 0.21 to 0.26 mm in diameter. The largest embryos observed were 0.55 mm in shell length.

Fecundity was a linear function of adult size (Figure 2). The coefficients of determination (r^2) for least-squares regression were greater than 0.76 for all months except March, August, and November 1981, when they were

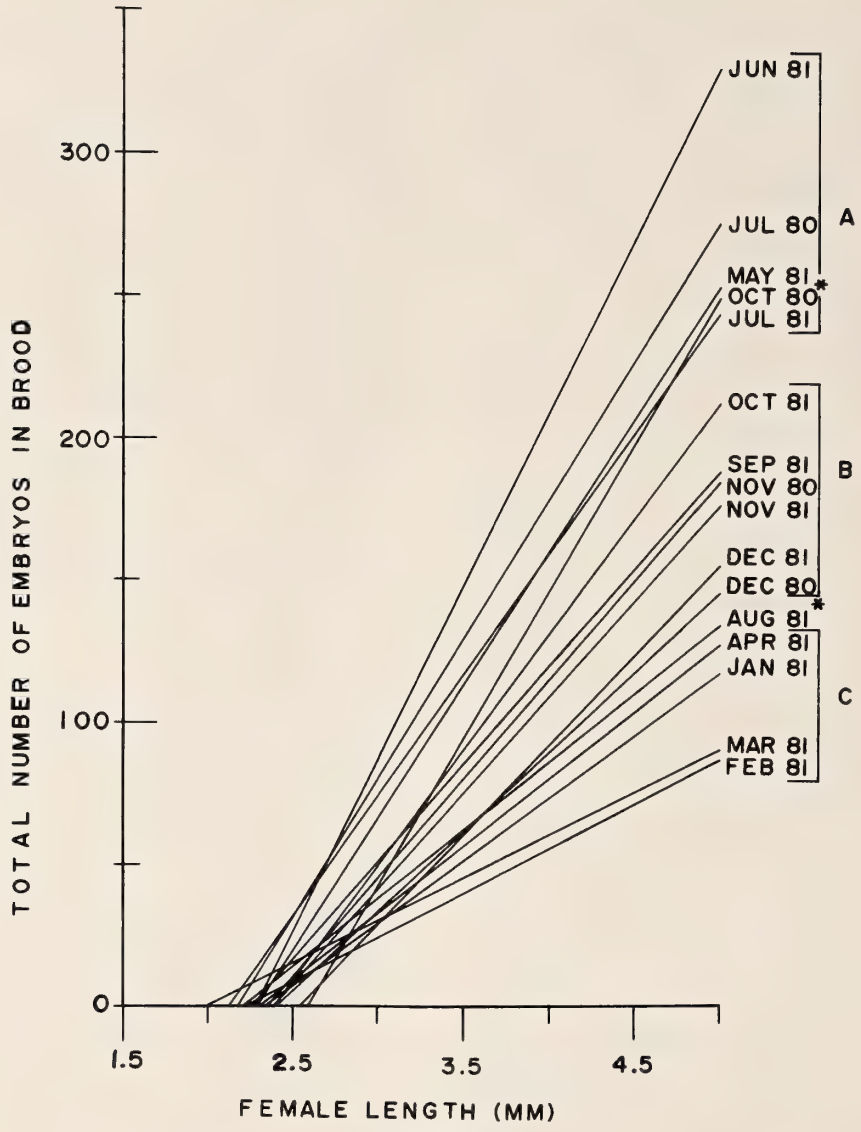


Figure 2

Seasonal change in the fecundity-size relationship of *Transennella tantilla* from the South Slough of Coos Bay, Oregon. Each line is the best fit regression line for data analyzed by least squares. Slopes range from 30 to 113; coefficients of determination (r^2) range from 0.61 (August 1981) to 0.94 (December 1980) ($P < 0.001$ for all regressions). The regression data were categorized into three seasonal groups (A, summer; B, fall; and C, winter–spring) and compared by ANCOVA ($P < 0.001$). *Data for August 1981 were assigned to the summer group and those for October 1980 to the fall group.

0.67, 0.61, and 0.69 respectively. All regressions were highly significant ($P < 0.001$).

Fecundity was seasonally variable (Figure 2). Data collected during the three seasons delineated in Figure 2 were combined and compared by an analysis of covariance (ANCOVA). Brood sizes of females of a given length were significantly larger during summer months than during late winter–early spring months and were intermediate in size during fall months (ANCOVA, $P < 0.001$).

The seasonal change in brood size occurred in females of all sizes and was similar during both years. Independent comparisons of data collected during the same months (July, October, November, and December of 1980 and 1981) were made using ANCOVA. There were no significant differences between any of the monthly pairs ($P > 0.10$). An inconsistent depression in brood size during August 1981 could not be explained.

In all but two monthly samples from Coos Bay, 2–24%

of the specimens examined had trematode sporozoites containing cercariae attached to their gonadal tissue. Parasitized females were randomly matched with non-parasitized females by shell length and collection date to correct for animal size and seasonal effects on brood size. Regressions of brood size on adult length for the resulting subset of 75 pairs of females were compared by ANCOVA. The brood sizes of animals with infected gonads were notably depressed (uninfected clams: Brood Size = 68 × Adult Length (mm) − 156, $r^2 = 0.53$; infected clams: Brood Size = 4 × Adult Length (mm) − 8; $r^2 = 0.03$; $P < 0.001$). As a result, females with infected gonads were excluded from the fecundity analyses above.

Release of Juveniles

Individual females (>2.67 mm long) maintained in field enclosures at Coos Bay released young during 11 of the 12 months they were monitored (Figure 3). Only two females survived during October and neither released young. The average (±SD) number of offspring released per female per month was 3 (±3) (Asson-Batres, 1982) which is lower than might be expected given the number of embryos known to be present in broods.

Periodic sediment burial and algal overgrowth led to anoxia in some cages. The sediment within these cages was black, indicating the presence of sulfide. Dead clams had blackened shells that were still articulated. Broods of dead eggs and shelled embryos were still present in dead females from these cages.

After one to two months of field exposure, cages that were sulfide-free mimicked the surrounding field community, with amphipods, cumaceans, tanaids, polychaetes, nemerteans, and nematodes established in the cage sediment. After field exposure, clams in these cages were alive except during October, when survivorship was inexplicably low.

It is unlikely that unnatural cage conditions induced females to release offspring because (1) shelled embryos of release size were found in the body cavities of dead females and (2) some living clams greater than 2.67 mm long (presumably the majority of these clams were female, see Table 1) did not release offspring (Figure 3). Thus, while cage artifacts may have depressed release rates, the results provide direct evidence that *Transennella tantilla* can release young year-around.

Representative monthly size-frequency distributions of *Transennella tantilla* collected from two of the South Slough study sites are presented in Table 2A, B (data from the other three sites are available in Asson-Batres, 1982). The first size class, which includes clams 0.59–0.74 mm in length, is underrepresented because the 500-μm mesh sieve did not retain newly released *T. tantilla* (the minimum shell dimension, clam height, is less than 0.5 mm). Thus, a lag of about one month exists between the actual time of juvenile release and the time when clams of the smallest size classes show up in the samples. As an example, the

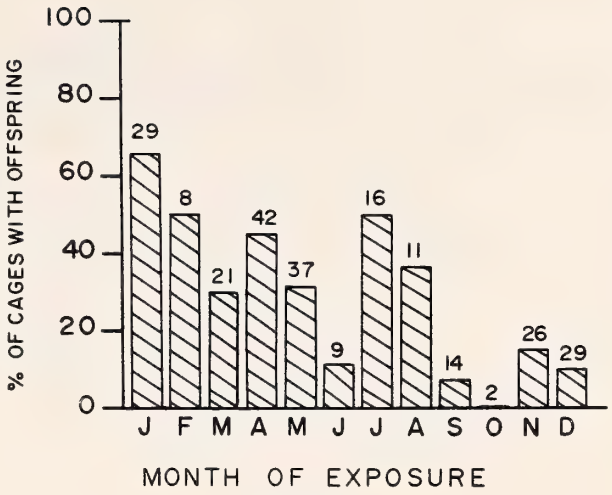


Figure 3

Percent of caged females (>2.67 mm long) with offspring. Field enclosures were maintained in the South Slough of Coos Bay, Oregon, and monitored monthly during 1981. Only cages with surviving females were examined for presence of offspring. The total number of cages examined each month is indicated above each bar.

majority of clams making up the second size class in the samples collected at site PA during March and April were probably released during February or March.

Juvenile clams were found at one or more sites during every month. Because the absolute number of juveniles is underrepresented in the sample (owing to the method of collection, see above), the second size class (0.81–1.04 mm) offers a better indication of the peak periods of juvenile release (Table 2A, B; Asson-Batres, 1982). Taking the lag period into consideration, peak release of juveniles occurred at sites PA, MP, and MS during February through April, and again at sites MP and MS during July and August. Except for a single surge in release of young at site PC during April, juvenile release was consistently low at sites PB and PC throughout the study period.

Growth

Individual *Transennella tantilla,* retained in cages on the Coos Bay mudflat, grew every month of the year (Table 3). The absolute change in shell length ranged from 0.07 to 0.56 mm per clam per month.

Distinct rings and zones were not present on the shells of animals in monthly field collections, suggesting that shell growth was continuous.

Mortality

A decline in the densities of large *Transennella tantilla* occurred at sites MP, PA, and PB from June to September. This is evident in Table 4, which compares the number (or relative percent) of clams greater than 2.0 mm in shell

Table 2

Size-frequency data for *Transennella tantilla* collected from two sites in the South Slough of Coos Bay, Oregon, during 1981. The number of clams comprising each size class are presented as percentages of the total number of clams present in the 0.1-m^2 sample. Sample sizes are included at the bottom of the table so that raw numbers can be generated, if desired.

Part A. Site PA

Size class (mm)	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0.59–0.74	2	1	1	0.7		0.5	0.4	0.7		0.6
0.81–1.04	51	48	23	24	21	12	5	4		20
1.11–1.33	29	25	44	33	23	23	11	4	7	8
1.41–1.63	8	11	22	31	37	26	19	7	1	2
1.70–1.92	4	6	7	10	17	27	26	19	3	6
2.00–2.22	2	3	2	0.7	3	11	23	30	8	13
2.29–2.52	2	3	1	0.5		1	14	20	24	19
2.59–2.81	0.8	1	0.4				1	11	23	13
2.89–3.11	0.2	1	0.3	0.2				4	11	14
3.18–3.40	0.5	0.3	0.4					0.7	13	4
3.48–3.70	0.3								3	0.6
3.77–4.00	0.3	0.1	0.1	0.2					7	
4.07–4.29	0.2	0.1							1	
Total number of clams in sample	593	1172*	1018	410	342	376	203	152	75	158

Part B. Site MP

Size class (mm)	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0.59–0.74	0.2		4	2	0.7	6	6	1	0.5	0.3	0.2
0.81–1.04	27	11	43	35	19	32	62	43	13	8	14
1.11–1.33	18	10	16	30	26	27	15	35	22	5	19
1.41–1.63	19	14	9	10	27	20	7	13	26	14	22
1.70–1.92	11	17	9	6	13	10	5	5	21	27	20
2.00–2.22	12	24	8	6	5	3	3	2	9	24	13
2.29–2.52	6	14	6	5	3	1	1	1	4	14	5
2.59–2.81	4	5	3	2	2	1	0.5	0.6	2	5	3
2.89–3.11	1	2	1	2	2	0.6	0.2		1	3	0.8
3.18–3.40	0.2	0.7	0.7	1	1	0.3			0.3	0.8	0.7
3. 48–3.70	0.8	0.7	0.1	0.4	0.7					0.5	0.3
3.77–4.00	0 .2	0.7					0.1				0.1
4.07–4.29				0.2	0.1						
4.37–4.59				0.1	0.1						
Total number of clams in sample	479	606	1418*	1355	1524	1163	929	1042	663	600*	1147

* Estimate based on two subsamples of 0.03 m^2 each.

length in monthly samples from the sites. Pre-decline densities of large clams were re-established at the sites during fall and winter months. Clams less than 2.0 mm in shell length did not decline during the summer at sites MP, PA, and PB (data not shown).

There was a precipitous decline in all sizes of *Transennella tantilla* at site PC in May (Asson-Batres, 1982). During June and July, repeated samples were checked for the presence of *T. tantilla,* but specimens retained by the 500-μm mesh screen were not present. Concomitant with the disappearance of live *T. tantilla* from the site was the appearance of numerous *T. tantilla* half-shells and shell fragments. Clams greater than 2.0 mm in shell length did not reach pre-decline densities at site PC (Table 4). A year later (June 1982), numerous (>10) samples were sieved (500-μm mesh) at the site and only one living *T. tantilla* was found. Such intensive sieving before the crash would have retrieved hundreds of clams visible to the naked eye.

Neither large (Table 4) nor small *Transennella tantilla* declined in number at site MS during summer months.

Life-History Characteristics of *Transennella tantilla* from False Bay

Fecundity was a linear function of adult size and was seasonally variable (Table 5). Females of a given size in False Bay had smaller broods than females of comparable size in Coos Bay and, although females in False Bay reached

Table 3

Growth of *Transennella tantilla* retained in field enclosures in the South Slough of Coos Bay, Oregon, during 1980–1981. One clam present per cage.

Month(s) of exposure	Number of survivors	% of survivors that grew	Change in length (mm) mean ± SD*
Dec–Feb	29	66	0.12 ± 0.06
Jan	54	72	0.11 ± 0.06
Jan–Mar	23	65	0.13 ± 0.06
Feb	26	15	0.06 ± 0.02
Feb–Apr	25	88	0.16 ± 0.10
Mar	48	75	0.11 ± 0.06
Mar–May	28	57	0.25 ± 0.20
Apr	66	53	0.15 ± 0.08
Apr–Jun	4	75	0.30 ± 0.20
May	69	38	0.12 ± 0.08
May–Jul	11	55	0.23 ± 0.10
Jun	21	48	0.11 ± 0.04
Jul	34	59	0.18 ± 0.14
Aug	26	81	0.12 ± 0.06
Sep	33	73	0.10 ± 0.04
Oct	4	75	0.12 ± 0.04
Nov	46	80	0.17 ± 0.08
Dec	42	7	0.07 ± 0.00

* The mean includes only those clams that showed an increase in length.

larger sizes than females in Coos Bay, the maximum brood sizes of False Bay animals were smaller than those of Coos Bay females during four of the six months sampled (Table 6).

Of the clams from the bimonthly collections from False Bay 2–17% were infected with trematode parasites. Parasitized females had significantly reduced brood sizes (ANCOVA, $P < 0.001$) and were excluded from the fecundity analyses.

Table 4

Number (%) of *Transennella tantilla* greater than 2.0 mm in shell length in monthly samples collected from each of the five study sites in the South Slough of Coos Bay, Oregon, in 1981.

Month	PC	PA	PB	MP	MS
Feb	198 (34)	—	44 (51)	116 (24)	38 (28)
Mar	229 (49)	37 (6)	71 (49)	285 (47)	68 (15)
Apr	266 (48)	100 (9)	422 (69)*	267 (19)	47 (7)
May	3 (2)	43 (4)	41 (59)	226 (17)	44 (7)
Jun	0 (0)	7 (2)	8 (24)	212 (14)	82 (18)
Jul	0 (0)	10 (3)	7 (7)	69 (6)	167 (27)
Aug	4 (7)	45 (12)	4 (3)	45 (5)	57 (27)
Sep	27 (73)	77 (38)	40 (49)	37 (4)	62 (11)
Oct	18 (83)	100 (66)	62 (67)	108 (16)	93 (24)
Nov	50 (94)	62 (82)	46 (49)	284 (47)	—
Dec	25 (80)	100 (64)	47 (30)	263 (23)	133 (38)

* The April sample size was spuriously high because the sample was collected from the slope by a pier where wave action deposited large individuals of *T. tantilla*.

Table 5

Brood size of *Transennella tantilla* collected from False Bay on San Juan Island, Washington. Regression data are for brood size (B) plotted over adult length (L) ($P < 0.001$ for all regressions).

Date	n*	Equation	r^2
Nov '80	31	B = 77L − 263	0.77
Feb '81	36	B = 20L − 62	0.85
Apr '81	65	B = 30L − 90	0.72
May '80	27	B = 41L − 128	0.64
Jun '81	48	B = 67L − 202	0.89
Aug '81	48	B = 82L − 303	0.85
Oct '81	39	B = 37L − 127	0.55

* n indicates the number of animals examined.

DISCUSSION

The field enclosure studies provide direct evidence that *Transennella tantilla* can reproduce and grow year-around in the South Slough of Coos Bay, Oregon. The results from monthly field samples support these observations. The presence of juvenile clams in all field collections supports the contention that release is continuous. Because it is known that variations in growth rate are recorded by distinct zones or rings on bivalve shells (NAYAR, 1955; JONES, 1983), the absence of such rings on the shells of *T. tantilla* in this location suggests that growth is continuous.

Continuous release of young by *Transennella tantilla* is not exceptional; other bivalves in northern waters also spawn year-around. *Mytilus californianus* spawns all year off the west coast of the United States (WHEDON, 1936; SUCHANEK, 1981) and at least part of the populations of *Astarte borealis* and *A. elliptica* in the Baltic Sea carry eggs and sperm year-around and spawn for a period of up to eight months (VON OERTZEN, 1972).

A majority of the clams between 1.85 and 2.37 mm in shell length from the sites in South Slough were males, whereas larger animals were predominantly females (Table 1). These results, along with HANSEN's (1953) demonstration (using histological techniques) that some individuals were in the process of a sex reversal, provide strong support for protandry in this species. The sex structure of the population was similar throughout the year at all sites, which suggests that sex reversal occurs throughout the year. The male-to-female sex ratios of populations sampled at sites PA and PB were 55:45 and from sites MP and MS were 61:39 (ASSON-BATRES, 1982). The proportion of males at each site is probably an underestimate because many animals smaller than the cut-off length of 1.85 mm likely were males.

Protandry is predicted when reproductive success is independent of size for males, but proportionally greater for large females than for small ones (GHISELIN, 1969; WARNER, 1975). Model simulations that assume these conditions predict that the smallest mature individuals in a

Table 6

Comparison of the mean ($\bar{x}$) brood size of *Transennella tantilla* by shell length (mm), month, and geographic location. The number (n) of animals examined is indicated. The animals were collected from False Bay on San Juan Island, Washington, and the South Slough of Coos Bay, Oregon.

Month	Female size class (mm)	False Bay		Coos Bay	
		$\bar{x}$	(n)	$\bar{x}$	(n)
Nov '80	2–3	—	—	24	(5)
	3–4	31	(8)	74	(9)
	4–5	74	(11)	127	(4)
	5–6	150	(12)	—	—
Feb '81	2–3	—	—	11	(16)
	3–4	9	(17)	32	(24)
	4–5	27	(19)	56	(4)
	5–6	—	—	88	(3)
Apr '81	2–3	3	(2)	20	(15)
	3–4	10	(25)	51	(32)
	4–5	37	(30)	96	(8)
	5–6	85	(8)	—	—
Jun '81	2–3	1	(6)	35	(26)
	3–4	12	(10)	150	(19)
	4–5	92	(12)	265	(5)
	5–6	169	(15)	275	(1)
	6–7	185	(5)	—	—
Aug '81	2–3	—	—	15	(20)
	3–4	6	(18)	53	(16)
	4–5	26	(17)	129	(1)
	5–6	145	(11)	—	—
	6–7	232	(2)	—	—
Oct '81	2–3	—	—	20	(6)
	3–4	21	(2)	73	(21)
	4–5	39	(29)	143	(1)
	5–6	61	(8)	—	—

population will be male. At some larger size, it will be more profitable to be female and, at this point, a change in sex will occur. Field studies of protandrous shrimp and plants offer evidence that the model is realistic (CHARNOV, 1979; POLICANSKY, 1981). Because large females of *Transennella tantilla* produce proportionally more embryos than small females, it is tempting to speculate that the model offers an appropriate explanation for protandry in this species. It is of interest that *Gemma gemma,* also a small (5 mm, maximum shell length) brooding venerid is dioecious. Female *G. gemma* begin brooding at about 2.0 mm in length, and fecundity increases logarithmically with female size. Juveniles are released when they are fully developed. Their life-span is thought to be 2 yr (SELLMER, 1967; GREEN & HOBSON, 1970). Although a positive correlation between fecundity and female size exists in both species, *T. tantilla* is a sex-changer and *G. gemma* is not. It is currently not possible to test the relative interspecific productivity of males. It may be that reproductive success is size-dependent for male *G. gemma* and size-independent for male *T. tantilla.*

The summer decline in densities of *Transennella tantilla* from four of the five study sites in Coos Bay was most likely due to predation. Juvenile *Cancer magister* (Dana) (13–30 mm in carapace width) forage for *T. tantilla* in the South Slough of Coos Bay, Oregon (ASSON-BATRES, 1986). When feeding on the clams, this crab characteristically separates the valves, leaving one half-shell intact (ASSON-BATRES, 1986). The megalops of *C. magister* were present in the Coos Bay estuary from mid-March to the end of May of 1981 (ROWELL, 1981) and would have metamorphosed to first instar juveniles throughout April to June. The coincidental disappearance of the clams and appearance of juvenile *C. magister,* and the concomitant appearance of half-shells and shell fragments at the site where the clams were found when alive, suggest that juvenile *C. magister* was a factor in the summer decline of *T. tantilla.* In support of this interpretation, it has been reported that small bivalves are a major part of the diet of first year *C. magister* (STEVENS *et al.,* 1982).

Shore birds and bottom-feeding fish that appear seasonally may have also contributed to the decline of *Transennella tantilla.* OBREBSKI (1968) indicated that the gut contents of unidentified shore birds collected near Bodega Bay contained *Transennella.* VIRNSTEIN (1977) reported that spot fish, *Leiostomus xanthurus,* were important predators on juvenile clams (1–3 mm, shell length) in the York River of Chesapeake Bay. Whether birds or fish feed seasonally on *T. tantilla* in South Slough has not been investigated. Juveniles of other species of crabs may have also preyed on *T. tantilla* during the summer, but none are likely to have been as abundant as juvenile *C. magister.*

The population decline of the large size classes at three of the five sites, and the population crash of all sizes at one site, suggest that mortality may be unpredictable for this species. Direct release of relatively immobile young can lead to the formation of groups of animals separated in space (patches). This could provide a refuge from predators, as they may overlook a prey patch. The stable population density observed at site MS during this study, concurrent with the decline of population densities at other sites, is consistent with such a prediction.

Individuals of *Transennella tantilla* from False Bay reach lengths up to 1.3 mm longer than their conspecifics in Coos Bay (Table 7). According to GRAY (1978), *T. tantilla* in Tomales Bay, California (38.4°N) reach 7.00 mm in length. Thus, the size of *T. tantilla* at False Bay, Coos Bay, and Tomales Bay is not correlated with the change in latitude.

Transennella tantilla is conspicuously distributed over much of the tideflat in False Bay. At mean lower low water, where the species is most dense in False Bay, it is a numerically dominant species (PAMATMAT, 1969; BRENCHLEY, 1981). In contrast, *T. tantilla* is smaller, less exposed, and distributed in isolated patches on the mudflat in the South Slough of Coos Bay, giving the impression

Table 7

Comparisons of life-history traits of *Transennella tantilla* from False Bay on San Juan Island, Washington, and the South Slough of Coos Bay, Oregon. Observations are personal except as indicated in parentheses. AB = Asson-Batres, 1982; H = Hansen, 1953.

	False Bay, Washington	Coos Bay, Oregon
Latitude	48.5°N	43.8°N
Shell length	0.65–6.60 mm	0.55–5.30 mm
Male size range	1.50–4.60 mm (H)	<1.85–3.48 mm
Female size range	>2.80 mm	>1.70 mm
Female reproductive behavior	Brood present all year; fecundity a linear function of size	Brood present all year; fecundity a linear function of size
Maximum brood size (adult length)	293 (5.6 mm)	327 (5.1 mm)
Diameter of uncleaved egg in brood chamber	0.25 mm (H, AB)	0.21–0.26 mm
Juvenile release size	0.65 mm (H, AB)	0.53–0.55 mm

that it is less abundant there than in False Bay. If abundance is greater in False Bay than in Coos Bay, it is not a result of increased brood sizes: females of similar size brood fewer embryos in False Bay than in Coos Bay (Tables 6, 7).

Females in both locations produce eggs of similar size (Table 7), but in False Bay, young are released at a larger size. The energetic costs of producing offspring should be equal at the two locations, if, as it is assumed (Hansen, 1953), embryos receive no nutrition from the parent during development. In this species, then, egg size appears genetically fixed, whereas other life-history traits are more plastic.

Parasitized animals from Coos Bay and False Bay had significantly smaller brood sizes. Kabat (1984) reported that 31% of the brooding females he examined from False Bay hosted parasites and produced only 40% as many embryos as non-parasitized females of the same size. In this study, the percentage of clams infected with gonad trematodes was extremely variable: 0–24% of the specimens collected at Coos Bay, and 2–17% of those from False Bay had parasitized gonads. There was no apparent correlation between the number of parasitized animals and the collection date (personal observation, unpublished).

Factors that restrict the productivity of female *Transennella tantilla* in Coos Bay and False Bay are the animal's life-span, the incidence of parasitism, and seasonal effects on egg production, embryonic growth, and juvenile release. Senility does not limit productivity because all non-parasitized, mature females are found with broods, and the oldest (largest) females have the largest broods. It is uncertain whether the allometry of egg production and brooding (Strathmann & Strathmann, 1982) limits productivity in *T. tantilla*. The linearity of the correlations between brood size and female size (recall that wet weight is correlated with length, see Results above) and the capacity of the organism to adjust its brood size upward during some seasons suggest that large *T. tantilla* have ample space to brood as many gametes as they are capable of producing. However, differences in the brood structures of animals from Coos Bay and False Bay may argue against this interpretation; a limitation in brood space could constrain females to brood either higher numbers of small young (as in Coos Bay) or lower numbers of large young (as in False Bay).

In summary, *Transennella tantilla* is a small, protandric, brooding bivalve that grows and reproduces year-around in the South Slough of Coos Bay, Oregon. It appears to be subject to intense seasonal predation by incoming settlements of juvenile *Cancer magister* and possibly shore birds and bottom-feeding fish. Maximum adult size is geographically variable, but there does not appear to be a correlation between animal size and latitude. Brood size, juvenile release size, age at maturity, and the size range of males and females vary between geographic sites (Table 7). Whether the comparative flexibility observed in many of the life-history characteristics of this species (Table 7) represents genetic differences or physiological adaptability to locally induced pressures has not been investigated. In this regard, a reciprocal transplant experiment and electrophoretic comparative analysis of the populations would be of interest.

ACKNOWLEDGMENTS

I thank P. W. Frank for encouragement and advice throughout the study and for assistance with preparation of the manuscript; R. R. Strathmann and R. I. Ingermann for helpful discussions; P. Rudy, Director of the University of Oregon Institute of Marine Biology, E. Kozloff, Acting Director of Friday Harbor Laboratories, and their staff for providing research facilities; and S. Batres for assistance in the design and construction of the experimental field cages. The field research was partially funded by a grant-in-aid from Sigma Xi. Preparation of the manuscript was supported in part by PHS Research Grant HD 15308.

LITERATURE CITED

Asson-Batres, M. A. 1982. The life history traits and population dynamics of the brooding bivalve, *Transennella tantilla* (Gould) in the South Slough of Coos Bay, Oregon. Master's Thesis, University of Oregon, Eugene. 73 pp.

Asson-Batres, M. A. 1986. The feeding behavior of the juvenile Dungeness crab, *Cancer magister* on the bivalve, *Transennella tantilla* (Gould), and a determination of its daily consumption rate. Calif. Fish Game 72:144–152.

Brenchley, G. A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. Jour. Mar. Res. 39:767–790.

Charnov, E. L. 1979. Natural selection and sex change in pandalid shrimp: test of a life history theory. Amer. Natur. 113:715–734.

Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press: Princeton. 355 pp.

Christiansen, F. B. & T. M. Fenchel. 1979. Evolution of marine invertebrate reproductive patterns. Theor. Pop. Biol. 16:267–282.

Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. Quart. Rev. Biol. 44:189–208.

Gould, A. A. 1852. Descriptions of shells from the Gulf of California and the Pacific coasts of Mexico and California. Bost. Jour. Natur. Hist. 6:374–408.

Gray, S. 1978. Comparative anatomy and functional morphology of two species of *Transennella* (Bivalvia: Veneridae). Master's Thesis, San Francisco State University, San Francisco. 68 pp.

Gray, S. 1982. Morphology and taxonomy of two species of the genus *Transennella* (Bivalvia: Veneridae) from western North America and a description of *T. confusa* sp. nov. Malacol. Rev. 15:107–117.

Green, R. H. & K. D. Hobson. 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). Ecology 51:999–1011.

Hansen, B. 1953. Brood protection and sex ratio of *Transennella tantilla* (Gould), a Pacific bivalve. Vidensk. Medd. fra Dansk naturh. Foren. 115:313–324.

Jones, D. S. 1983. Schlerochronology: reading the record of the molluscan shell. Amer. Sci. 71:384–391.

Kabat, A. R. 1984. Brooding, parasitism, and reproductive output in *Transennella tantilla* (Bivalvia). Amer. Zool. 24: 14A (abstract).

Keen, A. M. 1937. An abridged checklist and bibliography of west North American marine Mollusca. Stanford University Press: Stanford. 87 pp.

Menge, B. A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*. Mar. Biol. 31:87–100.

Narchi, W. 1970. The presence of byssus in adults of *Transennella tantilla* (Gould) (Bivalvia: Veneridae). Wasmann Jour. Biol. 28:233–236.

Nayar, N. N. 1955. Studies on the growth of the wedge clam, *Donax* (*Latona*) *cuneatus* Linnaeus. Ind. Jour. Fish. 2:325–348.

Obrebski, S. 1968. On the population ecology of two intertidal invertebrates and the paleoecological significance of size-frequency distributions of living and dead shells of the bivalve *Transenella* [sic] *tantilla*. Ph.D. Thesis, University of Chicago, Chicago. 102 pp.

Pamatmat, M. M. 1969. Seasonal respiration of *Transennella tantilla* Gould. Amer. Zool. 9:418–426.

Phillips, D. S. 1978. Basic statistics for health science students. W. H. Freeman & Co.: San Francisco. 185 pp.

Policansky, D. 1981. Sex choice and the size advantage model in jack-in-the-pulpit (*Arisaema triphyllum*). Proc. Natl. Acad. Sci. USA 78:1306–1308.

Rowell, D. L. 1981. The dispersal of *Cancer magister* larvae in the Coos Bay estuary. Master's Thesis, University of Oregon, Eugene. 66 pp.

Sellmer, G. P. 1967. Functional morphology and ecological life history of the gem clam *Gemma gemma* (Eulamellibranchia: Veneridae). Malacologia 5:137–223.

Stevens, B. G., D. A. Armstrong & R. Cusimano. 1982. Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. Mar. Biol. 72:135–145.

Strathmann, R. R. & M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. Amer. Natur. 119:91–101.

Suchanek, T. H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. Oecologia 50:143–152.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58:1199–1217.

von Oertzen, J. A. 1972. Cycles and rates of reproduction of six Baltic Sea bivalves of different zoogeographical origin. Mar. Biol. 14:143–149.

Warner, R. R. 1975. The adaptive significance of sequential hermaphroditism in animals. Amer. Natur. 109:61–82.

Whedon, W. F. 1936. Spawning habits of the mussel *Mytilus californianus* Conrad with notes on the possible relation to mussel poison. Univ. Calif. Publ. Zool. 41:35–44.

The Veliger 30(3):267–277 (January 4, 1988)

THE VELIGER

Aspects of the Life History and Population Biology of *Notospisula trigonella* (Bivalvia: Mactridae) from the Hawkesbury Estuary, Southeastern Australia

by

A. R. JONES AND A. MURRAY

Division of Invertebrates, The Australian Museum, P.O. Box A285, Sydney, 2000, Australia

AND

G. A. SKILLETER

School of Biological Sciences, University of Sydney, N.S.W. 2006, Australia

Abstract. Aspects of the life history of *Notospisula trigonella* and spatial and temporal variations in its abundance in the Hawkesbury Estuary, New South Wales, are described and related to physicochemical factors. Sexes were separate with a sex ratio close to 1:1. Spawning usually occurred between August and November but sometimes continued until February. Annual variation in the timing of onset and duration of spawning occurred and the nature of spawning cues is unclear. Recruitment always occurred between August and November, usually with a single cohort that appeared to survive about 1 yr. Growth rates were usually highest between November and February when cohorts of small size were present.

Spatial differences in abundance were usually significant but variable. The species was absent from salinities less than 10‰ and usually rare at sites closest to the ocean, where mean low-water salinities were 31.4‰. Water depth and sediment grade had little apparent effect on abundance as differences associated with the former were inconsistent and those with the latter were not significant. Temporal differences were somewhat cyclic in the middle estuarine reaches, with maximum abundance in November, but were variable in the lower reaches. Abundance fell to zero following a major flood. Much of the variability observed may ultimately be due to the unpredictable rainfall of the region.

INTRODUCTION

Notospisula trigonella (Lamarck, 1818) is a suspension-feeding mactrid bivalve found in estuaries and coastal waters of all Australian states (WILSON & KENDRICK, 1968). It inhabits a wide range of sedimentary habitats (ROBINSON & GIBBS, 1982) and can dominate the macrofaunal community with densities exceeding 2000 m^{-2} (GREEN, 1968). Despite this, little is known about its life history and population biology. Available information is limited to a study of mortality (where it was called *N. parva*) by GREEN (1968), fragmentary notes in several benthic community studies (*e.g.,* CHALMER *et al.,* 1976; STEPHENSON *et al.,* 1977; RAINER & FITZHARDINGE, 1981; POORE, 1982) and STEJSKAL (1985).

This paper is based on information collected during a long-term study of the macrobenthic community of the Hawkesbury River estuary in southeastern Australia. Because it was the dominant species in the study, the biology of *Notospisula trigonella* is treated here separately from the rest of the fauna. The aims are to describe aspects of the life history (reproductive cycle, sex ratio, recruitment, and growth) and population biology (spatial and temporal distributions) in relation to physicochemical factors.

MATERIALS AND METHODS

Field Sampling

Twelve across-estuary transects containing 29 sampling sites were located between the mouth of the Hawkesbury

Table 1

Mean values for depth, mean grain size (M_z), % mud, and bottom-water salinity (adjusted to low-water values) for most sites over the first five samplings (summer 1977 to summer 1978 inclusive). The sites upstream of 9.1 and 9.2 included both deep and shallow sites on each transect and all had sediments with <20% mud. Salinities decreased from 7.3‰ at transect 10 to <0.5‰ at transect 14. Site 7A was 20 m deep with muddy sand sediments and salinity similar to site 7.1.

Site	Depth (m)	M_z (ϕ)	Mud (%)	Salinity (‰)
1.1	4	6.0	59	31.4
1.3	10	4.4	31	31.4
2.1	4	6.1	61	29.7
2.2	5	6.0	60	29.7
2.3	12	7.7	88	29.7
3.1	12	5.4	49	27.9
3.2	6	3.1	17	27.9
3.3	5	8.1	93	27.9
6.2	8	4.4	36	24.0
6.3	8	1.7	6	24.0
7.1	12	5.7	51	20.5
7.2	8	2.1	13	20.5
7.3	6	7.6	83	20.5
8.1	6	6.0	57	16.8
8.2	16	3.4	17	16.8
9.1	20	6.2	63	11.8
9.2	6	3.0	20	11.8

Estuary and its junction with the Colo River (Figure 1). Sites on most transects varied in depth and sediment grade (Table 1). Samples were taken every season, with summer, autumn, winter, and spring being represented by February, May, August, and November respectively. All sites were sampled from February 1977 until February 1978 inclusive. Sampling was continued seasonally at sites 3.1 and 3.2 until spring (November) 1979 (*i.e.*, 3 yr total) and at sites 1.1, 1.3, 2.1, 2.2, 7.1, and 7.2 until summer (February) 1984 (*i.e.*, 7 yr total). No samples were taken at sites 1.3, 2.1, and 2.2 in autumn 1980 owing to equipment malfunction. Each sample comprised four 0.05-m^2 Smith-McIntyre grabs and material retained on a 1-mm sieve was preserved in buffered 10% formalin for subsequent laboratory processing under stereomicroscopes.

The salinity and temperature of bottom water were measured by a Goldberg temperature-compensated refractometer, a mercury thermometer (using water obtained by a closing water bottle), and a Martek Mark V *in situ* water quality analyzer whose sensors were lowered to the bottom. Sediment samples were taken from an additional grab taken at each time and site until autumn 1981. The sieve and pipette procedures of Folk (1974) were used to analyze the grain size composition of the sand and silt-clay components respectively. River-discharge data were obtained from the New South Wales Metropolitan Water Sewerage and Drainage Board's gauging station at Penrith upstream of the tidal limit.

Life History

In summer 1980, a dense population was discovered at site 7A (Figure 1) from which one or two grabs were collected every three months until spring 1983. Specimens from this site were used to describe the reproductive cycle and estimate sex ratios, recruitment, and growth. The minimum reproductive size was determined for specimens from sites 7A, 7.1, 7.2, 2.1, and 3.1.

The interval between sampling (three months) was imposed by the logistics of a long-term community study and is greater than would normally be used for accurate descriptions of reproductive cycles. However, it is possible to gain considerable insight into the reproductive cycle by considering seasonal reproductive changes in conjunction with size-frequency distributions and by relating periods of spawning to those of recruitment (Roberts, 1984).

Fifteen individuals of 8 to 15 mm shell length were selected from each sample from site 7A and tissue specimens were prepared for histology. The gonadal portion of the visceral mass was removed and dehydrated in graded alcohols, cleared in xylene, embedded in paraffin wax, sectioned at 7-μm intervals, and stained with Harris' hematoxylin and eosin (Carleton, 1957). At least 20 serial sections from each specimen were examined microscopically. Determination of the stage of gametogenesis was based on the classifications of Braley (1984) and Ropes (1968): *i.e.*, stage 0—resting or spent gonad; stage 1—early active; stage 2—late active; stage 3—ripe; stage 4—partially spawned; stage 5—spent. Allocation to a particular stage was made if more than 75% of the follicles showed this level of development.

Sex ratios and the minimum reproductive size were determined histologically and by observing the external condition (color) of the gonad in ripe individuals (stage 3). At other stages of gametogenesis, the color of the gonad could not be used to determine gender. In order to determine the minimum reproductive size, specimens ranging in size from 2 to 17 mm were examined for the presence of ripe gonad. Squash mounts of the gonad region of the visceral mass were used as a final check for small individuals without externally visible gonad.

Size Structure and Growth

Shell lengths of 200 randomly selected individuals from each sample taken at site 7A were measured with vernier calipers (±0.1 mm) and placed into 1-mm size classes. For samples with less than 200 specimens, all available individuals were measured. Estimates of mean cohort size from size-frequency distributions were made using normal probability paper (Cassie, 1954). Growth rates were then estimated from the displacement of the mean length of those cohorts that were clearly recognizable and could be followed through time.

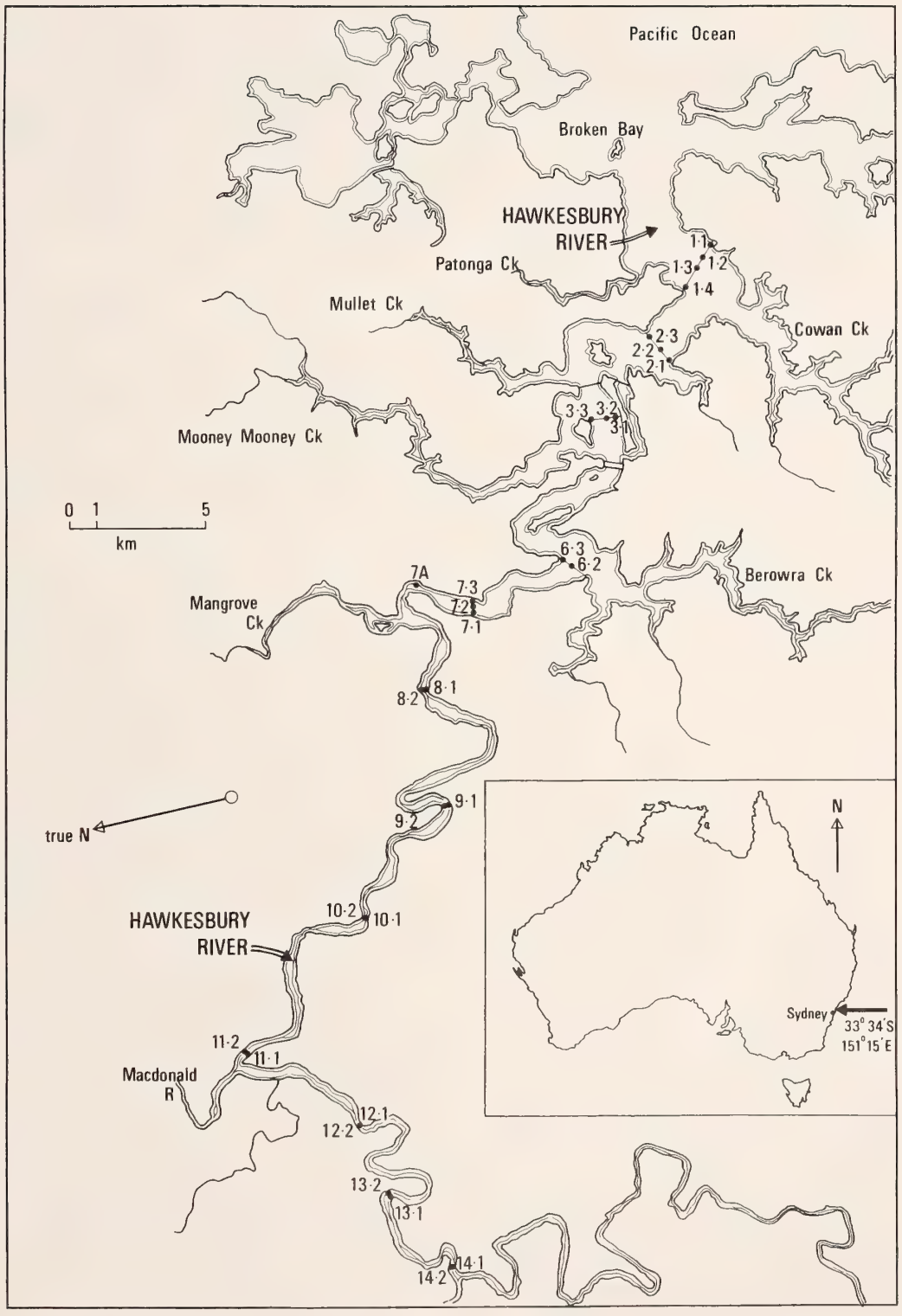


Figure 1

Map of Hawkesbury River estuary showing location of sampling sites. The transect number is indicated by the left hand numeral.

Data Analysis

Analyses of the relationship between the abundance of *Notospisula trigonella* and several abiotic variables (distance from the river mouth, water depth, sediment grade, season, year, river discharge, salinity, and temperature) were done. Some of these were confounded, *e.g.,* salinity varied with distance from the river mouth and sediment grade varied with both distance from the mouth and depth.

Differences in abundance associated with those variables whose levels could be fixed (distance from the river mouth, water depth, sediment grade, season, and year) were identified by analysis of variance (ANOVA) in various factorial combinations (see below) and *a posteriori* Student-Newman-Keuls (SNK) multiple comparisons. Cochran's test was used to test for variance heterogeneity and variance-stabilizing transformations were used where necessary. These ANOVAs deal with both spatial and temporal aspects of distribution and abundance.

Different spatial patterns during the first five sampling times were determined in the following ways. Patterns associated with distance from the mouth (along-estuary patterns) and depth (across-estuary patterns) arose from the transects containing both deep (>10 m) and shallow (3–6 m) sites. These data were analyzed by three-way fixed-factor ANOVAs (6 along-estuary positions × 2 depths × 5 times). Patterns associated with different sediments were identified by subjecting abundance data from transect 6 to a two-factor (sediment type × time) ANOVA. Only at transect 6 were sediment differences not confounded by depth differences. All the above ANOVAs included a time factor in order to assess the repeatability of various spatial differences in abundance.

Temporal patterns at transects with long-term data available (7 yr for transects 2 and 7) were analyzed by three-way fixed-factor ANOVAs (site × season × year). Year was considered a fixed factor because all available years were sampled. This fixed-factor model restricts inferences to the paricular sites, seasons, and years involved.

Relationships between abundance and those abiotic variables whose levels could not be fixed (temperature, salinity, and river discharge) were quantified using Spearman rank correlations and partial correlations. The latter provided statistical control for confounded variables, *i.e.,* the association between abundance and salinity (for example) could be quantified independently of the association with temperature and river discharge.

RESULTS

Physicochemical Characteristics of Sampling Sites

Considerable variation in physicochemical characteristics occurred. The mean salinity of bottom water varied from 31.4‰ at transect 1 to 11.8‰ at transect 9 (Table 1). No specimens of *Notospisula trigonella* were obtained in the lower salinities upstream of transect 9. There were temporal variations in salinity which were largely caused by a major flood in March 1978, minor floods in March 1977 and June 1978, and a major drought from 1979 until 1981 (Figure 2). Recorded temperature of bottom water at site 7A varied from 25.7 to 14.4°C. The range was approximately 2°C greater and less in the upper (transects 11–14) and 2°C less in the lower (transects 1–3) reaches respectively. The finest and coarsest sediments were located in the lower and upper reaches respectively, and sediment grade varied substantially across the estuary at transects 3–9 (Table 1).

Sex Ratio and Minimum Reproductive Size

Notospisula trigonella has separate sexes and the population at site 7A displayed a sex ratio of 1:1.05 (male: female, $n = 240$) which is not significantly different from 1:1 ($\chi^2 = 0.15$, $P > 0.05$). No hermaphrodites were observed.

The minimum recorded shell length of reproductively mature individuals at site 7A was 5 mm. However, at sites 7.1, 7.2, 3.1, and 2.1, it was only 3–4 mm.

Spawning and Recruitment

Spawning, as indicated by the presence of partially spawned individuals, usually occurred in November and sometimes continued until February of the following year (Figures 3A–D). However, the timing of both the onset of spawning and its duration appeared to vary among years. For example, in 1981, partially spawned specimens (stage 4) were present in August, whereas in 1983 and 1982, this stage was not observed until November and the following February respectively (Figures 3B–D). Furthermore, spawning had probably concluded by February in 1981 and 1982 but was continuing during February of 1980 and 1983. In fact, the presence of spent individuals as late as May in 1980 implies an exceptionally long duration for the spawning period starting in 1979 (Figure 3A).

Recruitment of a new cohort always occurred between August and November but variability in the number of cohorts per year among years was apparent (Figure 4). In 1982 for example, cohort 4 had settled prior to the August sampling and was supplemented by cohort 5, which had settled prior to the November sampling (Figures 4K, L). Each cohort appeared to survive about 1 yr, except cohort 4, which suffered high early mortality (Figures 4L, M). Although spawning in 1980 and 1983 continued until February (Figures 3A, D), no recruitment ensued (Figures 4A–C, M–O), although specimens too small to be sampled may have settled temporarily.

Growth

In all years except 1982, growth rates showed a single peak between November and February. In 1982, growth rates peaked in this period and also between August and November when settlement (cohort 4) occurred earlier than

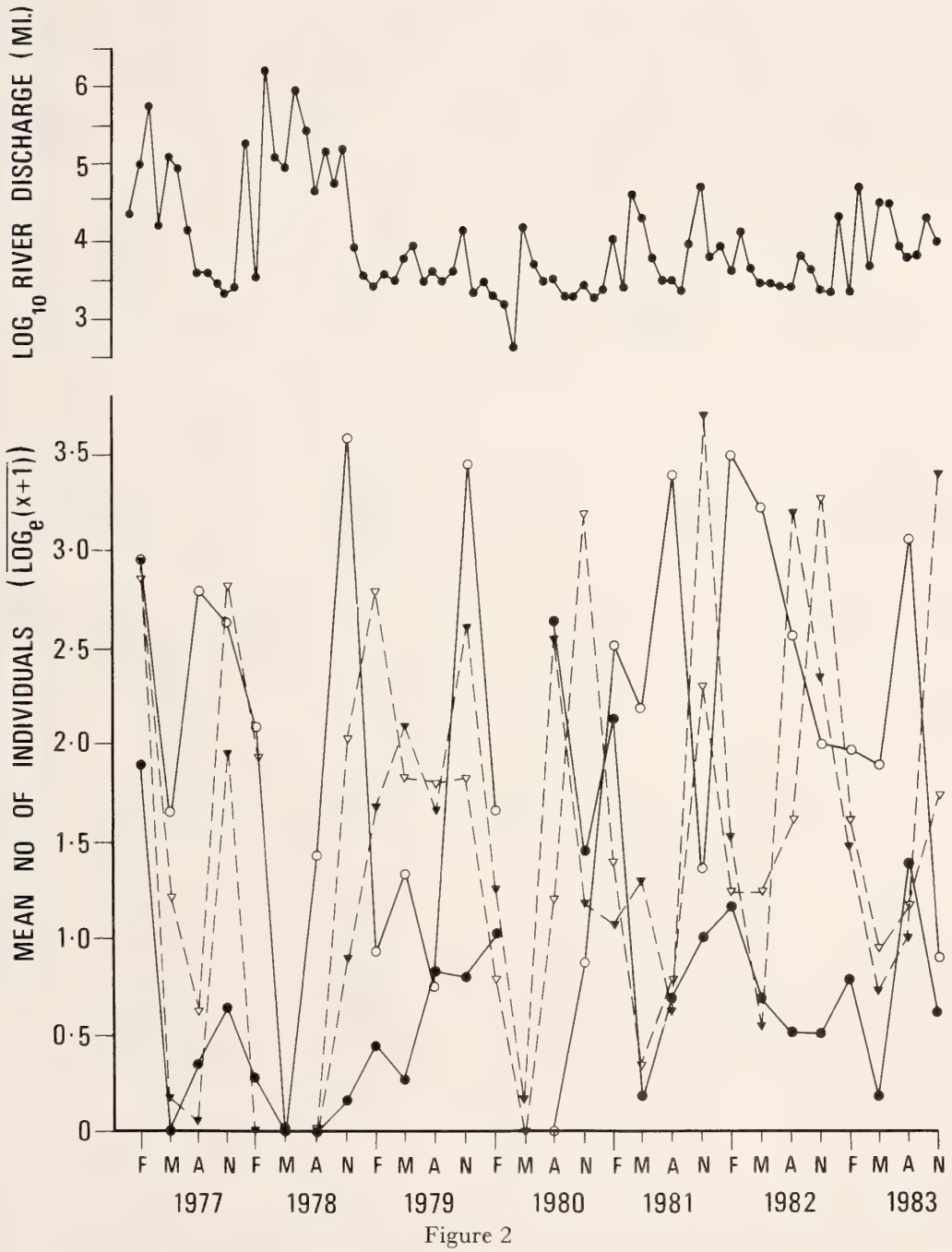


Figure 2

Temporal distribution (1977–1983 inclusive) of mean number of individuals per grab at sites 2.1 (●), 2.2 (○), 7.1 (▼), and 7.2 (▽). Standard errors are omitted for clarity but varied from 0.0 to 0.5 (2.1), 0.0 to 0.6 (2.2), 0.0 to 0.6 (7.1) and 0.0 to 0.8 (7.2) following data transformation to $\log_e(x + 1)$. Log_{10} river discharge volumes are included. Ml = megalitres.

for other years. Growth for these three-month periods varied from 4.0 mm for cohort 2 in 1980–1981 to 10.5 mm for cohort 3 in 1981–1982 (Figure 4). In addition to varying seasonally, growth rates also varied with cohort mean size. For example, the size of cohorts for all these high-growth periods was small, with mean shell lengths less than 5.6 mm. At other times, larger-sized cohorts (>8.4 mm mean length) were present and their growth

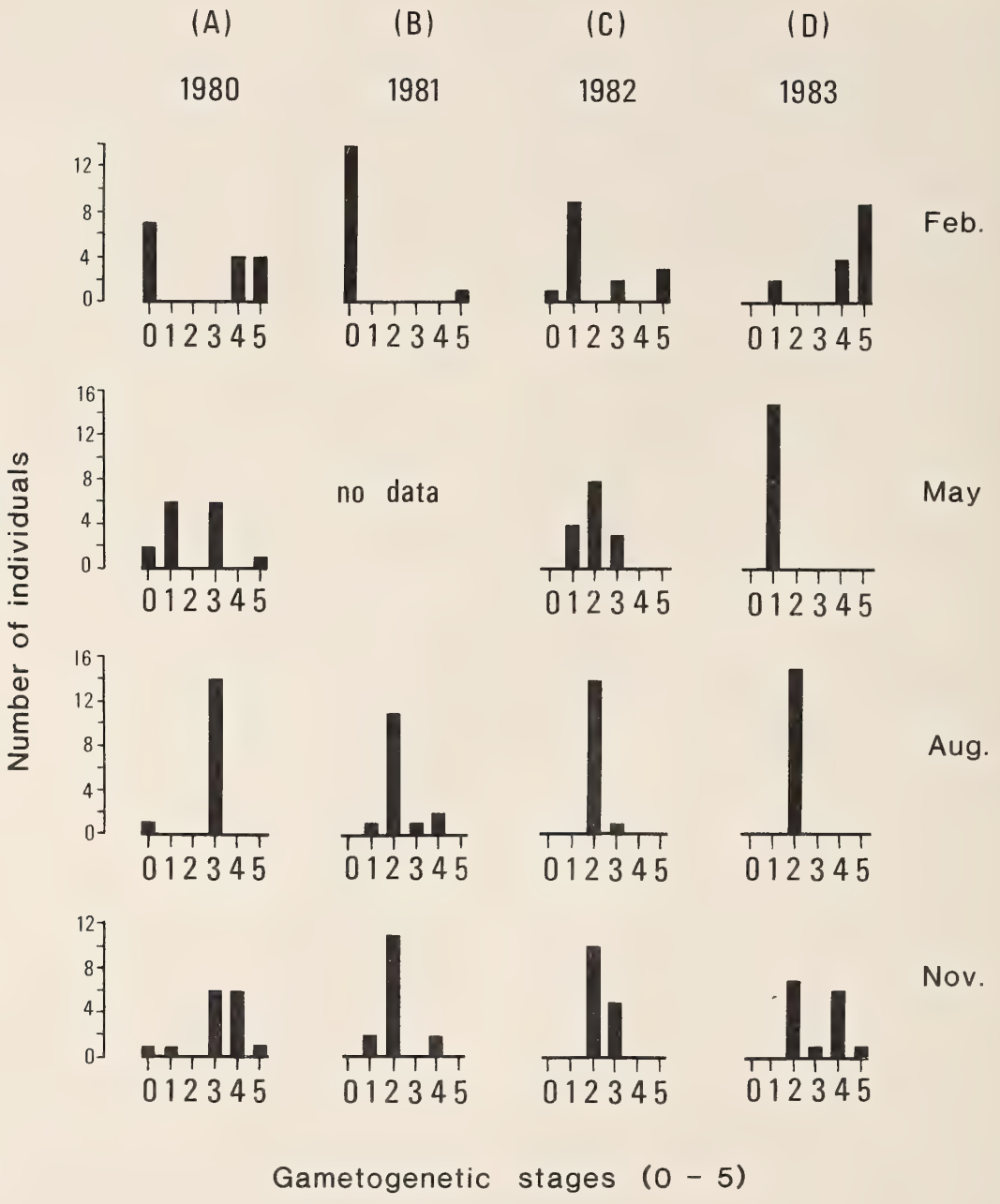


Figure 3

A–D. Temporal sequence of gametogenetic stages at site 7A from summer 1980 until spring 1983. The numbers 0 to 5 on the abscissa refer to gametogenetic stages with 0 = resting or spent gonad, 1 = early active, 2 = late active, 3 = ripe, 4 = partially spawned, and 5 = spent.

never exceeded 2.8 mm for any three-month period (Figure 4). Hence, the effect of season on growth rates was confounded by different sizes.

Growth rates also varied considerably among years. For example, growth for the November–February period of cohort 3 in 1981–1982 and cohort 5 in 1982–1983 was 10.5 mm and 4.8 mm respectively, even though the cohort mean size was identical (Figure 4).

Distribution and Abundance in Space and Time

Differences in abundance among transects, depths, and sediments, and with time, were often statistically significant. However, the patterns of difference were not consistent (ANOVA interaction terms significant) and, hence, any ecological importance of the main factors was obscured by complex interactions.

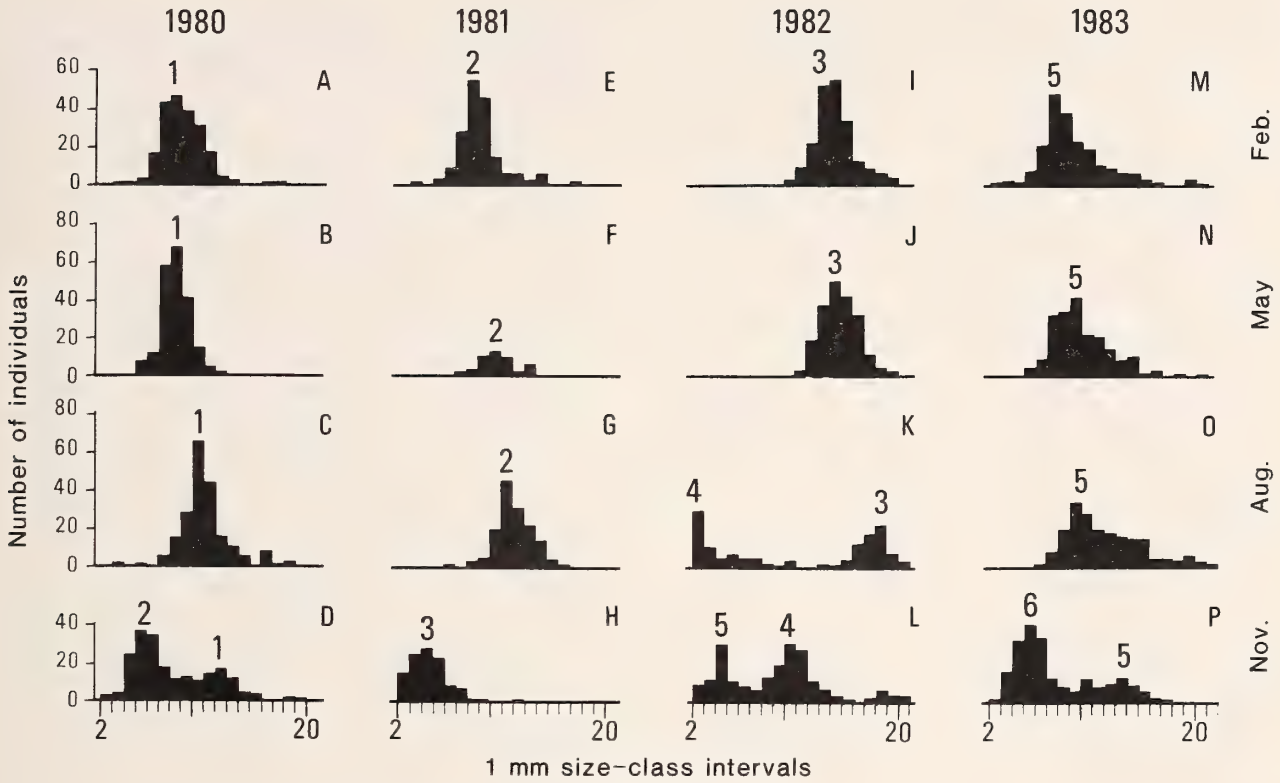


Figure 4

A–P. Size-frequency histograms for each sampling time at site 7A. n = 200 for all samples except F, G, H, and K where n = 46, 145, 110, and 140 respectively. The cohorts are numbered 1–6.

Along-estuary patterns: The occurrence of *Notospisula trigonella* was restricted to the lower and middle reaches of the estuary, *i.e.*, transects 1–9 inclusive. Although significant differences in abundance among these transects usually occurred (three-way ANOVA, $F_{transect} = 243.2$, $P < 0.001$; SNK tests), the pattern varied with both depth and time (three-way ANOVA, all interaction terms significant). The species was absent or rare from both deep and shallow sites on transects 1 and 9. At deep sites, transects 2 and 3 were usually significantly richer than all other transects, while no consistent along-estuary pattern of difference emerged from shallow sites (SNK tests, Figure 5).

Across-estuary patterns: Depth-related differences in abundance occurred at all transects analyzed (three-way ANOVA, $F_{depth} = 640.2$, $P < 0.001$). However, the pattern of difference varied with time (*i.e.*, the richer site was sometimes shallow and sometimes deep; ANOVA interaction terms significant, SNK tests) everywhere except at transect 3. At transect 3, the deep site always yielded more specimens than the shallow site although this depth-related difference was confounded by sedimentary differences between the sites (Table 1).

At transect 6, sediments (but not water depth) varied between the two sites (Table 1). Differences in abundance between these sites were not significant during the first five sampling times (two-way ANOVA, $F_{site} = 4.1$, $P > 0.05$; $F_{interaction} = 2.2$, $P > 0.05$).

Temporal patterns: For the long-term (7-yr) data, significant seasonal and annual differences in abundance occurred at both transect 2 ($F_{season} = 12.1$, $P < 0.001$; $F_{year} = 8.9$, $P < 0.001$) and transect 7 ($F_{season} = 56.7$, $P < 0.001$; $F_{year} = 20.3$, $P < 0.001$). However, at both transects the seasonal patterns varied with both site and year and the yearly patterns varied with both site and season (three-way ANOVAs, second order interaction significant). Despite this significant interaction, patterns were relatively cyclic at transect 7, where peaks often occurred in November and low densities in May or August (Figure 2). However, abundance varied irregularly at transect 2. Following a major flood in March 1978, *Notospisula trigonella* was absent from all sites sampled in May 1978 and relatively rare in August 1978 (Figure 2).

Abundances at transects 2 and 7 were related to temporally changing physicochemical factors in the following ways. Spearman correlations between abundance and each of salinity and one-month river discharge were significant at sites 2.1, 7.1, and 7.2, but not at 2.2. Correlations with temperature were significant only at sites 2.1 and 7.2 (Table 2). Variation in these physicochemical factors never accounted for more than 22% of variation in abundance.

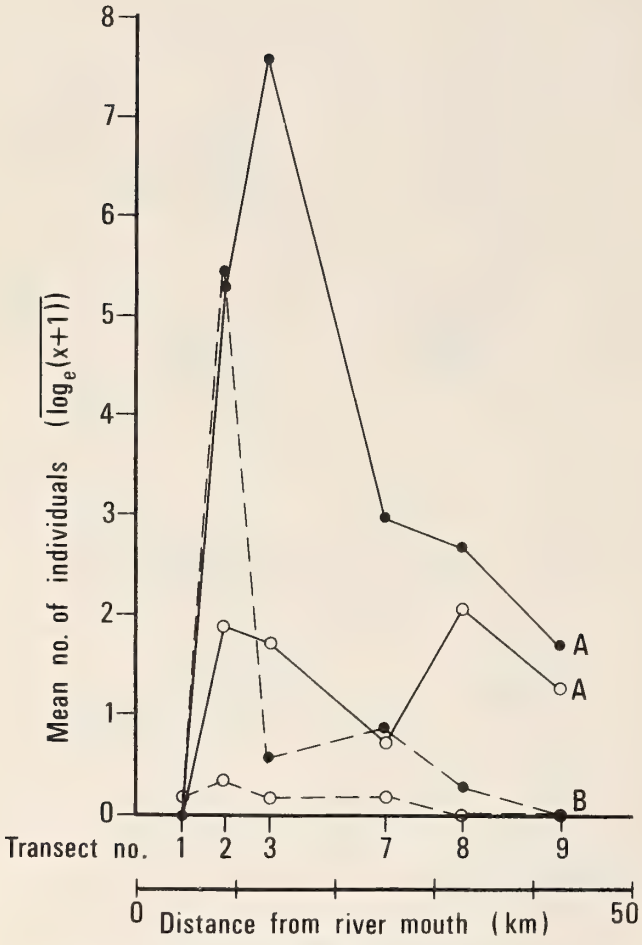


Figure 5

Along-estuary distribution of mean number of individuals per grab at shallow (○) and deep (●) sites for February 1977 (A) and August 1977 (B). Standard errors are omitted for clarity but varied from 0.0 to 0.5 (shallow, February), 0.0 to 0.5 (deep, February), 0.0 to 0.2 (shallow, August), and 0.0 to 0.4 (deep, August).

When the effects of two of the three physicochemical factors were held constant by second order partial correlation, only those correlations with salinity and temperature at site 7.2 were significant (Table 2).

DISCUSSION

Spawning and Recruitment

The appearance of a new cohort and the presence of partly spawned animals in November of most years (Figures 3, 4) indicate that spawning usually starts just prior to this month. This agrees with Hughes (personal communication) who found that specimens from the Swan Estuary in Western Australia first spawned in September–October. These findings suggest that rising temperature could be a spawning cue as found for other bivalve species (SASTRY, 1979). However, the variation in the onset and duration of spawning among years, despite similar temperature cycles, suggests that other factors could influence spawning.

Salinity changes can also cause spawning in some bivalve species (SASTRY, 1979) and spawning at low-flow (high-salinity) times would promote retention of planktonic larvae in the estuary. However, available evidence relating spawning in *Notospisula trigonella* with salinity changes are in conflict. For example, spawning occurred during increasing salinities in Western Australia (Hughes, personal communication) and apparently during decreasing salinities in Bramble Bay, Queensland (Stejskal, personal communication). Furthermore, partly spawned individuals were observed during both low- and high-flow conditions in the Hawkesbury Estuary. Hence, it appears that any role of salinity change as a spawning cue is either variable or else interacts with other factors.

Another feature of the life cycle of *Notospisula trigonella* is the relationship between spawning and recruitment. Although the length of the spawning period usually provided the opportunity for extended recruitment from November until February, only a single cohort appeared in most years

Table 2

Spearman (r_s) and partial (r_p) correlation coefficients between abundance of *Notospisula trigonella* and each physicochemical variable at sites (2.1, 2.2, 7.1, and 7.2) with 7 yr of data available. Partial correlations are second order, *i.e.*, both other physicochemical variables were controlled. *, **, *** = $P < 0.05$, 0.01, and 0.001 respectively, two-sided test.

		Site			
Physicochemical variable		2.1 (n = 112)	2.2 (n = 113)	7.1 (n = 116)	7.2 (n = 115)
Salinity	r_s	0.38***	−0.05	0.33***	0.46***
	r_p	0.12	0.15	0.12	0.23**
River discharge	r_s	−0.25**	0.03	−0.23**	−0.36***
	r_p	−0.17	0.15	0.03	−0.17
Temperature	r_s	0.25**	0.04	0.18	0.33***
	r_p	0.04	0.05	0.03	0.32***

(Figure 4), always early in the spawning season. Any settlement at other times did not yield specimens sufficiently large to be sampled. STEJSKAL (1985) also found recruitment in Bramble Bay, Queensland, restricted to single cohorts. In the present study, several factors may account for this pattern. For example, high river flows after November in some years (Figure 2) may have washed potential settlers downstream. Alternatively, the high densities present after settlement of the first cohort may impede further settlement through their suspension feeding on settling individuals (WOODIN, 1976). However, if this latter mechanism does apply, it was insufficient to prevent the settlement of two cohorts in 1982.

Growth

Growth rates varied seasonally, usually being highest between November and February. At this time, most specimens were small and, hence, the effects of season and size on growth rate were confounded. The decline in growth rate with size was probably caused by resources being diverted from somatic to gonadal growth following the onset of sexual maturity (CERRATO, 1980). However, other factors associated with changing seasons may also have influenced growth rates.

Growth rates also varied among years as shown by comparisons between cohorts of similar mean size from different years. From November 1981 to February 1982, the growth rate was the highest recorded and more than twice the rate for summer 1980–1981 and 1982–1983. This high-growth period coincided with increased river flows (but not of flood status) which may have enhanced the food supply, hence accounting for the high level of growth. Similarly, the growth rate for adults during spring (August to November) of 1983, which experienced high flows, was much greater than the growth rate of similar-sized animals in 1980 when flows were low. However, the relationship between growth and flow rate was non-monotonic, as abundance was low or zero following the floods of 1977 and 1978. Although few studies have related food availability and bivalve growth, WILDISH & KRISTMANSON (1985:237) showed that the growth of blue mussels "may be controlled by tidal current speed through its effect on seston supply." Further, JOSEFSON (1982) found that food supply rather than temperature affected the growth rate of *Abra alba*.

Growth rates of *Notospisula trigonella* also appear to vary with geographical location. For example, the Hawkesbury cohort 3 (Figures 4H–K) reached its maximum size (19 mm mean shell length) in nine months and may have persisted for only 12–15 months. By contrast, individuals of *N. trigonella* from Bramble Bay, Queensland, were only 14–16 mm long at an estimated age of 20–24 months (Stejskal, personal communication). Alternatively, the population at Bramble Bay may have grown more slowly because it was intertidal (and hence had less feeding time) rather than some geographical factor, or else because age estimates might have been in error.

Because of the limitations imposed by the low temporal resolution in sampling, the above life-history interpretations have provisional status only.

Distribution and Abundance

Spatial differences in abundance were not only usually statistically significant but also inconsistent. Such variability appears common both for *Notospisula trigonella* elsewhere (STEJSKAL, 1985) and for other bivalve species (O'FOIGHIL *et al.*, 1984; GIBBS, 1984). Although these inconsistent patterns make it difficult to suggest factors controlling abundance, available evidence suggests the upstream limit of *N. trigonella* may be influenced by salinity. Hughes (personal communication) found high mortality in laboratory populations held in salinities below 5‰, and both this study and that of POORE (1982) in the Gippsland Lakes failed to find this species below 10‰ in depths and sediment grades similar to populated sites of higher salinity.

Although no consistent downstream distributional limit was observed in the present study, *Notospisula trigonella* was absent or rare from transect 1 and also from the high-salinity sites near the mouth of the Gippsland Lakes (POORE, 1982). Furthermore, abundance in large marine bays can be enhanced near freshwater inputs (POORE & RAINER, 1974; STEJSKAL, 1985). These results suggest that marine salinities or some associated factor (see, *e.g.*, BOESCH, 1977) inhibit *N. trigonella*.

Significant across-estuary differences in abundance were sometimes associated with both depth and sediment grade. These patterns resemble those of other mactrid bivalve species (HOLLAND, 1985). However, neither depth nor sediment grade was useful for predicting abundance because the nature of the relationship varied with time, location, or both. Furthermore, at transect 6 where sediment changes were not confounded with depth, significant differences in abundance did not occur. These results suggest that sediment specificity is low in this species. Other studies have found *Notospisula trigonella* to occupy sediments ranging from mud (POORE & KUDENOV, 1978) to sand (MACPHERSON & GABRIEL, 1962; Hughes, personal communication). However, experimental work by Jones (personal communication) found that silt and fine sand attracted more specimens than coarse sand (which did not characterize any Hawkesbury site) where burrowing was difficult. Of course, factors such as hydrodynamic forces are confounded with water depth and sediment grade and may influence adult abundance through their effect on larval distribution or food supply.

Temporal Patterns

While temporal differences in abundance were often highly significant, the patterns of difference were very variable. For example, seasonal differences were not always repeatable over years. Some of this variation can be

explained by the occurrence of a major flood in March 1978 and a minor flood in March 1977 after which *Notospisula trigonella* was uniquely absent and rare respectively. Hence, the seasonal patterns of abundance were altered for these years.

Other estuarine invertebrate species also show substantial temporal variability (BOESCH *et al.,* 1976a; HOLLAND, 1985). One of these is the mactrid bivalve *Mulinia lateralis* which exhibits high fecundity, rapid growth, and early maturity (BOESCH *et al.,* 1976a). *Notospisula trigonella* shares some of these traits, which probably promote survival in a variable and disturbance-prone environment (GRASSLE & SANDERS, 1973).

In contrast, another estuarine mactrid bivalve, *Rangia cuneata,* has a life history that differs from the above species by having long life (at least 8 yr) and by being persistently present in samples taken between 1969 and 1975 (BOESCH *et al.,* 1976a). Temporal variability in abundance was also comparatively low. Consequently, attempts to generalize about estuarine life-history strategies, even among confamilial species, will fail. However, a partial explanation of these differing strategies arises from the following. Estuaries are far from uniform habitats, and species in different salinity zones often differ in their response to disturbance (BOESCH *et al.,* 1976b; Jones, in preparation). *Mulinia lateralis* and *Notospisula trigonella* both inhabit salinities exceeding 10‰ where flood-induced salinity depression, and hence the magnitude of disturbance, would be greater than for *R. cuneata,* which lives in salinities lower than 10‰. Unlike the other two mactrids, *R. cuneata* can survive severe flooding with the probable consequence of longer life and increased buffering of temporal fluctuations.

Although the decreased abundance of *Notospisula trigonella* associated with floods suggests that greatly decreased salinity lowers abundance, the effect of salinity is confounded with the sediment changes that accompany floods. Sediment erosion and deposition and turbidity can kill other bivalve species (PERKINS, 1974; PETERSON, 1985). Being a surface-dwelling suspension feeder with short siphons, *N. trigonella* would probably be particularly susceptible to these sediment changes, especially as Jones (personal communication) found sediment disturbance to affect significantly the abundance of this species.

Although some short-term changes can be explained by the effects of floods, factors such as salinity, river discharge, and temperature never explained more than 22% of the long-term variation (Table 2), a similar result to that obtained for *Mulinia lateralis* in the Chesapeake Bay (HOLLAND, 1985). Furthermore, most of the partial correlations concerning *Notospisula trigonella* were not significant. This high degree of unexplained variability is typical of the zoobenthos of the Hawkesbury Estuary, where rainfall is itself temporally unpredictable (Jones *et al.,* in preparation).

ACKNOWLEDGMENTS

We are grateful to malacologists at the Australian Museum (Dr. W. F. Ponder, Dr. W. B. Rudman, Mr. I. W. Loch, and Mr. P. Colman) and Dr. I. Stejskal and Professor D. T. Anderson for advice concerning taxonomy, biology, and histological interpretations. Dr. G. H. Pyke, Dr. Rudman, Mr. Loch, and two anonymous referees also made constructive comments on the manuscript. We also thank our boat skipper Mr. John Reed for his seamanship, Mr. R. Bateman and Mr. F. Byers for analyzing sediments, and the Coastal Council of N.S.W., the State Pollution Control Commission of N.S.W., and the Australian Museum Trust for financial support. The Metropolitan Water Sewerage and Drainage Board and the Water Resources Commission provided river discharge data. Above all, we are indebted to Mss. Robin Marsh and Charlotte Watson-Russell for their contributions to field and laboratory aspects of this project.

LITERATURE CITED

BOESCH, D. F. 1977. A new look at the zonation of benthos along the estuarine gradient. Pp. 245–266. *In:* B. C. Coull (ed.), Ecology of marine benthos. Univ. South Carolina Press: Columbia.

BOESCH, D. F., R. J. DIAZ & R. W. VIRNSTEIN. 1976b. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York Estuaries and the Lower Chesapeake Bay. Chesapeake Sci. 17:246–259.

BOESCH, D. F., M. L. WASS & R. W. VIRNSTEIN. 1976a. The dynamics of estuarine benthic communities. Pp. 177–196. *In:* M. Wiley (ed.), Estuarine processes. Vol. 1. Uses, stresses, and adaptation to the estuary. Academic Press: New York.

BRALEY, R. D. 1984. Mariculture potential of introduced oysters *Saccostrea cucullata tuberculata* and *Crassostrea echinata* and a histological study of the reproduction of *C. echinata.* Aust. Jour. Mar. Freshwater Res. 35:129–141.

CARLETON, H. M. 1957. Histological technique. 3rd ed. Chapter VII, pp. 93–100. Oxford University Press: London.

CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. Jour. Mar. Freshwater Res. 5:513–522.

CERRATO, R. M. 1980. Demographic analysis of bivalve populations. Pp. 417–465. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms: biological records of environmental change. Plenum Press: New York.

CHALMER, P. N., E. P. HODGKIN & G. W. KENDRICK. 1976. Benthic faunal changes in a seasonal estuary of South-western Australia. Rec. West. Aust. Mus. 4(4):383–410.

FOLK, R. L. 1974. Petrology of sedimentary rocks. Hemphill: Austin. 182 pp.

GIBBS, P. E. 1984. The population cycle of the bivalve *Abra tenuis* and its mode of reproduction. Jour. Mar. Biol. Assoc. U.K. 64:791–800.

GRASSLE, J. F. & H. L. SANDERS. 1973. Life histories and the role of disturbance. Deep-Sea Res. 20:643–659.

GREEN, R. H. 1968. Mortality and stability in a low diversity subtropical intertidal community. Ecology 49:848–854.

HOLLAND, A. F. 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. Estuaries 8:93–113.

JOSEFSON, A. B. 1982. Regulation of population size growth and production of a deposit-feeding bivalve: a long-term field study of three deep-water populations off the Swedish coast. Jour. Exp. Mar. Biol. Ecol. 59:125–150.

MACPHERSON, J. H. & C. J. GABRIEL. 1962. Marine molluscs of Victoria. Melbourne University Press: Melbourne. 475 pp.

McLachlan, A. & T. Erasmus. 1974. Temperature tolerances and osmoregulation in some estuarine bivalves. Zool. Africana 9(1):1–13.

O'Foighil, D., D. McGrath, M. E. Conneely, B. F. Keegan & M. Costelloe. 1984. Population dynamics and reproduction of *Mysella bidentata* (Bivalvia: Galeommatacea) in Galway Bay, Irish west coast. Mar. Biol. 81:283–291.

Perkins, E. J. 1974. The biology of estuaries and coastal waters. Academic Press: London. 678 pp.

Peterson, C. H. 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. Paleobiology 11:139–153.

Poore, G. C. B. 1982. Benthic communities of the Gippsland Lakes, Victoria. Aust. Jour. Mar. Freshwater Res. 33:901–915.

Poore, G. C. B. & J. D. Kudenov. 1978. Benthos of the Port of Melbourne: the Yarra River and Hobson's Bay, Victoria. Aust. Jour. Mar. Freshwater Res. 29:141–156.

Poore, G. C. B. & S. Rainer. 1974. Distribution and abundance of soft-bottom molluscs in Port Phillip Bay, Victoria, Australia. Aust. Jour. Mar. Freshwater Res. 25:371–411.

Rainer, S. F. & R. C. Fitzhardinge. 1981. Benthic communities in an estuary with periodic deoxygenation. Aust. Jour. Mar. Freshwater Res. 32:227–243.

Roberts, D. 1984. A comparative study of *Lasaea australis, Vulsella spongiarum, Pinna bicolor* and *Donacilla cuneata* (Mollusca; Bivalvia) from Princess Royal Harbour, Western Australia. Jour. Moll. Stud. 50:129–136.

Robinson, K. & P. Gibbs. 1982. A field guide to the common shelled molluscs of New South Wales estuaries. Coast and Wetlands Society: Sydney. 56 pp.

Ropes, J. W. 1968. Reproductive cycle of the surf clam, *Spisula solidissima,* in offshore New Jersey. Biol. Bull. 135:349–365.

Sastry, A. N. 1979. Pelecypoda (excluding Ostreidae). Chapter 5. *In:* A. C. Giese & J. S. Pearse (eds.), Reproduction of marine invertebrates. Vol. V. Molluscs: Pelecypods and lesser classes. Academic Press: New York.

Stejskal, I. 1985. The spatial and temporal patterns of the macrofauna of a subtropical muddy sandflat in southeast Queensland, Australia. Ph.D. Thesis, University of Queensland, Brisbane.

Stephenson, W., S. D. Cook & Y. I. Raphael. 1977. The effect of a major flood on the macrobenthos of Bramble Bay, Queensland. Mem. Queensl. Mus. 18:95–119.

Weinberg, J. R. 1985. Factors regulating population dynamics of the marine bivalve *Gemma gemma*: intraspecific competition and salinity. Mar. Biol. 86:173–182.

Wildish, D. J. & D. D. Kristmanson. 1985. Control of suspension feeding bivalve production by current speed. Helgolander wiss. Meeresunters 30:445–454.

Wilson, B. R. 1969. Survival and reproduction of the mussel *Xenostrobus securis* (Lamarck) (Mollusca; Bivalvia; Mytilidae) in a Western Australian estuary. Pt. II: Reproduction, growth and longevity. Jour. Natur. Hist. 3:93–120.

Wilson, B. R. & G. W. Kendrick. 1968. The recent appearance of *Notospisula parva* (Lamarck) (Mollusca; Bivalvia; Mactridae) in the Swan Estuary. Jour. Malacol. Soc. Aust. 1:25–31.

Woodin, S. A. 1976. Adult-larval interactions in dense faunal assemblages: patterns of abundance. Jour. Mar. Res. 34:25–41.

The Veliger 30(3):278–290 (January 4, 1988)

THE VELIGER

Reproduction in a Brackish-Water Mytilid: Gametogenesis and Embryonic Development

by

R. T. F. BERNARD,[1] B. R. DAVIES,[2] AND A. N. HODGSON[1]

[1] Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa
[2] Freshwater Research Unit, Department of Zoology, University of Cape Town 7700, South Africa

Abstract. The fine structure of gametogenesis, ultrastructure of the gametes, and embryonic development at a salinity of 9‰ and at three temperatures (15, 20, and 24°C) of the brackish-water mussel *Brachidontes virgiliae* (Barnard) are described. The spermatozoon is similar to that found in other Pteriomorphia, with a mid-piece of five or six mitochondria, a round electron-dense nucleus, and a hollow conical acrosome. Implications of spermatozoon structure in determining the taxonomic position of this species are discussed. Three stages of oogenesis were recognized: previtellogenic, and early and late vitellogenic. Cortical granules appear to be the source of the vitelline membrane material. The embryonic development of *B. virgiliae* is rapid at 24°C, with spat formation within 24 h of fertilization. Development slows by a factor of 1.5 at 20°C and 2.3 at 15°C. About 18% of developing ova fail to reach the spat stage at 20 and 24°C, increasing to 34% at 15°C. The embryonic development of the animal is discussed in the light of its ecology in southern Cape estuaries and coastal lakes.

INTRODUCTION

Brachidontes virgiliae (Barnard, 1964) is a mytilid bivalve mollusk found in South African waters from the Great Brak River to Mozambique (BARNARD, 1964). The mussel was first identified and named *Musculus virgiliae* by BARNARD in 1964, the name being confirmed by DAVIES (1980). More recently KILBURN & RIPPEY (1982) claim that the animal belongs to the genus *Brachidontes,* although they point out that this is by no means certain. Despite the uncertainty, however, we have elected to use the more recent classification and name.

Apart from descriptive work, there is limited information on the biology and ecology of the species. A few unpublished works deal with its distribution, feeding, reproduction, and spatfall (MCLAREN, 1977; PLUMSTEAD, 1976; SHARP, 1977; COETZEE, 1978). DAVIES (1980) noted that *Brachidontes virgiliae* inhabits the upper reaches of estuaries, favoring low, fluctuating salinities (<15‰) in areas where the substratum is relatively free of silt. Although a small bivalve (maximum shell length 30 mm), *B. virgiliae* is an extremely important component of the invertebrate standing stocks of many coastal lakes along the southern and eastern seaboard of South Africa (BOLTT, 1973; ALLANSON, 1981; DAVIES, 1982, 1984). A recent decline in standing stocks of the littoral macrophyte *Potamogeton pectinatus* Linnaeus in these coastal systems and a concomitant collapse of the *B. virgiliae* populations has had profound effects upon the food chains, with particularly severe consequences for the ichthyofauna (WHITFIELD, 1982, 1984). Clearly further ecological studies on this bivalve are called for, especially with regard to its association with *P. pectinatus* in these systems.

In this study we describe, using microscopic techniques, the fine structure of gametogenesis, the structure of the spermatozoon (which may aid the classification of this species), and the embryonic development of the organism.

MATERIALS AND METHODS

Gametogenesis

Specimens were collected during January and February 1984 from boulders at the head of the Kowie estuary (33°36′S, 26°54′E; Figure 1). Portions of testes and ovaries, which are found mainly in the mantle lobes, were excised from the animals and prepared for electron microscopy. Tissues were fixed in 2.5% phosphate buffered (pH 7.2) glutaraldehyde at 4°C and left overnight. After washing with phosphate buffer (pH 7.2) small pieces of tissue were post-fixed in 1.0% osmium tetroxide for 90 min, dehydrated, and embedded in Taab 812 resin via propylene oxide. Thin sections were cut with a glass knife, stained with uranyl acetate (30 min) and lead citrate (3 min), and examined with a JEOL 100 CXII microscope.

In Vitro Embryonic Development

In vitro fertilization experiments were carried out during the summer of 1978. Viable eggs and spermatozoa were obtained from animals kept in continuous culture and "wild" stocks from Swartvlei (34°0′S, 22°46′E) and the head of the Kowie estuary (Figure 1).

Swartvlei populations of *Brachidontes virgiliae* were normally sexually active at shell lengths from 5 to 6 mm, at which size the gonads could clearly be seen through the thin shell when viewed under transmitted light. The gonads within the mantle wall are typically branched structures: female, brown to russet in color (the species is dioecious), and male gonads, creamy white. Swartvlei stocks maintained in continuous culture systems at a salinity of 4‰ provided gametes at shell lengths between 6 and 10 mm, while those maintained at 9‰ provided viable gametes at shell lengths of 7 mm and larger. Stocks from the Kowie estuary provided viable gametes at shell lengths greater than 10 mm and showed no signs of sexual activity below this size. Because of the thickness of the shell, the sex and state of gonad development of these individuals could only be determined by opening the shell valves. Specimens from the estuarine population were frequently used for in vitro fertilization experiments, but shell lengths between 15 and 27 mm gave the most consistent results in terms of successful embryonic development. Animals from either source, which were less than 4.5 mm shell length, were invariably of indeterminate sex, although gonad development was visible in a few cases (mainly Swartvlei "wild" stocks).

In vitro fertilization experiments and observations of embryonic development were carried out in petri dishes containing filtered water maintained at a salinity of 9‰ and at temperatures of 15 ± 2, 20 ± 2, and 24 ± 2°C. Gametes were obtained by removing the right valve and rupturing the exposed mantle with a fine needle. Eggs and spermatozoa released in this way were rapidly caught up by the ciliary currents of the gills and carried along the feeding grooves to the labial palps. Here they collected and were either periodically gathered by the tip of the foot and pushed ventrally from the cavity or were picked up by currents along the inner mantle wall and discharged through the posterodorsal exhalant siphon. Gametes were transferred to cavity slides or glass wells using micropipettes, mixed, and subsequently monitored using a Wild stereomicroscope. Development was photographed using an Olympus Vanox automatic exposure system.

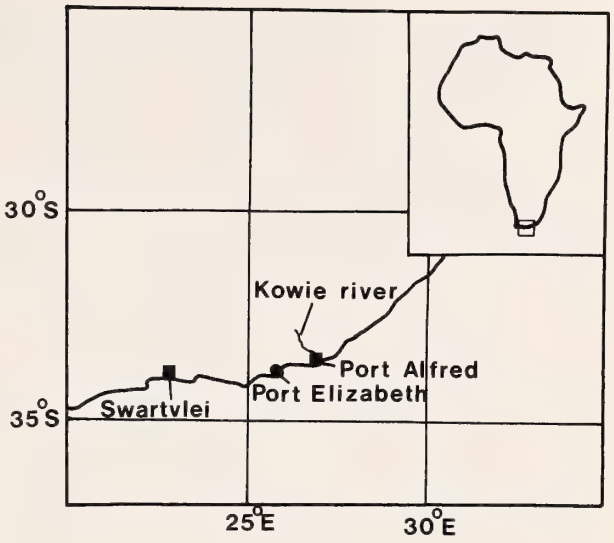


Figure 1

Map showing the positions of Swartvlei and Kowie estuaries on the coast of southern Africa, from which specimens of *Brachidontes virgiliae* were collected for studies of gametogenesis and embryonic development.

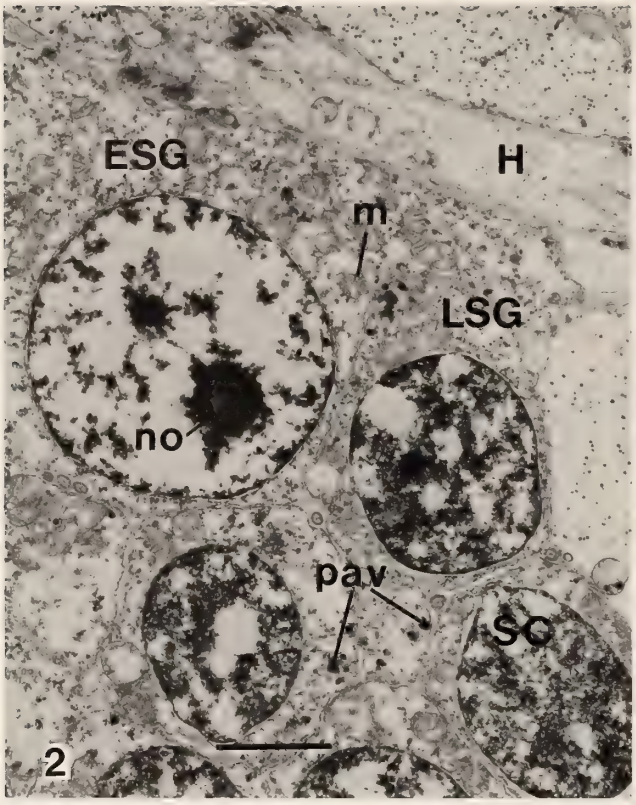
RESULTS

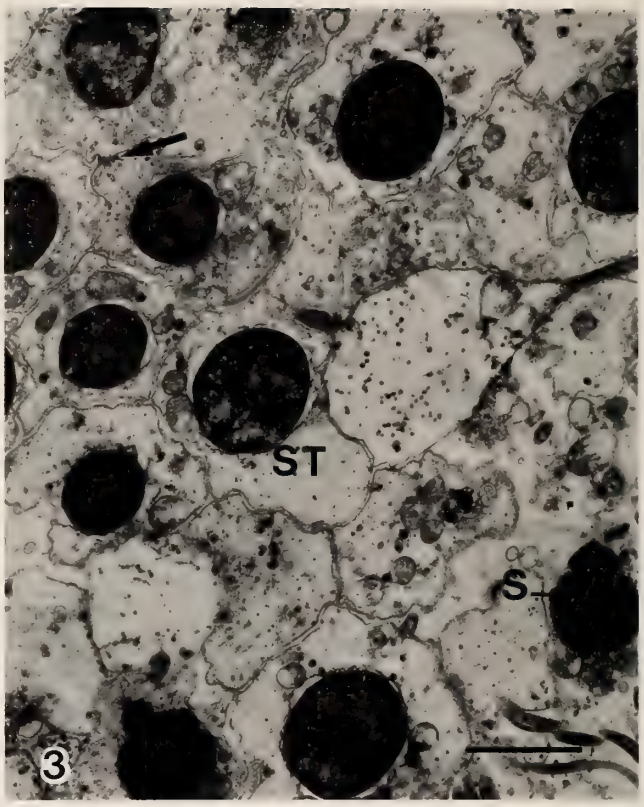
Spermatogenesis

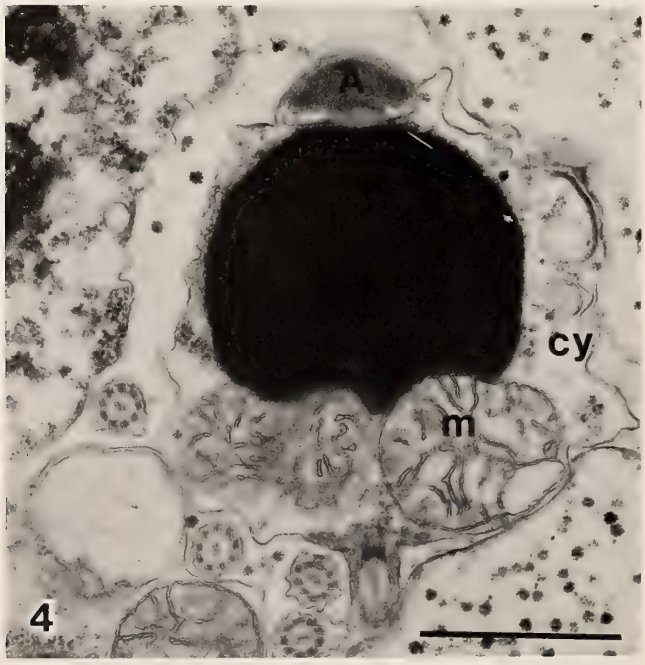
Most stages of spermatogenesis may be observed throughout the year. Early spermatogonia lie close to the haemocoelic space that surrounds each germinal follicle and are characterized by a large spherical or ellipsoidal nucleus (4 × 5 μm) with a prominent electron-dense nucleolus (0.7 μm diameter) (Figure 2). The nucleus contains small clumps of electron-dense chromatin which are often associated with the inner nuclear membrane. The cytoplasm contains numerous small mitochondria (0.3 μm diameter), free ribosomes, and rough endoplasmic reticulum. Late spermatogonia have a smaller nucleus (ca. 3 μm diameter) with a more granular electron-dense nucleoplasm (Figure 2).

Two stages of spermatocyte development, presumed to be primary and secondary, can be found in the walls of the germinal follicle of some specimens. The nucleus of the spermatocyte is similar in size and shape to that of the late spermatogonium; however, the nucleolus is no longer prominent and the chromatin is in the form of a patchwork (Figure 2). The cytoplasm contains a similar complement of organelles to the spermatogonia, as well as Golgi bodies and a few dense, osmiophilic granules—the proacrosomal vesicles (Figure 2)—which are formed by the Golgi bodies. Although similar in size and organelle complement to the primary spermatocyte, the secondary spermatocyte is characterized by less osmiophilic chromatin.

In the early stages of spermatid development the nucleus is spherical and occupies the center of the cell (Figure 3). The cytoplasm contains numerous mitochondria, rough endoplasmic reticulum, Golgi bodies, and proacrosomal vesicles. Intercellular bridges connect the spermatids. As they mature, spermatids are displaced towards the center of the germinal follicle, cytoplasm is lost by sloughing (although cells remain joined by bridges), and the nuclear contents begin to condense (Figure 3). Proacrosomal vesicles migrate to the presumptive anterior of the cell where they coalesce to form a single electron-dense vesicle (Figure







Explanation of Figures 2 to 4

Figure 2. Section through a germinal follicle wall in the testis of *Brachidontes virgiliae*. ESG, early spermatogonium; H, haemocoelic space; LSG, late spermatogonium; m, mitochondrion; no, nucleolus; pav, proacrosomal vesicles; SC, spermatocyte. Scale bar = 2 μm.

Figure 3. Portion of a germinal follicle showing spermatids (ST) and a mature spermatozoon (S). Note the intercellular bridge (arrow) linking two spermatids. Scale bar = 2 μm.

Figure 4. Longitudinal section through the middle of a late spermatid showing structure of the acrosome (A) after the proacrosomal vesicles have coalesced. Note the excess cytoplasm (cy) still surrounding the nucleus and the proximity of the mitochondria (m) to the nucleus. Scale bar = 1 μm.

4), while mitochondria become less numerous but increase in size.

As development progresses, the mitochondria come to occupy the end of the cell opposite the acrosome, forming the sperm mid-piece, and there is a steady loss of cytoplasm by sloughing, a decrease in nuclear size, and a condensation of nuclear material. The acrosomal vesicle assumes an oval shape with the short axis in the anteroposterior plane of

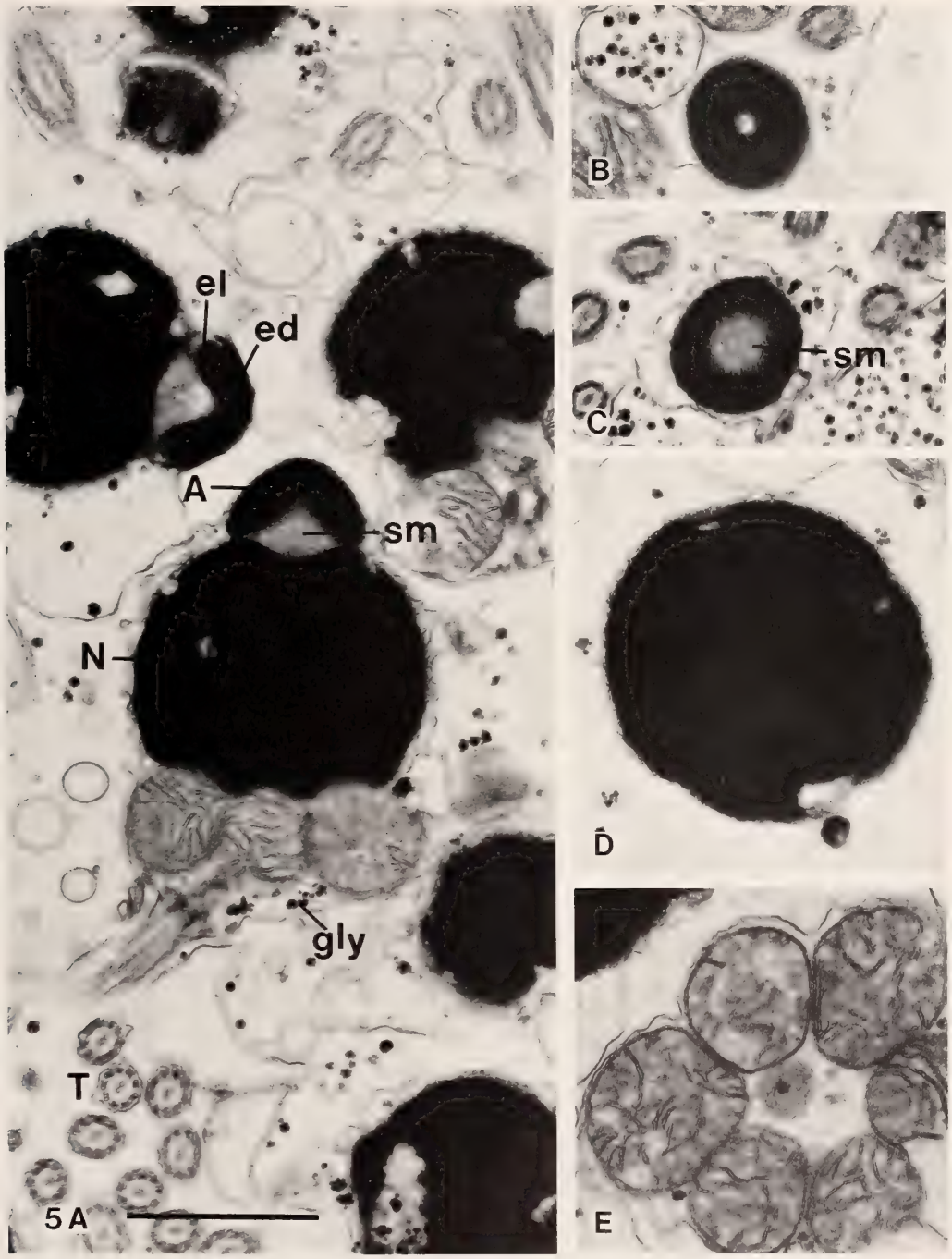
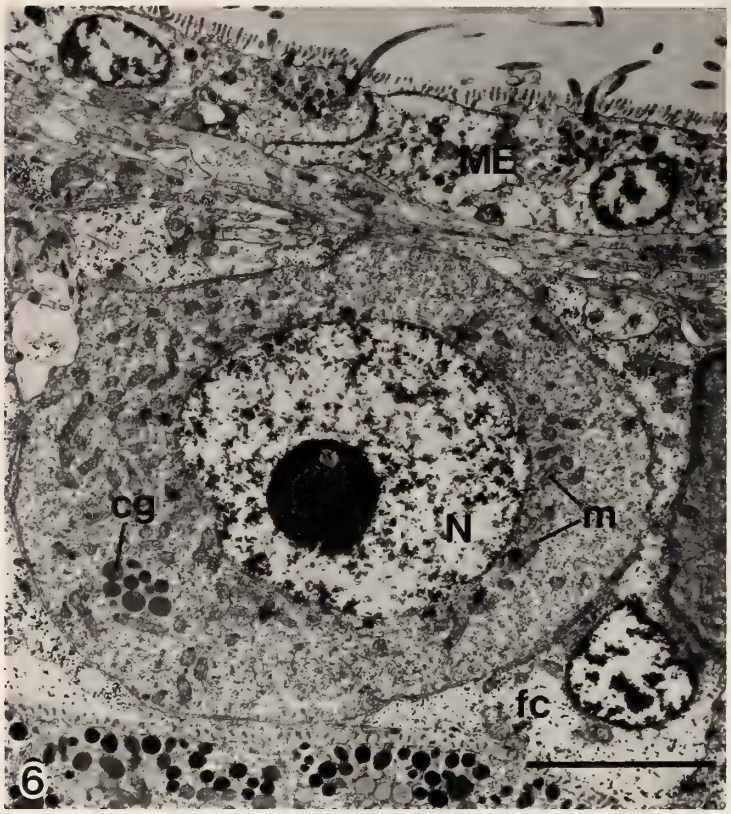


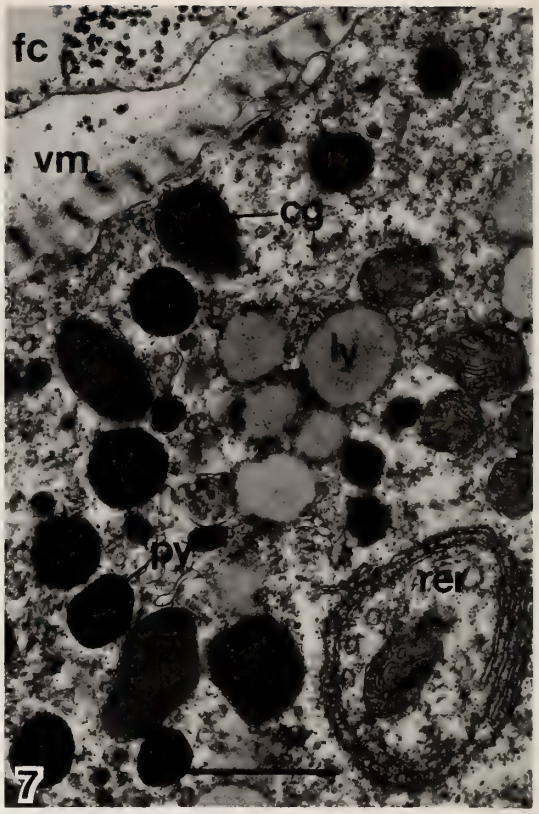
Figure 5

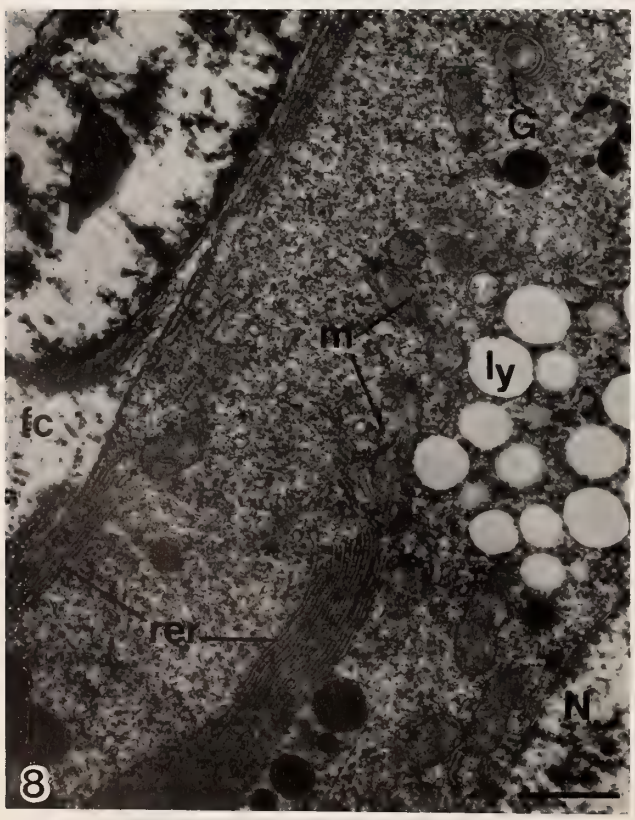
Longitudinal (A) and transverse (B–E) sections through a spermatozoon. B and C are sections through the acrosome; D through the nucleus, and E, the mid-piece. Key: A, acrosome; ed, electron-dense region of acrosome; el, electron-lucent region of acrosome; gly, glycogen; N, nucleus; sm, subacrosomal material; T, tail. Scale bar = 1 μm.

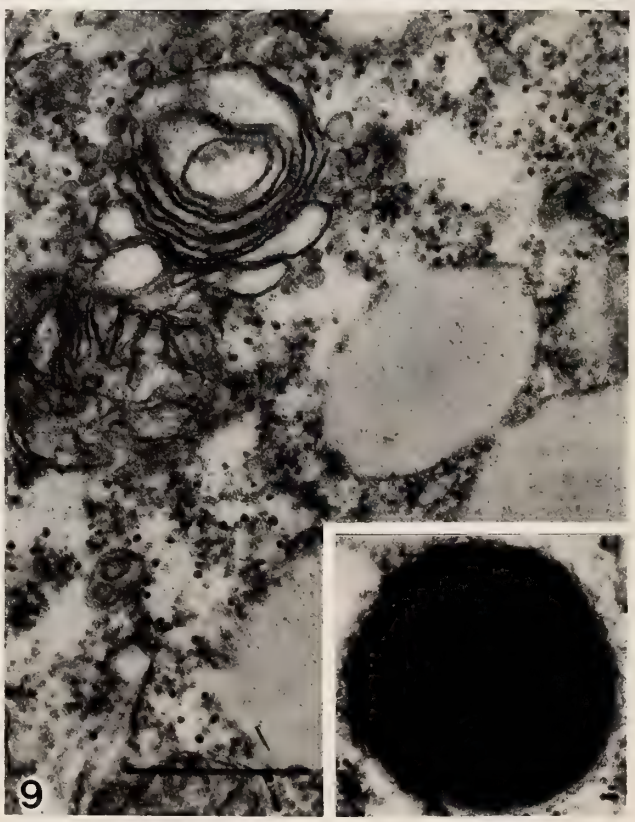
the spermatid (Figure 4). This is followed by invagination of the adnuclear surface and elongation to form the characteristic hollow conical-shaped acrosome (Figure 5).

Mature spermatozoa, each comprising head, mid-piece, and tail, occupy a more central position within the follicle. The head is a 1.8-μm long structure with a round to oval electron-dense nucleus (ca. 1.5 μm diameter) with a characteristic anterior fossa (Figure 5A) and an acrosome 0.5


ME
cg
N
m
fc
6


fc
vm
cg
ly
py
rer
7


G
m
ly
fc
rer
N
8


9

μm long. The hollow, conical acrosome has a uniformly thick wall and contains both an outer electron-dense and inner electron-lucent substance (Figure 5A). Beneath the acrosome is subacrosomal material that has a granular appearance (Figures 5A, C).

The mid-piece contains six (rarely five) spherical mitochondria (Figure 5E) which lie tightly against the nucleus. Glycogen granules lie between the mitochondria while in the center of the ring are the proximal and distal centrioles (Figures 5A, E). The tail, which originates from the distal centriole, has the typical 9+2 arrangement of microtubules (Figure 5A).

Oocyte Maturation

Three stages of oocyte maturation (previtellogenic, early vitellogenic, and late vitellogenic) can be recognized in the ovary of *Brachidontes virgiliae*. The previtellogenic oocyte is about 17 μm in diameter with a large (9 μm diameter) nucleus and a prominent nucleolus (Figure 6). The cell membrane has no microvilli and the vitelline membrane has not yet been formed. The cytoplasm is highly granular and contains numerous spherical and rod-shaped mitochondria, many of which are in a perinuclear position (Figure 6), some strands of rough endoplasmic reticulum, and a few cortical granules. The previtellogenic oocyte is surrounded by several follicular cells which are characteristically irregular in shape with large nuclei (Figure 6). The cytoplasm of the follicular cells is not as electron-dense as that of the oocyte and contains many glycogen granules, some mitochondria, and rough endoplasmic reticulum (Figures 6–8).

During the two vitellogenic stages there is production of lipid and protein yolk bodies and probably the continued production of cortical granules. Lipid yolk bodies, which are commonly found in association with mitochondria (Figure 8), are spherical and of variable size. They are not membrane bound, occur in clumps, and are relatively electron-lucent (Figures 7–9). Protein yolk bodies occur in two forms: in one, the contents appear to comprise numerous small vesicles, with areas of variable electron density (Figure 9, inset), while in the other, the contents are uniformly electron-dense (Figure 7). Both types of protein yolk body are spherical and membrane bound (Figures 7, 9). The cortical granules are of variable shape (often ovoid), occur singly, are membrane bound, and are of intermediate electron density (Figure 7).

During early vitellogenesis the cell membrane develops microvilli and the vitelline membrane is laid down (Figure 10). Associated with this deposition of the vitelline membrane is an arrangement of some of the cortical granules so as to be in contact with the oocyte cell membrane (Figure 10). Early vitellogenesis is further characterized by an increase in nuclear diameter to about 25 μm, with the nucleus becoming increasingly irregular in shape and the nuclear membrane more porous (Figures 10, 11). In addition to protein and lipid yolk bodies and cortical granules, the cytoplasm of the early vitellogenic oocyte contains numerous mitochondria, complex arrays of rough endoplasmic reticulum, and few Golgi bodies with associated vesicles (Figures 8, 9). In the early vitellogenic oocyte the cortical granules, protein, and lipid yolk bodies occur in the ratio 1:2:3. In the cytoplasm of the late vitellogenic or full-size oocyte (Figure 12), the cortical granules, protein, and lipid yolk bodies are abundant and occur in the ratio 1:4:5. At this stage the vitelline membrane is fully formed, and there has been no change in the complement of oocyte organelles. The follicular cells of the full-size oocyte are restricted to those parts of the oocyte that are in proximity to the germinal epithelium of the gonad.

In Vitro Embryonic Development

Development at 9‰ and 24 ± 2°C: Eggs are spherical, granular and russet-brown in color, with a mean diameter of 38.3 μm (SE = ±3.6 μm, n = 300) (Figure 13A). Embryonic development is rapid and the results for 23 separate in vitro fertilization experiments carried out at 9‰ and 24 ± 2°C are summarized in Table 1.

Within 5 min of mixing gametes, polar body extrusion is evident (Figure 13A; Table 1). The first division to produce a micro- and a megamere takes place within 25 min of fertilization (Figure 13A) and is followed by a second division within 45 min. Normally this takes place by division of the megamere (Figure 13A), but occasionally micromere divisions can be observed. The 8-cell stage is reached 115 min after fertilization (Table 1) and is followed by very rapid dexiotropic cleavage to form a blastula

←

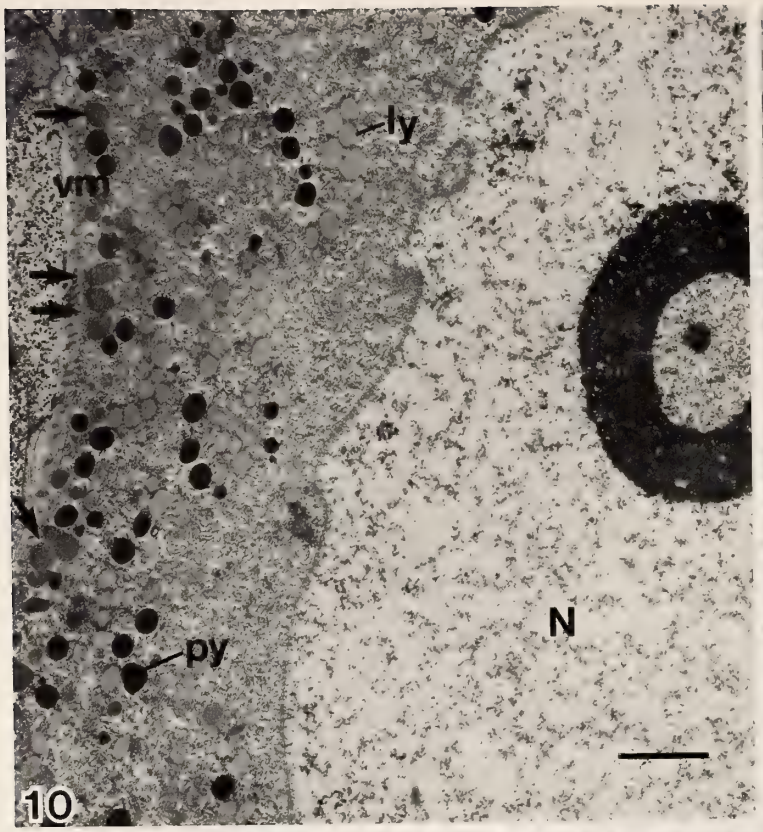
Explanation of Figures 6 to 9

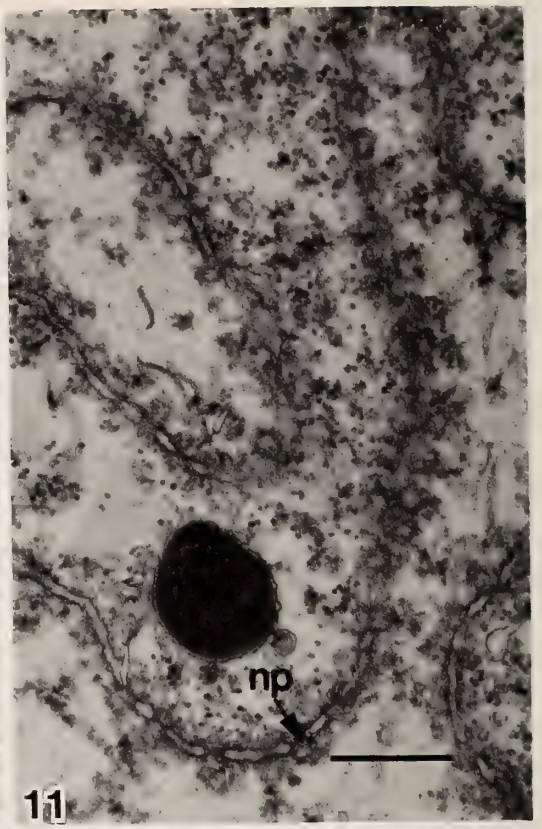
Figure 6. Section through a previtellogenic oocyte showing its peripheral position in the gonad. Note that the oocyte, with its nucleus (N) and prominent nucleolus is surrounded by follicular cells (fc). cg, cortical granule; m, mitochondria; ME, mantle epithelium. Scale bar = 5 μm.

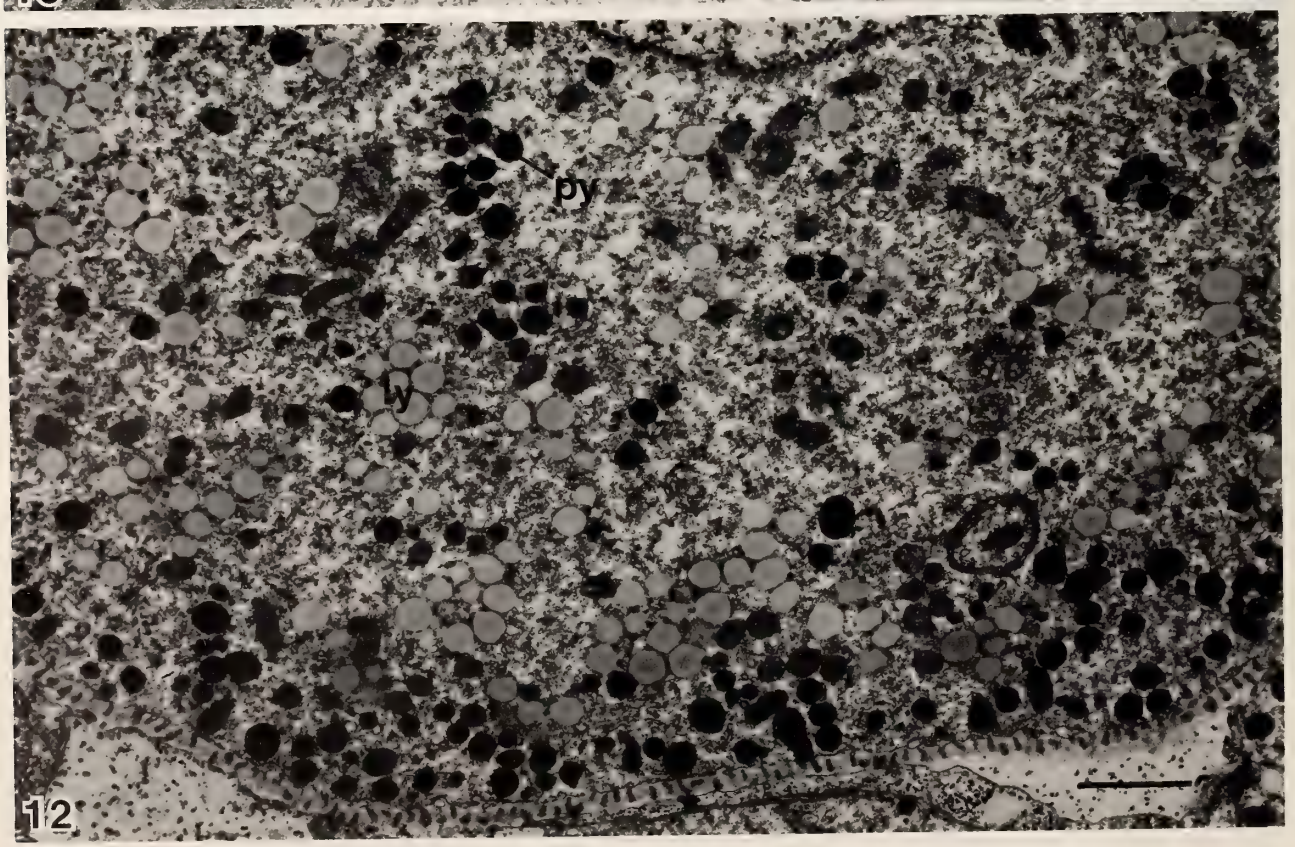
Figure 7. Section through part of a vitellogenic oocyte showing lipid yolk bodies (ly), protein yolk bodies (py), and cortical granules (cg). Note also the structure of the vitelline membrane (vm) and the glycogen in the follicular cell (fc). rer, rough endoplasmic reticulum. Scale bar = 1 μm.

Figure 8. Part of an early vitellogenic oocyte showing parallel arrays of rough endoplasmic reticulum (rer) and the close association of mitochondria (m) and lipid yolk bodies (ly). fc, follicle cell; G, Golgi body; N, nucleus. Scale bar = 1 μm.

Figure 9. Higher magnification of Golgi body and associated vesicles. Inset: protein yolk body from early vitellogenic oocyte. Scale for figure and inset the same, bar = 0.5 μm.


ly
vm
N
py
10


np
11


py
ly
12

(Figure 13B) some 4 h post-fertilization. Gastrulation (epibolic) occurs between 4 and 5 h (Figure 13C) and the morula begins to perform spiral swimming movements, as short ectodermal cirri begin to develop (Figure 14A).

Between 5 and 10 h after fertilization, the morula undergoes rapid organ differentiation, commencing with the development of velar cirri and velar lobes (Table 1), and by 10 h obvious veliger larvae (Figure 14B) are actively swimming, with more directed movements than the simple spiral swimming of earlier stages. After 20 h, embryonic development has progressed to the "early spat" stage, with the formation of the larval shell and regression of the velar lobes (Figure 14C). At this time, larvae respond to disturbance by cessation of swimming and sinking through the water column. A few hours later (ca. 24 h post-fertilization), the characteristic bilaterally flattened spat is obvious (Figure 14D), with a thickened shell and a pronounced hinge ligament. Adductor muscles are functional at this stage and, as before, the spat exhibit "avoidance" reactions to disturbance by closing the valves, cessation of swimming, and sinking to the bottom of the culture vessel. The rudimentary foot is ciliated and much of the swimming movements of spat are directed by this structure. The developing gut is visible through the transparent shell.

Additional observations indicate that spat remain active for at least a further 48 h (up to 72 h post-fertilization) after which they tend to reduce swimming activities and settle on the bottom of the culture vessel. Approximately 18% of fertilized ova fail to develop to the spat stage and of these, most fail to reach the 8-cell stage, while the remainder suffer deformity during transition from blastula to the early veliger larva.

Development at 9‰ and 15 ± 2 or 20 ± 2°C: In vitro embryonic development experiments at a salinity of 9‰ and at temperatures of 15 ± 2 and 20 ± 2°C were carried out during January 1979. The averaged results of four experiments at 15°C and seven at 20°C are listed in Table 2. Briefly, temperature reduction to 15°C slows development by a factor of 2.3 in terms of the time taken to reach the spat stage (up to 55 h post-fertilization). More important, perhaps, is the proportion of fertilized ova that fail to reach the spat stage—approximately 34%. In this case, most developmental failures occur in the very early stages (first and second cleavage). Embryonic development at 20°C slows by 12 h compared to that at 24°C (Table 2), while the failure rate is similar (ca. 16%).

At both 15 and 20°C, spat remain active for over 72 h post-fertilization and show no sign of settling. The longevity of spat at these temperatures is, however, unknown because of culture maintenance problems. Spat usually begin to show signs of osmotic stress after 70 h even after careful attempts to reduce water loss from culture vessels.

DISCUSSION

The structure of the spermatozoon of *Brachidontes virgiliae* is similar to that described for other bivalves of the subclass Pteriomorphia (Popham, 1979). The spermatozoa of such bivalves have a mid-piece of 4–6 mitochondria and a head comprising a round electron-dense nucleus capped by a conical acrosome. It has been suggested that, when evaluated correctly, the ultrastructure of spermatozoa can be used for taxonomic purposes or as an aid to the identification of invertebrates (Popham, 1979; Baccetti, 1979; Adiyodi & Adiyodi, 1983; Franzén, 1983). Recent work on two closely related species of *Mytilus, M. edulis* (Linnaeus) and *M. galloprovincialis* Lamarck, has shown this to be so (Hodgson & Bernard, 1986), for although these mussels are difficult to separate on shell characteristics, they are easily separated using spermatozoon morphology.

In the case of *Brachidontes virgiliae,* identification is still in doubt (Kilburn & Rippey, 1982); it was originally classified as *Musculus virgiliae* by Barnard (1964). In an attempt to shed some light on its position, we have compared the spermatozoon of *B. virgiliae* with that of *M. discors,* which was described by Franzén (1983). Figure 15 shows that the two spermatozoa are very different, suggesting that the two bivalves do not belong to the same genus. The difference, however, may be more closely linked to the mode of fertilization employed by each species. Franzén (1983), for example, has noted that some invertebrates having a modified reproductive biology have an elongate nucleus. *Musculus discors* has direct development, with simple brood protection (Thorson, 1935). *Brachidontes virgiliae,* on the other hand, employs external fertilization, and like all other bivalves with external fertilization, it has a primitive spermatozoon (Franzén, 1983). Clearly a comparative investigation of other species of *Brachidontes* and *Musculus,* supported by electrophoresis, is required before the problem of the correct identification of *B. virgiliae* can be solved.

The observations presented here on spermatogenesis mirror the findings of Longo & Dornfeld (1967) for *Mytilus edulis* and Bernard & Hodgson (1985) for *Perna perna* (Linnaeus). The greatest changes in cell morphology

←

Explanation of Figures 10 to 12

Figure 10. Section through an oocyte at the early vitellogenic stage showing the enlarged nucleus (N) with irregular border. Note the alignment of the cortical granules (arrows) next to the vitelline membrane (vm). Scale bar = 1 μm.

Figure 11. Section through an oocyte at the vitellogenic stage showing the irregular nuclear membrane, with numerous nuclear pores (np). Scale bar = 0.5 μm.

Figure 12. Section through part of the full-size oocyte showing the accumulation of lipid (ly) and protein (py) yolk bodies in the ooplasm. Scale bar = 2 μm.

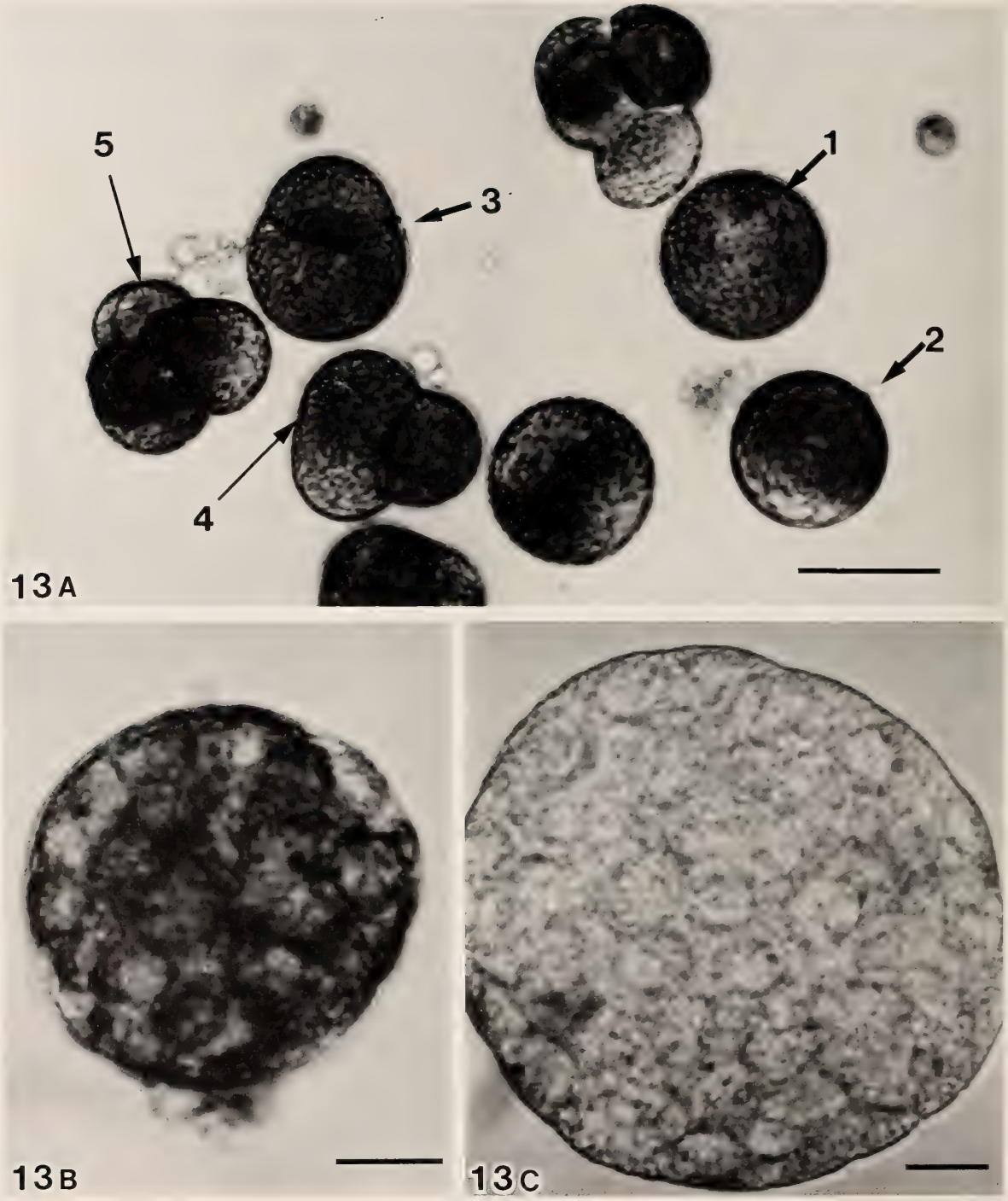


Figure 13

Photomicrographs of embryonic development of *Brachidontes virgiliae* at 24°C and 9‰. A. The newly fertilized egg (1) has a granular cytoplasm and vitelline membrane. Five minutes after fertilization the polar body (2) has been extruded, and first cleavage to produce distinct micro- and megamere (3) occurred within 30 min. (4) shows the first megamere about to cleave, and (5) a 4-cell embryo. Scale bar = 25 μm. B. Early blastula, 4 h post-fertilization. Scale bar = 10 μm. Early gastrula, approximately 4.5 h after fertilization. Scale bar = 5 μm.

occur at the spermatid stage, with nuclear chromatin condensation, mitochondrial fusion to form the mid-piece, and acrosome formation.

Two significant processes occur during oocyte maturation: the production and accumulation of yolk, and the deposition of the vitelline membrane. It is generally accepted that in mollusks, lipid yolk bodies are formed in association with mitochondria (Beams & Sekhon, 1966; Norrevang, 1968; De Jong-Brink *et al.*, 1983) and the close physical association between lipid yolk bodies and mitochondria in *Brachidontes virgiliae* supports this view. Several sources have been proposed for the protein yolk bodies (see Norrevang, 1968, for review). Humphreys (1962) has described bodies intermediate between mitochondria and protein yolk platelets in the oocytes of *Mytilus edulis*; such structures were not, however, seen in *B. virgiliae*. Beams & Sekhon (1966), Anderson (1969), and Taylor & Anderson (1969) have suggested that rough endoplasmic reticulum produces a precursor that is modified by the Golgi bodies and released as small vesicles, which later unite to form the definitive protein yolk body. Based on the abundance of rough endoplasmic reticulum, the presence of Golgi bodies, and the appearance of the two types of protein yolk body, we would suggest that these bodies in *B. virgiliae* are formed via a similar route, and further, that the protein yolk body in which small vesicles can be seen, is an intermediate stage.

The vitelline membrane, which is laid down in early vitellogenesis, is a product of the oocyte (De Jong-Brink *et al.*, 1983), and in *Mytilus edulis*, the cortical granules may be the source of this material (Humphreys, 1967). The arrangement of cortical granules, in contact with or very close to the cell membrane in *Brachidontes virgiliae* (present study) and *M. galloprovincialis* (Bernard & Hodgson, unpublished data), supports the suggestion of Humphreys (1967).

The follicular cells of *Brachidontes virgiliae* are arranged in a manner characteristic of the bivalves (De Jong-Brink *et al.*, 1983), and these authors have reviewed the functional roles suggested for follicle cells in the Mollusca. The cytoplasm of the follicle cells of *B. virgiliae* has large amounts of glycogen, rough endoplasmic reticulum, and mitochondria. The rough endoplasmic reticulum lies close to the cell membrane of the developing oocyte, suggesting that the follicle cells may play a significant role in the maturation of the oocyte. However, the exact function of the follicle cells of *B. virgiliae* remains to be elucidated.

The working temperatures and salinity used in the in vitro embryonic development studies were selected on the basis of data generated by Howard-Williams (1976, 1978) for Swartvlei. During the mouth-open phase of the lake, surface and mid-column salinities varied between 9 and 15‰, with the lowest end of the range occurring for 8 of 17 months of study, and the highest for 3. Temperatures varied between 14 (June–October, winter–spring) and 24°C (December–March, summer) during the same 17-month study period. Development of the mussel is very rapid at 24°C (fertilization to spat within 24 h) and is still relatively rapid at 15°C, while the difference in development time between 20 and 24°C (ca. 10 h) is, perhaps, surprising given the temperature variation overlap during the experiments.

Table 1

Summary of the in vitro early development of *Brachidontes virgiliae* at 24°C and a salinity of 9‰.

Time*	Development stage	Figure
5 min	Polar body extrusion	13A
25 min	First cleavage, micro- and megamere production	13A
70 min	3-cell stage developing	13A
80 min	4-cell stage	13A
115 min	8-cell stage; pronounced dexiotropic cleavage	
130 min	32-cell stage	
4 h	Early blastula free of the vitelline membrane	13B
5 h	Blastopore closing after epibolic gastrulation. Morula performing limited spiral movements; ectodermal cilia short.	13C
10 h	Development of velar cirri	
13–15 h	Developing velum; digestive system developing, directed swimming.	14B
20 h	Velar resorption commences; shell and hinge forming; characteristic bilateral symmetry.	14C
23–24 h	Free-swimming spat; shell well developed, adductor muscles forming; ciliated foot; avoidance response to disturbance.	14D

* Average development time from fertilization.

Coetzee (1978) has recorded high densities of "lamellibranch veliger larvae" in Swartvlei (*Brachidontes virgiliae* is the only possible source) between spring and early summer (October–December, with a peak of >40,000 m^{-3} at 6 m depth) and in autumn (April–May, between 37,000 and 39,000 m^{-3}). Spatfall on the submerged plant *Potamogeton pectinatus* reached >2.5 million individuals m^{-2} of lake bed in November 1978 and >1.25 million individuals m^{-2} in April (autumn) 1978 (Davies, unpublished data), confirming the main reproductive periods of *B. virgiliae* within the system. The double peak of spatfall is difficult to explain in terms of the ecology of the animal, particularly as the autumnal peak occurs as temperatures are falling within the system, and as the *Potamogeton* community is beginning to senesce (with concomitant loss of the enormous area available for attachment of *B. virgiliae*). Mortality must be very large indeed at this time.

The standing stocks of *Brachidontes virgiliae* within Swartvlei are enormous (Boltt, 1973; Davies, 1982, 1984). Indeed, they may constitute the highest standing

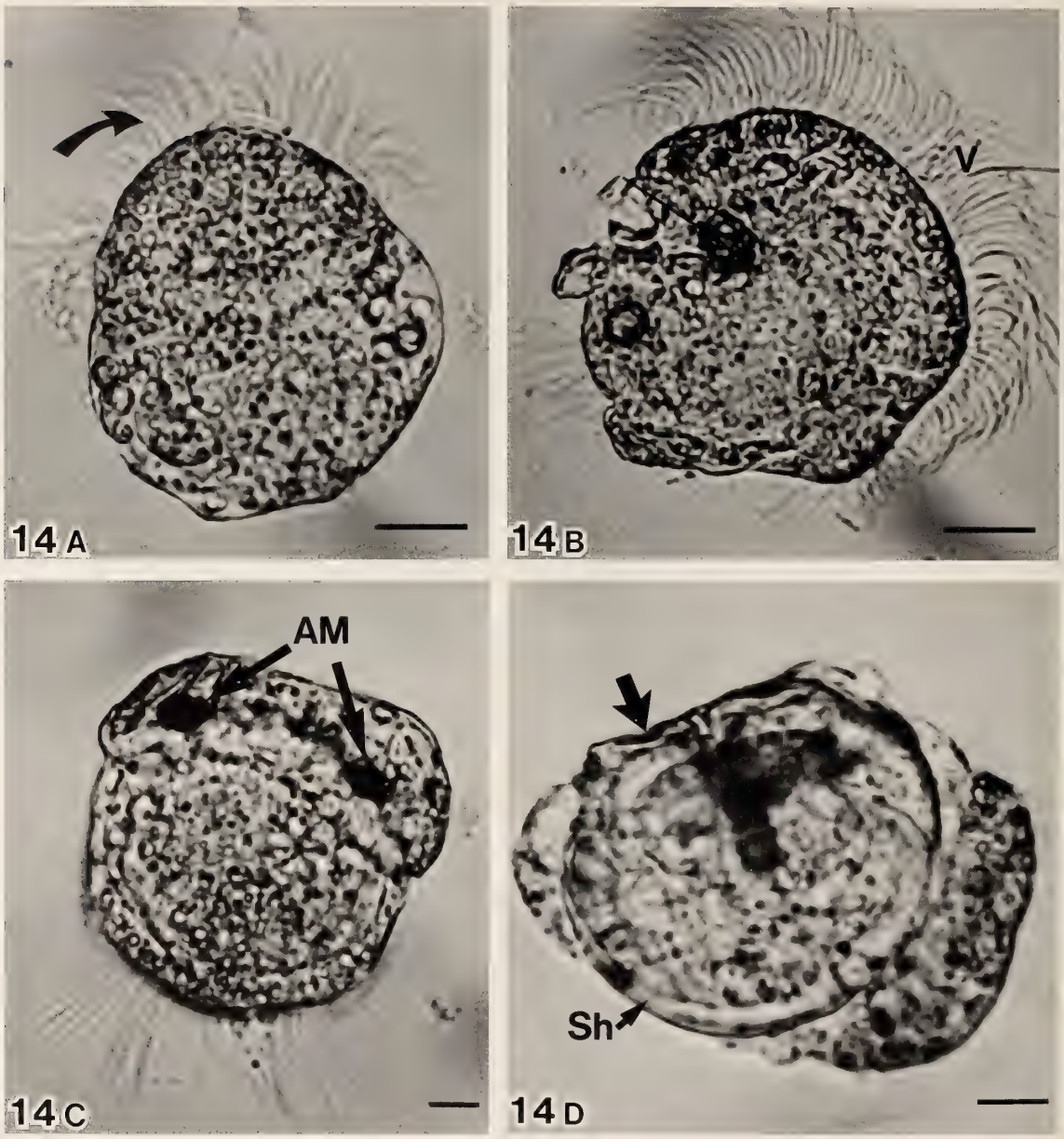


Figure 14

Photomicrographs of development of veliger and spat at 24°C and 9‰. Scale bars = 10 μm. A. Early veliger some 5 h post-fertilization showing development of ectodermal cirri (arrow). B. Veliger at between 5 and 10 h post-fertilization showing development of velar cirri (V) and early organ differentiation (arrow). C. Early spat with pronounced bilateral symmetry showing development of the adductor muscles (AM) and the dorsal aspect of the valves. D. Fully developed spat showing the hinge ligament (arrow), shell (Sh), and developing foot.

stocks of any invertebrate in any aquatic ecosystem anywhere in the world (Davies, 1982). Such densities may be a function of the ability of the mytilid to live attached to vertical surfaces (Davies, 1982, 1984). In the context of the annual cycle of *Potamogeton* (*e.g.*, Howard-Williams, 1978), the availability of a large area of substratum for attachment is temporally limited. This may account for the small size and early reproductive behavior of *B. virgiliae* populations in Swartvlei, as compared to populations from the estuaries of the eastern Cape. In Swartvlei, the animal is capable of commencing gamete production at 5–6 mm shell length (maximum shell length in Swartvlei = 12 mm) and development to the settling spat stage at ambient temperatures is rapid. By comparison

Table 2

Summary of the in vitro early development of *Brachidontes virgiliae* at 15 ± 2 and 20 ± 2°C and a salinity of 9‰.

Development stage	Development time from fertilization	
	15°C	20°C
Polar body extrusion	25 min	8 min
First cleavage	90 min	40 min
3-cell stage	3 h 30 min	100 min
4-cell stage	5 h	160 min
8-cell stage	12 h	3 h 15 min
32-cell stage	14 h	4 h
Early blastula	ca. 19 h	9 h
Gastrulation	ca. 23 h	ca. 12 h
Early veliger	ca. 31 h	20 h
Mature veliger	ca. 38 h	24 h
Velar resportion	ca. 48 h	ca. 30 h
Spat	ca. 56 h	ca. 36 h

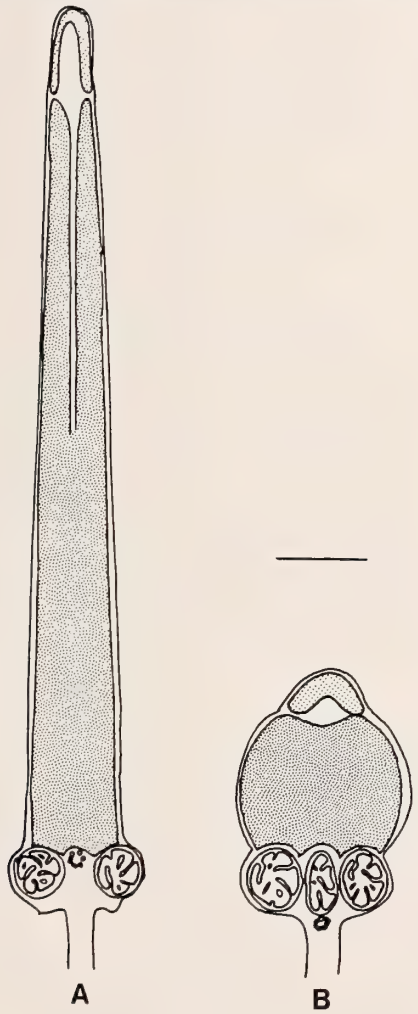


Figure 15

Diagrammatic representation of the structure of the spermatozoon of A, *Musculus discors* (after FRANZÉN, 1983), and B, *Brachidontes* (*Musculus*) *virgiliae* (present study). Scale bar = 1 μm.

populations found at the head of the Kowie estuary, where the substratum for attachment is limited to the protected undersurfaces of relatively large boulders, *B. virgiliae* grows to 30 mm shell length, but does not produce gametes until the shell is approximately 10 mm long. Densities and standing stocks are also very low (DAVIES, 1980, unpublished data). In addition to further studies on the taxonomic position of the species, possibly using the structure of the spermatozoon as a basis, information is also required on its growth, fecundity, and food requirements, together with a comparison between estuarine and coastal lake populations, in order to gain insight into the biology of this remarkable animal.

ACKNOWLEDGMENTS

The work on gametogenesis and gamete structure was supported by a grant from Rhodes University. Studies on the embryonic development of *Brachidontes virgiliae* were supported by the South African Council for Scientific and Industrial Research, Pretoria. These funding agencies are gratefully acknowledged. We would like to thank Mr. R. H. M. Cross for photographic assistance.

LITERATURE CITED

ADIYODI, K. G. & R. G. ADIYODI (eds.). 1983. Reproductive biology of invertebrates. Vol. II. Spermatogenesis and sperm function. John Wiley & Sons Ltd.: Chichester. 692 pp.

ALLANSON, B. R. 1981. The coastal lakes of southern Africa. Pp. 331–344. *In:* J. H. Day (ed.), Estuarine ecology, with particular reference to southern Africa. A. A. Balkema: Cape Town.

ANDERSON, E. 1969. Oocyte-follicle cell differentiation in two species of amphineurans (Mollusca), *Mopalia mucosa* and *Chaetopleura apiculata*. Jour. Morphol. 129:89–126.

BACCETTI, B. 1979. The evolution of the acrosomal complex. Pp. 305–329. *In:* D. W. Fawcett & J. M. Bedford (eds.), The spermatozoon. Urban and Swartzenberg: Baltimore.

BARNARD, K. H. 1964. Contributions to the knowledge of South African marine Mollusca. Part V. Lamellibranchiata. Ann. So. Afr. Mus. 47(3):361–593.

BEAMS, H. W. & S. S. SEKHON. 1966. Electron microscope studies on the oocyte of the fresh water mussel (*Anodonta*), with special reference to the stalk and mechanism of yolk deposition. Jour. Morphol. 119:477–502.

BERNARD, R. T. F. & A. N. HODGSON. 1985. The fine structure of the sperm and spermatid differentiation in the brown mussel *Perna perna*. So. Afr. Jour. Zool. 20:5–9.

BOLTT, R. E. 1973. Coastal lakes benthos. 3 pp. *In:* Report of the Institute for Freshwater Studies, Annual Reports and Reprints, 1972/3, Rhodes University, Grahamstown.

COETZEE, D. J. 1978. The zooplankton of the Wilderness Lakes. Ph.D. Thesis, University of Stellenbosch. 167 pp.

DAVIES, B. R. 1980. The identification of the mytilids *Musculus virgiliae* Barnard, *Arcuatula capensis* (Krauss) and *Brachidontes variabilis* Krauss, with corrections to the literature and a note on their distribution. Trans. Roy. Soc. So. Afr. 44: 225–236.

DAVIES, B. R. 1982. Studies on the zoobenthos of some southern Cape coastal lakes. Spatial and temporal changes in the benthos of Swartvlei, South Africa, in relation to changes in the submerged littoral macrophyte community. Jour. Limnol. Soc. So. Afr. 8:33–45.

Davies, B. R. 1984. The zoobenthos of the Touw River Floodplain. Part 1: The benthos of the Wilderness Lagoon, Touw River and the Serpentine, and the effects of submerged plant cutting. Jour. Limnol. Soc. S. Afr. 10:62–73.

De Jong-Brink, M., H. H. Boer & J. Joosse. 1983. Mollusca. Pp. 297–355. *In:* K. G. Adiyodi & R. G. Adiyodi (eds.), Reproductive biology of invertebrates. Vol. 1. John Wiley & Sons Ltd.: Chichester.

Franzén, Å. 1983. Ultrastructural studies of spermatozoa in three bivalve species with notes on evolution of elongated sperm nucleus in primitive spermatozoa. Gamete Res. 7: 199–214.

Hodgson, A. N. & R. T. F. Bernard. 1986. Observations on the ultrastructure of the spermatozoon of two mytilids from the south-west coast of England. Jour. Mar. Biol. Assoc. U.K. 66:385–390.

Howard-Williams, C. 1976. Swartvlei project. Background data on physical, chemical and biological aspects of the pelagic and littoral zones of Swartvlei November 1974–March 1976, and recommendations for future research. Institute for Freshwater Studies, Rhodes University, Grahamstown. 29 pp.

Howard-Williams, C. 1978. Growth and reproduction of aquatic macrophytes in a south temperate saline lake. Verhandlungen, Internationale Vereinigung für theoretische und angewandte Limnologie 20:1153–1158.

Humphreys, W. J. 1962. Electron microscope studies on eggs of *Mytilus edulis*. Jour. Ultrastr. Res. 7:467–487.

Humphreys, W. J. 1967. The fine structure of cortical granules in the eggs and gastrulae of *Mytilus edulis*. Jour. Ultrastr. Res. 17:314–326.

Kilburn, R. & E. Rippey. 1982. Sea shells of southern Africa. Macmillan: Johannesburg. 249 pp.

Longo, F. J. & E. J. Dornfeld. 1967. The fine structure of spermatid differentiation in the mussel *Mytilus edulis*. Jour. Ultrastr. Res. 20:462–480.

McLaren, E. C. K. 1977. Predation by the crab *Scylla serrata* (Forskal) on the sessile bivalves *Musculus virgiliae* Barnard and *Lamya capensis* (Krauss). Unpubl. B.Sc. Honours Project, Rhodes University, Grahamstown.

Norrevang, A. 1968. Electron microscopic morphology of oogenesis. Inter. Rev. Cytol. 23:113–186.

Plumstead, E. 1976. 'n Inleidende studie van die groei, reproduksie en osmoregulering van *Musculus vigiliae* (*sic*!). Unpubl. B.Sc. Honours Project, University of Port Elizabeth.

Popham, J. D. 1979. Comparative spermatozoon morphology and bivalve phylogeny. Malacolog. Rev. 12:1–20.

Sharp, B. J. 1977. The feeding and distribution of *Musculus virgiliae* Barnard in the Kowie Estuary, South Africa. Unpubl. B.Sc. Honours Project, Rhodes University, Grahamstown.

Taylor, G. T. & E. Anderson. 1969. Cytochemical and fine structural analysis of oogenesis in the gastropod *Ilyanassa obsoleta*. Jour. Morphol. 129:211–248.

Thorson, G. 1935. Biologische Studien uber die Lamellibranchier *Modiolaria discors* L. und *Modiolaria nigra* Gray in Ostgronland. Zoologischer Anzeiger 111:297–304.

Whitfield, A. K. 1982. Trophic relationships and resource utilization within the fish communities of the Mhlanga and Swartvlei estuarine systems. Ph.D. Thesis, University of Natal, Pietermaritzburg. 157 pp.

Whitfield, A. K. 1984. The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. Estuar. Coast. Shelf Sci. 18:315–329.

The Veliger 30(3):291–294 (January 4, 1988)

THE VELIGER

Effect of Eyestalk Ablation on Oviposition in the Snail *Lymnaea acuminata*

by

S. K. SINGH AND R. A. AGARWAL

Department of Zoology, University of Gorakhpur, Gorakhpur 273009 U.P., India

Abstract. The effects of eyestalk ablation on spawning in normal as well as cyclophosphamide-injected *Lymnaea acuminata* are reported. Unilateral or bilateral ablation of the eyestalk induced a spurt of spawning in snails. A second spurt of spawning could be induced in unilaterally ablated snails when the eyestalk of the other side was removed. Administration of cyclophosphamide, on the other hand, considerably reduced spawning. Eyestalk ablation, however, even in cyclophosphamide treated snails, stimulated egg laying to a considerable extent. It is proposed that, whereas the effect of cyclophosphamide is directly on the gonads, eyestalk ablation induces spawning through an endocrine mechanism.

INTRODUCTION

Information on the physiology of reproduction in pulmonate snails is fairly extensive; among these, the freshwater snail *Lymnaea stagnalis* (Basommatophora) has been studied in detail. The endocrine control of reproduction in the Basommatophora has been reviewed by JOOSSE & GERAERTS (1983) and GERAERTS & JOOSSE (1984). According to these authors, separate mechanisms regulate male and female systems in the hermaphrodite snail *L. stagnalis*. Specific neurohormones for the control of ovulation and the preparation of the egg mass have been suggested in these snails. In the stylommatophorans, optic tentacles are a source of an androgenic factor (RUNHAM, 1983) which helps in the differentiation of male sex cells. SINGH & AGARWAL (1981, 1983) demonstrated that injection of cyclophosphamide caused sterility in another hermaphrodite snail, *L. acuminata*.

In the present study the effect of eyestalk ablation on ovulation was studied in *Lymnaea acuminata*. Investigations were carried out on normal as well as on snails made sterile by the injection of cyclophosphamide (SINGH & AGARWAL, 1981, 1983). These studies have practical significance in that this snail is the intermediate host of the parasites *Fasciola gigantica* and *F. hepatica* which cause endemic fascioliasis in sheep and cattle.

MATERIALS AND METHODS

Adults of *Lymnaea acuminata* (2.6 ± 0.3 cm length) were collected from local freshwater ponds and kept in glass aquaria for 24 h in order to acclimatize them to laboratory conditions. Thereafter, the effect of eyestalk ablation on egg laying was studied in normal and cyclophosphamide injected snails. Groups of 20 snails were kept in 10-L capacity glass aquaria containing 3 L of dechlorinated tap water.

Egg masses of *Lymnaea acuminata*, which are laid in the form of gelatinous ribbons consisting of 5–120 eggs each, were collected every 24 h from the aquaria and transferred to 10-cm diameter petri dishes for counting the number of eggs. For ablation, the animals were gently picked out of an aquarium and either one or both eyestalks were quickly snipped off with a pair of iris scissors. Animals were then returned to the aquarium. Controls were likewise sham-operated on the foot.

Solutions of the desired strength of cyclophosphamide were prepared in distilled water and 50 μL was injected in the foot of the snails with an "Agala" micrometer syringe (SINGH & AGARWAL, 1981). Controls received distilled water alone.

Every experiment was conducted for six days on five groups of 20 snails each. Group A consisted of untreated controls; group B contained sham-operated controls kept in total darkness; group C consisted of eyestalk-ablated snails; group D consisted of ablated snails that were given 7 μg cyclophosphamide/snail daily for the first three days; group E received 7 μg of cyclophosphamide/snail daily for the first three days, following which their eyestalks were ablated.

Two sets of experiments were also conducted to study the effect of unilateral ablation. In one set, the left eyestalk was ablated and in the other set the right eyestalk was

Table 1

Effect of sham-operation, absence of light, and eyestalk ablation on egg laying in the snail *Lymnaea acuminata*. Table shows number of spawns and number of eggs laid by groups of 20 snails. Each value represents mean ± SE of 6 replicates with 20 snails in each replicate. Student's *t*-test were applied between the control and ablated snails to locate significant differences.

	Control (group A)		Sham-operated (kept in darkness) (group B)		Bilaterally ablated (group C)	
Period	Number of spawns	Number of eggs	Number of spawns	Number of eggs	Number of spawns	Number of eggs
24 h	7.33 ± 0.23	150.66 ± 5.37	5.66 ± 0.36*	131.5 ± 7.57	18.83 ± 0.91*	532.5 ± 29.12*
48 h	5.83 ± 0.18	148.66 ± 3.32	6.00 ± 0.40	129.66 ± 8.47	6.5 ± 0.54	154.5 ± 8.34
72 h	7.00 ± 0.28	131.32 ± 1.25	5.5 ± 0.37*	126.00 ± 5.78	3.83 ± 0.33*	92.83 ± 5.39*
96 h	6.33 ± 0.23	126.5 ± 4.77	5.5 ± 0.37	137.33 ± 7.13	2.5 ± 0.37*	41.33 ± 8.77*
120 h	6.33 ± 0.23	143.83 ± 9.31	5.33 ± 0.36	135.5 ± 8.68	1.66 ± 0.36*	17.66 ± 4.06*
144 h	6.16 ± 0.18	140.00 ± 3.29	5.33 ± 0.46	132.16 ± 3.36	0	0
Total number of eggs in 144 h		838		790		836

* Significantly ($P < 0.05$) different from control of corresponding period.

ablated. Controls were sham-operated as before. The eggs laid in both sets of unilateral ablation experiments were observed for 72 h. After this the eyestalk of the other side was also ablated and egg laying was studied for the next 72 h.

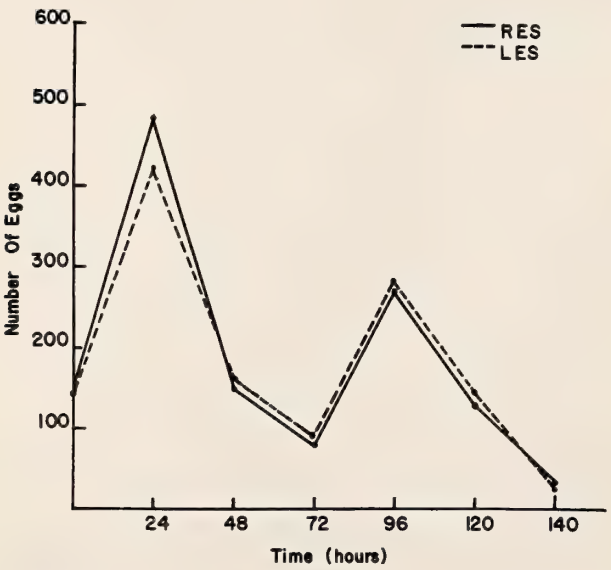


Figure 1

Graph showing effect of eyestalk ablation on pattern of egg laying in *Lymnaea acuminata* during 144-h period. Eggs were counted every 24 h. Data are mean of 6 replicates with 20 snails in each replicate. Zero time indicates number of eggs laid during the 24 h preceding ablation. Eyestalk of one side was removed and eggs were counted for the next 72 h; this was followed by removal of the eyestalk of the other side, with eggs counted for the subsequent 72 h. LES: initially left eyestalk was ablated, 72 h after which right eyestalk was ablated. RES: initially right eyestalk was ablated, 72 h after which left eyestalk was ablated.

Every experiment was replicated six times. Student's *t*-tests were applied to detect significant ($P < 0.05$) changes.

RESULTS

Groups of 20 normal *Lymnaea acuminata* together laid approximately 140 eggs/day during the six day observation period. An average of approximately 6 snails out of the group of 20 spawned every day (Table 1), indicating that over the entire observation period of 144 h each snail spawned approximately twice. The number of eggs laid by sham-operated controls kept in darkness did not differ significantly from non-operated controls kept in lighted aquaria (Table 1).

Bilateral removal of the eyestalks resulted in a sudden spurt of egg laying; during the first 24 h after eyestalk ablation an average of 18.83 spawns were laid. The number of eggs on the first day of ablation was 532 as compared to 150 in non-ablated snails (Table 1). This brisk rate of spawning, however, tapered off to no egg laying by the sixth day. The difference in the number of eggs between control and ablated snails was significant on five of six days ($P < 0.05$; *t*-test). The total number of eggs, however, laid by 20 snails in 144 h was 836 in the case of ablated and 838 in the case of non-ablated snails.

With unilateral eyestalk ablation also, there was a spurt of egg laying immediately after one of the eyestalks was removed. This started tapering off by the third day (Figure 1). Removal of the eyestalk on the other side, after 72 h, started a second spurt of egg laying (Figure 1). Thus, when the right eyestalk was removed 481 eggs were laid on the first day, 151 on the second, and 78 on the third. Removal of the other eyestalk resulted, after 24 h, in the laying of 273 eggs on the fourth day (Figure 1). Figure 1 also shows that right or left eyestalk ablation had the same effect on egg laying.

Table 2

Effect of cyclophosphamide treatment (7 μg/animal/day) and eyestalk ablation on egg laying in *Lymnaea acuminata*. Values are mean ± SE of 6 replicates of 20 snails each. All snails were injected with cyclophosphamide at 7 μg/day/animal for the first 3 days. Group D was ablated at the start of the experiment. Group E was ablated after 72 h. Student's *t*-test were applied to locate significant differences.

	Ablated on 1st day (cyclophosphamide injected for the first 3 days) (group D)		Ablated after 72 h (cyclophosphamide injected for the first 3 days) (group E)	
Period	Number of spawns	Number of eggs	Number of spawns	Number of eggs
24 h	8.16 ± 0.35	177.16 ± 8.98†	4.16 ± 0.18*,†	72.33 ± 1.80*,†
48 h	4.5 ± 0.24†	88.5 ± 2.93†	2.33 ± 0.23*,†	43.33 ± 1.95*,†
72 h	3.16 ± 0.33†	53.33 ± 6.63†	2.16 ± 0.33*	22.16 ± 4.54*,†
			(ABLATION)	
96 h	0	0	8.16 ± 0.44*,†	170.16 ± 5.13*,†
120 h	0	0	4.00 ± 0.28*,†	86.33 ± 3.07*,†
144 h	0	0	0	0

* Group E significantly ($P < 0.05$) different from group D.
† Significantly different from controls (Table 1).

Injection of cyclophosphamide at a dose of 7 μg/day for three days significantly ($P < 0.05$) reduced the number of eggs (Table 2). Thus, when cyclophosphamide was injected into non-ablated snails, the total number of eggs produced by 20 snails during the first three days was 137 as compared to 429 in control snails (Tables 1, 2). Injection of cyclophosphamide into ablated snails also reduced the number of eggs, but the reduction was significantly less than that observed in non-ablated snails during the first three days. In cyclophosphamide injected snails, however, oviposition ceased after three days (Table 2).

Eyestalk ablation, even in snails treated with cyclophosphamide for the first three days, resulted in a second spurt of egg laying for two days (Table 2). However, these eggs did not develop into young.

DISCUSSION

The present study clearly shows that ablation of the eyestalk(s) of *Lymnaea acuminata* initiates vigorous spawning activity within 24 h. In the beginning, the rate of oviposition was nearly 3.5 times higher than controls. From the number of spawns, eyestalk ablation apparently caused immediate spawning in nearly all of the snails. The rate of egg laying, however, gradually declined so that in the operated snails oviposition stopped completely after 120 h, even though the control snails continued to lay approximately the same number of eggs throughout the observation period. The present study also demonstrates that, even though eyestalk ablation changed the pattern of egg laying, the total number of eggs laid during the six day observation period was the same in both groups. Indeed, eyestalk ablation, although it causes a sharp increase in the rate of delivery of eggs immediately after ablation, did not cause any net increase in the number of eggs laid.

Data presented in this study shows that there was no change in the egg-laying pattern of sham-operated snails kept in total darkness. This rules out the possibility of blindness or injury being the cause of the egg-laying stimulus. Indeed, our study on unilateral ablation shows that removal of only one eyestalk of either side can cause increased egg laying. Moreover, a second spurt of spawning could be successfully started by the removal of the other eyestalk.

Singh & Agarwal (1981, 1983) demonstrated that the alkylating drug cyclophosphamide is a potent chemosterilant for *Lymnaea acuminata*. The present data show that ablation of eyestalks even in cyclophosphamide-treated snails caused a two-day spurt of egg laying. Since ablation can induce egg laying even in cyclophosphamide treated snails it is possible that ablation and cyclophosphamide act at different sites. Singh & Agarwal (1981, 1983) reported that cyclophosphamide reduced the DNA and RNA levels in the ovotestis of *L. acuminata*, thus indicating that the drug acts directly on gonads. It seems that ablation, which increases spawning in normal as well as in cyclophosphamide-injected snails, does not affect the gonads directly but through the neurohumoral system. Increased oviposition following ablation, three days after cyclophosphamide injection, also suggests that eyestalk removal can trigger the neurohumoral system even in sterile snails. There are a number of reports (Maat *et al.*, 1983; Scheerboom, 1978; Joosse & Veld, 1972; Bohlken & Joosse, 1982) that the caudo-dorsal cells in *L. stagnalis* release an ovulation hormone. It is possible that removal of the eyestalks in *L. acuminata* also stimulates the caudo-dorsal cells to release this hormone.

LITERATURE CITED

Bohlken, S. & J. Joosse. 1982. The effect of photoperiod on female reproductive activity and growth of the freshwater

pulmonate snail *Lymnaea stagnalis* kept under laboratory breeding conditions. Int. Jour. Invertebr. Reprod. 4:213–222.

GERAERTS, W. P. M. & J. JOOSSE. 1984. Freshwater snail (Basommatophora). *In:* K. M. Wilbur, A. S. Tompa, N. H. Verdonk & J. A. M. Van Den Biggelaar (eds.), The Mollusca 7:142–199. Academic Press, Inc.: New York.

JOOSSE, J. & W. P. M. GERAERTS. 1983. Endocrinology. *In:* A. S. M. Saleuddin & K. M. Wilbur (eds.), The Mollusca 4:318–390. Academic Press, Inc.: New York.

JOOSSE, J. & C. J. VELD. 1972. Endocrinology of reproduction in the hermaphrodite gastropod *Lymnaea stagnalis*. Gen. Comp. Endocrinol. 18:599–600.

MAAT, A. T., J. C. LODDER & M. WILBRINK. 1983. Induction of egg-laying in the pond snail *Lymnaea stagnalis* by environmental stimulation of the release of ovulation hormone from caudo-dorsal cells. Int. Jour. Invertebr. Reprod. 6:239–247.

RUNHAM, N. W. 1983. Mollusca, accessory sex glands. *In:* K. G. Adiyodi & R. G. Adiyodi (eds.), Reproductive biology of invertebrates. Wiley: England.

SCHEERBOOM, J. E. M. 1978. The influence of food quantity and food quality on assimilation, body growth and egg production in the pond snail *Lymnaea stagnalis* (L.), with particular reference to the haemolymph-glucose concentration. Proc. K. Acad. Wet. C81:173–183.

SINGH, R. & R. A. AGARWAL. 1981. Cyclophosphamide as a potential chemosterilant for harmful snails. Acta Pharmacol. Toxicol. 49:195–199.

SINGH, R. & R. A. AGARWAL. 1983. Chemosterilization and its reversal in the snail *Lymnaea acuminata*. Acta Pharmacol. Toxicol. 52:112–120.

The Veliger 30(3):295–304 (January 4, 1988)

THE VELIGER

A Review of the Genus *Agaronia* (Olividae) in the Panamic Province and the Description of Two New Species from Nicaragua

by

AL LÓPEZ,[1] MICHEL MONTOYA,[2,3] AND JULIO LÓPEZ[1]

[1] Universidad Centroamerica (UCA), P.O. Box A-90, Managua, Nicaragua
[2] Interamerican Institute for Cooperation on Agriculture (IICA), P.O. Box 4830, Managua, Nicaragua

Abstract. Three previously recognized Panamic species, *Agaronia testacea* (Lamarck, 1811), *A. propatula* (Conrad, 1849), and *A. griseoalba* (von Martens, 1897) (senior synonym here replacing *A. murrha* Berry, 1953), are reviewed and their occurrences reported for the Panamic province. Two new species, *A.* ***nica*** and *A.* ***jesuitarum***, are described, primarily from records in Nicaragua. Species are defined using parameters of protoconch type, spire height, aperture width, pillar lirae count, and shell length. Two distinct kinds of protoconch—acuminate and mammillate—are distinguished: species with acuminate protoconchs are *A. testacea, A. propatula,* and *A.* ***jesuitarum***; those with mammillate protoconchs are *A. griseoalba* and *A.* ***nica***.

INTRODUCTION

Two species, *Agaronia testacea* (Lamarck, 1811), and *A. propatula* (Conrad, 1849), have been regarded as broadly distributed in the Panamic province (*see* KEEN, 1958, 1971). A third species, *A. murrha* Berry, 1953, has been cited by Keen as known only from Corinto, Nicaragua. Previous authors have not realized that the latter species is broadly distributed in the southern Panamic province and has an older name. The extent to which the same patterns of color variation are shared by co-occurring species has not been understood. Here we demonstrate, based on meristic characters, that there are five Panamic species, two of which are new.

MATERIALS AND METHODS

The identity of previously described taxa presented a problem only for one of the names introduced by VON MARTENS, 1897: *Oliva* (*Agaronia*) *testacea* var. *griseoalba*. The type specimen was received on loan from the Zoologisches Museum of Humboldt-Universität in Berlin (ZMB) by Dr. McLean at the Los Angeles County Museum of Natural History, where it was photographed for inclusion here. Von Martens also proposed *Oliva* (*Agaronia*) *testacea* mut. *candida,* but that name is preoccupied by *Oliva candida* Lamarck, 1811, and need not be considered.

Specimens were collected by us at low tide and by wading and snorkling at a number of localities in Nicaragua and Costa Rica (Table 1). Information provided by Dr. McLean about the occurrences of these species elsewhere in the Panamic province is also included. We have also examined specimens received on loan from Carol Skoglund of Phoenix, Arizona, and David G. Robinson of Tulane University, New Orleans, Louisiana. Voucher specimens of previously described species and type specimens of the new species have been placed in the following institutional collections: CAS—California Academy of Sciences, San Francisco, California; LACM—Los Angeles County Museum of Natural History, Los Angeles, California; LSM—La Salle Museum of Natural History, San José, Costa Rica; UCA—Central America University, Managua, Nicaragua; UCRZ—Zoology Museum of University of Costa Rica, San José.

The meristics are based on 38 specimens of each of the five species. Measurements were made with vernier calipers, with an accuracy of 0.05 mm. Abbreviations for the physical parameters (Figures 1, 2, and text) are as follows: *a,* lateral spire height from tip of callus above aperture to protoconch tip; *b,* width, maximum distance from labrum

[3] Present address: P.O. Box 6327, San José, Costa Rica.

to opposite side; *c*, crest on fasciolar band; d_1, distance along labrum from suture to fasciolar band; d_2, same distance (suture to fasciolar band) on side opposite from lip; *e*, edge of pillar pleats; *f*, spire factor, a/w, a measure of spire acuteness; *g*, breadth factor, o/l, a measure of aperture width; *h*, maximum height; *k*, dorsal color band; *l*, length of shell from protoconch to tip of columella; *n*, number of specimens examined; *o*, maximum aperture width from tip of penult pillar pleat to edge of labrum; *p*, pillar pleats; *r*, relative growth factor d_1/d_2, a measure of relative growth of shell length; SD, standard deviation; s_1, posterior pillar lirae; s_2, anterior pillar lirae; *t*, terminal pleat; *w*, width of diameter of spire base measured from tip of callus above aperture to opposite point on suture.

SYSTEMATIC TREATMENT

Family Olividae Latreille, 1825

Subfamily Agaroniinae Olsson, 1956

Genus *Agaronia* Gray, 1839

Type species (monotypy): *Voluta hiatula* Gmelin, 1791. Recent, west Africa.

The shell is medium thick, ovate–fusiform, with a truncate flaring aperture extending about 0.7 of shell length. One strong terminal pleat (*t*) extends internally from the pillar through the spire whorls. Separated from it by a sulcus are 8 to 20 lirae on the inner surface of the pillar and the anterior parietal callus. The count of lirae provides a useful specific character. Some of these lirae are engraved and prolonged into the fasciole as strong pleats (*p*) over the pillar. The highest of these usually marks the posterior limit of the anterior pillar lirae (s_2), but more posteriorly there are a few posterior pillar lirae (s_1), particularly on *Agaronia griseoalba*. The average number of lirae, including the terminal pleat, varies from a minimum of 9.1 for *A. propatula* to a maximum of 16.7 for *A. griseoalba*. The slightly raised callus pad on the pillar and fasciole is microscopically wrinkled, white, sometimes suffused with purple. There is wide fasciolar band, covered with callus, that forms the base of the shell. The morphology of the fasciolar band is similar to that seen in the genus *Ancilla* Lamarck, 1799, which has an "ancillid" band and a fasciolar band separated by the "posterior fasciolar groove" (Kilburn, 1981). In *Agaronia* the two bands are fused together, but a very slight crest (*c*) corresponding to the posterior fasciolar groove of *Ancilla* is present. The callus of the fasciolar band is the same color as the spiral band callus, and both often have a slightly uneven surface, variegated with streaks of a different color. A short distance above the fasciolar band there is a dorsal color band (*k*), white or light purple, most easily seen on dark shells. Its background color is made up of a closely knit web of microscopic zigzag lines overset with larger, thin irregular streaks that are visible without magnification. These streaks are contained within the limits of the dorsal color band, but in large shells they sometimes occur on other parts of the dorsum. The surface of *Agaronia* is smooth and shiny, but not highly glazed except where covered with callus. The interior is dark purple in some shells and light purple, yellow, or white in other specimens, often with two well-marked purple bands. The edge of the lip reveals the color of the dorsum along its length.

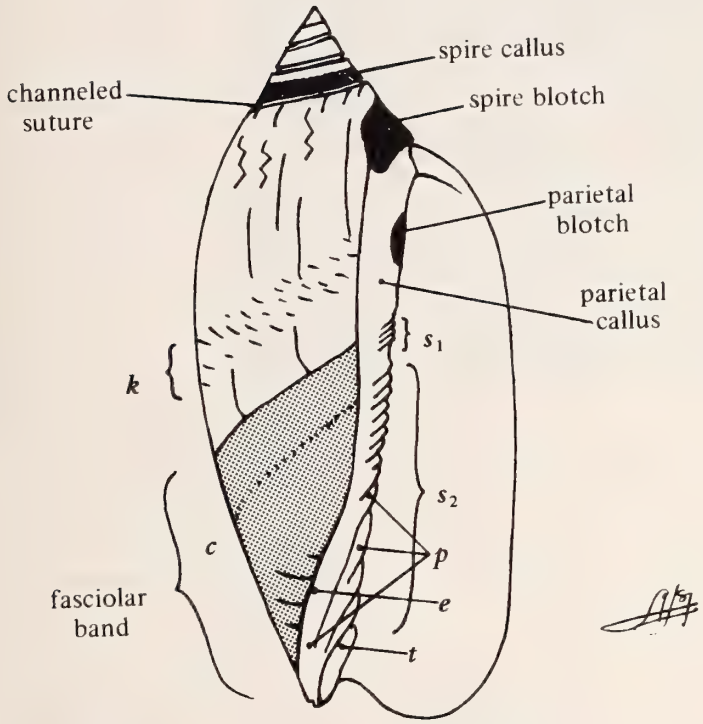
Table 1

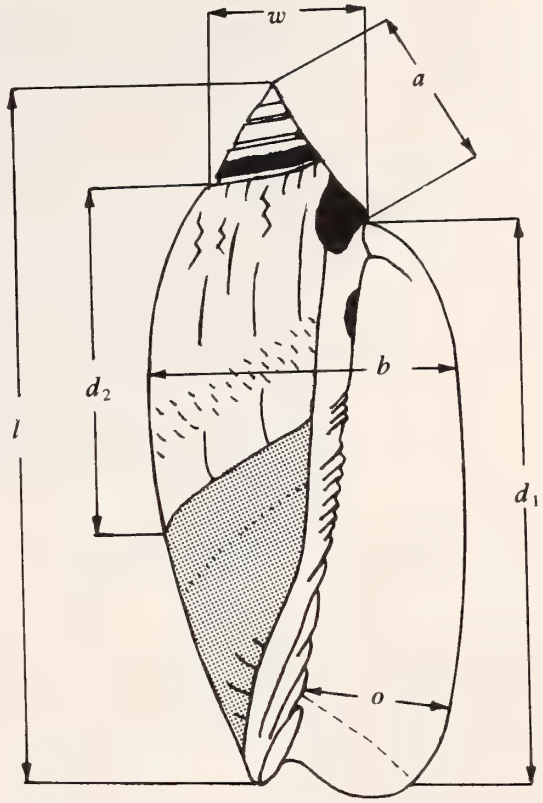
Latitude and longitude of collecting localities.

	N latitude	W longitude
Nicaragua		
Cosiguina, Chinandega	13°03′00″	87°34′00″
Jiquilillo, Chinandega	12°45′00″	87°31′30″
Aposentillo, Chinandega	12°37′52″	87°21′55″
Aserradores, Chinandega	12°36′27″	87°20′37″
Corinto, Chinandega	12°30′00″	87°10′00″
Poneloya, León	12°22′55″	87°02′49″
Los Playones, León	12°07′02″	86°44′42″
Masachapa, Managua	11°47′13″	86°31′01″
Pochomil, Managua	11°47′00″	86°30′30″
La Boquita, Carazo	11°40′40″	86°22′30″
Huehuete, Carazo	11°36′59″	86°19′34″
Chococente, Carazo	11°32′06″	86°11′15″
Rio Escalante, Rivas	11°31′04″	86°10′13″
Boca de Brito, Rivas	11°20′33″	85°58′37″
Majagual, Rivas	11°17′52″	85°55′00″
Marsella, Rivas	11°17′06″	85°54′14″
El Toro, Rivas	11°16′30″	85°53′59″
San Juan del Sur, Rivas	11°15′34″	85°52′49″
La Flor, Rivas	11°08′05″	85°47′38″
Ostional, Rivas	11°06′30″	85°46′00″
Costa Rica		
Playas del Coco, Guanacaste	10°33′32″	85°42′08″
Tamarindo, Guanacaste	10°18′07″	85°50′29″
Puntarenas, Puntarenas	9°58′52″	84°49′11″
Tivives, Puntarenas	9°52′10″	84°42′04″
Tárcoles, Puntarenas	9°45′49″	84°37′53″
Montezuma, Puntarenas	9°39′28″	85°04′17″
Jacó, Puntarenas	9°36′31″	84°37′30″
Esterillos, Puntarenas	9°31′31″	84°30′26″
Manuel Antonio, Puntarenas	9°23′42″	84°09′13″
Dominical, Puntarenas	9°13′22″	83°50′57″

The height and shape of the spire is important as a specific character. The spire has a channeled suture and three moderately callused whorls. There is a strongly marked spiral callus and blotch of darker color that often dips into the aperture. It is deep purple or brown on dark shells, light purple or yellow on light shells. Sometimes a light purple parietal blotch is apparent on fresh shells, but this may fade with time.

The protoconch is translucent or opaque, of 2 to 2.5 whorls, generally darker than the ground color of the spire. The protoconch is entirely devoid of sculpture, with the almost imperceptible suture developing into a channel on the last nepionic whorl. The contrast between the protoconch and the first whorl of the teleoconch is what determines a mammillate (Figure 3) or an acuminate (Figure 4) form of the protoconch. In the acuminate form, the





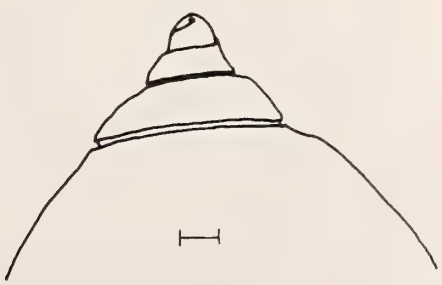
Explanation of Figures 1 and 2

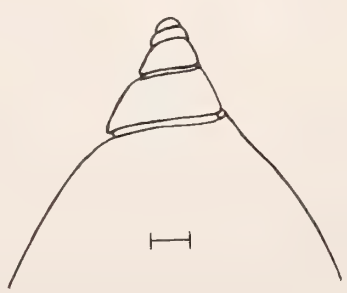
Figure 1. Shell features of *Agaronia*: *c*, crest on fasciolar band; *e*, edge of pillar pleats; *k*, dorsal band; *p*, pillar folds; s_1, posterior pillar lirae, s_2, anterior pillar lirae; *t*, terminal fold.

Figure 2. *Agaronia*: measurements taken for statistical analysis. See list in text.

increase in diameter of the whorls is gradual, so that protoconch and teleoconch fuse into a smooth, continuous cone with an angle of about 32 degrees. In the mammillate form, the first whorl of the teleoconch is about twice the diameter of the protoconch, which stands out nipple-like, and the cone forms an angle of about 50 degrees in *Agaronia griseoalba* and about 62 degrees in *A.* ***nica***. An additional difference between the two forms is that the diameter of the embryonic whorl varies from 0.45 to 0.7 mm in the three acuminate forms, *A.* ***jesuitarum***, *A. testacea*, and *A. propatula* respectively, and from 0.6 to 1.2 mm in *A.* ***nica*** and *A. griseoalba*, the two mammillate forms.

In order to quantify the height of the spire, we define a spire factor ($f = a/w$), where (a) is the lateral length of





Explanation of Figures 3 and 4

Figure 3. Protoconch, mammillate form of *Agaronia* ***nica*** sp. nov. Scale bar = 1 mm.

Figure 4. Protoconch, acuminate form of *Agaronia* ***jesuitarum*** sp. nov. Scale bar = 1 mm.

Figure 5

SEM view of radula of *Agaronia griseoalba,* showing tricuspid rachidian with closely adjacent secondary cusps, and single pair of hook-shaped lateral teeth. Scale bar = 20 μm.

the spire and (w) is the diameter of the spire base, both measured from the tip of the callus just above the aperture. The very sharp outline of the channeled suture makes it possible to duplicate the measurements. Average values for the spire factor for the Panamic species vary from 1.35 (SD, ±0.07) for *Agaronia testacea* to 1.01 (SD, ±0.04) for *A.* ***nica***. The latter has a convex spire, in contrast to the others, which have spires with straight or concave profiles.

The foot and body of *Agaronia* species are white to buff, more or less intensely speckled with purple; some animals appear to be entirely of this color except for a white, narrow edge around the foot. The siphon is ribbonlike but tubular, also buff and speckled with purple, but with an orange tip. The posterior lobe of the foot is easily broken off at a "tear" line. The gut is dark gray with a granular white or yellow digestive gland ventrally.

The animals live in the sand in the tidal zone. When active, the shells are nearly completely covered by the propodium and the parapodia. We have often seen them feeding on *Olivella semistriata* (Gray, 1839), which is abundant in Nicaragua and Costa Rica, and rarely on small Donacidae and Tellinidae. The prey is enveloped by the foot and then the *Agaronia* burrows into the sand while feeding (López, 1978). Dissection has also revealed remains of other small invertebrates in the stomach.

Contrary to previous descriptions (Keen, 1971:625; Abbott, 1974:238), Panamic *Agaronia* do not have an operculum. However, *A. travassosi* Morretes, 1938, which is endemic to Brazil, does have an operculum (Rios, 1975).

Radulae for all species except *Agaronia testacea* were examined; that of *A. griseoalba* is illustrated (Figure 5). As in all Olividae, the radula is rachiglossan with a tricuspid rachidian tooth, the central cusp being slightly smaller than the other two. Lateral to the two large cusps are small secondary cusps; in this detail, *Agaronia* and *Olivancillaria* d'Orbigny, 1840, differ from the rest of the Olividae, which do not have these denticles (Burch & Burch, 1964). Radulae of different *Agaronia* species show no detectable differences in the shape and spacing of cusps. In *A. propatula,* the external sides of the outer cusps are aligned, giving the ribbon a more regular appearance. In fresh specimens of *A.* ***jesuitarum***, the tips of the laterals have a marked golden hue not seen in the other species.

Only three fossil species of the Olividae have been reported to date from Central America. Olsson (1922) described *Oliva testacea* var. *costaricensis* from the Rio Banano Formation, now dated as being Pliocene in age, and *O. mancinella* from the Pleistocene Moín Formation, both from the Limón Province of Costa Rica. Later, Woodring (1964) reassigned these two taxa to the genus *Agaronia* and treated both as subspecies of *A. testacea.* He also described a new subspecies, *A. testacea hadra* from the Pliocene Gatún Formation of Panama. These fossil taxa need to be reviewed, taking into account their probable descendents in the Caribbean and Panamic biogeographic provinces.

Key to Living Panamic Species of *Agaronia*
(data from meristics under each species)

(1) Protoconch acuminate
  (a) Spire very high, f = 1.4 ..... *A. testacea*
  (lirae 10; length 34.5 mm)
  (b) Spire high, f = 1.2 ..... *A.* ***jesuitarum***
  (lirae 15; length 21.5 mm)
  (c) Spire medium, f = 1.1 ..... *A. propatula*
  (lirae 9; length 42.0 mm)

(2) Protoconch mammillate
  (a) Spire medium, f = 1.1 ..... *A. griseoalba*
  (lirae 18; length 32.0 mm)
  (b) Spire low, f = 1.0 ..... *A.* ***nica***
  (lirae 12; length 24.5 mm)

Agaronia testacea (Lamarck, 1811)

(Figures 6–9)

Oliva testacea LAMARCK, 1811:324; REEVE, 1850:pl. 18, fig. 36; MARRAT, 1871:26, pl. 348, figs. 334, 335.
Oliva (Agaronia) testacea: VON MARTENS, 1897:163, pl. 16, figs. 7, 12.
Agaronia testacea: BERRY, 1953:418, text fig. 6; HERTLEIN & STRONG, 1955:239; KEEN, 1958:422, fig. 629; BURCH & BURCH, 1964:111, pl. 6, fig. 2; KEEN, 1971:625, fig. 1370; ABBOTT, 1974:233, pl. 13, fig. 2548; ABBOTT & DANCE, 1982:196 [color fig.].
Agaronia reevei MÖRCH, 1860:87 [designated fig. 36 of REEVE, 1850].
Oliva (Agaronia) testacea var. *philippi* VON MARTENS, 1897: 165, pl. 15, figs. 13, 14.

Description: Spire straight-sided and highest among Panamic agaronias; protoconch acuminate, light colored; shell height 31–50 mm, profile subfusiform. The body color is usually grayish brown, with axial, brown irregular lines. The aperture is bluish white or gray, the edge of labrum white, often stained with brown; pillar is white. The spire callus band reaches only halfway across from suture to suture. The callus band and the fasciolar band callus are light brown, variegated with whitish streaks. The protoconch is acuminate and light colored. Spiral blotch weak to obsolete.

Meristics (n = 38): Spire factor 1.35 (SD, ±0.07); length 34.55 mm (SD, ±8.56); breadth factor 0.18 (SD, ±0.02); relative growth factor 1.37 (SD, ±0.07); lirae count 9.76 (SD, ±2.59).

Distribution: Empty shells were found in fair to good condition at nearly all sandy beaches in Nicaragua, but always in small numbers. Most of our specimens were collected from the northern beaches, from the Gulf of Fonseca to Aserradores. No live specimens were found. However, McLean reports (personal communication) that there are numerous live-collected records from the Gulf of California and southern Mexico, as well as Panama, in the LACM collection.

Material examined: MEXICO (Skoglund collection): Bahía Cholla, Sonora, 9 specimens; Playa Novillero, Nayarit, 7 specimens. NICARAGUA (UCA): Aserradores sea beach and estero beach: 5 lots, 24 specimens. Single shells and fragments from Cosiguina, Aserradores, Corinto, Huehuete, San Juan del Sur, La Flor. COSTA RICA: Tamarindo (LSM); Montezuma (UCRZ). PANAMA: Kobbe Beach, 2 specimens (Skoglund collection). Specimens from Aserradores had intact protoconchs and were used for spire measurements. This is the only species of *Agaronia* that we have not collected alive in Nicaragua.

Remarks: *Agaronia testacea* may readily be distinguished from the other species by its medium to large size, high spire, and accuminate protoconch.

Specimens from the Atlantic coast of Central America identified as this species have been reported by FLUCK (1905:18), HOUBRICK (1968:16), OLSSON & MCGINTY (1958:17), and WOODRING (1964:281). Those that we have collected at Moín, Puerto Limón, Atlantic coast of Costa Rica, do not agree with *A. testacea,* in having lower spires, broader apertures, and a lower count of lirae, and remain unidentified.

The holotype of *Oliva (Agaronia) testacea* var. *philippi* von Martens (Figure 9) is a small shell similar to those from Panama in the LACM collection. The locality Cobija, in northern Chile, quoted by VON MARTENS (1897), is obviously erroneous, as the species has not been recorded south of Panama.

Agaronia propatula (Conrad, 1849)

(Figures 10, 11)

Oliva propatula CONRAD, 1849:280, pl. 39, fig. 7.
Agaronia propatula: KEEN, 1958:422, fig. 629; KEEN, 1971: 625, fig. 1369 [copy Conrad fig.].
Not *A. propatula of* HEMMEN, 1981:128, pl. 27 [color fig.]; *of* ABBOTT & DANCE, 1982:196 [color fig.]. [=*A. griseoalba*].

Description: This is the largest and most massive of the Panamic agaronias. The spire is medium high, concave over the aperture owing to overhang of heavy callus, protoconch acuminate. Shell length about 42 mm, profile inflated, most globose of the five species. Lirae count lowest, about 9. The body color is often gray with dark gray zigzags, but it can also be light brown or terracotta marked by gray or brown axials that score the growth lines, giving the shell a woodlike appearance. These growth lines are somewhat sinusoid, as is the edge of the lip, especially in large specimens. The fasciolar band and the spire callus are dark purple-brown and highly glazed, this callus not reaching all the way from suture to suture on the spire and being variegated with whitish streaks. The aperture is bluish white or gray, the inner edge of the labrum whitish brown. The dorsal color band is white or purple, often with a blend of both. The protoconch is dark brown, contrasting with the first teleoconch whorl, which is usually white. The spiral blotch is dark brown, strongly marked, dipping well into the aperture, and extending along the spire callus.

Meristics (n = 38): Spire factor 1.11 (SD, ±0.08); shell length 42.31 mm (SD, ±10.66; breadth factor 0.22 (SD, ±0.01); relative growth factor 1.56 (SD, ±0.07); lirae count 9.1 (SD, ±1.66).

Distribution: Only a few live shells were taken at San Juan del Sur, La Flor, Chococente, and Poneloya in relatively coarse sand. Empty shells were found at many sandy beaches, especially at Aserradores. KEEN (1971) gave the range as southern Mexico to Ecuador. McLean reports (personal communication) that the LACM collection contains 9 lots of dead-collected specimens ranging from Guatemala to Panama.

Material examined: MEXICO: Bahía de Los Angeles, Baja California, 5 specimens (Skoglund collection); GUATE-

Explanation of Figures 6 to 23

Figures 6–9. *Agaronia testacea* (Lamarck, 1811). Figure 6: LACM 127342; Aserradores, Nicaragua; length 39.6 mm. Figure 7: LACM 127343; Bahía de Adair, Sonora, Mexico; length 50.8 mm. Figure 8: LACM 68-3; Novillero, Nayarit, Mexico; length 48.7 mm. Figure 9: Holotype, ZMB, *Oliva* (*Agaronia*) *testacea* var. *philippi* von Martens, 1897; length 31.2 mm.

Figures 10, 11. *Agaronia propatula* (Conrad, 1849). Figure 10:

MALA: San José, Escuintla, 2 specimens (D. G. Robinson collection); NICARAGUA (UCA): Living specimens from San Juan del Sur (2 lots); Chococente, 2 single lots; single lots from Poneloya and La Flor. Dead shells to 65 mm in length from Aserradores, Aposentillo, Corinto, Poneloya, Huehuete, La Boquita, Chococente, and El Toro. No specimens were found by us in Costa Rica.

Remarks: At Poneloya the living specimens occurred with *Agaronia* ***jesuitarum***. At Chococente they occurred with *A.* ***jesuitarum***, *A.* ***nica***, and *A. griseoalba*. We found this species to be only slightly less scarce than *A. testacea*.

Agaronia griseoalba (von Martens, 1897)

(Figures 12–17)

Oliva (*Agaronia*) *testacea* var. *griseoalba* VON MARTENS, 1897: 64, pl. 15, figs. 18, 19.

Agaronia murrha BERRY, 1953:417, pl. 29, fig. 1, text fig. 5; HERTLEIN & STRONG, 1955:240; BURCH & BURCH, 1964: 112 [not pl. 6, fig. 4]; KEEN, 1958:422, fig. 628; KEEN, 1971:725, fig. 1368.

"*A. propatula*" *of* HEMMEN, 1981:128, pl. 27 [color fig.]; *of* ABBOTT & DANCE, 1982:196 [color fig.]. Not *A. propatula* (Conrad).

Description: Spire straight or slightly concave, medium high, shell length about 32 mm, whorls somewhat inflated. Protoconch mammillate, lirae count highest of the five species, average 17, maximum 27. As noted by BERRY (1953), the typical form is "slightly grayish porcelain-white," with a white, yellow, or light brown callus on fasciole and spire, where it usually covers spire whorls from suture to suture. The aperture is dark purple or brown; the labrum has a white inner edge. Rarely the shell is pink with an orange aperture, with or without two purple bands. Variants from Costa Rica, Panama, and Ecuador include olive-brown shells with zigzag lines and some black shells (later turning gray) with an amorphous white dorsal band.

Meristics (*n* = 38): Spire factor 1.14 (SD, ±0.05); height 31.94 mm (SD, ±6.99); breadth 0.19 (SD, ±0.01); relative growth factor 1.47 (SD, ±0.06); lirae count 16.76 (SD, ±3.98).

Distribution: San José, Escuintla, Guatemala, to Canoa, Manabí, Ecuador. These represent new northern and southern distributional records beyond those reported in KEEN (1971).

Material examined: GUATEMALA: 1 large specimen from San José, Escuintla (D. G. Robinson collection). NICARAGUA (UCA): Jiquilillo, Aserradores, Corinto, Poneloya, Huehuete, Pochomil, Chococente, Rio Escalante, Majagual, Marsella, San Juan, La Flor. COSTA RICA: Playas del Coco, Puntarenas, Tivives, Tárcoles, Jacó, Esterillos, Dominical (UCA). PANAMA: Las Lajas, Playa Jobo (LACM). ECUADOR: Atacames, Esmeraldas (D. G. Robinson collection). This is the most abundant *Agaronia* in Costa Rica.

Remarks: BERRY (1953) proposed *Agaronia murrha* (Figure 13, holotype), from Corinto, Nicaragua, but overlooked the prior name *A. griseoalba* of VON MARTENS, 1897, from "Mexico," which we here reinstate, based on our examination of the type specimen (Figure 12). The species has not been frequently cited enough to warrant an effort to conserve Berry's name. Berry did not have material to demonstrate the color variation possible in this species, owing in part to the prevalence of the gray-white color form at his type locality and most localities throughout Nicaragua. Although he remarked in a footnote that a dark phase seemed to be present at San Juan del Sur, Nicaragua, these specimens prove to be *A.* ***nica***, described herein. Dark specimens of *A. griseoalba* (Figures 15, 16) have the size range, the lirae count, and the mammillate protoconch to match that of typical *A. griseoalba,* so there is no possible doubt as to their identity.

Agaronia ***nica*** A. López, Montoya & J. López, sp. nov.

(Figures 18–20)

"*Agaronia murrha,*" in part, *of* BERRY, 1953:419 [footnote only]; in part *of* BURCH & BURCH, 1964 [fig. 4 only].

Description: Shell solid, small, length about 25 mm, spire low, convex, body whorl inflated, lirae count medium, about 12. The light brown, mammillate protoconch of two

←

LACM 65-88; Mata de Limón, Costa Rica; length 46.8 mm. Figure 11: LACM 127344; Aserradores, Nicaragua; length 40.9 mm.

Figures 12–17. *Agaronia griseoalba* (von Martens, 1897). Figure 12: Holotype, ZMB, *Oliva* (*Agaronia*) *griseoalba* von Martens, 1897, "Mexico"; length 38.4 mm. Figure 13: Holotype, CAS, *Agaronia murrha* Berry, 1953; Corinto, Nicaragua; length 36.3 mm. Figure 14: LACM 127345; Huehuete, Nicaragua; length 37.2 mm. Figure 15: LACM 127346; Tivives, Costa Rica; length 39.4 mm. Figure 16: LACM 127346; Tivives, Costa Rica; length 34.7 mm. Figure 17: LACM 127346; Tivives, Costa Rica; length 35.8 mm.

Figures 18–20. *Agaronia* ***nica*** López, Montoya & López, sp. nov. Figure 18: Holotype, LACM 2269; San Juan del Sur, Nicaragua; length 24.7 mm. Figure 19: LACM 127347; San Juan del Sur, Nicaragua, collected by H. N. Lowe; length 25.5 mm. Figure 20: LACM 127348; Marsella, Nicaragua; length 23.5 mm.

Figures 21–23. *Agaronia* ***jesuitarum*** López, Montoya & López, sp. nov. Figure 21: Holotype, LACM 2271; Poneloya, Nicaragua; length 21.2 mm. Figure 22: Paratype, LACM 2272; Poneloya, Nicaragua; length 22.6 mm. Figure 23: Paratype, LACM 2272; Poneloya, Nicaragua; length 24.5 mm.

whorls is similar, and of about the same size as that of *Agaronia griseoalba,* although shells of *A.* ***nica*** are smaller. This is the most variable of the agaronias in color. We have seen uniform white shells and others that are black, as well as yellow, orange, brown, gray, and intermediate shades. Some are devoid of maculations, whereas others are partially or entirely covered with lines, dots, or zigzags. The aperture is dark purple in dark shells and lighter in others. The most common color combination (represented in the holotype) is dark gray with darker zigzags, dark brown spiral and columellar band callus, brown protoconch, bluish pillar, and dark aperture. The spire whorls are covered by callus from suture to suture.

Dimensions of holotype: length 24.7 mm, height 8.0 mm, width 11.1 mm, spire lateral height 5.7 mm, spire base diameter 5.8 mm; spire factor 1.017, lirae count 9.

Meristics (*n* = 38): Spire factor 1.01 (SD, ±0.04; length 24.41 (SD, ±2.82); breadth factor 0.22 (SD, ±0.01); relative growth factor 1.49 (SD, ±0.07); lirae count 12.21 (SD, ±1.80).

Type locality: San Juan del Sur, Rivas, Nicaragua.

Type material: Holotype, LACM 2269. Paratypes, LACM 2270; paratypes, CAS 050208 through 050212. Paratypes from all listed localities in Nicaragua (UCA).

Distribution: Sayulita, Nayarit, Mexico, to Puntarenas, Costa Rica.

Referred material: MEXICO: Sayulita, Nayarit (Skoglund collection); Playa Encantada, Acapulco (Skoglund collection); Acapulco (LACM 127386), 2 specimens from Earl Huffman collection, matching the "hypotype from Acapulco" figured by BURCH & BURCH (1964:fig. 4) and evidently from the same lot (J. McLean, personal communication). NICARAGUA (UCA): Jiquillo, Poneloya, Los Playones, Masachapa, Pochomil, La Boquita, Huehuete, Chococente, Boca de Brito, Marsella, San Juan del Sur, La Flor, Ostional (UCA). Numerous specimens from San Juan del Sur, Nicaragua, collected by H. N. Lowe in 1931 (Figure 19), now in LACM, San Diego Natural History Museum, and other collections. COSTA RICA: Puntarenas, a single specimen collected with *Agaronia griseoalba* by D. Shasky, Redlands, California.

Remarks: *Agaronia* ***nica*** is half the size of the three larger species (*A. testacea, A. propatula,* and *A. griseoalba*). Its mammillate protoconch separates it from *A. testacea, A. propatula,* and *A.* ***jesuitarum***, as well as its low, usually convex spire, even when the first two species are only half grown and about the same size as fully grown *A.* ***nica***. When comparing mature *A.* ***nica*** with juvenile *A. griseoalba* of the same color and length, the distinction lies in the low convex spire of *A.* ***nica***, its more inflated body, and its lower lirae count. Color differences are not reliable criteria for discrimination.

The footnote to BERRY's (1953) description of *Agaronia murrha* noted "a large series of small dark *Agaronia* in the San Diego Museum taken in 1931 by H. N. Lowe at San Juan del Sur, Nicaragua. These shells are mostly of purplish-gray coloring with deep brown (rarely light yellowish-brown) apex and fasciole, and appear to represent a dark phase of the species here described." The above mentioned specimens are typical *A.* ***nica***. A true dark phase of *A. griseoalba* is also now known to exist (Figures 15, 16).

This is the most common *Agaronia* in Nicaragua but has not previously been recognized as a distinct species, having been mistaken for juvenile *A. testacea* or *A. propatula.* As it is common in Nicaragua, we have named it ***nica***, the familar name by which persons and objects from Nicaragua are known throughout Central America.

Agaronia ***jesuitarum*** A. López, Montoya & J. López, sp. nov.

(Figures 21–23)

Description: Shell small, thin, subfusiform; spire high, straight sided, length about 22 mm, body whorl not inflated, lirae count relatively high, about 15. Protoconch acuminate, caramel colored. The body whorl is grayish or yellowish olive, profusely marked with broken zigzags or triangles. We have also seen several specimens with an orange ground color. The aperture is deep purple and the inner labrum edge matches the ground color or is mottled with purple. There is a subsutural band of slanted dashes, similar to those of *Agaronia testacea.* The spire and columellar band callus is yellowish brown and covers the whorls from suture to suture. The pillar callus pad is slightly more raised than in other agaronias, bluish white.

Dimensions of holotype: length 21.2 mm, height 6.5 mm, width 8.8 mm, spire lateral height 6.5 mm, spire base diameter 5.3 mm; spire factor 1.226, lirae count 15.

Meristics (*n* = 38): Spire factor 1.21 (SD, ±0.04), length 21.48 mm (SD, ±4.68); breadth factor 0.19 (SD, ±0.009); relative growth factor 1.46 (SD, ±0.06); lirae count 15.05 (SD, ±1.81).

Type locality: Poneloya Beach, at river mouth, León, Nicaragua.

Type material: Holotype, LACM 2271, 5 paratypes LACM 2272, 1 paratype CAS 050213. Twenty paratypes UCA.

Distribution: Poneloya to Boca de Brito, Nicaragua. About 40 specimens were found over the course of one year at Poneloya in coarse sand at low tide. The first six specimens were taken by Al and Julio López in December 1982. Four more specimens were collected at the same site a year later, where 30 additional specimens were also found by A. Fernandez, R. Meabe, and F. Zarrabe. Three were found in 1984 by Michel Montoya 6 km south of Poneloya and one at Boca de Brito, 100 km farther south. Some 20 additional specimens were found in 1985 at La Boquita and Huehuete, and four specimens at Chococente in 1986.

Remarks: *Agaronia* ***jesuitarum*** is the smallest of the Panamic agaronias and also the most distinct. It is easily separated from the others based on its small size and characteristic yellow or gray-olive ground color profusely covered with small aligned spots or zigzags. Because of its high spire and acute protoconch, it could be mistaken for a very small, immature *A. testacea*; but the color, high count of lirae, and subfusiform outline are distinctive.

This species is difficult to find. We are unable to explain why no dead specimens have been seen. The living specimens remain buried in the sand, rather than foraging on the surface, as observed in the other species. Feeding has not been observed. Other olivid species present at the type locality included *Agaronia griseoalba, A.* ***nica****, A. propatula, Oliva undatella,* and the ubiquitous *Olivella semistriata.* The specimens of *A.* ***jesuitarum*** were collected by Jesuits from the Central American University, and the name given to the species honors their dedication.

ACKNOWLEDGMENTS

We thank Dr. James H. McLean of the Los Angeles County Museum of Natural History, who suggested improvements, advised us of material in the LACM collection, edited the manuscript, and took the photographs. Dr. Romeo Martinez, Central Agronómico Tropical de Investigación y Ensenanza (CATIE), Turrialba, Costa Rica, helped us greatly with suggestions and techniques regarding the statistics used in this study. Carol Skoglund of Phoenix, Arizona, and David G. Robinson, Tulane University, made available from their collections several lots of *Agaronia* used in this study. Dr. R. Kilias, Zoologisches Museum of Humboldt-Universität in Berlin kindly loaned us the type specimens described by von Martens. Professor Dr. Rudolf Fisher, Geology and Paleontology Institute, Hannover University, West Germany, sent copies of papers by early German authors from the Senckenberg Museum, Frankfurt. Dr. Peter Sprechmann, Central American School of Geology, University of Costa Rica, granted us access to the W. P. Woodring collection of papers and documents. Lic. Teresita Aguilar, Department of Paleontology, University of Costa Rica, made available to us articles on fossil *Agaronia.* Professors Alejandro Cajina and Elda Garcia, Department of Ecology, Central American University, Managua, advised us on separating and mounting radulae. Professor Rolando López, Chairman, Department of Ecology, Central American University, allowed us the use of the instruments and laboratory in his department. Dr. Manuel Murillo, Department of Marine Sciences, University of Costa Rica, allowed access to the university mollusk collection. Brother Eduardo Fernandez, curator at the La Salle Museum of Natural History, San José, Costa Rica, showed us the mollusk collection and contributed some specimens. Ritha Sancho (Mrs. Michel Montoya) collected some of the specimens used in this study. Dr. Eugene V. Coan of Palo Alto, California, read and commented upon the manuscript.

LITERATURE CITED

Abbott, R. T. 1974. American seashells. Van Nostrand Reinhold: New York. 663 pp.

Abbott, R. T. & S. P. Dance. 1982. Compendium of seashells. Dutton: New York. 411 pp.

Berry, S. S. 1953. Notices of new west American marine Mollusca. Trans. San Diego Soc. Natur. Hist. 16:405–428.

Burch, J. Q. & R. L. Burch. 1964. The genus *Agaronia* J. E. Gray, 1928. Nautilus 77(4):110–112.

Conrad, T. A. 1849. The following new and interesting shells are from the coasts of Lower California and Peru, and were presented to the Academy by Dr. Thomas B. Wilson. Proc. Acad. Natur. Sci. Phila. 4:155–156.

Fluck, W. H. 1905. Shell collecting on the Mosquito coast of Nicaragua—II. Nautilus 19(2):16–19.

Gmelin, J. F. 1791. Caroli a Linne Systema naturae per regna tria naturae. Editio decima tertia. Leipzig, 1(6)(6), Vermes, pp. 3021–3910.

Gray, J. E. 1839. Molluscous animals and their shells. Pp. 103–155. *In:* F. W. Beechey (ed.), The zoology of Capt. Beechey's voyage . . . to the Pacific and Behring's Straits in his Majesty's ship *Blossom.* London.

Hemmen, J. D. 1981. Olividae of Jaco, western Costa Rica. *In:* D. Greifeneder (ed.), Contribution to the study of Olividae. Acta Conchiliorum of the Club Conchylia 1:128, 198–199.

Hertlein, L. G. & A. M. Strong. 1955. Marine mollusks collected during the "Askoy" Expedition to Panama, Colombia, and Ecuador in 1941. Bull. Amer. Mus. Natur. Hist. 107(2):159–318.

Houbrick, J. R. 1968. A survey of the littoral marine mollusks of the Caribbean coast of Costa Rica. Veliger 11(1):4–21.

Keen, A. M. 1958. Sea shells of tropical west America. Marine mollusks from Lower California to Colombia. Stanford University Press: Stanford. 624 pp.

Keen, A. M. 1971. Sea shells of tropical west America. Marine mollusks from Baja California to Peru. 2nd ed. Stanford University Press: Stanford. 1064 pp.

Kilburn, R. N. 1981. Revision of the genus *Ancilla* Lamarck, 1799 (Mollusca: Olividae: Ancillinae). Ann. Natal Mus. 24(2):349–463.

Lamarck, J. B. P. A. 1811. (Suite de la) Détermination des especes des mollusques testacés: continuation du genre Porcelaine et des genres Ovule, Tarrière, Ancillaire, et Olive. Annales du Muséum d'Histoire Naturelle 16:89–114, 330–338.

López, A. 1978. Jolly olivellas, hungry agaronias. Hawaiian Shell News 26(8):16.

Marrat, F. P. 1871. *Oliva* Bruguière. *In:* G. B. Sowerby (ed.), Thesaurus conchyliorum. London. Vol. 4:1–46, pls. 342–351.

Martens, E. von. 1897. Conchologische Miscellen II. Archiv fur Naturgesch. 63(1):157–180.

Mörch, O. A. L. 1860. Beiträge zur Molluskenfauna Central-Amerika's. Malakozool. Blätter 7(2):66–96.

Olsson, A. A. 1922. The Miocene of northern Costa Rica. Bull. Amer. Paleontol. 9(39):173–460.

Olsson, A. A. & T. L. McGinty. 1958. Recent marine mollusks from the Caribbean coast of Panama with the description of some new genera and species. Bull. Amer. Paleontol. 39(117):1–59.

Reeve, L. A. 1850. Monograph of the genus *Oliva.* Conchologia iconica: or illustrations of the shells of molluscous animals. London. 30 pls., text not paginated.

Rios, E. C. 1975. Brazilian marine mollusks iconography. Rio

Grande, Fundaçâo Universidade do Rio Grande, Centro de Ciências do Mar, Museu Oceanografico. 331 pp.
VON MARTENS, E. 1897. Conchologische Miscellen II. Archiv fur Naturgesch. 63(11):157–180.
WOODRING, W. P. 1964. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropods: Columbellidae to Volutidae). U.S. Geol. Survey Prof. Paper 306-C:240–297.
WOODRING, W. P. 1966. The Panama land bridge as a sea barrier. Proc. Amer. Phil. Soc. 110(6):425–433.

The Veliger 30(3):305–314 (January 4, 1988)

THE VELIGER

A Review of the Generic Divisions Within the Phyllidiidae with the Description of a New Species of *Phyllidiopsis* (Nudibranchia: Phyllidiidae) from the Pacific Coast of North America

by

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

AND

DAVID W. BEHRENS

Pacific Gas and Electric Company, Biological Research Laboratory, P.O. Box 117, Avila Beach, California 93424, U.S.A.

Abstract. The anatomy of *Ceratophyllidia africana* Eliot, 1903, and *Phyllidiopsis cardinalis* Bergh, 1875, the type species of their respective genera, is described. *Phyllidiopsis* ***blanca*** sp. nov. is described from the Pacific coast of southern California and Baja California. It differs from other species by its uniformly whitish coloration and low, poorly developed tubercles. Internally, it has a simple oral tube, without associated glands. The oral tube is elongate and convoluted. The buccal and gastro-esophageal ganglia are situated posteriorly from the circumesophageal nerve ring. The reproductive system is triaulic. The penis is lined with several rows of conical, chitinous spines.

The present species varies in its anal position. In one specimen the anus is located below the notum, while in the remaining five specimens it is located dorsally. Because the presence of a ventral anus is utilized to separate *Reyfria* Yonow, 1986, from *Phyllidia* Cuvier, 1797, the status of these genera is reviewed. The systematic position of *Phyllidiopsis* and *Ceratophyllidia* is discussed. Conflicting views of generic distinctions within the Phyllidiidae are also discussed.

INTRODUCTION

The Phyllidiidae are a family of nudibranchs that are characteristic of tropical, Indo-Pacific shallow-water habitats. Seven species have been described from the Mediterranean Sea and Atlantic Ocean. These represent the only species known outside of the Indo-Pacific. No members of the family have been recorded from the Pacific Ocean east of the Hawaiian Islands. The first record of a phyllidiid from the Pacific coast of North America was that of *Phyllidia* sp. (as *Phellidia* sp., Behrens, 1980). This species is undescribed and its morphology and systematic placement are the subject of this paper.

The generic divisions of the Phyllidiidae have been the subject of some disagreement. Part of the problem stems from the fact that the type species of two of the genera, *Phyllidiopsis* and *Ceratophyllidia,* have never been completely described. This study describes the anatomy of these species and discusses the relationships of the genera.

DESCRIPTIONS

Ceratophyllidia africana Eliot, 1903

(Figures 1A, 2)

Ceratophyllidia africana Eliot, 1903:250.
Ceratophyllidia grisea Eliot, 1910:436, pl. 25, figs. 3–7, syn. nov.

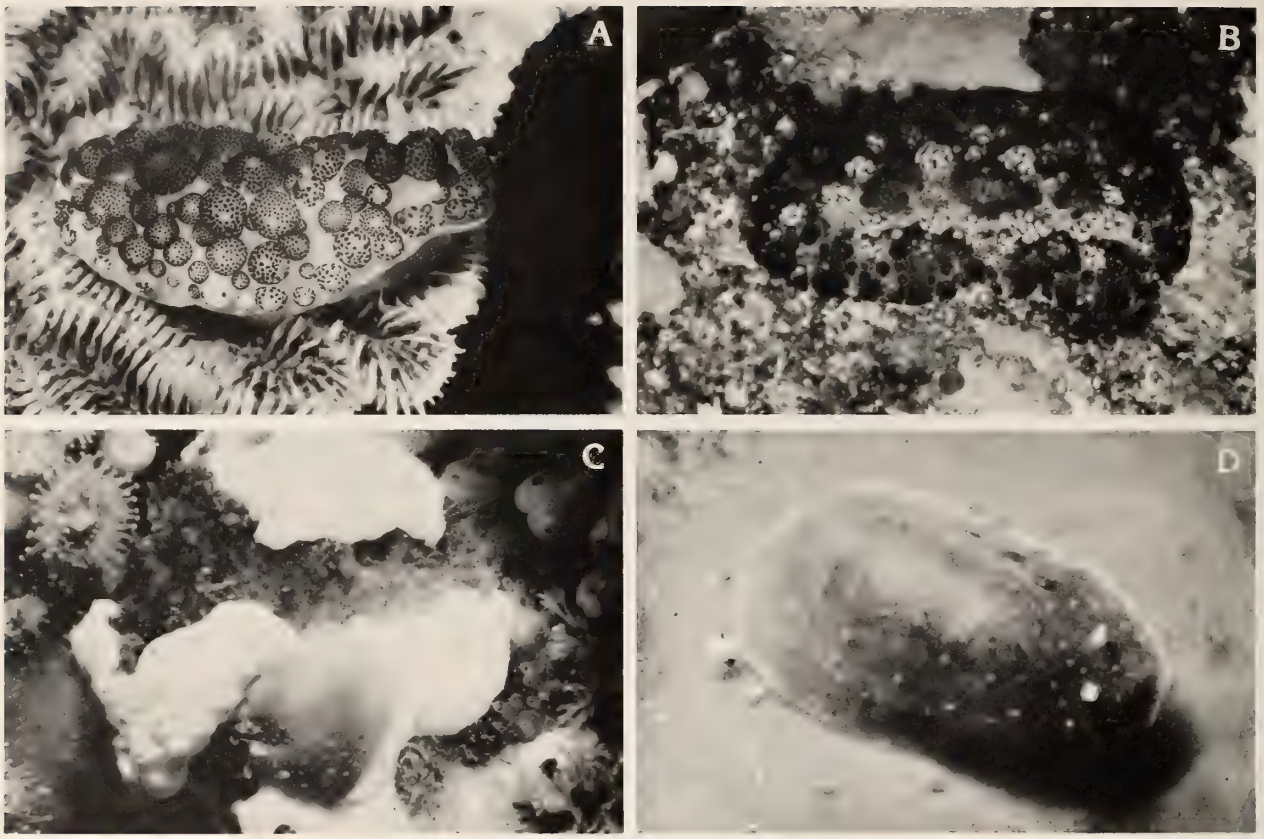


Figure 1

Living animals. A. *Ceratophyllidia africana* Eliot, 1903, Sodwana Bay National Park, South Africa, May 1981, photo by T. Gosliner. B. *Phyllidiopsis cardinalis* Bergh, 1875, Middle Camp, Aldabra Atoll, March 1986, photo by T. Gosliner. C, D. *Phyllidiopsis* ***blanca*** sp. nov., Islas San Benitos, August 1984, photos by Marc Chamberlin.

Distribution: This species is known only from the western Indian Ocean, where it has been recorded from Zanzibar (ELIOT, 1903), Coetivy Island in the Seychelles (ELIOT, 1910), South Africa (GOSLINER, 1987), and Aldabra Atoll, Seychelles (present study).

Material: South African Museum, Cape Town, SAM A 35625, one specimen, Nine Mile Reef, Sodwana Bay National Park, Natal, South Africa, 18-m depth, 20 May 1981, T. M. Gosliner. California Academy of Sciences, San Francisco, one specimen, CASIZ 063262, Passe du Bois, Aldabra Atoll, Seychelles, 10-m depth, 22 March 1986, T. M. Gosliner.

External morphology: The living animals (Figure 1A) were 20 and 30 mm in length. The general body color was yellowish white in the South African animal and grayish white in the Aldabran specimen. The densely perfoliate rhinophores were the same color as the body. The notum bears numerous soft, spherical papillae that are attached to the body by means of a short, slender stalk. The papillae are readily autotomized when the animals are disturbed. The diameter of the papillae varies from 1 to 4 mm. In living material, the diameter of the papillae expanded and contracted. The papillae bear black pigment spots, which are restricted to their apical half. The anus is situated on the dorsal surface, near the posterior end of the animal. The lateral margins of the body, between the notum and foot, bear approximately 90 simple gill leaflets per side. The oral tentacles are largely separate to their bases and have a longitudinal groove along their outer margin.

Digestive system (Figures 2A, B): Immediately posterior to the mouth, the oral tube expands into a broad, thin-walled vestibule. The posterior end of the vestibule narrows into a thicker-walled, glandular oral tube. The oral tube is invaginable and, in its contracted state (Figure 2B), is contained entirely within the vestibule. The esophagus exits at the anterior end of the oral tube. The esophagus is elongate and highly convoluted. Also entering the oral tube are the ducts of a pair of large oral glands. The ducts

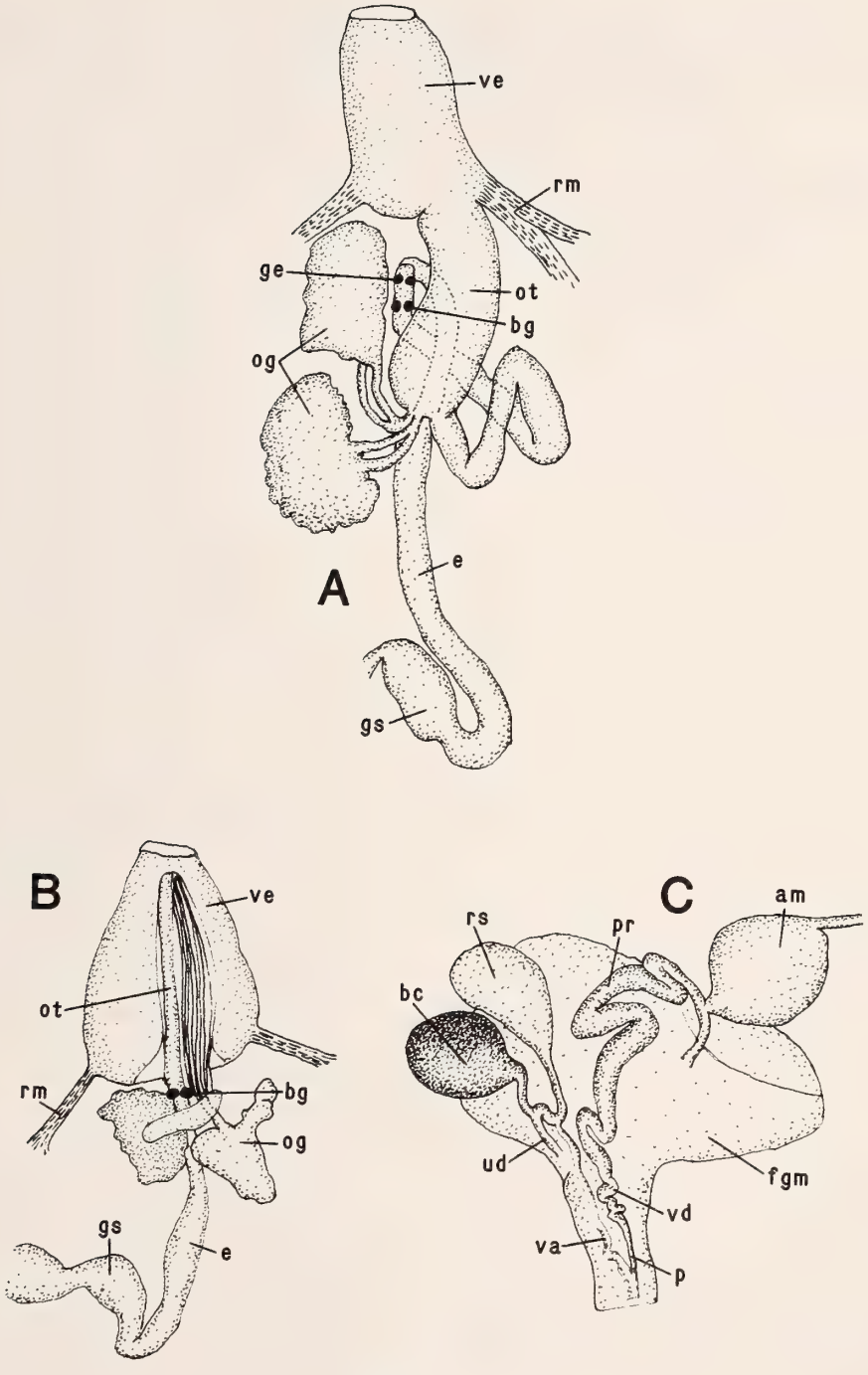


Figure 2

Ceratophyllidia africana Eliot, 1903. A. Digestive system retracted: bg, buccal ganglia; e, esophagus; ge, gastro-esophageal ganglia; gs, glandular segment of esophagus; og, oral glands; ot, oral tube; rm, retractor muscle; ve, vestibule. B. Digestive system everted, lettering same as A. C. Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; va, vagina; vd, vas deferens.

of these glands terminate at the anterior end of the oral tube, adjacent to the esophagus. Posteriorly, the esophagus expands into a short glandular segment prior to its entrance into the thin-walled stomach within the digestive gland.

Central nervous system: The ganglia forming the circumesophageal nerve ring are highly cephalized, with complete fusion of the cerebral and pleural ganglia. The cerebropleural ganglia are appressed to each other, without a distinct commissure. The pedal ganglia are separated by a short commissure. The buccal and gastro-esophageal ganglia are attached to the circumesophageal nerve by long connectives. When the oral tube is completely invaginated within the vestibule these ganglia are situated immediately ventral to the circumesophageal nerve ring.

Reproductive system (Figure 2C): The arrangement of organs is triaulic. The ampulla is short and saccate, narrowing abruptly near its division into the oviduct and vas deferens. The oviduct is short and enters the female gland mass near the albumen gland. The uterine duct emerges from the female gland mass and joins the duct of the pear-shaped receptaculum seminis. The spherical bursa copulatrix is thin-walled and black in both specimens examined. It has an elongate duct and joins the duct of the receptaculum and continues proximally to the vaginal opening, adjacent to the penis. The vas deferens is prostatic distally and narrows into a muscular, ejaculatory segment. The proximal portion is devoid of any chitinous spines.

Discussion: *Ceratophyllidia africana* Eliot, 1903, was described from a single specimen collected from Zanzibar. Eliot (1910) later described *C. grisea* from a single specimen collected in the Seychelles. He stated that *C. grisea* differed from *C. africana* in its gray rather than yellowish color and by having larger papillae that obscured most of the notum. No additional records of these species appeared until Gosliner (1987) reported *C. africana* from Natal, South Africa. This specimen, examined in the present study, was yellowish in color, but had large, dense papillae as described for *C. grisea*. The specimen collected at Aldabra was grayish in color with sparser papillae. In both living specimens, it was noted that the diameter of the papillae could be altered by expansion or contraction. Dissection of these specimens demonstrated no internal differences between them, except in the state of contraction of the buccal apparatus. Therefore, *C. grisea* is here regarded as a junior subjective synonym of *C. africana*.

Phyllidiopsis cardinalis Bergh, 1875

(Figures 1B, 3)

Phyllidiopsis cardinalis Bergh, 1875:670, pl. 16, figs. 11–15.

Distribution: This species is known throughout the Indo-Pacific tropics, from Aldabra Atoll to the Hawaiian Islands (present study).

Material: California Academy of Sciences, San Francisco, CASIZ 063263, one specimen, Poipu Beach Park, Kauai, Hawaiian Islands, under rock, intertidal zone, 16 February 1986, Michael Gosliner. CASIZ 063264, one specimen, Poipu Beach Park, Kauai, Hawaiian Islands, under rocks, intertidal zone, 19 February 1986, Michael Gosliner. CASIZ 063265, one specimen, Passe Houreau, off Middle Camp, Aldabra Atoll, Seychelles, 2-m depth, 18 March 1986, T. M. Gosliner.

External morphology: The living animals (Figure 1B) were 12–24 mm long. The color is complex. The foot, anal papilla, rhinophores, and notum are yellowish. This pigment is overlain with papillae that are dark brown marginally, lighter brown to cream more medially. The spaces between papillae are off-white to mustard yellow. The raised central portion is finely papillate, off-white to cream. Three central raised portions on this ridge are dirty brown. The rhinophores are densely perfoliate. The lateral margins between the notum and foot bear numerous, simple, leaflike gill lamellae. The tubercles covering the dorsum are composed of several small rounded tubercles. The anus is situated medially on the dorsum near the posterior end of the body. There are approximately 110 leaflets per side. The oral tentacles are united for their entire length and possess a groove along both lateral margins.

Digestive system (Figure 3A): The most anterior portion of the oral tube is rugose and glandular. More posteriorly, it is smooth and curves anteriorly. Slightly more anteriorly to this point, the oral tube narrows into the esophagus. A retractor muscle inserts into either side of the oral tube at its junction with the esophagus. The esophagus is elongate and convoluted, passing through the circumesophageal nerve ring. Near its posterior limit the esophagus expands slightly to a segment that contains circular muscle fibers. Posterior to this it curves and enters the stomach within the digestive gland.

Central nervous system: The ganglia of the circumesophageal nerve ring are highly concentrated. The cerebral and pleural ganglia are almost entirely fused. The cerebro-pleural ganglia are appressed to each other, without a distinct, narrowed commissure. The pedal ganglia are separated by a short commissure. The paired buccal and gastro-intestinal ganglia are situated posteriorly, immediately anterior to the muscular portion of the esophagus (Figure 3A).

Reproductive system (Figure 3B): The saccate ampulla narrows abruptly into the postampullary duct, prior to its division into the oviduct and vas deferens. The oviduct is short and enters the distal portion of the female gland mass. The elongate uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis at the duct that joins the receptaculum with the spherical bursa copulatrix. From the bursa copulatrix the elongate vaginal duct runs proximally to a joint gonopore with the

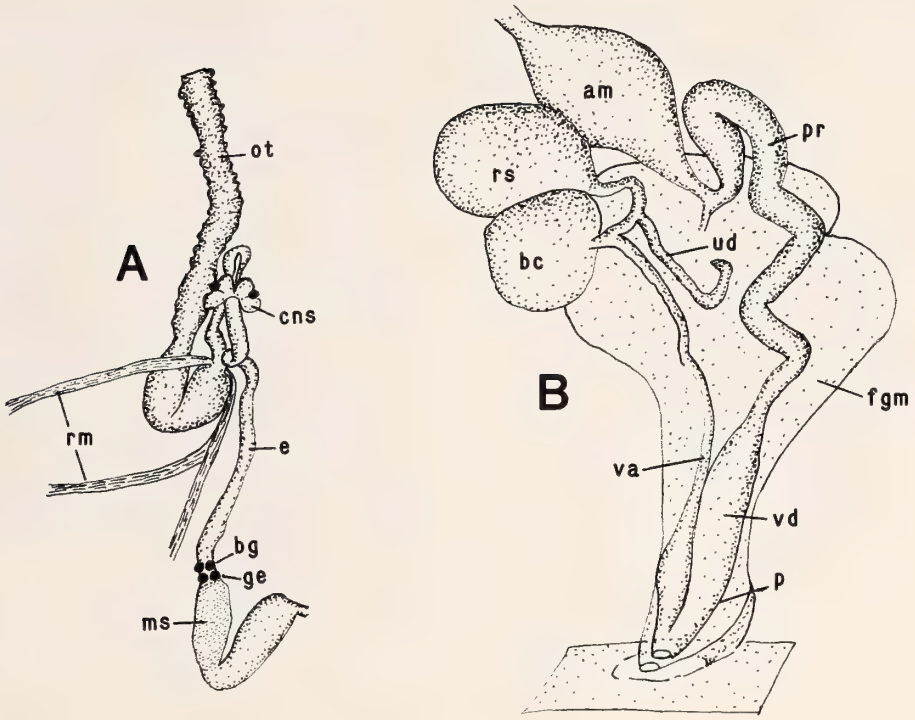


Figure 3

Phyllidiopsis cardinalis Bergh, 1875. A. Digestive system: bg, buccal ganglia; cns, central nervous system; e, esophagus; ge, gastro-esophageal ganglia; ms, muscular segment of esophagus; ot, oral tube; rm, retractor muscles. B. Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; va, vagina; vd, vas deferens.

penis. The vas deferens is prostatic distally and widens into a muscular portion. There are no cuticular spines associated with the penis.

Discussion: *Phyllidiopsis cardinalis* Bergh, 1875, is the type species of the genus. Some aspects of its morphology were described in the original description, but details of the reproductive anatomy were not examined. The digestive system is characterized by a short muscular segment at the posterior end of the esophagus. As far as is known, this is the only member of the genus to have this structure. Another species, *P. tuberculata* Risbec, 1928, is similar to the present species in that it also has compound tubercles and has similar coloration. As suggested by Pruvot-Fol (1957), this species is probably synonymous with *P. cardinalis*. In Risbec's (1928) description of this species, he indicates that a large salivary gland is present. This is likely the blood gland rather than a salivary gland.

Phyllidiopsis ***blanca*** Gosliner & Behrens, sp. nov.

(Figures 1C, D, 4, 5)

Phellidia (*sic*) sp.: Behrens, 1980:100, fig. 144.
Phyllidia sp.: Behrens & Gatewood, 1986:139.

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 063266, San Nicolas Island, ¾ mi (1.2 km) S of Sand Spit Light, 33°12′N, 120°25′W, CIRP Station SNI-2, 40 ft (13 m) deep, 22 October 1982, Jack Engle, 25 mm preserved. Paratypes, CASIZ 063267, 5 specimens, Isla San Benitos, 28°20′N, 115°40′W, 11 m deep, 6 August 1984, Jim Gatewood and Marc Chamberlin.

Distribution: Pacific coast of California and Baja California, Mexico, from Santa Barbara Island to Isla San Benitos. Specimens examined in this study were collected from San Nicolas Island and Isla San Benitos. Photographs of specimens made available to us indicate that this species occurs at least as far north as Santa Barbara Island and from several localities within this range.

External morphology: The living animals (Figures 1C, D, 4A) are 10–25 mm long. The general body color is white to grayish white. The sparsely perfoliate rhinophores are the same color as the body. The notum bears numerous soft, low tubercles. Although varying in diameter, these tubercles are more or less evenly dispersed over the notal surface. No gradation in size occurs as the tubercles near the notal margin. In five of the six specimens

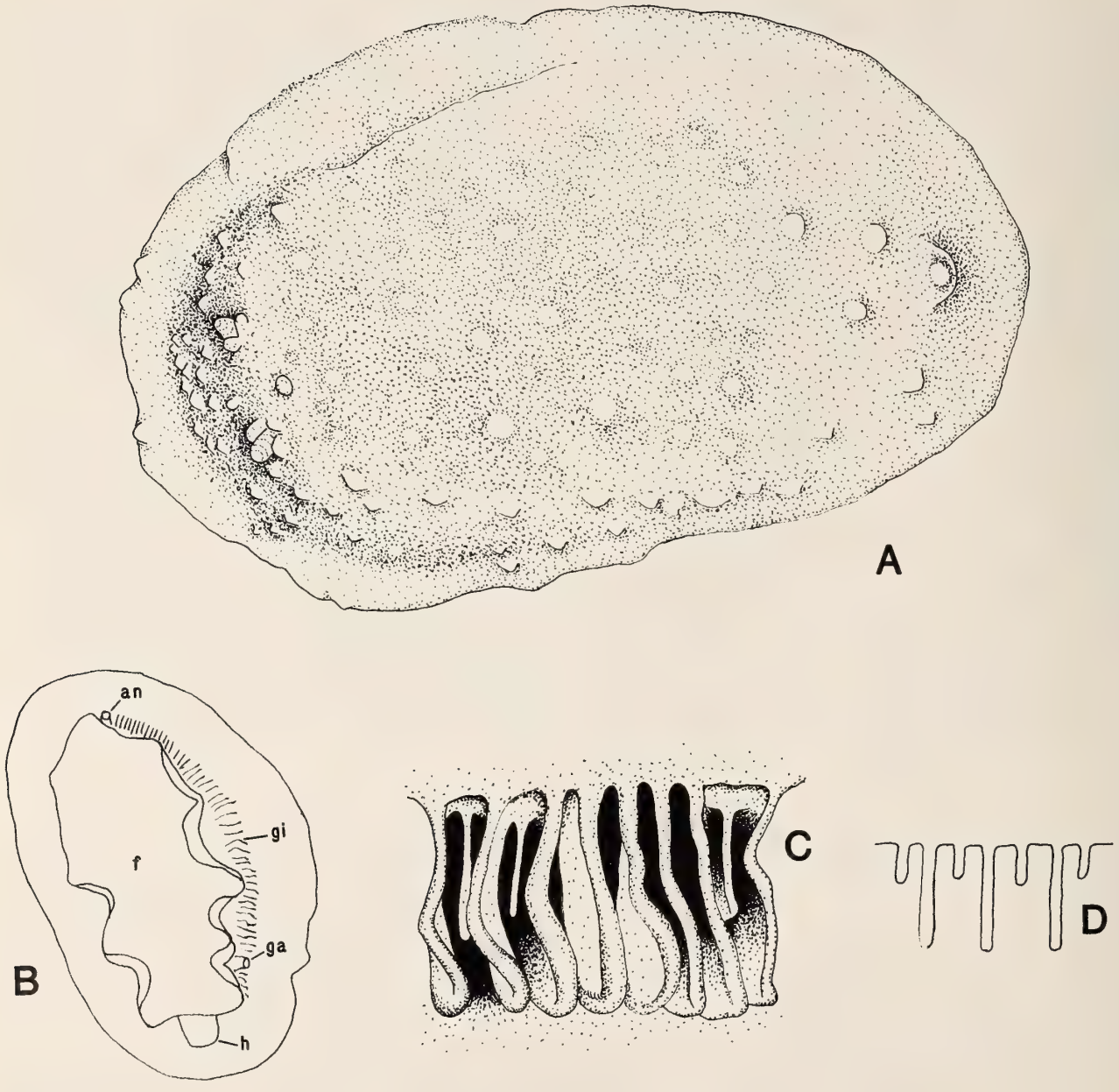


Figure 4

Phyllidiopsis ***blanca*** sp. nov. A. Dorsal view of living animal. B. Ventral view of preserved specimen with ventral anus: an, anus; f, foot; ga, genital apertures; gi, gills; h, head. C. Section of gills. D. Schematic view of gills, showing alternation of large and small gill filaments.

examined, the anus was located dorsally, near the posterior end of the animal. In the sixth specimen (Figure 4B) from Islas San Benitos, the anus is located posteroventrally on the hyponotum. The gills are arranged laterally, between the notum and foot. It is difficult to establish the exact number of gill leaflets, as the gill is a series of large lamellae irregularly interdigitated by smaller gill leaflets (Figures 4C, D). A count of the major gill elements in the holotype indicates that they may not be bilaterally equal, with the left side bearing about 70 leaflets and the right side approximately 60. This is due to the interruption of the leaflets on the right side, in the vicinity of the gonopores. Remnants of oral tentacles are present as grooves along either side of the flattened, quadrangular head.

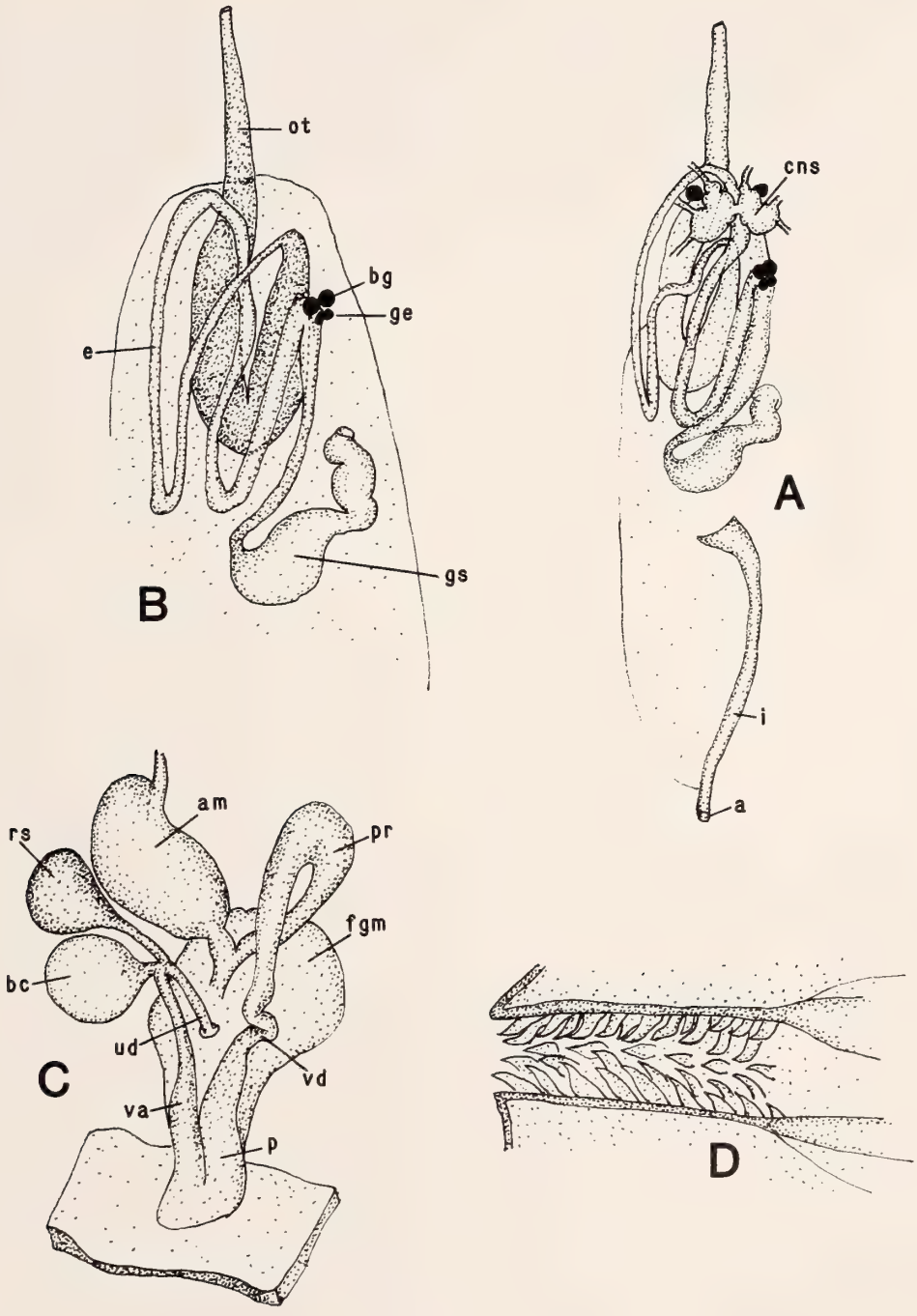


Figure 5

Phyllidiopsis ***blanca*** sp. nov. A. Digestive system with central nervous system: a, anus; cns, central nervous system; i, intestine. B. Detail of digestive system with central nervous system removed: bg, buccal ganglia; e, esophagus; ge, gastro-esophageal ganglia; gs, glandular segment of esophagus; ot, oral tube. C. Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; va, vagina; vd, vas deferens. D. Penial armature.

Digestive system (Figures 5A, B): The oral tube is narrowest at the mouth, gradually widening posteriorly. The oral tube is simple throughout its length and is devoid of associated oral glands. It recurves anteriorly and narrows abruptly into the esophagus. The esophagus consists of several convolutions, which traverse the length of the oral tube. Near its posterior limit, the esophagus expands into a glandular segment, curves anteriorly, and enters the digestive gland. More posteriorly, the intestine emerges again from the digestive gland and continues posteriorly to its termination at the anus.

Central nervous system: The ganglia constituting the circumesophageal nerve ring are highly concentrated. The paired cerebral and pleural ganglia are largely fused. The cerebral ganglia are appressed to each other, without a distinctly narrowed commissure. The pedal ganglia are separated by a short commissure. Extending posteriorly from the cerebro-pleural ganglia are the elongate buccal nerves. They are joined to the paired buccal ganglia along the sides of the esophagus. Immediately posterior to the buccal ganglia are the gastro-esophageal ganglia. In one specimen the buccal and gastro-esophageal ganglia are situated near the posteriormost loop of the esophagus. In a second specimen, they are situated even more posteriorly, just anterior to the glandular swelling of the esophagus.

Reproductive system (Figure 5C): The reproductive system is triaulic. The ampulla is short and saccate. Proximally, it narrows into the postampullary duct just prior to its bifurcation into the oviduct and vas deferens. The oviduct enters the female gland mass after a short distance. The various nidamental glands that constitute the female gland mass cannot be differentiated, owing to poor preservation. The uterine duct emerges from the female gland mass near its juncture with the oviduct. It joins the receptaculum seminis and bursa copulatrix at their common base. The receptaculum has a short duct while the bursa is inserted directly on to the uterine duct. Emerging from the proximal end of the juncture of the uterine duct, receptaculum, and bursa, is the vaginal duct. It is elongate and widens gradually towards the gonopore. The vas deferens is prostatic distally following its separation from the oviduct at the proximal terminus of the postampullary duct. It narrows into a muscular ejaculatory segment that terminates adjacent to the vaginal and nidamental openings. The proximal end of the ejaculatory segment (Figure 5D) contains 4 or 5 rows of sharp, chitinous spines, with approximately 12 spines per row.

Discussion: *Phyllidiopsis* ***blanca*** is placed in *Phyllidiopsis* because it lacks a ring of oral glands present in *Phyllidia* and *Reyfria*. The presence of a ventral anus in one specimen of *P.* ***blanca*** represents an acquisition of this character independently from that of *Reyfria*.

The known morphology of species of *Phyllidiopsis* is compared in Table 1. *Phyllidiopsis* ***blanca*** and *P. berghi* Vayssière, 1902, are the only known species within the family that have uniformly whitish coloration. All other species have complex color patterns and, with the exceptions of *P. cardinalis* and *P. tuberculata,* possess some black pigment on the notum. *Phyllidiopsis berghi* differs from *P.* ***blanca*** in having a distinct vestibule at the anterior end of the oral tube and a much longer oral tube (Bouchet, 1977:fig. 17). *Phyllidiopsis* ***blanca*** is also similar to *P. gynenopla* Bouchet, 1977, in its arrangement of the digestive system, but lacks the distinct armature surrounding the nidamental opening of the female reproductive system.

DISCUSSION OF GENERA

The distinctions between genera within the Phyllidiidae have been discussed by several workers (Bergh, 1875, 1889; Pruvot-Fol, 1956, 1957; Marcus & Marcus, 1962; Edmunds, 1972; Wägele, 1985; Yonow, 1986). The major characteristics utilized to separate genera are the elaboration of the oral tube and associated glands, the position of the anus, and the elaboration of the oral tentacles.

Most studies have differentiated *Phyllidia* and *Reyfria* (as *Fryeria*) from *Phyllidiopsis* and *Ceratophyllidia* on the basis of the possession of a large mass of oral glands surrounding the oral tube in the former two genera.

In *Phyllidiopsis* and *Ceratophyllidia* the arrangement of oral glands, when present, is more complex. The type species of *Phyllidiopsis, P. cardinalis* Bergh, 1875, and most other members of the genus lack oral glands (Table 1), as in *P. blanca. Phyllidiopsis papilligera* Bergh, 1890 (Marcus & Marcus, 1962:fig. 24) and *P. molaensis* have a single nodular oral gland, which enters the posterior end of the oral tube. In *P. papilligera* there is a caecum at the distal end of the gland that is absent in *P. molaensis. Phyllidiopsis tuberculata* (Risbec, 1928) was reported to have a large oral gland, but Pruvot-Fol (1957) has suggested that this is actually the blood gland. There is some question as to whether *P. tuberculata* may actually be a junior synonym of *P. cardinalis* Bergh, 1875. Both species have compound tubercles and are similar in their coloration. *Ceratophyllidia africana* has a pair of large oral glands with ducts entering the oral tube and running its length adjacent to the esophagus (Eliot, 1903; present study).

Phyllidia has also been characterized by having well developed retractor muscles, while they are apparently absent in *Phyllidiopsis* (Pruvot-Fol, 1957). On the basis of lacking retractor muscles, Edmunds (1972) placed a phyllidiid species in *Phyllidiopsis,* despite the fact that it had prominent oral glands surrounding the oral tube. Similarly, *Ceratophyllidia africana* has large retractor muscles but lacks a ring of distinct glands. Thus, the presence of both a mass of oral glands and retractor muscles cannot be used to separate *Phyllidia* from *Phyllidiopsis* and *Ceratophyllidia.* It seems that the mass of oral glands in *Phyllidia* and *Reyfria* is far more likely to represent a unique derivation within the Phyllidiidae, and should be afforded greater weight in differentiating these genera from *Phyl-*

Table 1

Morphological variability of *Phyllidiopsis*.

	Distribution	Tubercles	Oral tentacles	Oral tube	Oral glands	Cerebro-buccal connective	Gills	Vas deferens	References
P. cardinalis Bergh, 1876	Indo-Pacific	compound	largely fused	no vestibule	absent	elongate	75 +	unarmed	PRUVOT-FOL, 1957; present study
P. tuberculata (Risbec, 1928)	New Caledonia	compound	—	with large vestibule	absent ?	—	—	—	RISBEC, 1928; PRUVOT-FOL, 1957
P. papilligera Bergh, 1890	W. Atlantic	simple, low warts	round, largely fused	thick vestibule	present ventral	elongate	100 per side	armed	BERGH, 1890; MARCUS & MARCUS, 1962
P. molaensis Meyer, 1977	Atlantic coast of Panama	simple, conical	conical, separate	thick vestibule	present dorsal	—	—	—	MEYER, 1977
P. berghi Vayssière, 1902	E. Atlantic	simple, round	short, united at base	with thicker vestibule	absent	elongate	70–80 per side	armed	VAYSSIÈRE, 1902; BOUCHET, 1977
P. gemmata Pruvot-Fol, 1957	?	simple, round	largely united	no vestibule	absent	elongate with buccal glands situated anterior to nerve ring	numerous	—	PRUVOT-FOL, 1957
P. krempfi Pruvot-Fol, 1957	Viet Nam	compound	united	with thicker vestibule	absent	—	—	—	PRUVOT-FOL, 1957
P. striata Bergh, 1889	Thailand	simple, conical	short, separate	no vestibule	present ?	elongate	—	armed	BERGH, 1889
P. gynenopla Bouchet, 1977	E. Atlantic	simple, hemispherical	largely united	no vestibule	absent	elongate	—	armed	BOUCHET, 1977
P. ***blanca*** sp. nov.	E. Atlantic	simple, round	united throughout	no vestibule	absent	elongate	60–70 per side	armed	present study

lidiopsis and *Ceratophyllidia*. Hence, EDMUNDS' (1972) species should be placed in *Phyllidia*.

The systematic position of *Ceratophyllidia* has been the subject of confusion. Since its original description (ELIOT, 1903), most workers have considered *Ceratophyllidia* as a junior synonym of *Phyllidiopsis* (THIELE, 1931; PRUVOT-FOL, 1957; FRANC, 1968). MARCUS & MARCUS (1962) suggested that *Ceratophyllidia* should be regarded as a distinct genus on the basis of its possession of stalked papillae. Unfortunately, the opinions regarding its generic status were based solely on ELIOT's incomplete descriptions (1903, 1910). Examination of the present material provides a more complete basis of comparison. The fleshy, stalked, readily detachable papillae are unique to *Ceratophyllidia*. Also the presence of paired oral glands with ducts running parallel to the esophagus within the oral tube is known only from *Ceratophyllidia*. This additional fact lends support to the contention that *Ceratophyllidia* represents a distinct genus.

The systematic position of *Fryeria* Gray, 1853, had never been in question. Recently, however, YONOW (1986) correctly pointed out that the name *Fryeria* had been incorrectly applied to *F. ruppelli* rather than to *Phyllidia pustulosa* Cuvier, 1804. She considered *Fryeria* as a junior synonym of *Phyllidia*, because *P. pustulosa* has a dorsal anus, and substituted the *Reyfria* for the species with a ventral anus. The fact that specimens of *Phyllidopsis* ***blanca*** examined in this study are variable in the position of the anus (dorsal in five specimens, ventral in one) casts serious doubts as to whether *Reyfria* should be separated from *Phyllidia*. Certainly, the degree of intraspecific variability of this character within the Phyllidiidae must be examined in greater detail.

ELIOT (1903) stated that, although it was not possible to examine the vas deferens of *Ceratophyllidia africana*, it was likely that it was armed with hooks, as in other members of the family. THIELE (1931) also characterized the family as having spines within the male duct. However, WÄGELE (1985) observed that the male duct of *Phyllidia pulitzeri* lacked armature. Similarly, the type species of *Phyllidiopsis* and *Ceratophyllidia* also lack any armature (present study). It appears that this character varies within genera.

ACKNOWLEDGMENTS

We thank Jim Gatewood, Marc Chamberlain, and Jack Engle for kindly providing us with specimens of *Phyllidiopsis blanca*. Marc Chamberlain also graciously permitted us to use his photographs of this species. We also thank Marc Charnow of the California Academy of Sciences for printing the final photographic prints of the living animals.

LITERATURE CITED

BEHRENS, D. 1980. Pacific nudibranchs. A guide to the opisthobranchs of the northeastern Pacific. Sea Challengers: Los Osos, California. 112 pp.

BEHRENS, D. & J. GATEWOOD. 1986. New opisthobranch records for the west coast of Baja California Shells and Sea Life 18(9):139–142.

BERGH, R. 1875. Neue Bieträge zur Kenntniss der Phyllidiaden. Verh. der k. k. zool-bot Gesell. Wien 25:659–674.

BERGH, R. 1889. Malacologische Untersuchungen, 3, Nudibranchien vom Meere der Insel Maritius. *In:* C. Semper (ed.), Reisen im Archipel der Philippinen. Wiss. Res. 2, 3 (16) pt. 2:815–872.

BERGH, R. 1890. Report on the nudibranchs. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–1878) and in the Caribbean Sea (1879–1880), by the U.S. Coast Survey steamer "Blake," Lieut. Commander C. D. Sigsbee, U.S.N. and Commander J. R. Bartlett, U.S.N. commanding. Bull. Mus. Comp. Zool. Harv. 19:155–181.

BOUCHET, P. 1977. Opisthobranches de profondeur de l'océan atlantique: II—Notaspidea et Nudibranchiata. Jour. Moll. Stud. 43:28–66.

EDMUNDS, M. 1972. Opisthobranchiate Mollusca from the Seychelles, Tanzania and the Congo, now in the Tervuren Museum. Rev. Zool. Bot. Afr. 85:67–92.

ELIOT, C. 1903. On some nudibranchs from East Africa and Zanzibar. II. Proc. Zool. Soc. Lond. 1903(1):250–257.

ELIOT, C. 1910. Nudibranchs collected by Mr. Stanley Gardiner from the Indian Ocean in H.M.S. Sealark. Trans. Linn. Soc. Lond. 13:411–438.

FRANC, A. 1968. Sous-classe de opisthobranches. *In:* P. Grassé (ed.), Traité de Zoologie, 5 (3), Mollusques Gasteropodes er Scaphopodes. Masson et Cie: Paris.

GOSLINER, T. 1987. Nudibranchs of southern Africa. A guide to opisthobranch molluscs of southern Africa. Sea Challengers: Monterey, California.

MARCUS, EV. & ER. MARCUS. 1962. Opisthobranchs from Florida and the Virgin Islands. Bull. Mar. Sci. 12(3):450–488.

MEYER, K. 1977. Dorid nudibranchs of the Caribbean coast of the Panama Canal Zone. Bull. Mar. Sci. 27(2):299–307.

PRUVOT-FOL, A. 1956. Revision de la famille des Phyllidiadae. 1. Jour. Conchyl. 96:55–80.

PRUVOT-FOL, A. 1957. Revision de la famille des Phyllidiadae. 2. Jour. Conchyl. 97:104–135.

RISBEC, J. 1928. Contribution a l'étude des nudibranches Néo-Calédoniens. Faune Colon. Française 2(1):1–328.

THIELE, J. 1931. Handbuch der Systematischen Weichterkunde. 1. Gustav Fischer: Jena.

VAYSSIÈRE, A. 1902. Opisthobranches. Pp. 221–270. *In:* Expéditions scientifiques du "Travailleur" et du "Talisman" pendant les annees 1880–1883. Ouvrage publie sous les auspices du ministre de l'instuction publique, Paris.

WÄGELE, H. 1985. The anatomy and histology of *Phyllidia pulitzeri* Pruvot-Fol, 1962, with remarks on the three Mediterranean species of *Phyllidia* (Nudibranchia, Doridacea). Veliger 28(1):63–79.

YONOW, N. 1986. Red Sea Phyllidiidae (Mollusca, Nudibranchia), with descriptions of new species. Jour. Natur. Hist. 20:1401–1428.

The Veliger 30(3):315–318 (January 4, 1988)

THE VELIGER

A New Species of *Gastropteron* (Gastropoda: Opisthobranchia) from Reunion Island, Indian Ocean

by

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

AND

GARY C. WILLIAMS

Department of Marine Biology, South African Museum, P.O. Box 61, Cape Town 8000, South Africa

Abstract. *Gastropteron* ***michaeli*** sp. nov. is described from Reunion Island. Aspects of its external and internal morphology clearly differentiate this species from other members of the genus.

INTRODUCTION

During the course of a collecting expedition to Reunion Island in the western Indian Ocean in July 1977, one of us (G.C.W.) and Michael Gosliner collected 16 species of opisthobranch gastropods. Included in this collection is an undescribed species of *Gastropteron*. This paper describes the morphology of this species and compares it with closely allied congeners.

METHODS

Penial morphology was determined by clearing and staining of the material. The whole penis was stained in a dilute solution of 70% EtOH and acid fuchsin for 1 min. It was then dehydrated in a series of three alcohols (80%, 95%, 100% EtOH, for 1 min each). The specimen was then cleared in xylene for 2 min and mounted in Permount on a microscope slide.

DESCRIPTION

Family GASTROPTERIDAE Swainson, 1840

Gastropteron Meckel (in Kosse), 1813

Gastropteron ***michaeli*** Gosliner & Williams, sp. nov.

(Figures 1, 2)

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 063270, 2 km S of St. Giles, Reunion Island, Indian Ocean, under rocks on dead coral reef, 2 m depth, 28 July 1977, Michael L. Gosliner. Paratype, one specimen, CASIZ 063271, 2 km S of St. Giles, Reunion Island, under rocks on dead coral reef, 2 m depth, 28 July 1977, M. L. Gosliner.

Etymology: This species is named after Michael L. Gosliner. He has been an enthusiastic collector and supporter of our research efforts. He collected both of the specimens of this species.

External morphology: The living animals (Figure 1) were 3–5 mm in length. The body was uniformly yellow-orange with large maroon-brown spots scattered over the surface of the head shield, posterior shield, and dorsal and ventral surfaces of the foot.

The head shield is roughly triangular in shape, broadest anteriorly. Its posterior end is involuted to form a siphon with a thin, cylindrical medial crest. The parapodia are thin and low, barely extending on to the dorsal surface of the animal. The posterior shield is ovoid and elongate, without a flagellum or auxiliary appendages. The foot is not distinctly separated from the parapodia. When the animal is actively crawling, the foot is extended well behind the posterior end of the visceral hump. A distinct pedal gland was not observed on the ventral side of the foot, but this may be a result of preservation. The simply plicate

Figure 1

Gastropteron ***michaeli*** sp. nov., living animal.

ctenidium is poorly developed, consisting of 3 or 4 simple leaflets. The anus is located immediately posterior to the ctenidium. The genital aperture is situated anterior to the ctenidium. From it, the sperm groove runs anteriorly to the male genital aperture on the right side of the head. Owing to fixation of the material in Bouin's solution, the shell, if present, was dissolved.

Digestive system: The buccal mass is muscular throughout its length. From the posterior end of the buccal mass, emerges the narrow esophagus. It expands into a short, thin-walled crop, which approximates the buccal mass in size. The crop is devoid of chitinous plates or folds. It narrows again posteriorly, where a short esophageal portion enters the digestive gland. The intestine emerges from the digestive gland, curves posteriorly, and emerges at the anus, posterior to the gill.

Within the buccal mass the jaws are poorly developed, devoid of distinct chitinous rodlets, and reduced to a thin cuticular lining. The radular formula is 21–22 × 3.1.0.1.3. in the two specimens examined. The inner lateral tooth (Figure 2A) is broad with an elongate cusp and a broad base. The masticatory border of the tooth may be entirely smooth or with up to five irregular denticles along its margin. The presence or absence of denticles varies within the radula of a single individual. The outer laterals are narrow with a broader base. They are devoid of denticles.

Central nervous system (Figure 2B): The arrangement of ganglia is euthyneurous and highly cephalized, with a short visceral loop. The cerebral ganglia are large and appressed to each other. Large nerve thickenings emerge from the anterior and lateral sides of each cerebral ganglion. The pedal ganglia are as large as the cerebrals, and are separated from each other by a short, narrow commissure. The left pleural ganglion is separated from the left cerebral and pedal ganglia by a short connective. Immediately posterior and appressed to the left pleural is the subintestinal ganglion. The larger visceral ganglion is directly behind the subintestinal ganglion. Emanating from the posterior end of the visceral ganglion are three nerves. The innermost of these is the visceral loop. The short visceral loop joins the posterior end of the supraintestinal ganglion adjacent to the osphradial nerve. The supraintestinal ganglion is partially fused with the right pleural ganglion.

Reproductive system (Figure 2C): The system is monaulic. The ovotestis consists of numerous round bodies. The ampulla is narrow and winding. It narrows further proximally and winds around the outer surface of the

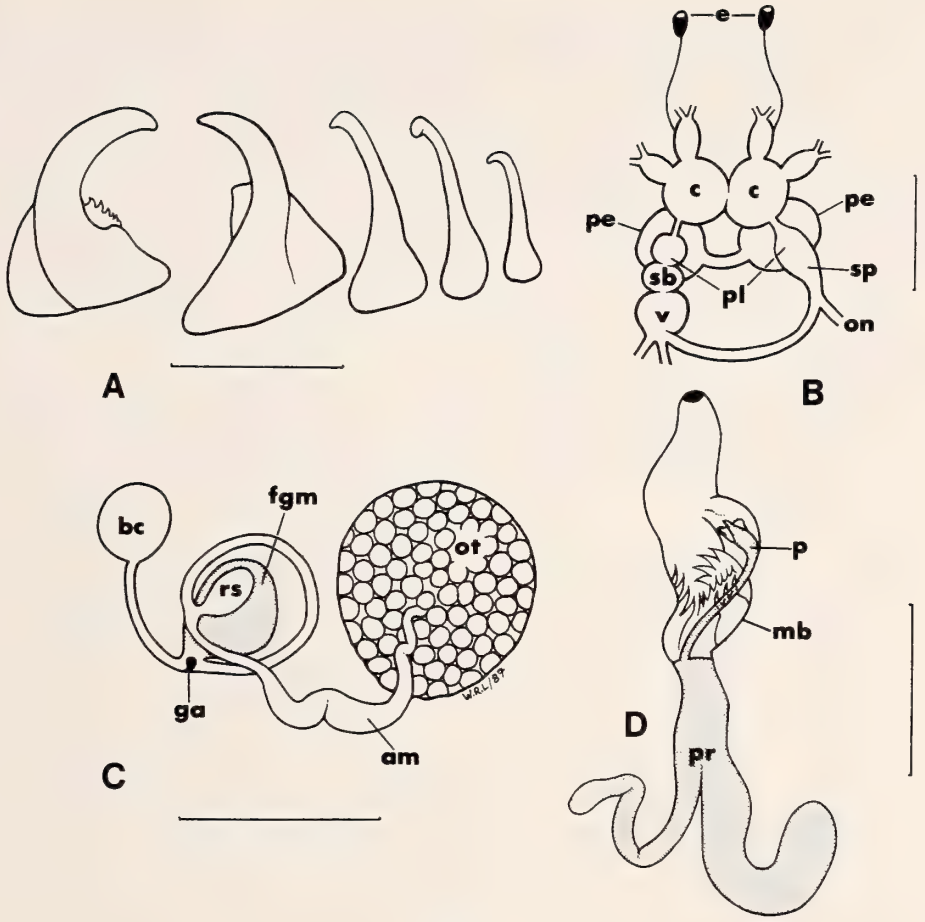


Figure 2

Gastropteron ***michaeli*** sp. nov. A. Radular teeth, showing variation in inner lateral tooth and outer laterals, scale = 20 μm. B. Central nervous system. Key: c, cerebral ganglion; e, eye; on, osphradial nerve; pe, pedal ganglion; pl, pleural ganglion; sb, subintestinal ganglion; sp, supraintestinal ganglion; v, visceral ganglion; scale = 250 μm. C. Reproductive system. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ga, genital atrium; ot, ovotestis; rs, receptaculum seminis; scale = 1.0 mm. D. Penis. Key: mb, muscular bulb with chitinous spines; p, penial papilla; pr, prostate; scale = 0.5 mm.

female gland mass. Near the middle of the hermaphroditic duct, a short duct leds to the pyriform receptaculum seminis. The hermaphroditic duct curves proximally and terminates at the common genital atrium. The spherical, thin-walled bursa copulatrix has a narrow, elongate duct, which also joins the common genital atrium near the gonopore. The female glands could not be differentiated from one another in the fully dissected specimen.

The penis (Figure 2D) is well developed and complex in its structure. The prostate is bilobed, with one of the lobes significantly thicker than the other. The two lobes are united for their proximal one-third. From the proximal end of the prostate, a narrow duct emerges and enters the small, conical penial papilla. A curved fleshy, papilla is situated more proximally, within the penial sac. The largest portion of the prostate enters a bulbous, muscular section. Within this muscular region are four rows of curved, chitinous spines. The left lobe has four spines, the posteriormost three, the middle lobe seven, and the anteriormost four. The anterior end of the muscular portion joins the penial sac anteriorly. The penial sac is thin and elongate, terminating at the male gonopore.

DISCUSSION

In a recent review of the genus, Gosliner (1984) listed 15 described species of *Gastropteron*. Since then, one additional species, *G. vespertilium* Gosliner & Armes, 1984, has been described. Of these 16 species, only six are known to lack a flagellum or other auxiliary process on the posterior shield. *Gastropteron brunneomarginatum* Carlson & Hoff, 1974, was recorded as lacking a flagellum. However,

examination of specimens of this species from New Guinea (present study) indicates that a flagellum may be present or absent in individuals from a single population.

Of the species that always lack a flagellum, only *Gastropteron flavobrunneum* and *G.* ***michaeli*** are yellowish with brown spots (GOSLINER, 1984). *Gastropteron flavobrunneum* is lighter in color and lacks any orange pigment. The radula of *G. flavobrunneum* has six or seven teeth per half row, while in *G.* ***michaeli*** there is a maximum of four teeth per half row. The inner lateral teeth of *G. flavobrunneum* lack any denticles on the masticatory border, while in *G.* ***michaeli*** denticles may be present or absent. The penial morphology of the two species differs markedly. The penis of *G. flavobrunneum* has a distinct spermatic bulb, in addition to the single prostate, and the penial papilla has a discoidal apex. In *G.* ***michaeli*** the prostate is bilobed, there is a muscular region with chitinous spines, and the penial papilla is conical.

The penial morphology has been described for only six of the 16 known species. It varies considerably between species. Of the described species, only *Gastropteron ladrones* Carlson & Hoff, 1974, is similar to that of *G.* ***michaeli*** in having a muscular region with cuticular spines and a separate duct leading to the penial papilla (GOSLINER, in press). At least one other undescribed Indo-Pacific *Gastropteron* species has a similar penial morphology. It appears that further examination of this character, by staining and clearing of preparations, will provide information useful in establishing natural groupings of species within the Gastropteridae.

ACKNOWLEDGMENTS

We thank Bill Liltved for preparing the final figures, with the exception of the living animal, and Michael Gosliner for collecting the specimens.

LITERATURE CITED

CARLSON, C. & P. HOFF. 1974. The Gastropteridae of Guam, with descriptions of four new species (Opisthobranchia: Cephalaspidea). Publ. Seto Mar. Biol. Lab. 21(5/6):345–363.

GOSLINER, T. 1984. Two new species of *Gastropteron* (Gastropoda: Opisthobranchia) from southern Africa. Publ. Seto Mar. Biol. Lab. 29(4/6):231–247.

GOSLINER, T. In press. The Philinacea (Gastropoda: Opisthobranchia) of Aldabra Atoll, with descriptions of five new species and a new genus. Proc. Biol. Soc. Wash.

GOSLINER, T. & P. ARMES. 1984. A new species of *Gastropteron* from Florida (Gastropoda: Opisthobranchia). Veliger 27(1): 54–64.

The Veliger 30(3):319–324 (January 4, 1988)

THE VELIGER

The First Record of *Polycerella* Verrill, 1881, from the Pacific, with the Description of a New Species

by

DAVID W. BEHRENS

Biological Laboratory, Pacific Gas and Electric Company, P.O. Box 117, Avila Beach, California 93424, U.S.A.

AND

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. A new species of *Polycerella, P.* ***glandulosa*** is described from the Pacific coast of California and the Gulf of California. It differs from the Atlantic *P. emertoni,* the only other member of the genus, in several aspects of its external and internal morphology. *Polycerella* ***glandulosa*** is characterized by its few rhinophoral lamellae and its compoundly digitate extra-branchial appendages.

INTRODUCTION

Specimens of an undescribed *Polycerella* were abundant along the California coast from Morro Bay to San Diego, in late 1982 and throughout 1983. Specimens have also been collected commonly at various localities within the Gulf of California. This paper describes the morphology and aspects of the biology of this species and compares them to the only other known member of the genus, *Polycerella emertoni* Verrill, 1881.

Polycerella ***glandulosa*** Behrens & Gosliner, sp. nov.

(Figures 1–4)

Type material: Holotype: California Academy of Sciences, San Francisco, CASIZ 063272, one 7 mm specimen, Punta Gringa, Bahia de los Angeles, Baja California, Mexico, 10 m depth, 1 October 1984, T. M. Gosliner. Paratypes: CASIZ 063273, four specimens, Punta Gringa, 10 m depth, 1 October, 1984, T. M. Gosliner; CASIZ 063268, 8 specimens, Los Islotes, north of La Paz, Baja California Sur, Mexico, 15–20 m depth, 22 July 1985, T. M. Gosliner.

Etymology: The specific name ***glandulosa*** is chosen to call attention to the yellow glandular structure occurring distally on the extra-branchial appendages.

Distribution: *Polycerella* ***glandulosa*** has been found along the Pacific coast of California from Morro Bay south to San Diego. Within the Gulf of California it has been found from the La Paz region north to Bahia de los Angeles.

Natural history: *Polycerella* ***glandulosa*** has generally been collected in association with the ctenostomatous bryozoan *Zoobotryon* sp. Specimens, together with egg masses, are commonly found crawling on *Zoobotryon* colonies, on floating docks, and in the shallow subtidal zone to a depth of 20 m. Specimens from Morro Bay were collected in association with another bryozoan, *Bugula* sp.

External morphology: The living animals reach 8 mm in length. The limaciform body is typically polycerid. It is compressed laterally and is highly arched dorsomedially, near the branchial region (Figures 1, 2A). The foot is linear and tapers posteriorly into a bluntly pointed tail. The anterior corners of the foot form a pair of triangular points (Figure 2A). The head is rounded and bears rounded lobes laterally. The distinct, semicircular frontal veil consists of 5 papillae. These papillae are simple, elongate, and cylindrical, tapering to a point apically. There are 2 extra-branchial appendages, situated posterolaterally to the branchial plume. These appendages are irregularly ramified and are slightly swollen at the most distal ramus (Figure 2B). This swelling is yellowish and glandular, and

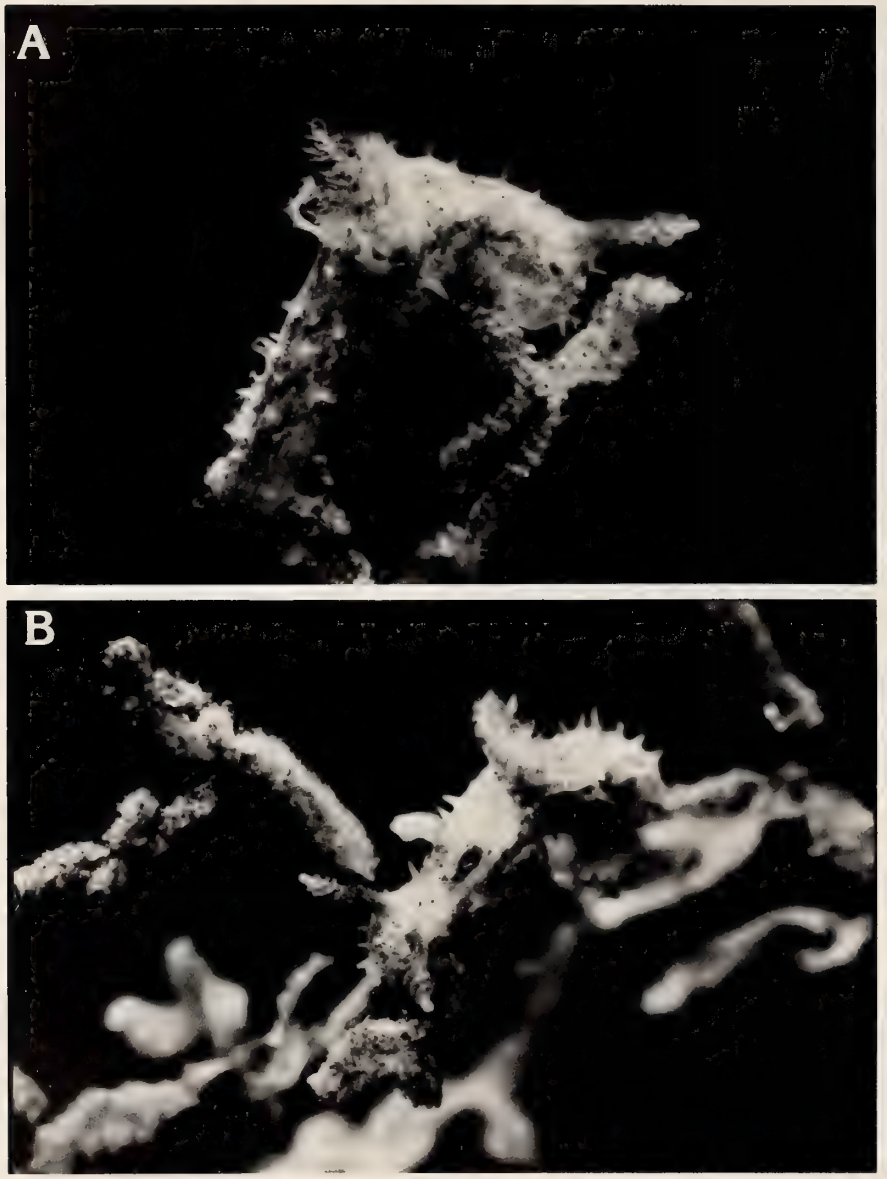


Figure 1

A and B. Living animal (8 mm in length) of *Polycerella* ***glandulosa*** sp. nov., collected from Mission Bay, San Diego, California, November 1982. Photos by Jeff Hamann.

appears granular internally. The function of this organ is unknown. The non-retractile rhinophores (Figure 2C) are perfoliate with 3 or 4 lamellae. The clavus of the rhinophores is short, less than one-third of the entire rhinophore. The shaft tapers slightly towards the clavus. The branchial plume is semicircular and consists of 6 or 7 irregularly bipinnate gills. The posterior 2 gills are smaller than the anterior ones. The notum is ornamented with numerous cylindrical papillae. The anus is situated within the branchial plume. The genital apertures are located on the right side of the body at approximately the level of the anteriormost portion of the branchial plume.

The ground color is translucent white to cream. The notum bears a series of irregular subepidermal brown streaks and blotches. The notum is covered with yellow-white and dark brown specks. The living animals appear dirty white in color and are exceedingly cryptic when on colonies of *Zoobotryon*.

Digestive system: The buccal mass is well developed and muscular. A pair of short, cylindrical salivary glands is present at the juncture of the narrow esophagus with the posterior portion of the buccal mass. The jaws (Figure 3A) are ovoid and brown in color. Their surface is or-

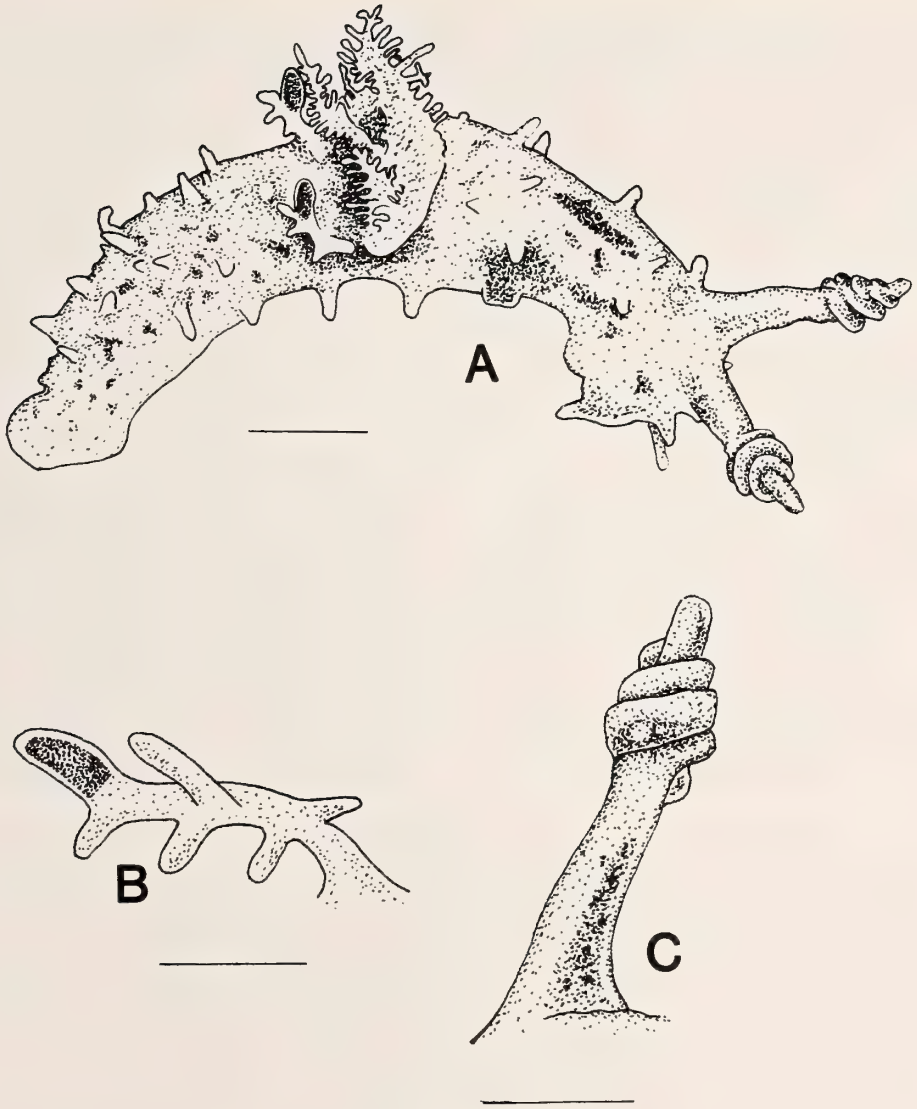


Figure 2

Polycerella ***glandulosa***. A. Living animal drawn from color transparency, scale = 1.0 mm. B. Extra-branchial process, scale = 0.25 mm. C. Rhinophore, scale = 0.5 mm.

namented with flattened polygonal rodlets (Figure 3B). The radula is minute and details of its morphology are discernible only by means of scanning electron microscopy. The radular formula is 28–40 × 3·1–2·0·1–2·3 in three specimens examined. The shape and configuration of the radular teeth varies from one end of the radula to the other. The formative portion of the radula is widest and tapers significantly towards the older portion. In the oldest portion of the radula the inner two laterals are fused to form a single elongate tooth with four denticles (Figure 4A). After approximately the 15th radular row, these two laterals become entirely separate. More posteriorly, the inner lateral teeth (Figure 4B) are roughly triangular in shape, with simple apical and basal hook-shaped denticles. The second lateral is largest with an acutely pointed, triangular denticle near the apex. A thickened medial portion runs basally to the triangular basal denticle. In the oldest portion of the radula the third laterals are simply hook-shaped teeth. More posteriorly, they are roughly rectangular, devoid of denticles, with a thickened medial portion (Figures 4C, D). In the older portion of the radula the outer two teeth are elongate and sickle-shaped. More posteriorly, the fourth tooth has a thickened base, while the fifth tooth remains narrow and elongate.

Reproductive system (Figure 3C): The preampullary duct is narrow and expands into a short, saccate ampulla. More proximally the ampulla narrows into a postampul-

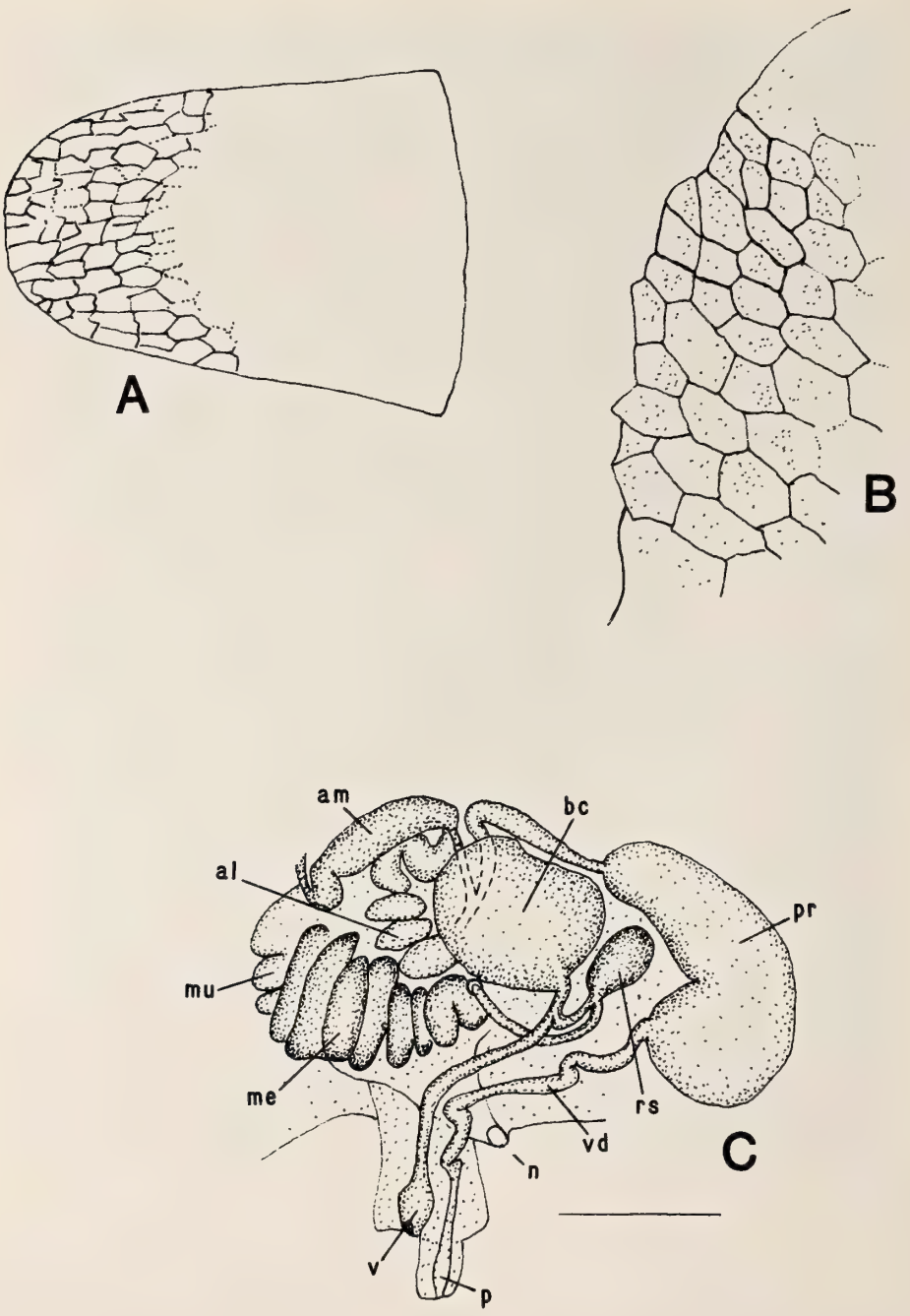


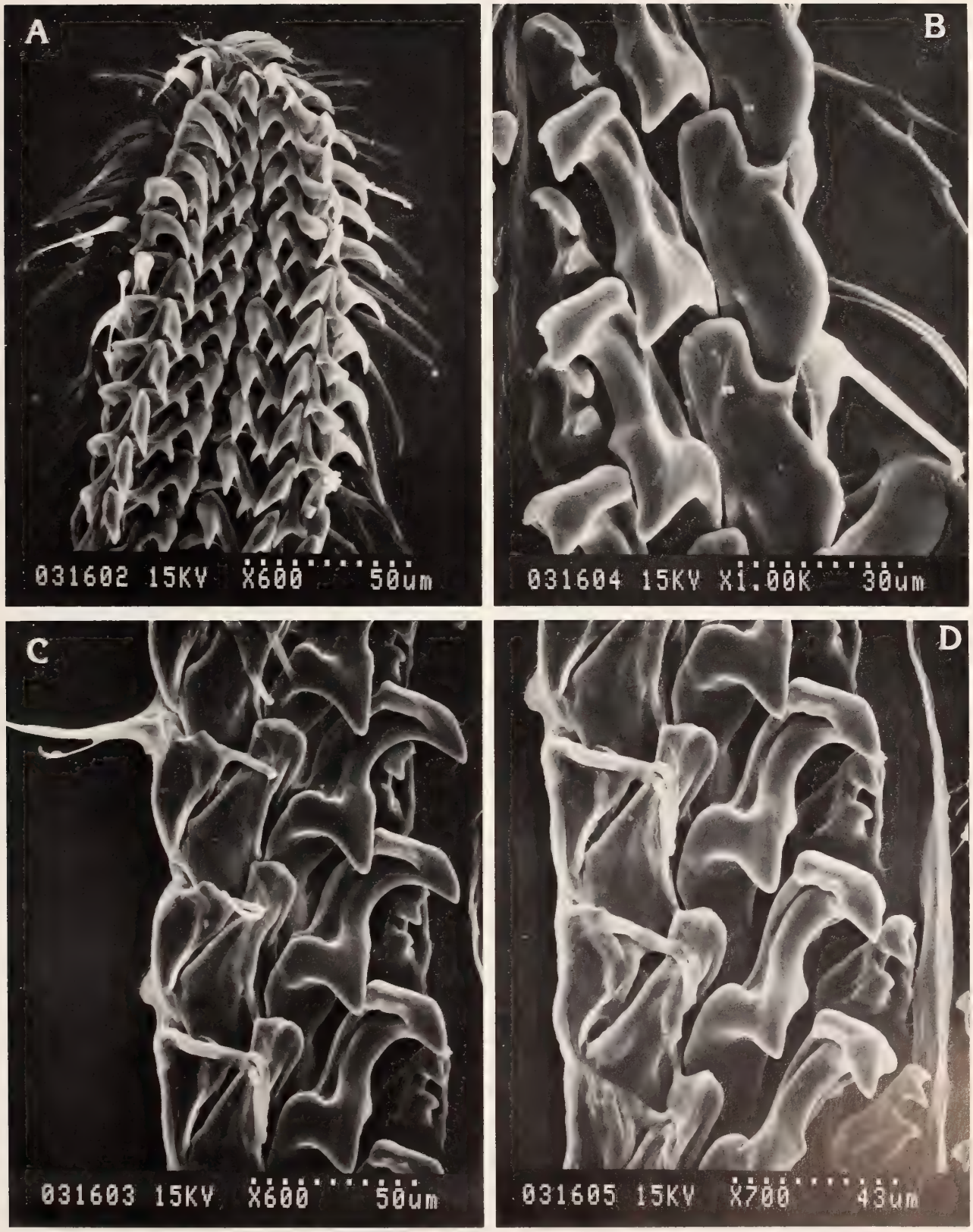
Figure 3

Polycerella ***glandulosa***. A. Jaw, ×200. B. Jaw rodlets, ×400. C. Reproductive system, scale = 1.0 mm: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; n, nidamental opening; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, vas deferens.

→

Figure 4

Polycerella ***glandulosa***. Scanning electron micrographs of radula. A. Oldest portion of radula. B. Middle of radula. C and D. Newest portion of radula.


A
031602 15KV X600 50um
B
031604 15KV X1.00K 30um
C
031603 15KV X600 50um
D
031605 15KV X700 43um

lary duct that divides into the oviduct and vas deferens. The oviduct enters the female gland mass in the vicinity of the albumen gland. The uterine duct also emerges from the female gland mass close to the oviduct. It continues as a narrow duct to the base of the pyriform receptaculum seminis, where it joins with the receptaculum duct. The receptaculum duct joins the vaginal duct prior to their common entrance into the thin-walled, spherical bursa copulatrix. The narrow vagina is elongate and expands immediately prior to its exit adjacent to the penis. The albumen gland is the smallest portion of the female gland mass. The membrane gland is slightly larger, consisting of numerous whitish folds. The membrane gland is smooth, with several distinct lobes. The female glands terminate at the nidamental gonopore ventral to the vaginal and penial apertures. The narrow vas deferens expands into the large prostate gland a short distance from its division from the ampulla. At its proximal end the prostate abruptly narrows again into an ejaculatory segment. Its proximal end contains several rows of minute, curved chitinous hooks. No distinct penial papilla is present.

DISCUSSION

The genus *Polycerella* Verrill, 1881, includes species with a narrow radula, consisting of more rows of teeth than *Polycera* Cuvier, 1817, and smooth, rather than perfoliate, rhinophores. In *Polycerella,* the jaws are less well developed than in *Polycera.* Four species of *Polycerella* have been described from the Atlantic coasts of North and South America and the Mediterranean. Franz & Clark (1972) considered *Polycerella davenporti* Balch, 1899, to be a junior synonym of *P. emertoni* Verrill, 1881. Ev. Marcus (1976) stated that *P. conyna* Er. Marcus, 1957, and *P. recondita* Schmekel, 1965, are also junior synonyms of *P. emertoni.* This synonymy was also supported by Schmekel & Portmann (1982). Thus, there appears to be only one species of *Polycerella* inhabiting the Atlantic and Mediterranean.

The present species differs significantly from *Polycerella emertoni* in several aspects of its external anatomy. The rhinophores are perfoliate, with 3 or 4 lamellae, rather than smooth. The extra-branchial processes are ramified rather than simple. There are only 3 gills in *P. emertoni* and 6 or 7 in *P. **glandulosa***. The papillae are longer and more numerous in *P. **glandulosa*** than in *P. emertoni.*

There are also some significant internal differences separating the species. The radular teeth of *Polycerella **glandulosa*** are thicker and more strongly developed than those of *P. emertoni.* In *P. emertoni* the third lateral teeth are elongate hooks, while in *P. **glandulosa*** they are short and thick. There is only a single row of inner lateral teeth in *P. emertoni,* while there are two rows present in most of the radula of *P. glandulosa.*

In view of the addition of *P. **glandulosa*** to *Polycerella,* the genus must be expanded to include species with smooth and perfoliate rhinophores. *Polycera* differs from *Polycerella* in having numerous (12–17) densely packed rhinophoral lamellae, a narrow radula with quadrate, rather than elongate, outer lateral teeth, and strongly developed jaws.

ACKNOWLEDGMENTS

We thank Jeff Hamann for first bringing this species to our attention, based on specimens he collected from Mission Bay, California, in 1982. We also thank him for permission to use his photograph of the living animal. Mary Ann Tenorio and Marc Charnow of the California Academy of Sciences kindly prepared the final scanning electron micrographic prints and photos of the living animal.

LITERATURE CITED

Franz, D. & K. Clark. 1972. A discussion of the systematics, reproductive biology, and zoogeography of *Polycerella emertoni* and related species (Gastropoda: Nudibranchia). Veliger 14(3):265–270.

Marcus, Ev. 1976. Marine euthyneuran gastropods from Brazil (3). Stud. Neotrop. Fauna Environ. 11:5–23.

Schmekel, L. & A. Portmann. 1982. Opisthobranchia des Mittelmeers. Springer-Verlag: Berlin.

The Veliger 30(3):325–328 (January 4, 1988)

THE VELIGER

Anatomical Information on *Thorunna* (=*Babaina*) (Nudibranchia: Chromodorididae) from Toyama Bay and Vicinity, Japan

by

KIKUTARÔ BABA

Shigigaoka 35, Minami-11-jyo, Sango-cho, Ikoma-gun, Nara-ken, Japan 636

Abstract. *Glossodoris florens* Baba, 1949, was referred to the new genus *Babaina* by Odhner in Franc, 1968, but it was transferred to *Thorunna* Bergh, 1878, by Rudman, 1984. This species, the type of *Babaina,* was studied again. It agrees with *Thorunna* proper in the anatomy of the genital system, but it differs somewhat from *Thorunna* proper in details of the tooth morphology and shape of the oral tube.

INTRODUCTION

Collections made from different stations of Japan during recent years provided a number of both recorded and unrecorded species of the Chromodorididae. This paper describes the taxonomy and anatomy of a species that has not been extensively characterized before.

Thorunna florens (Baba, 1949); Hanairo-umiushi

(Figures 1–3)

Synonymy

Glossodoris florens Baba, 1949:53, 143–144, pl. 19, fig. 67, text-fig. 60—Hayama, Sagami Bay; Abe, 1964:49, pl. 22, fig. 79—Tsuruga Bay, *etc.*

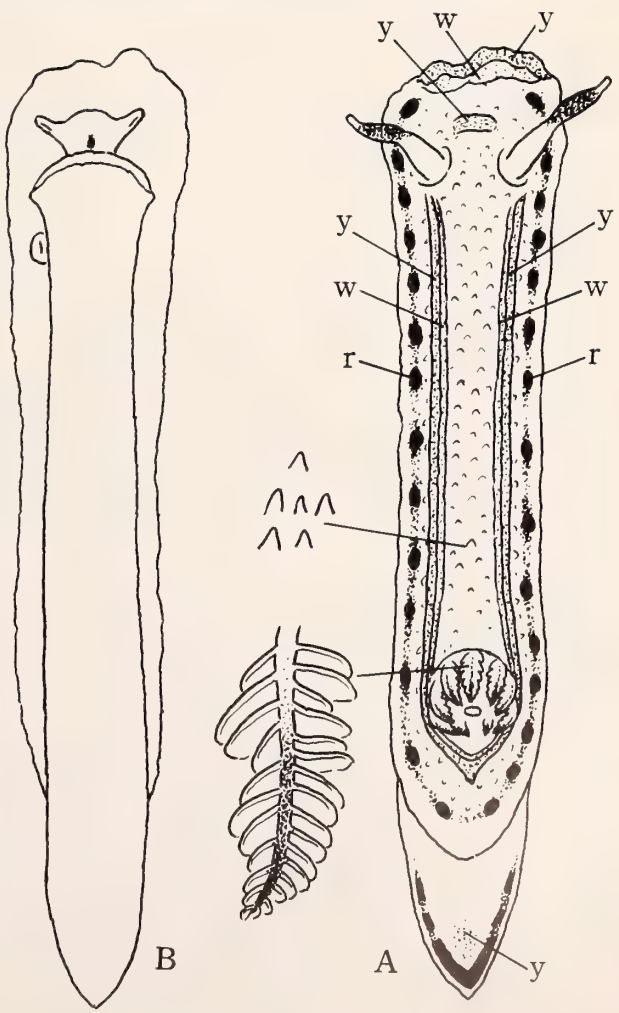
Babaina florens: Takaoka Biol. Club, 1978:6, photo (color)—Abugashima, Toyama Bay.

Thorunna florens (*Babaina florens*): Baba, 1985:225, figs. 2F, 4F, 5F, 10—Echizen-cho, Echizen Coast; Ogi, Toyama Bay; Togi-Kazanashi, Noto Pen.

See also:

Thorunna Bergh, 1878:575 (type: *Thorunna furtiva* Bergh, 1878—Philippines); Rudman, 1984:216, 225–226, 264.

Thorunna furtiva: Rudman, 1984:216–220, figs. 76, 77, 80—Heron Is., *etc.,* Australia.



→

Figure 1

Thorunna florens. A and B, from material no. 1. A. Entire animal in actively crawling position, from above, total length 17 mm; part of the dorsal tubercles and a branchial plume are shown enlarged. B. Same animal from below. r, reddish purple; w, opaque white; y, yellow.

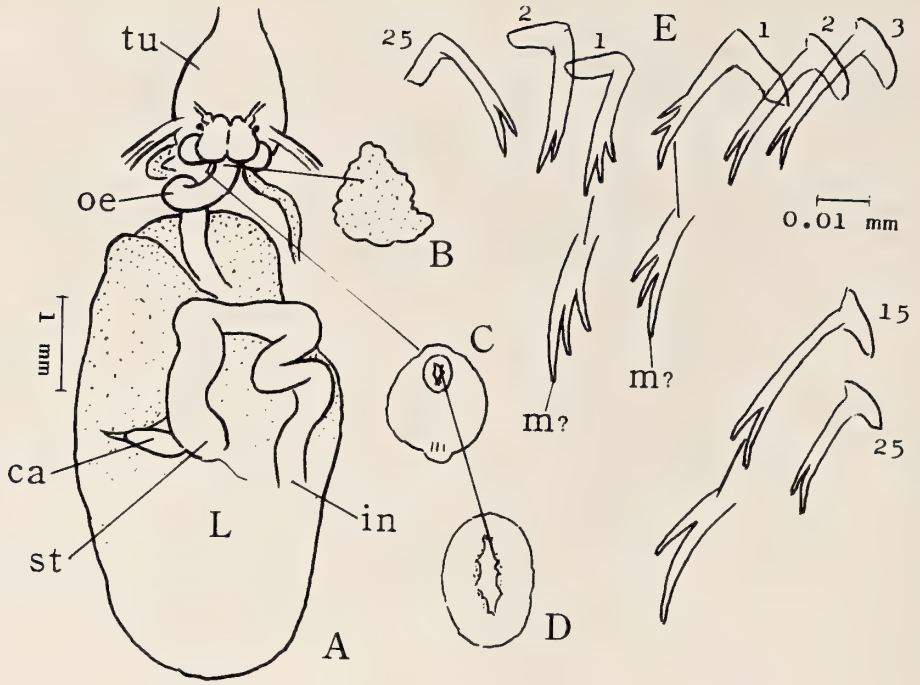


Figure 2

Thorunna florens. A–D, from material no. 2; E, from material no. 1. A. Digestive system from above. B. Blood gland (not to scale). C. Pharynx in frontal view (not to scale). D. Labial disc (not to scale). E. A transverse row of radula. ca, caecum; in, intestine; L, liver; m?, main cusp; oe, oesophagus; st, stomach; tu, oral tube.

Babaina ODHNER in Franc, 1968:867 (type: *Glossodoris florens* Baba, 1949—Sagami Bay, Japan).

Main material: All the specimens were collected by the Takaoka Biological Club. No. 1. Echizen-cho, Echizen Coast, Japan, 11 Aug. 1966, 1 specimen, total length 17 mm (external figures and radula). No. 2. Ogi, Toyama Bay, Japan, 5 Aug. 1962, 11 specimens, length 8–10 mm preserved (digestive system, labial disc, and genital system). Additional specimens were collected from many stations of the central Japan Sea coast between Sado Island and Tsuruga Bay, since the year 1951.

Description: A small species. The upper surface of the mantle is covered with minute conical tubercles. No mantle glands are present. The simply pinnate gills, about 9 in number, are set in a circle which is open behind.

An example of the color pattern of the body is shown in Figure 1A. The ground color of the back is slightly yellowish white, but a fleshy tint of the viscera shines through the integument of the mid-dorsum. The chrome-yellow stripe or band running down each side of the back from behind the rhinophore to the rear of the branchial circle is accompanied with an opaque white line on the inside. This chrome-yellow band is usually entire, but is sometimes discontinuous. A short chrome-yellow arc occurs just in front of the rhinophores. The anterior edge of the mantle is marked with a double band of chrome yellow and opaque white. On the inside of the mantle margin there is a row of reddish purple spots. Each rhinophore is yellow on the club and whitish on the stalk. The gills are whitish. Each plume is tinged with yellow on the rachis. The tail end has a submarginal reddish purple band. The underside of the body (Figure 1B) is colorless.

In *Thorunna* the pharynx is greatly reduced in size in contrast to the large, elongate oral tube. In *T. florens* the oral tube (Figure 2A) is short, swollen, and bulbous. The cuticular labial disc appears to be naked. The radula is extremely small with the formula of 33 × 20–25.0.20–25. In *Thorunna* proper the first lateral tooth is somewhat stronger than the next lateral teeth. In *T. florens,* however, all the lateral teeth are similarly elongated (Figure 2E), narrow, and spatular in shape. In constitution the first lateral tooth has two denticles on the inside of the main cusp and the next lateral teeth have each a single denticle on the inside of the main cusp. In *T. florens,* both these cusps and denticles tend to become finer and rather unusually tapering to the tips. A stomach caecum is present in *T. florens.* The blood gland lies on the oesophagus just behind the nerve center.

The genital system of *Thorunna florens* is fundamentally as in *Thorunna* proper (Figure 3). That is, the spermatocyst is sausage-shaped, and the spermatheca is larger and

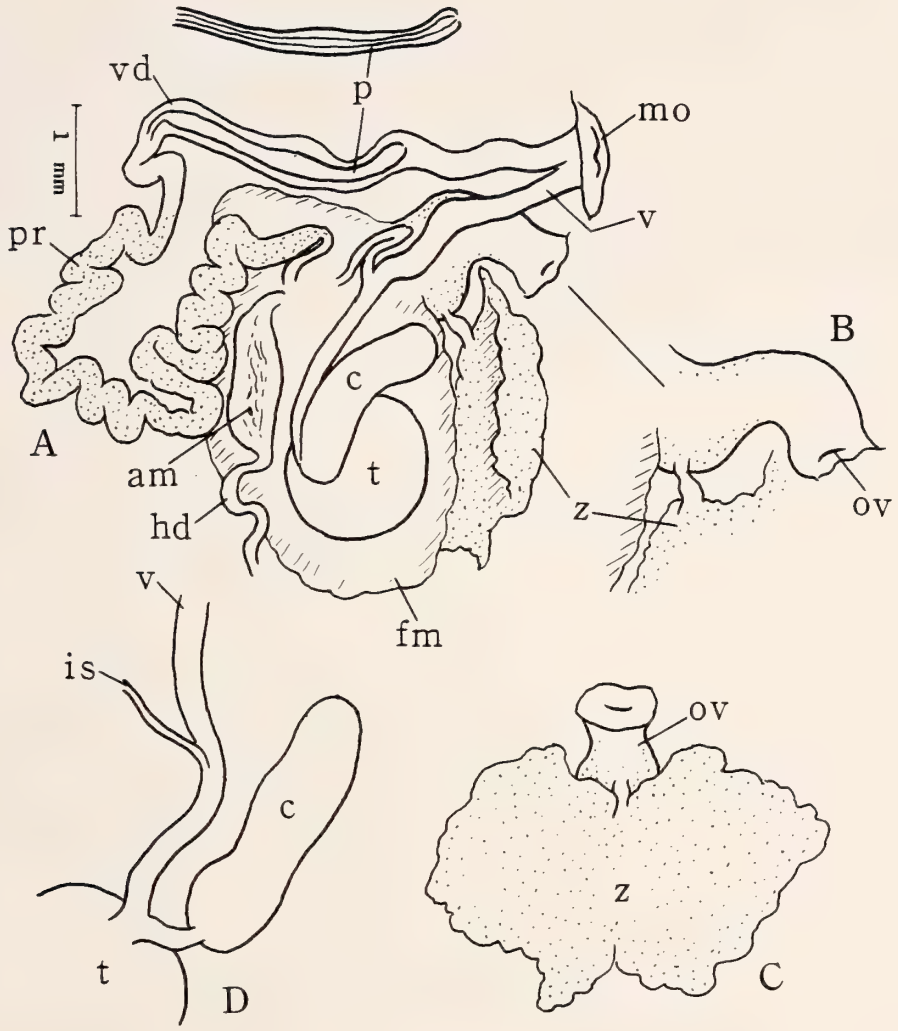


Figure 3

Thorunna florens. A–D, from material no. 2. A. Main part of the genital system from above. B. Oviducal part analyzed. C. Vestibular gland in surface view. D. Vaginal part analyzed. am, ampulla; c, spermatocyst; fm, female gland mass; hd, hermaphrodite duct; is, insemination duct; mo, male orifice; ov, oviduct and oviducal orifice; p, penis; pr, prostate; t, spermatheca; v, vagina; vd, vas deferens; z, vestibular gland.

spherical. There is a well-developed vestibular gland leading to the oviducal vestibulum. The vagina is slender, but it is not winding. The penis is unarmed.

Remarks: *Babaina* as represented by *Thorunna florens* may be synonymized with *Thorunna* following RUDMAN (1984): *T. florens* agrees with *Thorunna* proper (*e.g., T. furtiva*) in the marked development of a vestibular gland. However, it is noted that *T. florens* differs more or less from *Thorunna* proper in the shape of the first lateral tooth, which is not differentiated in size from the rest of the lateral teeth of the radula. The cusps and denticles on the lateral teeth are apt to be tapering to the tips. The bulbous oral tube of *T. florens* is also different from the elongate oral tube of *Thorunna* proper. The rodlets of the labial disc in *Thorunna* proper that were mentioned by Rudman (1984) were not seen in my mounted specimen. Thus, *T. florens* is a somewhat rare example of a species that may be included in the genus *Thorunna* in an expanded sense.

ACKNOWLEDGMENTS

My thanks are due to the members of the Takaoka Biological Club, Toyama-ken, Japan, for affording me specimens for field and laboratory study. The manuscript of this paper was critically read and improved by two anonymous reviewers.

LITERATURE CITED

Abe, T. 1964. Opisthobranchia of Toyama Bay and adjacent waters. Hokuryu-Kan: Tokyo. 99 pp., 36 pls.

Baba, K. 1949. Opisthobranchia of Sagami Bay, collected by his Majesty the Emperor of Japan. Iwanami Shoten: Tokyo. 194 pp., 50 pls.

Baba, K. 1985. An illustrated key to the Chromodoridinae genera of Japan (Mollusca: Nudibranchia: Doridídae). Shells and Sea Life 17(10):225–228.

Bergh, R. 1878. Malacologische Untersuchungen. *In:* C. Semper (ed.), Reisen im Archipel der Philippinen. Wiss. Res. 2(13):547–601, pls. 62–65.

Odhner, N. 1968. Opisthobranches. *In:* P. Grassé (ed.), Franc, Gastéropodes. Traité Zool. 5(3):834–893, pls. 10–11.

Rudman, W. B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zool. Jour. Linn. Soc. 81:115–273.

Takaoka Biological Club. 1978. Photographic illustration of the Opisthobranchia on the central Japan Sea coast. 53 pp., 1 map (in Japanese).

The Veliger 30(3):329–330 (January 4, 1988)

THE VELIGER

Notes, Information & News

California Malacozoological Society

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed 6 January 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger*. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); or Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C.M.S., Inc., are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, and devises are deductible for Federal estate and gift tax purposes under sections 2055, 2106, and 2522 of the Code. Upon request, the Treasurer of the C.M.S., Inc., will issue suitable receipts which may be used by donors to substantiate their tax deductions.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on 8 October 1987, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 31 of *The Veliger*. For affiliate members of the Society, the subscription rate for Volume 31 will be US$28.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will be US$56.00, also now with postage to domestic addresses included. An additional US$4.00 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. There is a one-time membership fee of US$2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription.

Send all business correspondence, including subscription orders, membership applications, payments for them, and changes of address to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Page Charges

Although we would like to publish papers without charge, high costs of publication require that we ask authors to defray a portion of the cost of publishing their papers in *The Veliger*. We wish, however, to avoid possible financial handicap to younger contributors, or others without financial means, and to have charges fall most heavily on those who can best afford them. Therefore, the following voluntary charges have been adopted by the Executive Board of the California Malacozoological Society: $30 per *printed* page for authors with grant or institutional support and $10 per page for authors who must pay from personal funds (2.5 manuscript pages produce about 1 printed page). In addition to page charges, authors of papers containing an extraordinary number of tables and figures should expect to be billed for these excess tables and figures at cost. It should be noted that even at the highest rate of $30 per page the Society is subsidizing well over half of the publication cost of a paper. However, authors for whom the regular page charges would present a financial handicap should so state in a letter accompanying the original manuscript. The letter will be considered an application to the Society for a grant to cover necessary publication costs.

We emphasize that these are *voluntary* page charges and that they are unrelated to acceptance or rejection of manuscripts for *The Veliger*. Acceptance is entirely on the basis of merit of the manuscript, and charges are to be paid *after* publication of the manuscript, if at all. Because these contributions are voluntary, they may be considered by authors as tax deductible donations to the Society. Such contributions are necessary, however, for the continued good financial health of the Society, and thus the continued publication of *The Veliger*.

Reprints

While it was hoped at the "*birth*" of *The Veliger* that a modest number of reprints could be supplied to authors free of charge, this has not yet become possible. Reprints are supplied to authors at cost, and requests for reprints should be addressed directly to the authors concerned. The Society does not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

Patronage Groups

Since the inception of *The Veliger* in 1958, many generous people, organizations, and institutions have given our journal substantial support in the form of monetary donations,

either to *The Veliger* Endowment Fund, *The Veliger* Operating Fund, or to be used at our discretion. This help has been instrumental in maintaining the high quality of the journal, especially in view of the rapidly rising costs of production.

At a recent Executive Board Meeting, we felt we should find a way to give much-deserved recognition to those past and future donors who so evidently have our best interests at heart. At the same time, we wish to broaden the basis of financial support for *The Veliger,* and thus to serve our purpose of fostering malacological research and publication. Accordingly, it was decided to publicly honor our friends and donors. Henceforth, donors of $1000.00 or more will automatically become known as **Patrons** of *The Veliger,* donors of $500.00 or more will be known as **Sponsors** of *The Veliger,* and those giving $100.00 or more will become **Benefactors** of *The Veliger.* Lesser donations are also sincerely encouraged, and those donors will be known as **Friends** of *The Veliger.* To recognize continuing support from our benefactors, membership in a patronage category is cumulative, and donors will be listed at the highest applicable category. As a partial expression of our gratitude, the names only of donors in these different categories will be listed in a regular issue of the journal. Of course, we will honor the wishes of any donor who would like to remain anonymous. The Treasurer of the California Malacozoological Society will provide each donor of $10.00 or more with a receipt that may be used for tax purposes.

We thank all past and future donors for their truly helpful support and interest in the Society and *The Veliger.* Through that support, donors participate directly and importantly in producing a journal of high quality, one of which we all can be proud.

Notes to Prospective Authors

The increasing use of computers to prepare manuscript copy prompts the following notes. We request that the right margin of submitted papers be prepared "ragged," that is, *not* justified. Although right-justified margins on printed copy sometimes look "neater," the irregular spacing that results between words makes the reviewer's, editor's, and printer's tasks more difficult and subject to error. Similarly, the automatic hyphenation capability of many machines makes for additional editorial work and potential confusion; it is best not to hyphenate words at the end of a line. Above all, manuscripts should be printed with a printer that yields unambiguous, high-quality copy. With some printers, especially some of the dot-matrix kinds, copy is generally difficult to read and, specifically, the letters "a, p, g, and q" are difficult to distinguish, especially when underlined as for scientific names; again, errors may result.

Other reminders are (1) that three copies of everything (figures, tables, and text) should be submitted to speed the review process, and (2) absolutely everything should be double-spaced, including tables, references, and figure legends.

Because *The Veliger* is an international journal, we occasionally receive inquiries as to whether papers in languages other than English are acceptable. Our policy is that manuscripts must be in English. In addition, authors whose first language is other than English should seek the assistance of a colleague who is fluent in English *before* submitting a manuscript.

International Commission on Zoological Nomenclature

The following applications have been received by the Commission and have been published in Vol. 44, Part 1, of the *Bulletin of Zoological Nomenclature* (23 March 1987). Comment or advice on these applications is welcomed for publication in the *Bulletin* and should be sent to the Executive Secretary, ICZN, % British Museum (Natural History), London SW7 5BD, U.K.

Case No. 2563. *Conus floridanus* Gabb, 1869 (Mollusca: Gastropoda): proposed conservation of the specific name by the suppression of an unused senior subjective synonym, *Conus anabathrum* Cross, 1865.

Case No. 2548. *Harpa articularis* Lamarck, 1822 (Mollusca: Gastropoda): proposed conservation of the specific name, which is threatened by the unused senior synonyms *Harpa delicata* and *Harpa urniformis* Perry, 1811.

Western Society of Malacologists 1988 Annual Meeting

The 21st Annual Meeting of the Western Society of Malacologists will be held in Darwin Hall on the campus of Sonoma State University, Rohnert Park, California, 17–21 July 1988. Contributed papers are welcome on any aspect of molluscan neontology and paleontology, including research on terrestrial, freshwater, and marine mollusks.

In keeping with its long standing tradition of emphasis on eastern Pacific molluscan faunas, the WSM will convene two special Symposia: "Biogeography and Evolution of the Molluscan Fauna of the Galápagos Islands" (Chaired by Matthew J. James) and "Marine Plant–Molluscan Herbivore Interactions" (Chaired by Cynthia Trowbridge, Marine Science Center, Newport, Oregon 97365).

For further information and registration materials, contact Matthew J. James, Geology Department, Sonoma State University, Rohnert Park, California 94928. Telephone: (707) 664-2301.

The Veliger 30(3):331–332 (January 4, 1988)

THE VELIGER

BOOKS, PERIODICALS & PAMPHLETS

Nudibranchs of Southern Africa A Guide to Opisthobranch Molluscs of Southern Africa

by TERRENCE GOSLINER. 1987. Sea Challengers, Monterey, and Jeff Hamann, El Cajon. 136 pp. Price: $34.95 (plus 6% tax for California residents) and shipping charge.

This is an excellent book. Dr. Gosliner has written a superbly informative text and has beautifully photographed a marvelous fauna. *Nudibranchs of Southern Africa* is a field guide to be read; whether intensely studied or casually perused, it is a remarkable learning experience.

The book can be conveniently divided into three parts. The Introduction is a terse, comprehensive account of opisthobranch evolutionary history, defense mechanisms, feeding, and reproduction. A discussion of the habits and characteristics of the higher taxonomic units, hints of where and how to see living opisthobranchs, and an insightful discussion of the biogeography of opisthobranchs from southern Africa complete the Introduction. The biogeography section is especially well written. A table showing graphically the faunal affinities of the opisthobranch taxa in this region conveys much information and deserves careful study. It demonstrates a classic faunal replacement along a geographic and environmental gradient. Dr. Gosliner's explanations about the distributional patterns of these organisms are carefully argued; throughout the book, his decisions and opinions are supported with ample evidence.

Part two consists of a species list (including all known species from southern Africa, not just the species discussed in this book), excellent line drawings (rendered by Bill Liltved) of representative living animals and significant anatomical features, and a dichotomous key to the 268 species of opisthobranchs treated in this book. Heed the author's caveat that this key is to be used for living animals.

The third part, comprising the majority of the book, is the Species Accounts. Each animal, whether identified to species or not, is described with a definitive text. The text summarizes the taxonomy (with synonyms or significant morphological characteristics), natural history, and the occurrence and distribution of the species. It is extremely readable. Field guide descriptions usually tend to be tediously repetitive, but this book has a polished, variable text that does justice to the foudroyant evolutionary diversity of opisthobranch mollusks. When I finished reading the species accounts, I kept turning the pages, hoping to find more!

The final pages of the book include references, a species index, map of southern Africa (titling the book after a geographic rather than political entity is an appreciated sensitivity), and a list of sizes of the animals photographed (hopefully these will be placed on the same page as the text or illustration of the animal in future editions).

The book is dedicated to Mrs. Eveline Marcus. She should be quite pleased, because it is a most worthy present.

Hans Bertsch

A History of Shell Collecting

by S. PETER DANCE. 1986. E. J. Brill: Leiden, The Netherlands. 265 pp. + 32 pls. Price: 94 guilders (about US$42.75).

This book is a revision of Dance's *Shell Collecting: an Illustrated History* published in 1966. As that first edition has been out of print for a number of years, a revision was undertaken. According to the author's Preface, "although substantially identical to the first edition the text has been considerably rearranged and enlarged." Perhaps the greatest change has been in the illustrations, many of which are different from those in the first edition. The history itself has not been carried forward, however, and the text still does not extend far into the twentieth century.

What is still presented in this second edition is an enjoyable, informative account of the collectors, dealers, and students of "shells," from Aristotle in the fourth century B.C. through the seminal works of Buonanni, Lister, and Rumphius in the seventeenth century to Linnaeus, Lamarck, Cuming, and beyond (but, unfortunately, not much beyond World War I). The reader is given a look at the shell cabinets, catalogs, and publications of the early shell collectors, most of whom collected for the beauty (and sometimes the status) of their specimens and some later for the scientific benefits as well.

In addition to the main body of text, the book contains four appendices and an extensive bibliography. The first two appendices ("Shell cabinets of the early eighteenth-century arranged by location and vocation of owners" and "Shell books in 1948") are primarily of historical interest, although those who frequent bookstores in search of old books on shells may find the latter appendix useful today.

The third appendix, titled "Conchology or malacology?," is an interesting, if peculiar, explanation as to why Dance has used "conchology" exclusively to signify the study of mollusks throughout his book, "carried there by logical reasoning." Dance attempts to synonymize the terms conchology and malacology, and therefore to establish a preference for conchology because it is the older term. Although this argument would seem to be a logical extension of the principle of priority, so essential in zoological nomenclature, it is not, because the two terms simply are not commonly held as strict synonyms. As Dance acknowl-

edges (p. 199), how things stand today is that ". . . we still have the terms conchology and malacology in use at the same time, the former implying the study of shells merely, the latter implying the study of the molluscan animals, and, incidentally, their shells." As such, the terms are not identical but rather provide useful, commonly understood shades of meaning. Indeed if one of the terms should be deleted from our lexicon, a notion I do not advocate, a strong functional argument could be made for deleting conchology, as that term seems to be the one with the more ambiguous meaning.

The fourth appendix is a "Guide to collections: a list of some shell collections of scientific importance and their present locations." This is not only of historical interest, but may be useful as well to present-day taxonomists in need of locating type collections.

Notwithstanding some specific flaws, among them an annoyingly large number of typographical errors, *A history of shell collecting* is a worthwhile book to have. This malacologist greatly enjoyed gaining a historical perspective on the study of mollusks and will appreciate having the volume on the shelf for reference.

D. W. Phillips

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

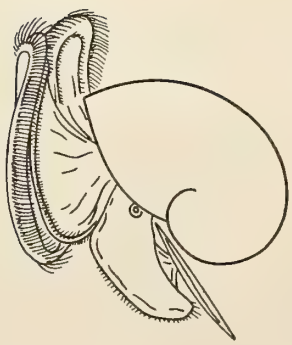
It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

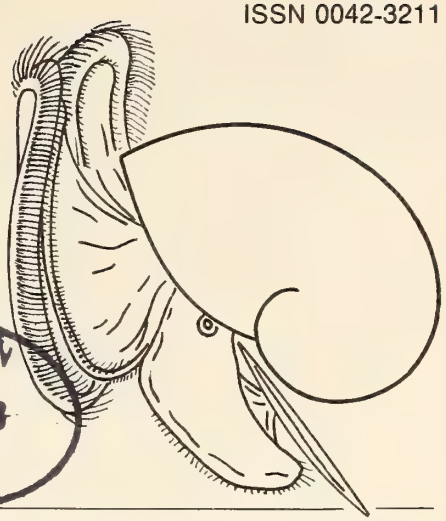
An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.



ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 30 April 1, 1988 Number 4

Contents

Contents — *Continued*

The Veliger (ISSN 0042-3211) is published quarterly on the first day of July, October, January and April. Rates for Volume 30 are $25.00 for affiliate members (*including* domestic mailing charges) and $50.00 for libraries and nonmembers (*including* domestic mailing charges). An additional $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Department of Zoology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Scope of the journal

The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

Membership and Subscription

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. As an affiliate member, a person may subscribe to The Veliger for US $25.00 (Volume 30), which now *includes* mailing charges to domestic addresses. There is a one-time membership fee of US $2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription; a reinstatement fee of US $3.00 will be required if membership renewals do not reach the Society on or before April 1 preceding the start of the new Volume. If a receipt is required, a self-addressed, stamped envelope (or in the case of foreign members, the envelope and two International Postal Reply coupons) should be included with the membership or subscription request.

The annual subscription rate to The Veliger for libraries and nonmembers is US $50.00 (Volume 30), which now *includes* mailing charges to domestic addresses.

An additional US $3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Memberships and subscriptions are by Volume only (July 1 to April 1) and are payable in advance to California Malacozoological Society, Inc. Single copies of an issue are US $25.00 plus postage.

Send all business correspondence, including subscription orders, membership applications, payments for them, changes of address, to: C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709, USA.

Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616, USA.

The Veliger 30(4):333–341 (April 1, 1988)

THE VELIGER

The Possible Rôle of Gut Bacteria in Nutrition and Growth of the Sea Hare *Aplysia*

by

TIMOTHY Z. VITALIS, MARGOT J. SPENCE,
AND THOMAS H. CAREFOOT

Department of Zoology, University of British Columbia, Vancouver, Canada V6T 2A9

Abstract. The rôle of bacteria in nutrition and growth of the sea hare *Aplysia* was investigated by: (1) comparing growth of *Aplysia juliana* Quoy & Gaimard on three algal diets in seawater media with and without antibiotics, (2) assessing the number and types of bacteria in the guts of *Aplysia dactylomela* Rang and *A. juliana* on different algal diets, (3) determining in vivo and in vitro effects of various antibiotics on these bacteria, (4) measuring the degree to which bacteria isolated from the gut of *A. juliana* break down various algal storage products and structural polysaccharides, and increase the pool of free amino acids in a culture medium containing the green alga *Ulva fasciata* Delile, and (5) assessing possible direct effects of antibiotics on the sea hare itself.

Aplysia juliana grew significantly less under antibiotic treatment (10 mg penicillin-G and 10 mg streptomycin sulfate per L seawater) on each diet. The antibiotic treatment reduced the number of gut bacteria in *A. juliana* by approximately one order of magnitude. Twelve colony types (assumed to represent 12 bacterial types) were found in the gut of *A. juliana* and 23 different types in *A. dactylomela.* Five bacterial types seemed to be residential in the two species and varied little with changes in diet. Bacteria isolated from the gut of *A. juliana* were capable of breaking down carbohydrates in test media and increasing the pool of free amino acids in a culture medium of the green alga *Ulva fasciata.* Neither behavior nor rate of oxygen consumption in *Aplysia* was significantly affected by exposure to concentrations of antibiotics up to five times those employed in the growth studies, suggesting that the antibiotics reduced the nutritional contribution of the bacteria by reducing their numbers in the gut, rather than having a directly deleterious effect on the sea hares themselves. The results suggest that gut bacteria may contribute significantly to nutrition and growth in *Aplysia.*

INTRODUCTION

The relationship between animals and their symbiotic gut bacteria is well understood in vertebrates and in commercially and medically important insects (BROOKS, 1964; MCBEE, 1971). In marine invertebrates, however, the relationship is not as clear. Several recent studies on marine invertebrate herbivores have pointed to a nutritional rôle for the gut bacteria (PRIM & LAWRENCE, 1975; FONG & MANN, 1980; CAREFOOT, 1981a, b), although the extent of nutritional contribution in some forms has been questioned (LAWRENCE, 1975; PRIM & LAWRENCE, 1975). FONG & MANN (1980) showed clearly that amino acids produced by gut bacteria in the sea urchin *Strongylocentrotus droebachiensis* were absorbed from the gut and used in the synthesis of the host's own tissues. FISHER & CHILDRESS (1986) also demonstrated that a large proportion (>45%) of the carbon fixed by symbiotic chemautotrophic bacteria inhabiting the gills of the gutless bivalve *Solemya reidi* is translocated to, and used by, the host. In neither study was the importance of such contribution to the host animal's overall nutrition investigated. Indirect evidence that the sea hare *Aplysia kurodai* may employ bacterially produced amino acids in its own nutrition was provided by CAREFOOT (1981b). There, young animals maintained steady weight on several chemically defined artificial diets with deficiencies in amino acids known to be essential for the rat, over a 24-day experimental period. The most likely explanation for this was that gut bacteria were providing the necessary amino acid nutrients, assuming that sea hare requirements for amino acids are the same as found for other animals. Another study on juvenile *A. dactylomela* (CAREFOOT, 1981a) showed that animals eating a chemical diet deficient in arginine (essential for the rat) and containing antibiotics gradually lost weight over a 20-day period. The weight loss was reversed when the arginine-deficient diet was

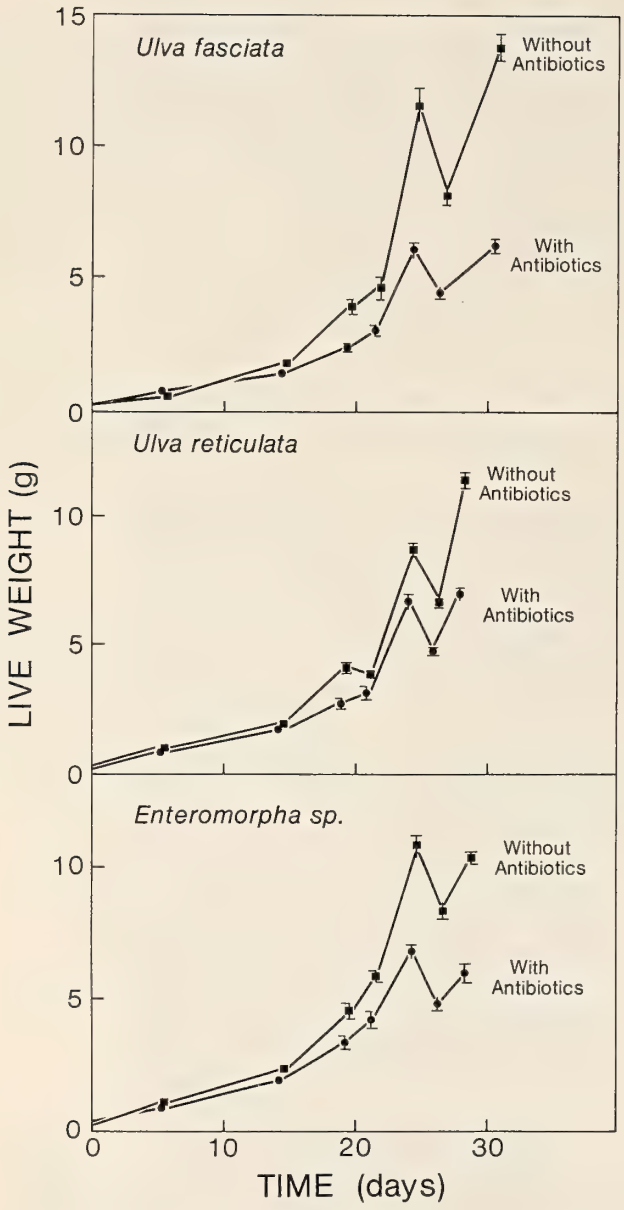


Figure 1

Change in live weight of *Aplysia juliana* on diets of the green algae *Ulva fasciata, U. reticulata,* and *Enteromorpha* sp., with and without antibiotic treatment (10 mg streptomycin sulfate and 10 mg penicillin-G·L seawater^{-1}) at 25°C. Each point represents the $\bar{X}$ ± SE of six animals.

replaced by one complete in all nutrients. In vitro studies by Prim & Lawrence (1975), on the ability of bacteria isolated from the guts of sea urchins to digest algae and various storage products of algae, have further supported the notion that symbiotic gut bacteria are generally involved in the nutrition of marine invertebrate herbivores. This contribution could be especially significant in instances where less than optimally nutritious seaweeds or other plants are eaten, where foods are particularly indigestible, or where for reasons of temporal or spatial shortages a variety of seaweeds must be consumed.

The present study investigates the possible rôle of gut bacteria in the nutrition and growth of the sea hare *Aplysia.* It involves five major approaches: (1) a comparison of growth rates of animals treated and not treated with antibiotics, (2) an assessment of the number and types of bacteria in the guts of the sea hares, and whether these change with change in diet, (3) an assessment of the effects of various antibiotics on these bacteria, (4) a measure of the degree to which algal storage products and structural polysaccharides are broken down by bacteria isolated from the guts of sea hares, and the extent to which bacteria can increase the pool of free amino acids in an *Ulva fasciata* culture medium, and (5) an assessment of the direct inhibitory effects, if any, that the antibiotics might have on the sea hares themselves.

Effect of Antibiotic Treatment on Growth Rates

Individuals of *Aplysia juliana* were metamorphosed from a single batch of eggs following procedures outlined in Switzer-Dunlap & Hadfield (1977). Forty-two animals were successfully metamorphosed. When they reached a live weight of 0.15–0.30 g, 36 were divided into 6 groups of 6 animals each, such that each group had approximately the same mean live weight and variance (0.25 ± 0.001 g). Each group was kept in a plastic tub (10 × 10 × 14 cm) and supplied with its own flow of seawater (33‰, 25°C). The groups were randomly divided into three double sets (control and experimental), each set receiving as food one of the green seaweeds *Enteromorpha* sp., *Ulva fasciata,* or *U. reticulata* Forsskal. After a 5-day holding period, the experimental group in each set was treated with antibiotics in an attempt to sterilize the animals' digestive tracts. The antibiotic treatment consisted of 10 mg streptomycin sulfate and 10 mg penicillin-G delivered per L of seawater over the 28-day period of study. The antibiotics were administered dropwise from a stock solution (containing 1 g of mixed antibiotics per L seawater) into the seawater flowing through the system. At the start of the antibiotic treatment all animals were given rations just sufficient to satisfy their appetites (based on data from previous growth studies; Carefoot, 1970). This minimized "superfluous" feeding (feeding in excess, which results in quicker passage of food through the gut and less efficient digestion) and thus ensured that the gut bacteria had maximal time to act on the ingested algae. The animals were weighed every few days over the 28-day experimental period.

Figure 1 shows change in live weight of *Aplysia juliana* on three seaweed diets with and without antibiotics. In each case, animals treated with antibiotics grew significantly less than did untreated animals ($P < 0.001$, ANOVA). Animals grew fastest and showed greatest response to the antibiotics on a diet of *Ulva fasciata,* the alga most

Table 1

Description of bacterial colonies isolated from the guts of *Aplysia juliana* (Nos. 1–6) and *A. dactylomela* (Nos. 1–4, 6–24). Standard descriptive characteristics from BUCHANAN & GIBBONS (1974).

	Macroscopic colony morphology							Microscopic colony morphology				
No.	Size (mm)	Shape	Margin	Pigmentation	Colony under reflected light	Colony under transmitted light	Elevation	Gram stain	Shape	Spore-forming	Arrangement	
1	2–3	round	entire	creamy	smooth	opaque	slight	−	cocci	no	pairs random	20% 80%
2	0.5–1.5	round	entire	white	smooth	opaque	slight	−	cocci	no	pairs triplets	70% 30%
3	5–6	round	entire	yellow-creamy	rough	transparent	slight	−	rods: long and slender	no	random	100%
4	0.5–1	round	entire	yellow	smooth	opaque	raised	−	cocci	no	pairs chains random	20% 40% 40%
5	2	irregular	entire	orange, grainy	smooth	transparent	very slight	−				
6	1–3	round	entire	orange	smooth	opaque	slight	−	rods: length/width = 2/1	no	chains random	50% 50%
7	varying	irregular	convoluted	yellow	rough	transparent	slight	−	cocci	no	random	100%
8	0.5–1	round	entire	yellow	smooth glossy	opaque	very slight	−	cocci	no	random	100%
9	varying	irregular	convoluted	pale yellow	smooth	transparent	very slight	−	rods	no	random	100%
10	0.5–1	round	entire	colorless	smooth	transparent	raised	−	cocci	no	random	100%
11	10	irregular	convoluted	creamy edge, dark center	smooth	transparent	slight	−	cocci	no	pairs random	20% 80%
12	0.5–1	round	entire	creamy	smooth	opaque	slight					
13	1–2	round	convoluted	colorless	smooth	transparent	slight	−	rods	no	random	100%
14	1	round	entire	black	smooth	opaque	slight	−	cocci	no	random	100%
15	2–3	round	entire	cream with dark center	glossy smooth	opaque	raised	−	rods: length/width = 2/1	no	random	100%
16	1–1.5	round	entire	colorless	smooth	transparent	slight	−	rods: length/width = 3/1	yes	random	100%
17	varying	irregular	convoluted	yellow	rough	opaque	slight	−	cocci	no	random	100%
18	2	round	irregular	yellow	rough	opaque	very raised	+	cocci	no	random	100%
19	varying	irregular	irregular	colorless	smooth	transparent	slight					
20	≤0.5	round	entire	colorless	smooth	transparent	none					
21	1–4	round	entire	white	smooth	opaque	slight	−	rods: length/width = 2/1	no	pairs random	20% 80%
22	2	round	entire	pink center, white edge	smooth	opaque	very raised					
23	1–3	round	entire	cream	smooth	transparent	slight	−	rods: length/width = 3/1	no	grouped random	40% 60%
24	0.5–1	round	entire	colorless	smooth	transparent	slight	−	cocci	no	chains random	45% 55%

Table 2

Number and types of bacteria isolated from the guts of *Aplysia*. Values are based on the means of counts from 2 to 6 animals.

Diet	Total number of colony types	Predominant colony types		Number of bacteria/mL gut fluid
		Number	Identity (Nos. refer to Table 1)	
Aplysia juliana				
Ulva spp.	12	6	Nos. 1–6	43×10^5
Enteromorpha sp.	12	6	Nos. 1–6	—
Aplysia dactylomela				
Ulva fasciata	7	4	Nos 1, 2, 4, 9	53×10^5
Spiridea sp.	17	5	Nos. 1, 7, 9, 10, 24	—
Laurencia sp.	10	7	Nos. 1, 4, 7–9, 19, 24	—
starved (5 days)	11	4	Nos. 1, 4, 9, 24	—
artificial	—	—		25×10^5

preferred by field animals and one known to be a good settlement-inducer in this species of sea hare (Switzer-Dunlap & Hadfield, 1977). Overall, the antibiotic treatment reduced growth of the animals by 40–53% on the three diets. Neither diet nor the interaction of antibiotics and diet had a significant effect on growth rates ($P = 0.11$ in each case, ANOVA). A pump malfunction in the seawater system bathed the animals for one day with supersaturated seawater (a leak caused air to be pumped into the seawater under pressure), and this feeding interruption explains the conspicuous drop in weight shown by all animals on day 26 of the experiment (see Figure 1).

Number and Types of Bacteria in the Guts of *Aplysia*

At the end of the growth experiment the gut was dissected from each *Aplysia juliana* and the total contents of the crop and gizzard regions removed with a sterile Pasteur pipette. The contents were diluted 1000-fold in autoclaved seawater and an aliquot plated onto nutrient agar. The culture medium consisted of 10 g bactopeptone (Difco), 15 g agar (Difco), and 1 L of membrane-filtered and autoclaved seawater. To this was added 15 mL 50% w/v separately autoclaved glucose solution. Two culture media were used, one with a pH of 6 to match that of the crop of *Aplysia,* the other with a pH of 8 to match that of the gizzard. The inoculated plates were incubated for 4 days at 25°C, after which the colonies were counted and characterized according to standard morphological features (methods outlined in Buchanan & Gibbons, 1974). The bacteria were not identified as to species. Similar platings were made from the guts of *A. dactylomela* feeding on several algal diets, from some that had been starved for 5 days, and from ones eating a chemically defined artificial diet.

Twenty-four colony types were identified in platings from crop and gizzard contents of *Aplysia juliana* and *A. dactylomela* (Table 1). In *A. juliana,* six of these isolates were abundant and appeared consistently (Nos. 1–6, Table 1; another six appeared in the *A. juliana* platings, but only sporadically and in low numbers, and thus are not described in Table 1). There was no obvious correlation between the presence or absence of a bacterial type and the diet or treatment (with or without antibiotics) in this sea hare species. The number of bacteria was highly variable, but averaged about $43 \times 10^5 \cdot$mL gut fluid^{-1} in normal animals, and $4–10 \times 10^5 \cdot$mL gut fluid^{-1} in antibiotic-treated animals.

In comparison, 23 bacterial types were identified in platings from the buccal mass, crop, gizzard, and digestive gland of *Aplysia dactylomela.* Of these, 4–7 types predominated depending on diet, 4 of which were present in the guts of animals starved for 5 days. There was no evident correlation of bacteria types with seaweed diet in *A. dactylomela* (Table 2). Animals starved for 5 days had 11 types spread through the various regions of the gut, as many or more than in the guts of some normally feeding animals. Of the 6 commonest types isolated from *A. juliana,* 5 appeared identical to types from *A. dactylomela* (Nos. 1–4, 6; Table 1). All but one of the total of 24 different types present in abundance in the two species of *Aplysia* had Gram-negative staining characteristics. Finally, there was no consistent pattern either in the types or numbers of bacteria with the location in the gut in *A. dactylomela.*

Effect of Antibiotics on the Gut Bacteria

The effectiveness of antibiotics in reducing the numbers of gut bacteria in *Aplysia juliana* was determined by treating six animals (11–14 g live wt) over a 6-day period with seawater containing antibiotics (50:50 mix of streptomycin sulfate and penicillin-G) in concentrations ranging from 0 to 1000 mg·L seawater^{-1}. All animals were allowed to feed *ad libitum* on *Ulva fasciata* and *U. reticulata.* The animal in zero concentration of antibiotics was a control. At the end of the 6-day period of treatment the gut contents were removed and plated onto agar discs, as described

Table 3

Resistance of selected bacterial types from the gut of *Aplysia dactylomela* (colony Nos. 10 and 24, Table 1) to various antibiotics. The antibiotics were administered in the form of Difco-discs containing standardized antibiotics dosages. Response of the bacteria is indicated as S = susceptible, I = intermediate susceptibility, and R = resistant.

Antibiotic	Dosage in each disc (μg)	Response of bacteria	
		No. 10	No. 24
Ampicillin	10	I	I–S
Chloromycetin	10	S	S
Erythromycin	5	I–S	R
Kanamycin	10	I	R
Neomycin	10	I–S	R
Penicillin	3	R	R
Polymycin B	10	I	R
Streptomycin	5	R	R
Tetracycline	10	R	I–S

previously, and the total number of bacteria growing at each dosage of antibiotics was counted.

Figure 2 shows the bacterial cell counts in relation to antibiotic dosage. The antibiotics appeared to reduce markedly the number of bacteria, even at comparatively low dosages. The control *Aplysia juliana* had 43 × 10^5 bacteria·mL^{-1} in its crop/gizzard, comparable to values of 48 and 59 × 10^5 bacteria·mL^{-1} counted in the digestive contents of two specimens of *A. dactylomela* feeding on *U. fasciata* (see also Table 2). The *A. juliana* treated with 70 and 1000 mg antibiotics·L seawater^{-1} each had counts of 1 × 10^5 bacteria·mL gut fluid^{-1}. Based on these observations and bacterial counts of animals used in the growth experiments, the concentration of antibiotics used in the growth experiment reduced the number of gut bacteria approximately one order of magnitude.

A number of antibiotics were tested in vitro for their effectiveness against gut bacteria in *Aplysia dactylomela.* Difco discs containing standard dosages of the antibiotics ampicillin, chloromycetin, erythromycin, kanamycin, neomycin, penicillin, polymycin B, streptomycin, and tetracycline were tested against two of the most prevalent types of bacteria found throughout the guts of sea hares (Nos. 10 and 24; see Table 1). The standard dosages in the discs were 10 μg for all except erythromycin and streptomycin, which were 5 μg, and penicillin which was 3 μg. The response of *Escherichia coli* to the same antibiotics was used as a standard of comparison for the responses of the *Aplysia* gut bacteria. A standard test procedure was employed as outlined in Buchanan & Gibbons (1974).

The results of the Difco-disc series of experiments are presented in Table 3. Ampicillin and chloromycetin were the most effective antibiotics on the two bacterial types tested. With the exception of some intermediate levels of susceptibility of one or other of the bacterial isolates to erythromycin, neomycin, and tetracycline, the bacteria were generally resistant to all of the other antibiotics.

Utilization of Plant Constituents by *Aplysia* Gut Bacteria

Utilization of various plant constituents by bacteria isolated from the gut of *Aplysia juliana* was determined using carbohydrate-vitamin-nitrogen (CVN) media as described by Prim & Lawrence (1975). Each CVN medium contained a single carbohydrate source. Carbohydrates tested included glucose, maltose, starch, carrageenan, and cellulose. After a 4-day incubation at 25°C with each of the six main bacterial types isolated from *A. juliana,* utilization of a carbohydrate was judged to have occurred if the culture medium turned cloudy, if sediment accrued at the bottom, or if growth occurred at the surface (Prim & Lawrence, 1975). CVN media without bacteria and inoculated CVN media without a carbon source were used as controls. Each

Table 4

Utilization of carbohydrates by each of six types of bacteria isolated from the gut of *Aplysia juliana.* The bacteria were incubated for 4 days at 25°C in carbohydrate-vitamin-nitrogen media at pH = 6 (as found in the crop of *Aplysia*) and pH = 8 (gizzard).

Bacterial isolate	Carbohydrate substrate									
	Glucose		Maltose		Starch		Carrageenan		Cellulose	
	pH 6	pH 8	pH 6	pH 8	pH 6	pH 8	pH 6	pH 8	pH 6	pH 8
1	+	+	+	+	−	+	+	+	−	−
2	+	+	−	−	−	−	+	+	−	−
3	+	+	+	+	+	+	+	+	−	−
4	+	+	+	+	−	−	+	+	−	−
5	+	+	+	+	+	+	+	+	−	−
6	+	+	+	+	+	+	+	+	−	−
Control (no carbohydrate)	−	−	−	−	−	−	−	−	−	−
Control (no bacteria)	−	−	−	−	−	−	−	−	−	−

Table 5

Concentration of free amino acids in 10-mL aliquots of three *Ulva fasciata* media: one, incubated 4 days at 25°C with a mixture of the six predominant bacterial types from the gut of *Aplysia juliana*; the other, a sterile control medium incubated 4 days at 25°C; the last, a fresh homogenate of the seaweed. The final column gives the approximate ×-fold change in concentration of each amino acid resulting from bacterial action. Dashes indicate no data available. Amino acids in block type are those known to be essential for the rat.

	Concentration (μM) of free amino acids in *Ulva fasciata* media			
	Control (incubated 4 days with no bacteria)	Fresh homogenate	Incubated 4 days with gut bacteria	×-fold change in amino acid concentration
ARGININE	—	trace	516	—
Alanine	17	62	319	+8
Aspartic acid	22	34	32	nil
Glutamic acid	23	14	214	+11
Glycine	25	59	661	+16
HISTIDINE	trace	41	23	nil
ISOLEUCINE	10	12	—	—
LEUCINE	16	16	—	—
LYSINE	16	20	21	nil
METHIONINE	7	—	134	+19
Ornithine	26	38	24	nil
PHENYLALANINE	10	7	107	+12
Proline	—	—	461	—
Serine	34	110	50	nil
Threonine	11	22	12	nil
TYROSINE	9	7	49	+6
VALINE	—	173	114	nil

test of a carbohydrate was replicated three times at pH values of 6 and 8, representing values recorded from the crop and gizzard, respectively, of *A. juliana*.

Table 4 shows that all six bacterial isolates were able to grow on the CVN media containing either glucose or carrageenan at pH levels present in the crop and gizzard. The maltose- and starch-containing media showed lack of growth in some instances. Neither the cellulose-containing medium nor the controls supported growth of any of the bacteria.

In addition, the ability of the gut bacteria to digest seaweed was tested; a change in the concentration of free amino acids in the culture was used as a measure of bacterial activity. Two 50-mg samples of oven-dried (60°C) *Ulva fasciata* were each mixed with separate 2.5-mL portions of seawater to slurry consistency and autoclaved for 15 min. Following this, one sample (the control) was made up to 10 mL with 3.75% sulfosalicylic acid in 0.2 N lithium citrate buffer, sealed, and stored in the dark at 2°C. The remaining sample was made up to 10 mL with autoclaved seawater and inoculated with a mixture of the six predominant bacterial isolates from *Aplysia juliana* and incubated for 4 days at 25°C. At the end of the 4-day period, a third 50-mg sample of dried *Ulva* was homogenized in 0.2 N lithium citrate buffer and made up to 10 mL. All three samples were then centrifuged at 13,000 RPM for 5 min at 0°C. Aliquots (100 μL) of the supernatant were analyzed for the presence of free amino acids using a Beckman Model 118C amino acid analyzer.

Table 5 indicates that bacterial action markedly increased the pool of free amino acids in a culture medium containing only seawater and the alga *Ulva fasciata*. The values for the test culture were compared with the averages of values for control (no bacteria) and freshly prepared homogenate. There was no consistent difference between these last two media with respect to levels of free amino acids, suggesting that the bacteriocidal sulfosalicylic acid treatment had no, or only minor, chemically degrading effect on any free amino acids originally present in the homogenate. Several essential (for the rat) amino acids showed marked increases in concentration following incubation of the seaweed with the bacteria (methionine, phenylalanine, tryosine, and possibly arginine), as did some non-essential ones (alanine, glutamic acid, and glycine). Several amino acids remained in much the same concentration as at the start, while none showed any marked decrease in concentration.

Other Effects of the Antibiotics

The question remains as to whether antibiotic treatment had any effect on the sea hares beyond reducing their levels of gut bacteria. The animals' feeding behavior was not inhibited by antibiotic treatment. None of the animals died during the experiments and none showed evidence of poor health. However, since this was a critical point in interpretation of the results, a further experiment was performed to show that metabolic rate was not markedly affected by antibiotic treatment. *Aplysia dactylomela* was used in this experiment instead of *A. juliana,* as none of the latter was available. The two species are similar in size and share common behavioral attributes (*e.g.,* both are nocturnal). *Aplysia dactylomela* readily eats the ulvoid species favored as food by *A. juliana* and growth rates are comparable in the two species. The experiment employed an antibiotic concentration five times that in the *A. juliana* growth study (a total of 100 mg antibiotics·L seawater^{-1}), and tested the immediate effects of the antibiotics on oxygen uptake. A flow-through respirometer system with a YSI Model 58 Dissolved-Oxygen Meter was used to monitor oxygen levels (see CAREFOOT, in press, for details of respirometry methods). The antibiotics were administered directly from a stock solution into the seawater line flowing to the respirometer. An animal was allowed 30 min of equilibration time in the respirometer before its rate of oxygen uptake was measured. Then, to test for instantaneous effects of the antibiotics, a 1-h baseline level of oxygen uptake was established before the supply of normal

seawater was switched to that containing antibiotics. Rates of oxygen uptake were monitored for a further 2-h period after the start of antibiotics administration. All measurements were made between 1100 and 1400 h at a temperature of 28.5°C during the animals' normal daytime state of quiescence.

Figure 3 shows that there were no apparent acute effects of the antibiotics in oxygen consumption in *Aplysia dactylomela*. Rates were maintained at a fairly constant level of 3.75–3.85 mL $O_2 \cdot indiv^{-1} \cdot h^{-1}$ ($P = 1.00$, ANOVA) despite perfusion of antibiotics-containing seawater (five times the concentration used in the growth experiment) over the *Aplysia*. Because it took some time for the antibiotics-treated seawater to replace completely the normal seawater in the respirometer flask, and because this varied with each run (depending on volume of the flask and flow rate), the data in Figure 3 were re-expressed to show the rate of oxygen consumption in relation to the actual concentration of antibiotics. These data are presented in Figure 4 and again show no significant effect of the antibiotics on the rate of oxygen uptake in *Aplysia* over short-term exposure ($P = 0.99$, ANOVA). While a larger sample size and further information on possible long-term effects of the antibiotics on the metabolic rate in *Aplysia* would make these results more convincing, the data do suggest that the level of antibiotics employed in the growth study had no directly deleterious effects on the sea hares.

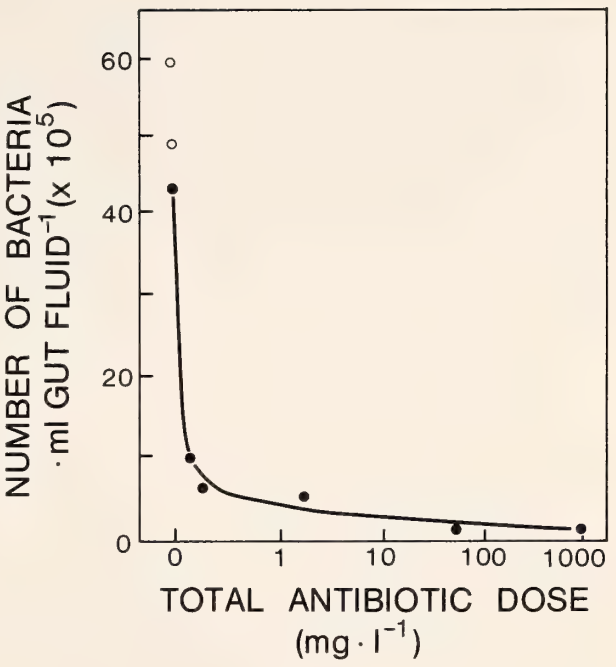


Figure 2

Change in number of bacteria in the gut contents of *Aplysia juliana* after a 6-day exposure to different concentrations of antibiotics in the seawater bathing the animals, at 25°C. The antibiotic solution was a 50:50 mixture of streptomycin sulfate and penicillin-G in seawater. Solid dots, *A. juliana*; open dots, *A. dactylomela*. The latter were normal (untreated with antibiotics) animals feeding for the same length of time as *A. juliana* on the same green alga foods, *Ulva fasciata* and *U. reticulata*, and are included for comparison. Each point represents a single animal.

DISCUSSION

Several points of interest emerge from these data. First, antibiotic treatment significantly reduces the growth of juvenile *Aplysia juliana*. Second, bacteria are abundant both in the number of individuals and the types throughout the gut of sea hares, including the buccal region, crop, gizzard, and digestive gland. Finally, bacterial isolates from the gut of *A. juliana* readily break down various plant constituents, such as maltose, starch, and carrageenan, and increase the concentration of free amino acids in a seaweed culture medium.

These facts point to a possible nutritional contribution by the gut bacteria to their hosts. However, an alternative explanation is that the antibiotics directly inhibit growth of juvenile sea hares. Of the two antibiotics used in the growth study, penicillin is the least likely to produce growth-inhibiting side-effects in metazoans. Its antibacterial activity involves the disruption of formation of cross-linkages in the structurally unique bacterial cell wall (Franklin & Snow, 1975) and its action appears to be specific against bacteria (Hammond & Lambert, 1978). In comparison, streptomycin affects bacteria more generally, inhibiting protein synthesis on ribosomes by interfering with the coding sequence of amino acids in the elongating peptide chains (Hammond & Lambert, 1978). Streptomycin is known to inhibit specifically the incorporation into peptide linkages of arginine, glutamic acid, histidine, phenylalanine, and threonine (Franklin & Snow, 1975). The potency of a penicillin and streptomycin mixture results from synergistic effects of the component antibiotics, which reduce bacterial cell counts more effectively than if either antibiotic is used individually (Brown *et al.*, 1979). The blocking of cross-linking in the peptidoglycan structure of the bacterial cell wall by penicillin facilitates the movement of streptomycin into the cell (Brown *et al.*, 1979). Of the two antibiotics, then, streptomycin would appear to be potentially most deleterious to the sea hares.

Chernin (1959) tested the effects of various antibiotics on the freshwater snail *Australorbis glabratus* under axenic conditions. He found that streptomycin stunted growth of the snail at concentrations of 100 $\mu g \cdot mL^{-1}$. No inhibition occurred at a concentration of 10 $\mu g \cdot mL^{-1}$ (equivalent to that used in the present study), and the author noted that small additions of $CaCl_2$ to the culture medium negated certain stress-induced behavioral effects caused by the antibiotic, even at fairly high concentrations (100 $\mu g \cdot mL^{-1}$; Chernin, 1959). Penicillin had no effect on growth of *Australorbis* at concentrations up to 60 $\mu g \cdot mL^{-1}$ (Chernin & Schork, 1959; six times the concentration used in the present study). Thus, if sea hares responded in a manner

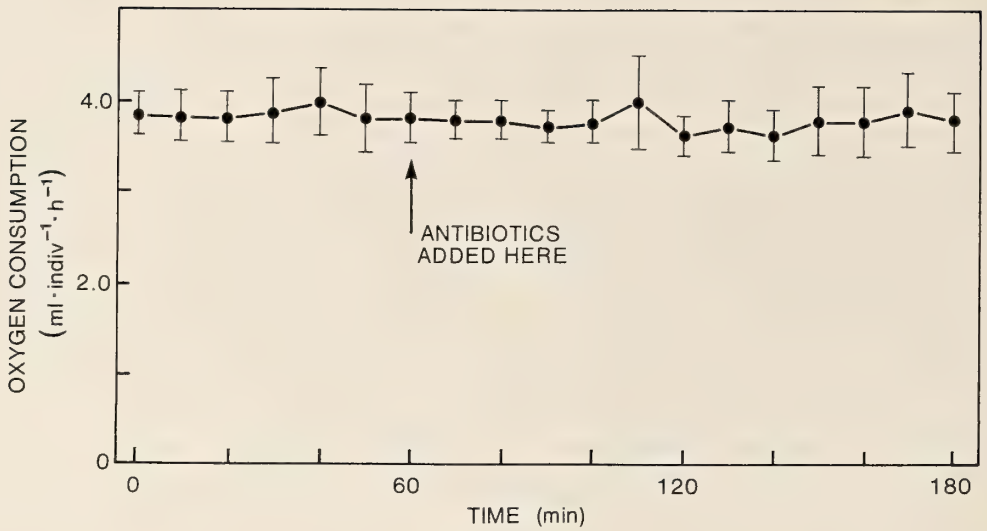


Figure 3

Effect of antibiotics on oxygen uptake in *Aplysia dactylomela*. After 60 min to establish a baseline level of oxygen consumption, seawater containing 100 mg antibiotics·L^{-1} (50 mg each of streptomycin sulfate and penicillin-G) was introduced into the respirometer at normal rates of flow. Owing to a scarcity of animals only four experiments were run. Animal weights ranged from 150 to 307 g live. All values for oxygen consumption (V_{O_2}) were converted to a standard animal weight of 200 g live using the equation $V_{O_2(200\ g)} = 200/\text{exper wt})^{0.926} \cdot V_{O_2(exper)}$ (see CAREFOOT, 1987). Each point represents the $\bar{X} \pm$ SE. Temperature = 28.5°C.

similar to *Australorbis,* the decreased growth rate of *Aplysia juliana* could not be attributed to an antibiotic effect. As well, the relatively high concentration of calcium ions in seawater could have ameliorated any potentially undesirable behavioral side-effects streptomycin might have had on the sea hares.

Oxygen consumption measurements on *Aplysia dactylomela* treated with five times the concentration of antibiotics employed in the *A. juliana* growth study showed no significant deviations from baseline values. If the antibiotic treatment had created stress or caused illness in the sea hares it would presumably have been manifested as a change in metabolic rate, reflected in either increased or decreased levels of oxygen consumption. As noted earlier, the animals appeared to be normal throughout the growth experiment and, even when subjected to a 50-fold greater concentration of antibiotics than that used in the growth experiment (Figure 2), the sea hares showed no observable change in activity or in the rate of feeding. While these observations are circumstantial, they nonetheless support the idea that the negative effects of the antibiotics on the growth of *A. juliana* were indirect effects due to a reduction in the numbers of gut bacteria, and not directly deleterious effects on the sea hares themselves.

Bacteria certainly seem to be involved in the breakdown of plant materials in the guts of marine invertebrate herbivores. They have been shown capable of releasing glucose from carbohydrate storage materials such as maltose and starch, and from such structural materials as carrageenan (but not cellulose) during in vitro studies using bacteria from sea urchins (PRIM & LAWRENCE, 1975) and bacteria from sea hares (present study, see Table 4). In addition, bacterial isolates from the gut of *Aplysia juliana* have been shown in the present study to increase the concentration of free amino acids in an *Ulva fasciata* culture medium. The absorption and utilization of such bacterially produced amino acids and fixed carbon by host animals in the synthesis of their own tissues have been demonstrated in the sea urchin *Strongylocentrotus droebachiensis* (FONG & MANN, 1980) and the gutless bivalve *Solemya reidi* (FISHER & CHILDRESS, 1986). While no similar experiments have been done with sea hares, it can be expected that any bacterially mediated breakdown product of seaweeds, whether glucose or amino acids, would be readily absorbed and used by an animal in its own metabolism. Indeed, there could even be a degree of exploitative competition for food resources occurring within the gut between the bacteria and host.

The sea hare has several possible sources of amino acids due to bacterial activity: (1) from normal extracellular digestion of algal protein by the bacteria, (2) from synthesis by bacteria and the release to the gut lumen, (3) from digestion of bacteria by other bacteria, (4) from autolysis of bacteria, and (5) from digestion of bacteria by the sea hare's own digestive enzymes. The high steady-state concentration of gut bacteria (even in starved animals), combined with their diversity, point to a potentially important rôle played by them in the nutrition of their hosts. FONG & MANN (1980) suggest, in this regard, that the ability of sea urchins to use a wide variety of seaweeds as foods

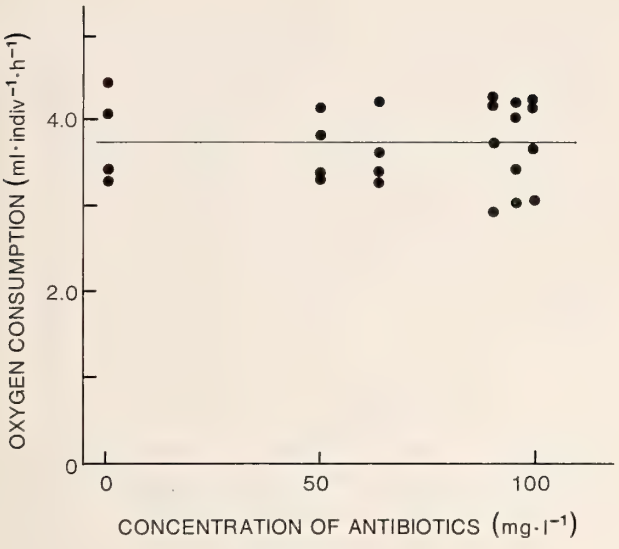


Figure 4

Relationship of oxygen consumption to antibiotics concentration in *Aplysia dactylomela*. Data from the experiment outlined in Figure 3. Regression statistics for the equation $Y = a + bX$ are $a = 3.74$ and $b = -0.093$. The correlation coefficient $r = -0.138$ is not significantly different from zero ($P > 0.50$).

stems from the clandestine nutritional contributions made by bacterial symbionts.

In summary, antibiotic treatment inhibited growth of juvenile sea hares either through an unknown and unobserved directly deleterious effect or through an indirect effect of nutrient loss through reduction in the number of gut bacteria. The post-metamorphic rate of growth is high in sea hares, and thus demand for amino acids is high. Removal of gut bacteria, a potential source of amino acids and glucose beyond those available from the breakdown of algal protein, would limit the rate of protein synthesis and metabolism and thus limit growth. We showed an approximately one order of magnitude reduction in the number of gut bacteria in *Aplysia* after treatment with antibiotics. This is considerably less than the five orders of magnitude reduction shown by Fong & Mann (1980) to occur in the sea urchin *Strongylocentrotus droebachiensis* after 2 days of treatment with the same antibiotics (but using a higher concentration: 90 mg·L seawater^{-1}) but, nevertheless, represents a considerable reduction in bacterial numbers. We believe that gut bacteria do contribute significantly to the nutrition of *Aplysia*, as they seem to do for other marine invertebrate herbivores, and represent a factor largely neglected in past studies of growth, nutrition, and dietary preferences in marine invertebrate herbivores in general.

ACKNOWLEDGMENTS

We thank Robert Kane, Director of the Kewalo Marine Laboratory, University of Hawaii, and Wayne Hunte, Director of the Bellairs Research Institute of McGill University, for providing research space and facilities. We are grateful to Marilyn Switzer-Dunlap for use of her research facilities, for supplying us with newly metamorphosed *Aplysia juliana*, and for teaching us the fine art of rearing *A. dactylomela*. We also thank Francis of Speightstown for special laboratory assistance during the Barbados part of the study and Barbara Taylor for helpful comments on the manuscript. The research was supported by Natural Science and Engineering Research Council of Canada Summer Research Fellowships to T. Vitalis and M. Spence, and by an operating grant from NSERC to T. Carefoot.

LITERATURE CITED

Brooks, M. A. 1964. Symbiotes and the nutrition of medically important insects. Bull. World Health Org. 31:555–559.

Brown, M. R. W., P. Gilbert & R. M. M. Klemperer. 1979. Influence of the bacterial cell envelope on combined antibiotic action. Pp. 69–86. *In:* J. D. Williams (ed.), Antibiotic interactions. Academic Press: London. 183 pp.

Buchanan, R. E. & N. E. Gibbons (eds.). 1974. Bergey's manual of determinative bacteriology. Williams and Wilkins Co: Baltimore. 1268 pp.

Carefoot, T. H. 1970. A comparison of absorption and utilization of food energy in two species of tropical *Aplysia*. Jour. Exp. Mar. Biol. Ecol. 5:47–62.

Carefoot, T. H. 1981a. Nutrition of a coral rubble-inhabiting herbivore, the sea hare *Aplysia*. Proc. Fourth Intl. Coral Reef Symp., Manila, 1981, 2:665–669.

Carefoot, T. H. 1981b. Studies on the nutrition and feeding preferences of *Aplysia*: weight changes on artificial diets deficient in specific amino acids. Can. Jour. Zool. 59:445–454.

Carefoot, T. H. In press. Diet and its effect on oxygen uptake in the sea hare *Aplysia*. Jour. Exp. Mar. Biol. Ecol.

Chernin, E. 1959. Cultivation of the snail, *Australorbis glabratus*, under axenic conditions. Ann. N.Y. Acad. Sci. 77: 237–245.

Chernin, E. & A. R. Schork. 1959. Growth in axenic culture of the snail, *Australorbis glabratus*. Amer. Jour. Hyg. 69:146–160.

Fisher, C. R. & J. J. Childress. 1986. Translocation of fixed carbon from symbiotic bacteria to host tissues in the gutless bivalve *Solemya reidi*. Mar. Biol. 93:59–68.

Fong, W. & K. H. Mann. 1980. Role of gut flora in the transfer of amino acids through a marine food chain. Can. Jour. Fish. Aquat. Sci. 37:88–96.

Franklin, T. J. & G. A. Snow. 1975. Biochemistry of antimicrobial action. Chapman and Hall: London. 224 pp.

Hammond, S. M. & P. A. Lambert. 1978. Antibiotics and antimicrobial action. Edward Arnold: London. 63 pp.

Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. Oceanogr. Mar. Biol. Ann. Rev. 13: 213–286.

McBee, R. H. 1971. Significance of intestinal microflora in herbivory. Ann. Rev. Ecol. Syst 2:165–176.

Prim, P. & J. M. Lawrence. 1975. Utilization of marine plants and their constituents by bacteria isolated from the gut of echinoids (Echinodermata). Mar. Biol. 33:167–173.

Switzer-Dunlap, M. & M. G. Hadfield. 1977. Observations on development, larval growth and metamorphosis of four species of Aplysiidae (Gastropoda: Opisthobranchia) in laboratory culture. Jour. Exp. Mar. Biol. Ecol. 29:245–261.

The Veliger 30(4):342–346 (April 1, 1988)

THE VELIGER

Penetration of the Radial Hemal and Perihemal Systems of *Linckia laevigata* (Asteroidea) by the Proboscis of *Thyca crystallina*, an Ectoparasitic Gastropod

by

D. A. EGLOFF, D. T. SMOUSE, Jr., and J. E. PEMBROKE

Department of Biology, Oberlin College, Oberlin, Ohio 44074, U.S.A.

Abstract. The proboscis of female *Thyca crystallina* (Mollusca) penetrates the body wall of *Linckia laevigata* (Echinodermata) and terminates in the middle of the ambulacral ridge where it opens within the perihemal sinus near the radial hemal strand. The proboscis does not penetrate the perivisceral coelom of its host, nor can it be withdrawn because the attachment disc of the adult snail is fused to the epidermis of the host. Except for a partial alteration in size and texture of a few ambulacral ossicles, and loss or reduction in size of the host's ampullae at the site of infection, other host organs and tissues are relatively unaffected by the penetration of the proboscis. Presumably *T. crystallina* obtains nutrients from the hemal-perihemal systems of its asteroid host.

INTRODUCTION

Because females of the ectoparasitic snail *Thyca crystallina* (Gould, 1846) are fused to their hosts, *Linckia laevigata* (Linnaeus), lack mouth parts, and have reduced digestive and enlarged salivary glands, many authors have concluded that they must be utilizing nutrients not requiring complex digestion (Sarasin & Sarasin, 1887; Kükenthal, 1897; Koehler & Vaney, 1912; Adam, 1934; Cheng, 1964). To this extent the snail-host relationship has been well described. However, both early and more recent published discussions (Taylor & Lewis, 1970; Yonge & Thompson, 1976; Elder, 1979) have not described the pathway of the snail's proboscis into the host. Most investigators have heretofore asumed that *T. crystallina* sucks internal fluids or tissues from *L. laevigata* but have not identified the probable source of nutrients for the snail.

In the Echinodermata, nutrient transport from sites of intake or storage has been attributed to one or more of the following coelomic derivatives: the perivisceral coelom, the water vascular system, the hemal system, and the perihemal system (Hyman, 1955; Anderson, 1966; Ferguson, 1969, 1982; Binyon, 1972). To the extent that any or all of these systems are rich in nutrients, they could serve as a potential source of nutrients for *Thyca crystallina.*

In the present study we traced the route of penetration of an ectoparasitic snail's proboscis into a sea star's arm to determine which of the host's internal systems are contacted. Our discovery that the snail's proboscis terminates within the perihemal system near the radial hemal strand suggests that these systems serve as a source of nutrients for *Thyca crystallina.*

MATERIALS and METHODS

Specimens of the sea star *Linckia laevigata* were examined from collections made in May 1965, December 1970, and August 1976 on the reef flats east of the ship channel at Suva, Fiji. Thirty-two specimens of the 224 (14.3%) collected in 1965 were infected by one or more individuals of *Thyca crystallina* (a limpetlike prosobranch gastropod in the family Capulidae). Specimens were examined alive or were preserved in buffered 4% formaldehyde. Gross dissections were prepared with the aid of razor blades or a small, motor-driven, circular saw. Specimens for sections were decalcified for 2–3 days in a modified Heidenhain's Susa fixative (10 mL glacial acetic acid, 50 mL 40% formaldehyde, and 20 g trichloroacetic acid in 200 mL 70% ethyl alcohol), embedded in paraffin in a low vacuum, sectioned at 10–16 μm, and stained with hematoxylin and Gomori's trichome or in Cason's rapid one-step Mallory-Heidenhain.

RESULTS

We found that female specimens of *Thyca crystallina* are attached to their hosts by a circular disc as described by

Adam (1934). We also found the males of this species attached under the shell of the females. The proboscises of the males that we examined lay freely in the space under the female shell and did not penetrate the integument of the sea star.

The attachment discs of the female *Thyca crystallina* are fused in the largest specimens to the host's integument by fibrous connective tissues. The female proboscis extends from the center of this attachment disc through a hole up to 1 mm in diameter into the tegument of the host. Gross dissections revealed that the proboscis enters the sea star's arm between the marginal dermal ossicles, progresses through the thick connective and muscular tissue of the dermis, and terminates in the middle of the ambulacral ridge (Figures 1, 2A). By angling towards the ambulacral ridge, the proboscis bypasses the perivisceral coelom, penetrates the thick body wall, and enters the ambulacral ossicles so that one or more ampullae of the host's water vascular system are lost or displaced. The only superficial evidence of the proboscis on the internal surface of the ambulacral ridge is the absence or reduction in size of 1–3 ampullae and a darkening of the ambulacral ridge in the area directly overlying the infected area; inside the ambulacral ridge this may involve the reduction in size of 2–4 ambulacral ossicles on the infected side. Discoloration results from a replacement of the ambulacral ossicle(s) lying above the proboscis by an abnormal area of hypertrophied muscular and connective tissue. These alterations in the ambulacral ossicle may be seen by comparing Figures 2B and C.

In 3 of 18 dissected specimens we observed a small hole in the depression on the aboral side of the ambulacral ridge in the middle of the discolored, infected area. In another specimen we found a small hole opening downward from the proboscis area into the ambulacral groove. Because these openings were not present in most specimens nor in any of the 12 sectioned specimens we assume they do not represent the normal condition.

The proboscis of female *Thyca crystallina* terminates in the area occupied by the hemal and perihemal systems. When uninfected areas are viewed in cross-section, these systems form a triangular area bounded on the lower side by the V-shaped radial nerve and on the upper side alternately by the lower transverse ambulacral muscle and, in the spaces between the muscles, by the radial water canal (Figure 2C). These relationships are identical in infected arms of *Linckia laevigata* proximal and distal to the infection site, *i.e.*, there is no histological evidence that the ectoparasite affects the radial systems of the host on either side of the point of infection. However, in the area penetrated by the proboscis, an extensive displacement of all systems occurs. The radial water canal is pushed to one side and the radial nerve is flattened and also pushed to the far side of the ambulacral groove; hemal tissues are often more abundant in the region near the end of the proboscis (Figure 2B). Despite the enlargement of the hemal tissue, we traced the perihemal sinus through the infected area beween unaltered distal and proximal regions in 11 serially sectioned specimens. In a 12th specimen the hemal tissue filled the space in front of the proboscis, thereby locally obliterating the perihemal sinuses.

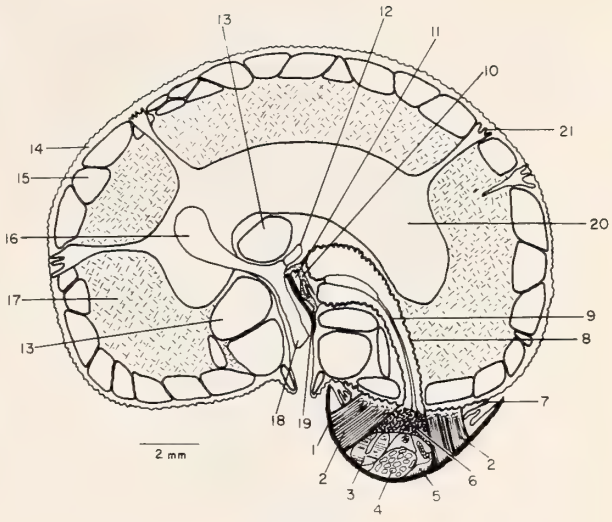


Figure 1

Schematic cross-sectional view of an arm of *Linckia laevigata* to which an ectoparasitic *Thyca crystallina* is attached. View is towards the central disc of the sea star. The snail's proboscis bypasses the perivisceral coelom, displaces 1–3 ampullae, penetrates the radial perihemal sinus, but does not interrupt the water vascular or nervous systems. *Thyca crystallina*: 1, shell; 2, columellar muscle; 3, capsule gland; 4, digestive gland; 5, nephridium; 6, salivary gland; 7, attachment disc, left anterior edge; 8, proboscis; 9, esophagus. *Linckia laevigata*: 10, hemal tissue; 11, perihemal sinus; 12, radial water canal; 13, ambulacral ossicle; 14, epidermis; 15, dermal ossicle; 16, ampulla; 17, dermis; 18, tube foot; 19, radial nerve; 20, perivisceral coelom; 21, papula.

The proboscis of *Thyca crystallina* consists of a sheath through which extends two salivary gland ducts and a thin-walled esophagus that terminates in a thick-walled pharyngeal mass (Figure 2D). In preserved specimens the wall of the proboscis is contracted and therefore highly folded in longitudinal sections. Except for a distinct outer epithelium, the proboscis is filled with connective tissue, blood, and blood cells. At its distal end the proboscis is folded on its outer surface, forming a groove that encloses tissues of the host (Figure 2E). This groove is continuous with the internal proboscis space through which runs the pharyngeal mass and esophagus. Inside the proboscis the groove becomes a crescentric chamber surrounding the mouth (Figure 2F); the mouth opens at the tip of the muscular pharyngeal mass. Salivary gland ducts attach to the outer surface of the muscular pharyngeal mass (Figure 2G) and empty at its distal end. Internally the pharyngeal mass is divided into a tripartite food canal which is continuous proximally with the thin-walled esophagus (Figure 2H).

Strands of host cells converge at the end of the proboscis (Figure 2B). These cells appear to originate from both the

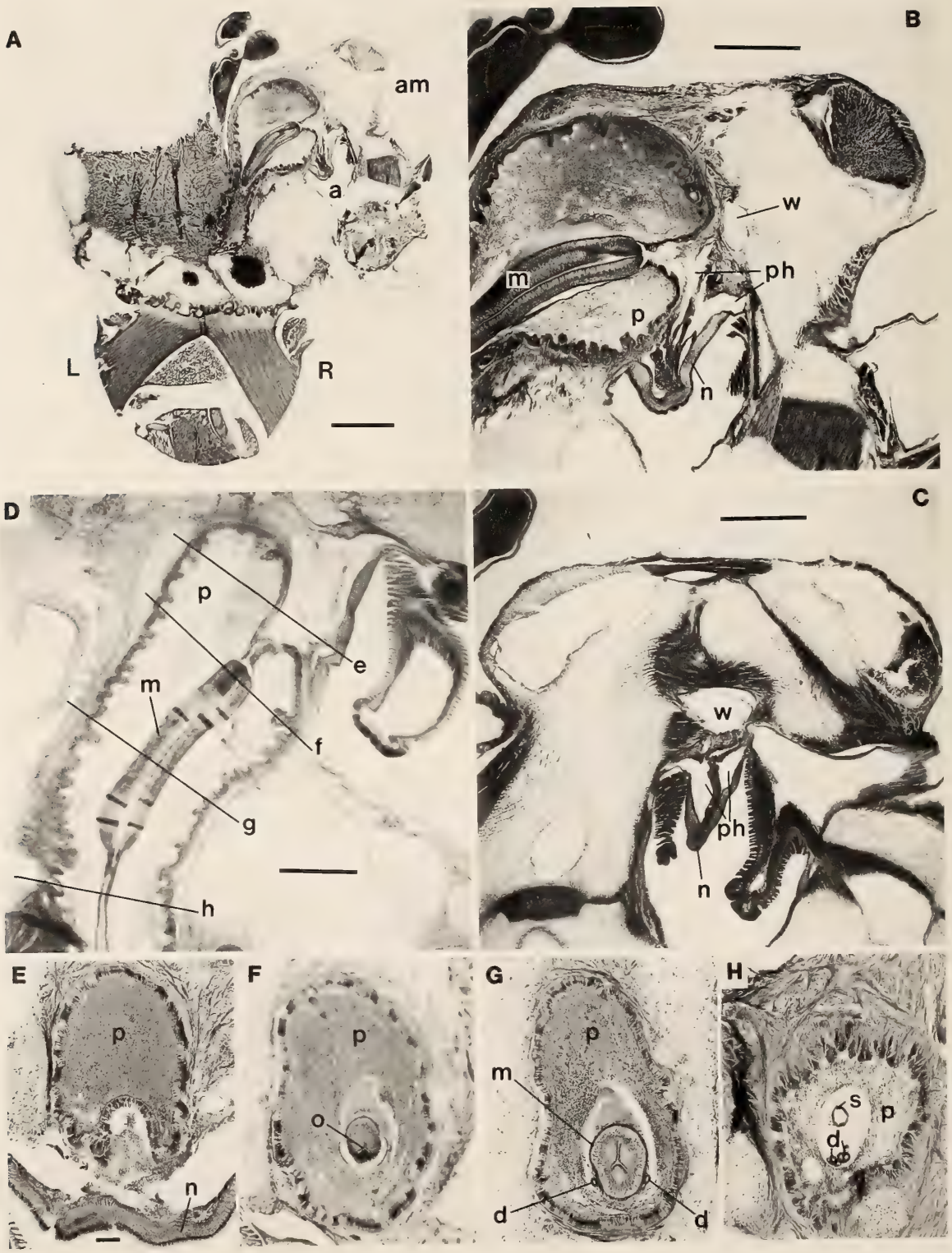


Figure 2

Photomicrographs of *Linckia laevigata* arms with and without (Figure 2C) attachment or penetration by the snail *Thyca crystallina*. A. A section through an entire snail and a fragment of a seastar arm at the level where the proboscis penetrates the perihemal sinus. The section is oriented with the ambulacrum (a) on the lower side and

host's body wall surrounding the distal end of the proboscis and from hemal tissue. The contents of the esophagus, although sparse in sectioned specimens, occasionally include nuclei of cells in addition to larger quantities of amorphous material.

DISCUSSION

The route of penetration of the proboscis of the female *Thyca crystallina* into *Linckia laevigata* suggests that sufficient food is available from some combination of hemal, perihemal, and surrounding fluids and tissues to sustain the ectoparasitic snail. This deduction is based on the fact that the proboscis of large snails cannot be withdrawn because the attachment disc is fused with the tissue of the host and the fact that the proboscis has access to no other sources of nutrients inside the host.

Alternative routes are possible but not utilized. For example, holes in the body wall occupied by papulae (Figure 1), provide a short and direct access to the perivisceral coelom, but in no specimens we examined did the proboscis of *Thyca crystallina* take this path. Instead, the proboscis bypasses the perivisceral coelom and proceeds deeper into the host. This penetration must require extensive digestion of dense dermal tissue and dissolution of calcareous ossicles. The energetic costs of creating this circuitous route to the hemal-perihemal complex ultimately must be more than offset by a flow of nutrients to the snail.

The tissues of the host at the site of penetration are not grossly injured; in fact, the opposite appears to be the case. The region at the end of the proboscis has an abundance of cells derived from the host's body wall and from hemal tissue. This suggests that the host is capable of replacing the apparent loss of cells to the snail.

Thyca crystallina presumably shuns the more spacious perivisceral coelom in favor of the relatively small hemal-perihemal complex because the latter is a more concentrated source of nutrients than is the perivisceral coelom (Ferguson, 1982; Beijnink & Voogt, 1984). This hypothesis is consistent with the observations in another asteroid, *Echinaster graminicolus,* where a radioisotopic tracer appeared within 12–24 h in the ambulacral radial hemal tissue after injection of C^{14}-labeled amino acids (Ferguson, 1970) or after feeding C^{14}-labeled clams or liquid glucose-amino acid medium (Ferguson, 1984). The proteins, glycoproteins, and possibly glycolipids stored in the hemal strand of *Asterias rubens* (Beijnink & Voogt, 1986) would provide a rich source of complex nutrients for *T. crystallina* if present in *Linckia laevigata.*

In addition, the snail may be obtaining soluble food produced at remote sites and transported to the snail through the perihemal sinuses. The presence of flagellated cells in the perihemal sinus (Cuénot, 1948; Walker, 1979) of some asteroids provides a means of moving nutrients in solution through this system. Based on these observations, Ferguson (1984) concluded that nutritive metabolites are translocated by some combination of movement and storage within the hemal-perihemal complex.

Given the reported anatomical relationships and the probable role of the hemal-perihemal complex in nutrient transport and storage in asteroids, the stage is set for an experimental determination of the kinds and rates of nutrient transfer through the hemal-perihemal complex of *Linckia laevigata* by using *Thyca crystallina* as a natural probe.

ACKNOWLEDGMENTS

Field work in 1965 was done by the first author while a participant on Stanford University's *Te Vega* Cruise #7 supported by N.S.F. G17465. Laboratory work in 1978 was supported by Oberlin College Research and Development Committee. We gratefully acknowledge the 1970 collections by the late Alan Banner and the advice and encouragement of Charles Walker and Matthew Wilks.

LITERATURE CITED

Adam, W. 1934. Prosobranches parasites. Mem. Mus. Roy. Hist. Natur. Belg. 2(14):87–115.

Anderson, J. M. 1966. Aspects of nutritional physiology. Pp. 329–357. *In:* R. A. Boolootian (ed.), Physiology of Echinodermata. Interscience Publishers: New York.

Beijnink, F. B. & P. A. Voogt. 1984. Nutrient translocation in the sea star: whole-body and microautoradiography after

←

ampulla (am) in the perivisceral coelom on the upper side. The left (L) and right (R) sides of the snail are indicated. B. Higher magnification of the section in Figure 2A at the distal end of the proboscis (p), which encloses the pharyngeal mass (m). The radial water canal (w), hemal tissue and associated perihemal sinuses (ph) lie above the radial nerve (n). C. A section of an uninfected part of the same seastar arm proximal to the section shown in Figures 2A, B. D. Section through the proboscis of another specimen showing the extent of the muscular pharyngeal mass (m) in the proboscis (p). Lines (e–h) indicate the level of cross sections through the proboscis of a third specimen shown in Figures 2E, F, G and H, respectively. E. Section of the proboscis (p) distal to the pharyngeal mass and mouth. The groove in the proboscis appears to surround hemal tissue lying aborally to the radial nerve (n) of the seastar. F. Section through the proboscis (p) at the point where the mouth (o) opens into the pharyngeal mass. G. Section through the middle region of the muscular pharyngeal mass (m). Ducts (d) of the salivary gland adhere closely to the outer edge of the pharyngeal mass. H. Section proximal to the pharyngeal mass showing the esophagus (s) and the ducts of the salivary gland (d). Scale bars: A, 1 mm; B–D, 0.5 mm; E, 0.1 mm (the same scale applies to F–H).

ingestion of radiolabeled leucine and palmitic acid. Biol. Bull. 166:669–682.

Beijnink, F. B. & P. A. Voogt. 1986. The aboral haemal system of the sea star, *Asterias rubens* (Echinodermata, Asteroidea): an ultrastructural and histochemical study. Zoomorphology 106:49–60.

Binyon, J. 1972. Physiology of echinoderms. Pergamon Press: Oxford. 264 pp.

Cheng, T. C. 1964. The biology of animal parasites. Saunders Company: Philadelphia. 727 pp.

Cuénot, L. 1948. Anatomie, éthologie et systématiques des Échinodermes. *In:* P. P. Grassé (ed.), Traité de zoologie 11: 3–275. Masson: Paris.

Elder, H. Y. 1979. Studies on the host parasite relationship between the parasitic prosobranch *Thyca crystallina* and the asteroid starfish *Linckia laevigata.* Jour. Zool. (Lond.) 187: 369–391.

Ferguson, J. C. 1969. Feeding, digestion and nutrition in Echinodermata. Pp. 71–100. *In:* M. Florkin & B. T. Scheer (eds.), Chemical zoology. Vol. III. Echinodermata, Nematoda, and Acanthocephala. Academic Press: New York.

Ferguson, J. C. 1970. An autoradiographic study of the translocation and utilization of amino acids by starfish. Biol. Bull. 138:14–25.

Ferguson, J. C. 1982. Nutrient translocation. Pp. 373–393. *In:* M. Jangoux & J. M. Lawrence (eds.), Echinoderm nutrition. Balkema: Rotterdam.

Ferguson, J. C. 1984. Translocative functions of the enigmatic organs of starfish—the axial organ, hemal vessels, Tiedemann's bodies, and rectal caeca: an autoradiographic study. Biol. Bull. 166:140–155.

Hyman, L. 1955. The invertebrates. Vol. IV. Echinodermata. McGraw-Hill Book Company: New York. 763 pp.

Koehler, R. & C. Vaney. 1912. Nouvelles formes de Gastéropodes ectoparasites. Bull. Sci. Fr. Belg. 46:191–217.

Kükenthal, W. 1897. Parasitische Schnecken. Abh. Schneckenbergishen Ges. 24:1–14.

Sarasin, P. & F. Sarasin. 1887. Ueber zwei parasitische Schnecken. Ergeb. Naturwiss. Forsch. Ceylon 1:1–32.

Taylor, J. D. & M. S. Lewis. 1970. The flora, fauna and sediments of the marine grass beds of Mahé, Seychelles. Jour. Natur. Hist. 4:199–220.

Walker, C. W. 1979. Ultrastructure of the somatic portion of the gonads in Asteroids, with emphasis on flagellated-collar cells and nutrient transport. Jour. Morphol. 162:127–162.

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

The Veliger 30(4):347–350 (April 1, 1988)

THE VELIGER

Gastric Contents of *Fissurella maxima* (Mollusca: Archeogastropoda) at Los Vilos, Chile

by

CECILIA OSORIO

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

M. ELIANA RAMIREZ

Sección Botánica, Museo Nacional de Historia Natural, Casilla 787, Santiago, Chile

AND

JENNIE SALGADO

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

Abstract. The study of the gastric contents in 92 specimens of *Fissurella maxima* from Los Vilos, Chile (31°51′S, 71°32′W) showed the presence of partially digested algal remains of 13 species. Diatoms were present, as were whole animals. The macroalgae *Chondrus*, *Gelidium*, and *Ulva*, found throughout the 13-month study period, had the greatest relative abundance in gastric contents. Other macroalgae were occasionally present, with wide fluctuations in abundance; still others were recorded only once. The analysis of the feces of keyhole limpets maintained in an aquarium showed abundant undigested diatoms and remains of digested *Gelidium* and *Porphyra* which had been given as food. We conclude that *F. maxima* is mainly a primary consumer which grazes on macroalgae in the rocky intertidal zone.

INTRODUCTION

Fissurella maxima Sowerby, 1835, is found on intertidal rocks from Huarmey in Peru to Lirquen (Concepción) in Chile (McLean, 1984). Like other keyhole limpets, this one is an important economic resource in Chile. Extraction in 1985 was 3.653 tons and in 1986 was 2.159 tons (Anuario Estadístico de Pesca, 1986).

Data available on *Fissurella maxima* include taxonomic aspects (Osorio *et al.*, 1979; McLean, 1984), age and growth (Bretos, 1982) and the reproductive cycle (Bretos *et al.*, 1983; Herrera, 1983; Aviles & Osorio, unpublished data). There are no data in the literature on the feeding habits of *F. maxima*. Such information would be essential for the knowledge of the trophic position of the species and its interactions with other intertidal organisms. Several authors (*e.g.*, Moreno & Jaramillo, 1983; Jara & Moreno, 1984; Santelices *et al.*, 1986; Oliva & Castilla, 1986) consider that the action of certain herbivorous gastropods—trophic generalists of large body size—could influence the abundance and species composition of intertidal algal communities.

To document its feeding habits, we have analyzed the stomach contents of *Fissurella maxima* during a 13-month period in the intertidal zone of a northern Central Chilean beach.

MATERIALS AND METHODS

The study site was Caleta "El Ñague" at Los Vilos (31°51′S, 71°32′W). For the gastric analysis, 92 specimens of *Fissurella maxima* were collected, 6–8 specimens monthly, with sizes ranging from 85 to 139 mm (reproductive size); only five collected individuals were smaller than 85 mm. Samplings were conducted from March 1983 through March 1984.

Specimens collected were immediately injected with formalin in seawater in order to stop digestion. In the laboratory, the stomach contents were emptied into a glass cylinder and the total volume was measured. For analysis, 4 mL of the contents per stomach were used, *i.e.*, about 50% of the total volume. When the volume was under 4 mL, the total content of the stomach was analyzed. Individual food items were separated under the microscope and

their presence recorded. Histological sections were made in order to identify the algal remains. The total volume per month of each algal item was quantified by measuring its volume displacement in a 1.25-mL cylinder graduated to 0.25 mL. Values were expressed as the percentage of relative abundance of each item in the total sample.

Feces of specimens kept in an aquarium were analyzed under the microscope in order to determine whether diatoms were digested. Some keyhole limpets survived for 3 months in the aquarium. During this time they were fed *Porphyra* and *Gelidium.*

RESULTS

All of the 92 examined stomachs contained algal and microalgal remains. In general the diet did not vary with size. The gastric contents of the five individuals smaller than 85 mm did not differ from those of the larger sizes. Animal remains were found only occasionally. The microalgal genera most frequently found were diatoms of several genera: *Synedra, Lichmophora, Thalassiosira, Cocconeis, Pleurosigma,* and *Coscinodiscus.* Diatoms did not show signs of digestion.

Among the animals were small crustaceans (copepods and cypris larvae), a few gastropods, bivalve post-larvae, and two individuals each of polychaetes and medusae. It is worth noting that these animals showed no signs of trituration or digestion.

Macroalgae were abundant and, unlike the former groups, they showed clear evidence of digestion. Thirteen species were found: *Chondrus canaliculatus* (C. Ag.) Grev., *Glossophora kunthii* (C. Ag.) J. Ag., *Halopteris funicularis* (Mont.) Sauv., *Corallina officinalis* var. *chilensis* (Dec.) Kutz., *Lessonia nigrescens* Bory, *Codium dimorphum* Svedelius, *Adenocystis utricularis* (Bory), *Porphyra columbina* Mont., *Pterosiphonia dendroidea* (Mont.) Salk., *Gelidium* sp., *Ulva* sp., *Cladophora* sp., and *Enteromorpha* sp. Of these, nine species were present in considerable amounts and could be quantified.

Chondrus, Gelidium, and *Ulva* were found throughout the 13 months of sampling, being present in 71%, 70%, and 54% of the examined stomachs respectively. *Glossophora, Halopteris, Cladophora, Corallina,* and *Lessonia* were present for at least 8 months. *Codium, Adenocystis,* and *Porphyra* occurred during only 4 months. In terms of relative abundance, the most important genera were *Chondrus, Gelidium, Ulva,* and *Glossophora,* the total volumes of which added up to 80%.

The monthly variation of the most frequently found algae, arranged by major taxa, is represented in Figure 1. The most abundant Rhodophyta were *Chondrus* and *Gelidium* (Figure 1a). *Chondrus* exhibited high values from May through October, with maximum abundance in August (62.5%). On the other hand *Gelidium* showed higher variations in abundance than *Chondrus,* with two peaks, one in September (50%) and another in December (45.4%).

Phaeophyta were less abundant (Figure 1B) and their maximum values reached only 30%. In this group, *Glossophora* and *Halopteris* were the most abundant, but with discontinuous values during the year.

Among the Chlorophyta, *Ulva* was recorded the year round with maximum abundance in March 1983 and March 1984 (29.4% and 33.3% respectively). The values for *Ulva* were markedly lower from August to December. *Cladophora* appeared somewhat irregularly with maximal abundance from November to January.

The analysis of the trophic spectrum per month disclosed that *Fissurella maxima* ingests simultaneously from 5 to 10 macroalgal species, with variable abundance throughout the year. The largest variety was observed in summer—January, February—with 9 or 10 species, whereas in June, November, and December only 5 algal species were recorded as food items. All the remaining species of macroalgae showed wide temporal fluctuations in abundance, particularly *Corallina, Lessonia, Codium, Adenocystis,* and *Porphyra.* Two algae were recorded only once during the study period: *Pterosiphonia* (March 1983) and *Enteromorpha* (August 1983).

The specimens maintained in the aquarium fed at night, and no apparent activity was recorded during the day. The analysis of the feces obtained during the first six days revealed abundant diatoms (*Lichmophora, Synedra, Navicula, Grammatophora, Amphora, Cocconeis, Nitzchia, Cymbella, Ceratoneis, Entophyla, Rhabdonema, Rhoicosphenia, Pleurosigma, Coscinodiscus,* and *Pinnularia*) with no signs of digestion; thecae and chloroplasts were still present. Feces after 30 and 60 days contained only scarce diatoms (*Cocconeis, Pinnularia,* and *Grammatophora*) and residues of *Gelidium* and *Porphyra,* which had been fully digested.

DISCUSSION

The diet of *Fissurella maxima* at Caleta El Ñague in Los Vilos consisted mostly of macroalgae. Other organisms such as diatoms, seemed to be less important in nutrition, since they may have passed through the gut undigested. They were probably passively ingested with the macroalgae.

Fissurella maxima seems to be a generalist herbivore feeding especially on *Chondrus, Gelidium,* and *Ulva.* Occasionally it consumes other algae such as *Corallina, Lessonia, Codium, Adenocystis,* and *Porphyra.* Another keyhole limpet, *Fissurella crassa* Lamarck, 1822, is also a generalist herbivore whose diet at a nearby site in Pelancura (33°35'S, 71°38'W), between April 1983 and April 1984, consisted of microalgae, macroalgae (ulvoids, *Schottera, Gelidium,* and calcareous algae), invertebrate remains, and spores (Santelices *et al.,* 1986). However, the diets of the two species seem to differ in their composition. Such differences could be related to the ecological distributions of the two *Fissurella* species. *Fissurella maxima* inhabits the low intertidal zone, while *F. crassa* is mostly found on the upper intertidal zone, where it reaches higher levels than other keyhole limpets (McLean, 1984). On the other hand *F.*

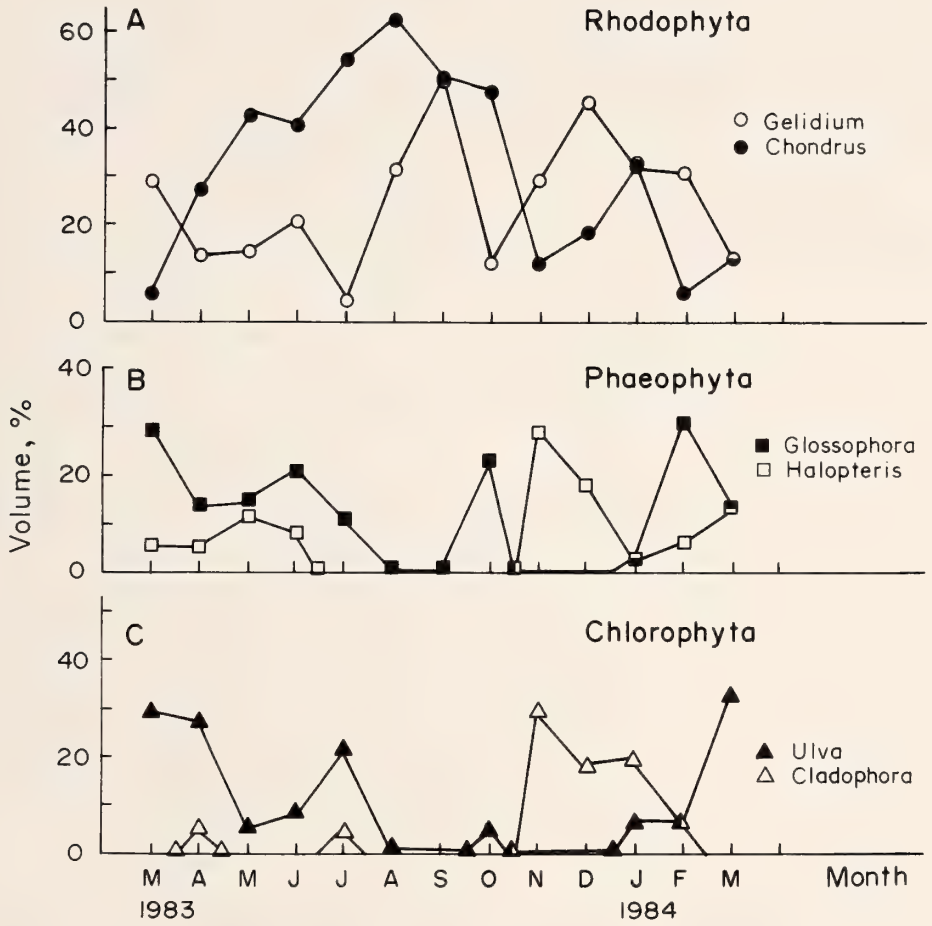


Figure 1

Monthly variation of the main algae in the gastric contents of *Fissurella maxima* at Los Vilos, Chile, from March 1983 to March 1984.

barbadensis (Gmelin, 1791), found in Barbados (WARD, 1966), has been reported to ingest preferably green and blue-green algae, sand grains, diatoms, small crustaceans, bivalves, and occasionally Foraminifera. The only food items this species seems to share with *F. maxima* are *Cladophora* and *Ulva*. These differences in diet could be explained by the different ecological conditions of their habitats.

The variations in relative abundances of algae in the stomach contents may or may not relate to the relative abundances of algae in the community. For example, 12 species of the macroalgae identified in the stomachs of *Fissurella maxima* are known to occur the year round in the rocky intertidal zone of central Chile (SANTELICES & VERA, 1984). However, without more detailed knowledge of the relative abundances we cannot ascertain preferences in this keyhole limpet.

SANTELICES (1981) suggests that *Codium* and *Gelidium* may escape herbivory owing to their growth patterns, which result in a continuous cover. In turn, *Lessonia* and *Corallina* may also escape predation, the former because of its large size and the latter on account of its rough texture. However, the presence of all these species in the stomach of *Fissurella maxima* questions these hypotheses. Furthermore, STENECK & WATLING (1982) consider that the rhipidoglossan radula of *F. maxima* would not be adequate for grazing on rough textured algae. The finding of *Corallina* in the stomach of this species challenges this notion, and supports SANTELICES *et al.* (1986) who suggest that the different shapes of gastropod radulas do not necessarily relate to the kind of algae ingested.

Based on its gastric contents, we conclude that *Fissurella maxima* is "euriphycophagous" and a primary consumer of macroalgae in the rocky intertidal zone of Chile.

ACKNOWLEDGMENTS

The authors thank N. Bahamonde and D. Soto for valuable suggestions and revision of the manuscript; V. Montecino

for identifying diatoms; C. Fernandez for the diagrams and M. Bustos for technical assistance; and two anonymous reviewers for valuable suggestions.

This study was supported by Project N 1754-8522 of the Departamento de Investigación y Bibliotecas de la Universidad de Chile.

LITERATURE CITED

Anuario Estadistico de Pesca. 1986. Servicio Nacional de Pesca, Chile.

Bretos, M. 1982. Biología de *Fissurella maxima* (Moll; Archaeogastropoda) en el norte de Chile I. Caracteres generales, edad y crecimiento. Cahiers Biol. Mar. 23:159–170.

Bretos, M., I. Tesorieri & L. Alvarez. 1983. The biology of *F. maxima* in northern Chile. II. Notes on its reproduction. Biol. Bull. 165:559–568.

Herrera, G. 1983. Análisis estacional del ciclo sexual en ovario de *F. maxima* en el norte de Chile. Resumen, Reunión Soc. Biol. 1983.

Jara, F. H. & C. Moreno. 1984. Herbivory and structure in a midlittoral, rocky community: a case in southern Chile. Ecology 65:28–38.

McLean, J. 1984. Systematics of *Fissurella* in the Peruvian and Magellanic faunal provinces (Gastropoda: Prosobranchia). Contribution in Science No. 354:1–70. Natur. Hist. Mus. Los Angeles.

Moreno, A. C. & E. Jaramillo. 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coast near Valdivia. Oikos 41:73–76.

Oliva, D. & J. C. Castilla. 1986. The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. Mar. Ecol. 7(3):201–217.

Osorio, C., J. Atria & S. Mann. 1979. Moluscos marinos de importancia económica en Chile. Biol. Pesq. 11:3–47.

Santelices, B. 1981. Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. I. Cinturones de macroalgas. Medio Ambiente 5(1–2):175–189.

Santelices, B., J. Vasquez & I. Meneses. 1986. Patrones de distribución y dietas de un gremio de moluscos herbívoros en habitats intermareales expuestos de Chile central. Monografías Biológicas 4:147–171.

Santelices, B. & M. E. Vera. 1984. Variación estacional de floras marinas en Caleta Horcón, Chile central. Phycol. Lat. Amer. 2:83–101.

Steneck, R. S. & L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Mar. Biol. 68:299–319.

Ward, J. 1966. Feeding, digestion and histology of the digestive tract in the key hole limpet *Fissurella barbadensis* Gmelin. Bull. Mar. Sci. 16(4):668–683.

The Veliger 30(4):351-357 (April 1, 1988)

THE VELIGER

Variable Population Structure and Tenacity in the Intertidal Chiton *Katharina tunicata* (Mollusca: Polyplacophora) in Northern California

by

TIMOTHY D. STEBBINS

Department of Biological Sciences, University of Southern California,
Los Angeles, California 90089, U.S.A. and
Invertebrate Zoology Section, Los Angeles County Museum of Natural History,
Los Angeles, California 90007, U.S.A.

Abstract. Populations of the chiton *Katharina tunicata* (Wood, 1815) were studied at three rocky intertidal areas in northern California, each subjected to a different degree of wave exposure. The spatial density and size structure of *Katharina* populations varied with the degree of exposure to wave action. Chiton densities increased and body sizes decreased with increased exposure to wave action. Laboratory experiments showed that tenacity (adhesion strength, or resistance to shear force) of *Katharina* significantly increased with a decrease in body size. This increased capacity of smaller chitons to resist removal from the substratum may provide a mechanism for the observed patterns of abundance and size-distribution of *Katharina*.

INTRODUCTION

Organisms living in rocky intertidal areas on exposed shores encounter a number of biological and environmental factors that interact to regulate population and community structure (see reviews by CONNELL, 1972; STEPHENSON & STEPHENSON, 1972; RICKETTS *et al.*, 1985). Waves are an important agent of disturbance on rocky shores and may be extremely important in structuring intertidal populations and communities (*e.g.*, JONES & DEMETROPOULOS, 1968; PAINE & LEVIN, 1981; DENNY, 1985; DENNY *et al.*, 1985). Analyses of intraspecific variation of important intertidal organisms at sites varying in exposure may yield information critical to our understanding of community ecology.

Chitons are conspicuous components of intertidal communities in many areas of the world (BOYLE, 1970; GLYNN, 1970; PAINE, 1980; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985; OTÁIZA & SANTELICES, 1985). The role of motile herbivores like chitons in regulating algal composition and ultimately community structure may be extremely important (PAINE & VADAS, 1969; DAYTON, 1975; LUBCHENCO & MENGE, 1978; LUBCHENCO & GAINES, 1981). Aside from studies on reproductive biology (HIMMELMAN, 1978, 1979, 1980; PEARSE, 1978; SAKKER, 1986) relatively little is known about the ecology of intertidal chitons (see BOYLE, 1970; GLYNN, 1970; ANDRUS & LEGARD, 1975; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985; OTÁIZA & SANTELICES, 1985).

The chiton *Katharina tunicata* (Wood, 1815) (hereafter as *Katharina*) is an important member of mid- to low-intertidal communities along the Pacific coast of North America (HIMMELMAN, 1978; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985), and has a geographic range from Alaska to southern California (HADERLIE & ABBOTT, 1980; RICKETTS *et al.*, 1985). Despite the abundance and importance of *Katharina* in structuring intertidal communities (DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985) little is known regarding intraspecific variation in this chiton.

Preliminary observations suggested that the population structure of *Katharina* varied at different sites in northern California. In this study abundances and size distributions of *Katharina* were quantified at three rocky intertidal areas and correlated with the degree of wave exposure at the sites. In addition, the tenacity (adhesion strength) of chitons was measured in the laboratory to determine if tenacity varied with body size. Finally, several alternative hypotheses are discussed that may explain the observed patterns of *Katharina* population structure.

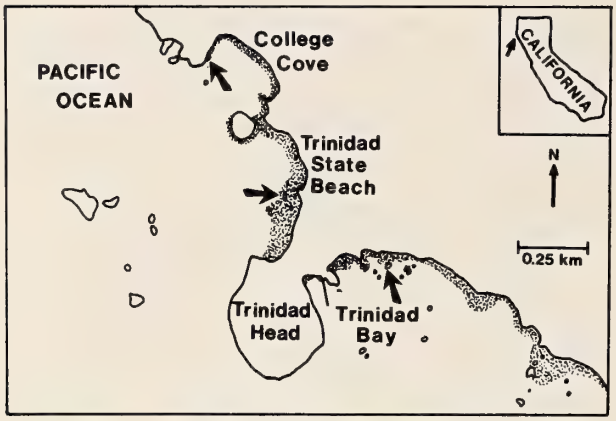


Figure 1

Location of study areas (arrows) near Trinidad, northern California (41°03′07″N, 124°07′51″W). In order of decreasing exposure to wave action the study sites are Trinidad State Beach, College Cove, and Trinidad Bay.

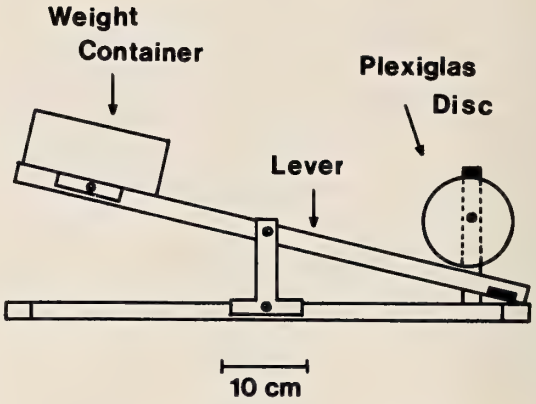


Figure 2

Apparatus used to measure tenacity of chitons on a hard substrate (Plexiglas) and subjected to shear forces.

MATERIALS AND METHODS

Study Areas

The study was conducted at three rocky intertidal areas near Trinidad, in northern California (Figure 1). The sites were similar in terms of inclination and heterogeneity of the substratum and were covered primarily with crustose coralline algae and clumps of the laminarian *Hedophyllum sessile* (C. Agardh) Setchell. *Katharina tunicata* was the most prominent herbivore at the sites, although the limpets *Lottia pelta* (Rathke, 1833) (=*Collisella pelta*) and *Tectura scutum* (Rathke, 1833) (=*Notoacmea scutum*) were also common. The seastar *Pisaster ochraceus* (Brandt, 1835) occurred at all sites below the zone of *Katharina,* although it was more abundant at the most exposed site.

Transects were initially established at each study site through belts of *Hedophyllum* at about 0.5 m below to 0.5 m above mean lower low water. These transects were oriented perpendicular to the direction of wave impact and marked by permanent 5-cm^2 markers bolted to the substratum.

The three study areas differ in their degree of exposure to wave action. Trinidad State Beach faces west-northwest and receives the full force of waves and swells. College Cove is slightly protected from wave action by a projecting headland. The south-facing Trinidad Bay site is largely protected from most waves and swells by Trinidad Head and numerous offshore rocks. A more objective "exposure index" similar to that described by MENGE (1976) was calculated for each area (Table 1) and supported the subjective observations. In order of decreasing exposure to wave action, the study areas were Trinidad State Beach, College Cove, and Trinidad Bay.

Table 1

Exposure indices at three study areas in northern California from April 1980 to April 1981. Exposure index = (no. of transect markers lost ÷ no. of marker-months) × 100. A marker-month is one marker in place for 1 month.

Study area	Exposure index
Trinidad State Beach	26.9 (7/26)
College Cove	13.8 (4/29)
Trinidad Bay	0 (0/36)

Sampling Procedures

Katharina populations were examined monthly at each site over a 13-month period from April 1980 to April 1981, except in January 1981 when severe wave action prohibited access. Monthly population densities and size-class distributions were estimated from 10 randomly chosen 0.25-m^2 quadrats along the transects at each study site. All chitons occurring within the quadrats were counted, and body lengths measured to the nearest 0.1 mm with calipers. Mean numbers of individuals per 0.25 m^2 and mean body lengths were calculated monthly for each site.

Experimental Procedures

Sixty-four individuals of *Katharina* between 1.0 and 10.0 cm in body length were studied to determine if their ability to resist removal from a hard substrate (defined as tenacity) varied with body size. Chitons were collected near the field sites between April and August 1981 and maintained in running seawater aquaria at the Telonicher Marine Laboratory (Trinidad, California) of Humboldt State University. All test specimens were used within 2 weeks of collection and each animal was used in only one test. Only healthy animals were tested. Tenacity, expressed as the force per unit area required to dislodge a chiton, was measured using an apparatus that applied a shear force parallel to the chiton's foot (Figure 2). Test substrates

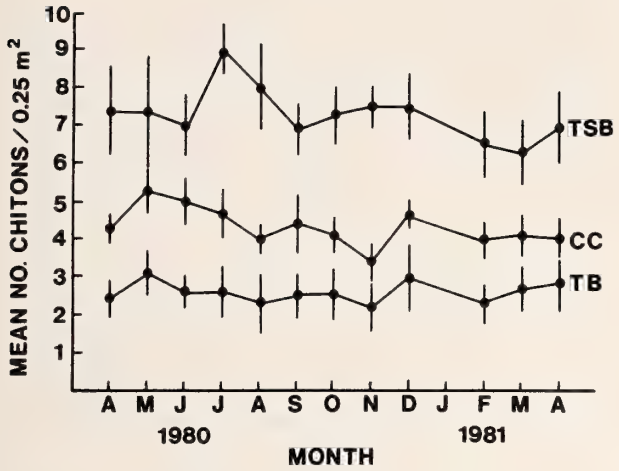


Figure 3

Population densities of *Katharina tunicata* at Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB) in northern California. Data for each month are expressed as mean number of chitons per 0.25 m^2 ± 1 SE.

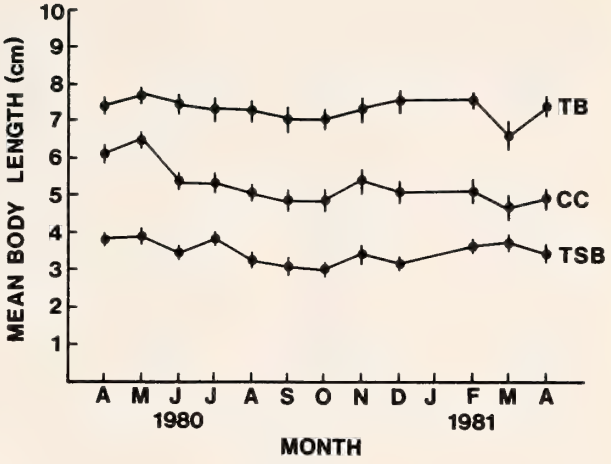


Figure 4

Mean body sizes of *Katharina tunicata* at Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB) in northern California. Data for each month are expressed as mean body length (cm) of chitons ± 1 SE.

were roughened Plexiglas discs 10 cm in diameter. Chitons were allowed to remain attached to the test surface for approximately 2 h prior to testing. After attachment, the test disc was attached to the apparatus and the lever positioned parallel to the plane of the foot of the attached chiton. Each individual was tapped lightly immediately before testing to induce it to adhere to the substratum as tightly as possible. Weights were then added to the container in 25 g increments every 2.5 sec until the chiton was dislodged from the surface; the maximum weight (g) necessary to cause detachment was recorded. The body length and weight of each individual were measured after testing. The foot surface area (cm^2) was determined by placing the chiton on a transparent grid. Tenacity was calculated as total weight applied per foot area, and converted to newtons per m^2 ($N \cdot m^{-2}$).

RESULTS

Abundance and Size Distribution

The average numbers of *Katharina* per 0.25 m^2 were plotted over the study period for each study site (Figure 3). These mean densities throughout the year differed significantly between sites ($P < 0.005$; Kruskal-Wallis Analysis of Variance). The chiton densities at Trinidad Bay were significantly lower than at College Cove and Trinidad State Beach, and the densities at College Cove were significantly lower than those at Trinidad State Beach ($P < 0.001$; Mann-Whitney U-test). The densities during the study ranged from 0 to 16 chitons per 0.25 m^2. The animals tended to aggregate around and under clumps of *Hedophyllum,* accounting for an observed patchiness. Generally there were no significant seasonal trends in density fluctuations. However, the decreases in *Katharina* densities between December 1980 and February 1981 may be related to severe storm activity during that period.

The mean body lengths of *Katharina* were plotted for each area over the study period (Figure 4) and were found to differ significantly between sites ($P < 0.001$; one-way ANOVA). Trinidad Bay chitons were significantly larger than those at College Cove and Trinidad State Beach, and the chitons at College Cove were significantly larger than those at Trinidad State Beach ($P < 0.05$; Student-Newman-Keuls test). The body lengths of individuals ranged from 0.72 to 10.15 cm during the study with maximum mean lengths occurring in May 1980 at all sites. The size-class distributions clearly show the distinct nature of the three *Katharina* populations (Figure 5). Greater than 70% of the chitons at Trinidad State Beach, the most exposed site, were consistently less than 5.0 cm in length, while chitons in this size range consistently made up less than 20% of the population at the least exposed site, Trinidad Bay. The size range of College Cove chitons was intermediate between the two extreme sites.

Recruitment

Katharina grows to a length of 2.5 cm during its first year (Hyman, 1967). The relative frequency of juvenile chitons less than 2.0 cm long was plotted for each site over the study period and used as an estimate of recruitment (Figure 6). From these data it appears that recruitment differed significantly at the sites, at least immediately preceding and during this study. Juveniles of *Katharina* were a conspicuous component of the chiton population throughout the year at Trinidad State Beach, with a noticeable peak following the summer of 1980. This peak corresponds with a main spawning period in June as reported by Him-

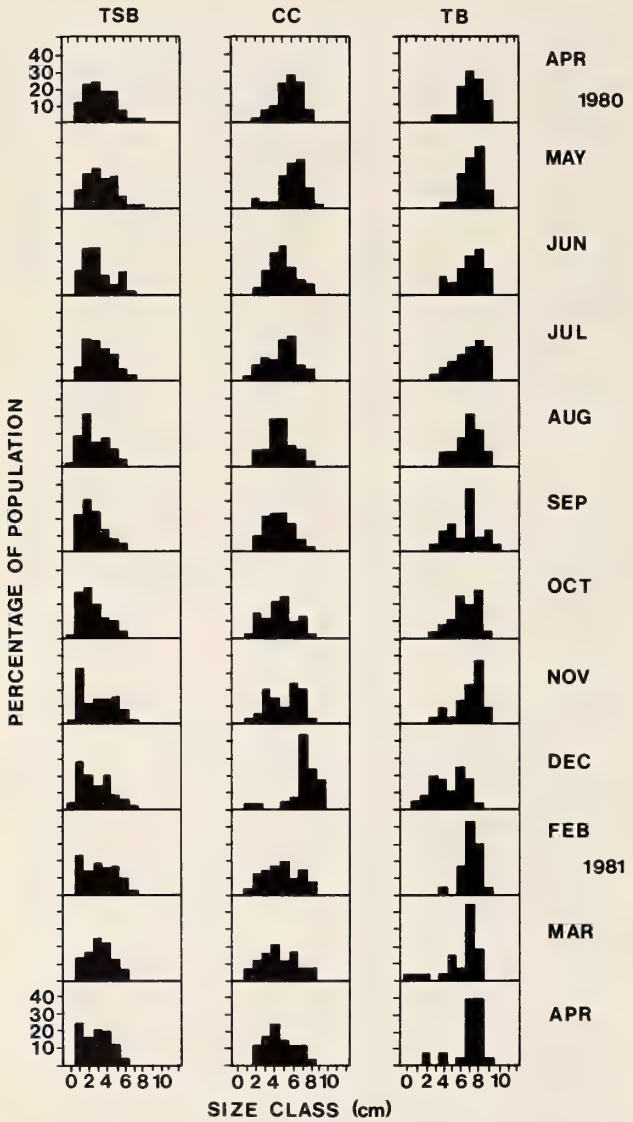


Figure 5

Katharina tunicata. Size-frequency distributions of chitons at three study areas in northern California: Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB).

MELMAN (1978). In contrast, juveniles were much rarer at the other two study sites.

Juvenile *Katharina* occurred in five different microhabitats during low tides: (1) in cracks or crevices on exposed surfaces, (2) in cracks or crevices under blades of *Hedophyllum*, (3) on bare rock or coralline crusts under *Hedophyllum* blades, (4) under adult *Katharina*, and (5) within *Hedophyllum* holdfasts. Another chiton, *Lepidochitona dentiens* (Gould, 1846) (=*Cyanoplax dentiens*), often coexisted with *Katharina* juveniles within kelp holdfasts.

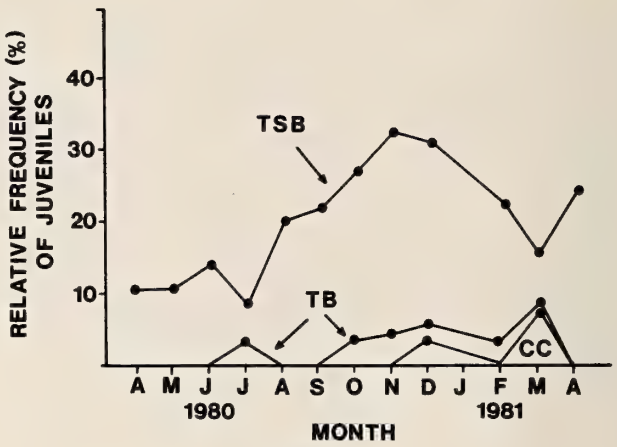


Figure 6

Recruitment of *Katharina tunicata* as estimated by the relative frequency of juveniles (length < 2.0 cm) in chiton populations at Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB).

Tenacity

There was a significant decrease of tenacity ($N \cdot m^{-2}$) with increasing body size ($P < 0.001$; see Figure 7). Small chitons (2–3 cm long) were up to twice as resistant to removal as were large individuals (8–10 cm). Resistance of animals ranged from 0.87×10^4 $N \cdot m^{-2}$ (a 9.31 cm individual) to 5.10×10^4 $N \cdot m^{-2}$ (a 2.16 cm individual and a 2.49 cm individual). Mean tenacity for all *Katharina* tested ($n = 64$) was $2.45 \pm 1.00 \times 10^4$ $N \cdot m^{-2}$ ($\bar{x} \pm$ SD). LINSENMEYER (1975) reported a lower mean resistance value for *Katharina* equivalent to $1.45 \pm 0.38 \times 10^4$ $N \cdot m^{-2}$ ($n = 12$); however, he provided no data on body sizes. Linsenmeyer's lower value may simply reflect his use of larger individuals.

DISCUSSION

Katharina tunicata is a major determinant of intertidal community structure in the eastern North Pacific whose importance stems from its size, density, and generalist feeding behavior (DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985). However, little is known regarding variation between populations of this chiton. *Katharina* was the dominant herbivore at my study sites, averaging approximately 10–36 individuals per m^2. These densities are comparable to those described for more northern populations (PAINE, 1980; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985). The density and size structure of *Katharina* populations were shown to vary with the degree of exposure to wave action (Figures 3–5). There was an inverse correlation between population densities and body size of chitons at the three study sites; density increased and body size decreased with increased exposure to wave action.

Andrus & Legard (1975) reported similar observations for *Katharina* in central California. Similar patterns of abundance and size distribution have been reported for other motile invertebrates including limpets in Great Britain (Jones, 1948; Southward, 1953; Southward & Orton, 1954; Ballantine, 1961) and Australia (Meyer & O'Gower, 1963). Harger (1970, 1972) and Paine (1976a, b) have shown that temperate mussels and seastars also increase in size where wave action is less, while Connell (1972) has shown a similar trend for some marine algae. In contrast, Otáiza & Santelices (1985) reported that the large Chilean chitons *Acanthopleura echinata* (Barnes, 1824) and *Chiton latus* Sowerby, 1825, displayed an opposite trend, with larger individuals occurring in the most exposed habitats.

Patterns of intertidal population and community structure are the result of complex interactions of predation, competition, biological disturbance, exposure to wave action, and the inclination and heterogeneity of the substratum (Dayton, 1971; Menge, 1976). The inclination and heterogeneity of the substratum were similar at my three northern California study sites and were probably not responsible for differences between *Katharina* populations. Intraspecific competition was probably not important since neither food nor space ever appeared to be limiting. Interspecific competition was probably minor since no major competitors for the large macrophytic algae (*e.g., Hedophyllum*) occurred in these areas. The only other common herbivores at these sites were the limpets *Lottia pelta* and *Tectura scutum*. These limpets have been described as "indirect commensals" of *Katharina* (Dethier & Duggins, 1984) and probably have little effect on chiton population structure. Predation pressure may vary between sites since the predatory seastar *Pisaster ochraceus* was more abundant at the most exposed site, Trinidad State Beach. Although *Pisaster* is known to eat *Katharina* (Paine, 1966; Dayton, 1975; Carefoot, 1977), I never noticed an instance of predation in three years of observation. Thus, it seems unlikely that seastar predation plays a major role in regulating chiton populations near Trinidad, although these observations were restricted to periods of low tides. More information on the feeding habits of *Pisaster* during high tides is needed before definitive conclusions can be made regarding the effect of predation on *Katharina*.

Many motile invertebrates (*e.g.,* seastars, limpets, and chitons) can withstand the direct force of waves by adhering tenaciously to the substratum. The effects of wave action on populations of these organisms cannot be easily predicted. However, degree of wave action may have important consequences on the age or size structure of intertidal populations, since waves are more likely to remove large than small individuals from the substratum (Denny *et al.*, 1985). Larger chitons may have a greater likelihood of being detached because, as body length increases, the area of attachment (*i.e.,* the foot) does not increase proportionately. Consequently, large animals have a greater ratio of body size to attachment surface and higher profile than small individuals, and could be more susceptible to detachment by wave action. If such is the case, wave action could regulate *Katharina* population structure by removing larger animals in greater numbers than small animals. If this hypothesis is correct, one would expect large chitons to be less abundant than small individuals at areas of high wave impact, and more abundant at more protected areas. Such was the case at the northern California sites. These observations suggest that small chitons have an advantage over large individuals at withstanding forces associated with wave shock. Although Linsenmeyer (1975) demonstrated that the force required to dislodge different species of chitons was directly related to the degree of wave action in the habitat of each species, no attempt was made to determine if resistance to removal (tenacity) varied with body size.

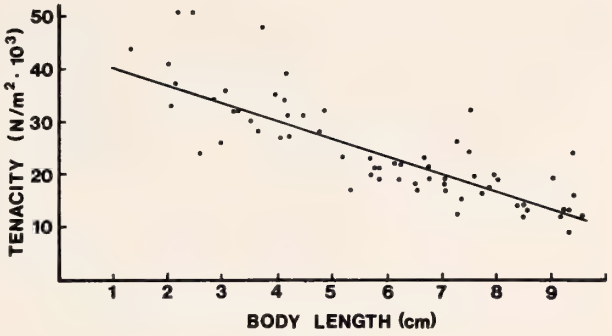


Figure 7

Tenacity of *Katharina tunicata*. Resistance of chitons on a hard substrate (Plexiglas) to removal by a shear force. Least-squares linear regression of tenacity ($N \cdot m^{-2}$) as a function of body size (length in cm). Regression line ($y = 45418 - 3576x$) significant at $P < 0.001$ ($n = 64$).

In this study, there was a significant relationship between the body size and tenacity of *Katharina*; tenacity increased with decreased body size (Figure 7). This increased capacity of smaller chitions to resist removal from the substrate may explain the observed patterns of abundance and size distribution of these animals near Trinidad, by way of limiting the size of chitons at more exposed areas. Although this differential size resistance may explain the observed population structure of *Katharina,* this hypothesis depends upon several assumptions. First, the adhesive abilities of *Katharina* will limit populations only if chitons actually are washed off the substrate. At present there is no direct evidence that they are. Secondly, the chitons must experience shear forces near their adhesive strengths if they are going to be dislodged. This is difficult to determine for *Katharina* because tenacity values were calculated using an unnaturally smooth substrate (Plexiglas), and therefore probably represent underestimates of

this chiton's true adhesive abilities (see MILLER, 1974; LINSENMEYER, 1975; DENNY *et al.*, 1985). Furthermore, chitons may not adhere in the lab with a tenacity approaching that in nature. However, these estimates of *Katharina* tenacity ($\sim 1\text{–}5 \times 10^4$ N·m^{-2}) are only an order of magnitude lower than values for limpets ($\sim 1\text{–}4 \times 10^5$ N·m^{-2}) (BRANCH & MARSH, 1978; GRENON & WALKER, 1982; DENNY *et al.*, 1985) on natural surfaces. It seems likely that *Katharina* has adhesive strength at least comparable to limpets under natural conditions. DENNY *et al.* (1985) and others have concluded that, at least for limpets, adhesion is much stronger than typical wave shear. In addition, GLYNN (1970) reported that the Caribbean chitons *Acanthopleura granulata* (Gmelin, 1791) and *Chiton tuberculatus* Linnaeus, 1758, were capable of surviving forces equivalent to those generated by waves 5.5 m high. Finally, there is evidence that normal (lift) forces may be more important than the shear forces measured here (DENNY *et al.*, 1985).

Although the size-resistance hypothesis may explain the observed patterns of abundance and size distribution of *Katharina*, several other alternative hypotheses also explain these patterns. (1) Topographic irregularities (*e.g.*, holes and crevices) may provide greater refuge from wave impact to small chitons than large individuals; large chitons would be selectively removed from areas of high wave impact owing to the lack of suitable refuge. The restriction of juvenile *Katharina* to some type of shelter (under kelp or adult chitons, in cracks or crevices) lends support to this hypothesis. (2) Differential recruitment may be important. Increased recruitment rates at areas at high wave exposure could explain the observed patterns. However, these patterns may be variable in time and space and have little to do with the sites themselves. (3) Less feeding time at areas of high wave impact, due to the increased turbulence in these areas, could cause lower growth rates in chitons; these lower growth rates could result in smaller individuals at areas of high wave exposure. (4) The reduced body size of chitons at areas of high wave shock may be due to increased mortality rates (decreased mean longevity) associated with the severity of the environment.

Knowledge of intraspecific variation of important intertidal species is essential to developing a clear understanding of community organization and structure. More data on chiton hydrodynamics and on feeding times, recruitment, growth rates, and longevity for *Katharina* at areas of varied exposure to wave action are needed to interpret adequately the role that various factors play in regulating the population structure of this animal. Wave action may mediate the population structure of this chiton through complex interactions of some or all of the above proposed hypotheses.

ACKNOWLEDGMENTS

I wish to thank Drs. M. J. Boyd and G. J. Brusca for their advice and guidance throughout this project. I gratefully acknowledge: P. Bixler, L. Bott, K. Cooper, G. Crandell, C. Diebel, V. Frey, R. Rasmussen, and D. Richards for discussions; P. Collins for computer advice; and R. Holsinger for design and construction of the tenacity apparatus. The director and staff of the Telonicher Marine Laboratory kindly provided use of their facilities. I am deeply indebted to P. Bixler, S. Birks, and Jesse for field assistance. This manuscript benefitted substantially from critical reviews by G. J. Bakus, M. J. Boyd, G. J. Brusca, R. C. Brusca, P. M. Delaney, M. W. Denny, and J. F. Quinn. This work is based in part on a M.A. Thesis submitted to the Department of Biological Sciences at Humboldt State University, California.

LITERATURE CITED

ANDRUS, J. K. & W. B. LEGARD. 1975. Description of the habitats of several intertidal chitons (Mollusca: Polyplacophora) found along the Monterey Peninsula of central California. Veliger 18(Suppl.):3–8.

BALLANTINE, W. J. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. Field Studies 1:1–19.

BOYLE, P. R. 1970. Aspects of the ecology of a littoral chiton, *Spharochition pelliserpentis* (Mollusca: Polyplacophora). N.Z. Jour. Mar. Freshwater Res. 4:364–384.

BRANCH, G. M. & A. C. MARSH. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. Jour. Exp. Mar. Biol. Ecol. 34:111–130.

CAREFOOT, T. H. 1977. Pacific seashores. A guide to intertidal ecology. University Washington Press: Seattle. 208 pp.

CONNELL, J. H. 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. 3:169–191.

DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.

DAYTON, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45:137–159.

DENNY, M. W. 1985. Wave forces on intertidal organisms: a case study. Limnol. Oceanogr. 30:1171–1187.

DENNY, M. W., T. L. DANIEL & M. A. R. KOEHL. 1985. Mechanical limits to size in wave-swept organisms. Ecol. Monogr. 55:69–102.

DETHIER, M. N. & D. O. DUGGINS. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. Amer. Natur. 124:205–219.

DUGGINS, D. O. & M. N. DETHIER. 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. Oecologia 67:183–191.

GLYNN, P. W. 1970. On the ecology of the Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linné: density, mortality, feeding, reproduction, and growth. Smithson. Contrib. Zool. 66:1–21.

GRENON, J.-F. & G. WALKER. 1982. The tenacity of the limpet *Patella vulgata* L.: an experimental approach. Jour. Exp. Mar. Biol. Ecol. 54:277–308.

HADERLIE, E. C. & D. P. ABBOTT. 1980. Polyplacophora: the chitons. Pp. 412–428. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, California.

HARGER, J. R. E. 1970. The effect of wave impact on some aspects of the biology of sea mussels. Veliger 2:401–414.

HARGER, J. R. E. 1972. Competitive coexistence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. Veliger 14:387–410.

HIMMELMAN, J. H. 1978. The reproductive cycle of *Katharina tunicata* Wood and its controlling factors. Jour. Exp. Mar. Biol. Ecol. 31:27–41.

HIMMELMAN, J. H. 1979. Factors regulating the reproductive cycles of two northeast Pacific chitons, *Tonicella lineata* and *T. insignis*. Mar. Biol. 50:215–225.

HIMMELMAN, J. H. 1980. Reproductive cycle patterns in the chiton genus *Mopalia* (Polyplacophora). Nautilus 94:39–49.

HYMAN, L. H. 1967. The invertebrates: volume VI, Mollusca I. McGraw-Hill: New York. 792 pp.

JONES, N. S. 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. Proc. Trans. Liverpool Biol. Soc. 56:60–77.

JONES, W. E. & A. DEMETROPOULOS. 1968. Exposure to wave action: measurements of an important ecological parameter on rocky shores on Anglesey. Jour. Exp. Mar. Biol. Ecol. 2:46–63.

LINSENMEYER, T. A. 1975. The resistance of five species of Polyplacophora to removal from natural and artificial surfaces. Veliger 18(Suppl.):83–86.

LUBCHENCO, J. & S. D. GAINES. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst. 12:405–437.

LUBCHENCO, J. & B. A. MENGE. 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 59:67–94.

MENGE, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46:355–393.

MEYER, G. R. & A. K. O'GOWER. 1963. The ecology of six species of littoral gastropods. I. Association between species and associations with wave action. Aust. Jour. Mar. Freshwater Res. 14:176–193.

MILLER, S. L. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. Jour. Exp. Mar. Biol. Ecol. 14:99–156.

OTÁIZA, R. D. & B. SANTELICES. 1985. Vertical distribution of chitons (Mollusca: Polyplacophora) in the rocky intertidal zone of central Chile. Jour. Exp. Mar. Biol. Ecol. 86:229–240.

PAINE, R. T. 1966. Food web complexity and species diversity. Amer. Natur. 100:65–75.

PAINE, R. T. 1976a. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57:858–873.

PAINE, R. T. 1976b. Biological observations on a subtidal *Mytilus californianus* bed. Veliger 19:125–130.

PAINE, R. T. 1980. The third Tansley lecture. Food webs: linkage, interaction strength and community infrastructure. Jour. Anim. Ecol. 49:667–685.

PAINE, R. T. & S. A. LEVIN. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51: 145–178.

PAINE, R. T. & R. L. VADAS. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Mar. Biol. 4:79–86.

PEARSE, J. S. 1978. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. III. The chitons *Acanthopleura haddoni* Winckworth and *Onithochiton lyelli* (Sowerby), and the abalone *Haliotis pustulata* Reeve. Bull. Mar. Sci. 28:92–101.

RICKETTS, E. F., J. CALVIN & J. W. HEDGPETH (revised by D. W. PHILLIPS). 1985. Between Pacific tides. 5th ed. Stanford Univ. Press: Stanford, California. 652 pp.

SAKKER, E. R. 1986. Seasonal reproductive cycles of three Australian species of chitons (Mollusca: Polyplacophora). Int. Jour. Invert. Repro. Devel. 10:1–16.

SOUTHWARD, A. J. 1953. The ecology of some rocky shores in the south of the Isle of Man. Proc. Trans. Liverpool Biol. Soc. 59:1–50.

SOUTHWARD, A. J. & J. H. ORTON. 1954. The effects of wave action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. Jour. Mar. Biol. Assoc. U.K. 33:1–19.

STEPHENSON, T. A. & A. STEPHENSON. 1972. Life between tidemarks on rocky shores. W. H. Freeman & Co.: San Francisco. 425 pp.

The Veliger 30(4):358–368 (April 1, 1988)

THE VELIGER

Observations on the Larval and Post-Metamorphic Life of *Concholepas concholepas* (Bruguière, 1789) in Laboratory Culture

by

LOUIS H. DiSALVO

Department of Aquaculture, Universidad del Norte, Casilla 480, Coquimbo, Chile

Abstract. Observations were made in the laboratory on the postcapsular life of the Chilean "loco," *Concholepas concholepas*. Spontaneously eclosed veligers were cultured on two separate occasions, initiated in October 1984 and in July 1985. Veligers fed on monospecific cultures of microalgae grew from an initial shell length of 250 μm to near 1700 μm during periods of 111 to 124 days. Of several tens of thousands of early larvae, only seven individuals could be brought through metamorphosis, of which only one survived and was cultured to juvenile size. About 60 competent veligers were captured at sea with a neuston net, and returned to the laboratory where about 50% passed metamorphosis. Of these, 11 were cultured to 10–20 mm during a 3-mo period.

Aspects of the external morphology, growth, and behavior of larvae and postlarvae are reported for the first time for this species. The larvae produce a four-lobed velum and employ a byssal thread for flotation. They produce a distinctive lip on the larval shell indicating readiness for metamorphosis. The propodium functions actively in adherence to substrates at metamorphosis, making this species highly adapted for recruitment in the wave-swept Chilean intertidal zone.

INTRODUCTION

Concholepas concholepas (Bruguière, 1789), an unusual muricid gastropod of the South American temperate west coast, is both biologically interesting and of high commercial value. It is the last surviving species of a genus whose other six members became extinct before or during the Pleistocene (STUARDO, 1979). The existing species, commonly referred to in Chile as the "loco," occurs from the intertidal zone to depths of 40 m, and has a geographical range from the central coast of Peru to the southern tip of Chile. Ecologically, locos are first-level carnivores that prey upon filter feeders such as the barnacles, mussels, and tunicates abundant on the rocky Chilean coast (CASTILLA *et al.*, 1979). Locos reproduce by depositing egg capsules on subtidal rocks, primarily during the winter months. After an incubatory period of one or two months, veliger larvae hatch from the capsules and enter the coastal plankton for periods estimated to be about three months, after which the later veligers settle in the high intertidal zone during the spring and summer months (CASTILLA, 1982).

Concholepas concholepas represents the largest gastropod fishery in the world (FAO, 1981). Fueled by a strong export demand beginning in the 1970s, landings of this species reached 24,858 metric tons (MT) by 1980 (CASTILLA & JEREZ, 1986). By 1984 the total catch had dropped to 11,100 MT (SERNAP, 1985) with declines in catch per unit effort demonstrated on a localized basis (GEAGHAN & CASTILLA, 1986). The author participated on an advisory panel in 1986 and 1987 convened by the Chilean national fisheries service (SERNAP) in order to help plan regulations designed to avoid overexploitation of the loco fishery. Among the panel's recommendations has been the need to study the planktonic and early recruitment phase of the loco life cycle, and the feasibility of its mass production under artificial conditions. Although numerous studies have been made on diverse aspects of the biology of the loco (see review in CASTILLA, 1982) it had not, until the present study, been cultivated in the laboratory.

The present study investigated aspects of the larval and postlarval biology of *Concholepas concholepas,* and used some elements of our bivalve hatchery facilities to examine the feasibility of its mass culture. The first successful laboratory culture of the species is now reported, with observations on its external morphology and behavior through the planktotrophic phase and metamorphosis. The behavior of loco veligers in laboratory aquaria led us to sample

for wild specimens in coastal surface waters. Success in this endeavor included the first recovery of advanced veliger larvae, followed by their metamorphosis and growth in the laboratory; these results lent critical support to the otherwise limited success of larval culture in the laboratory.

MATERIALS AND METHODS

Attempts at culture of postcapsular veligers of *Concholepas concholepas* were initiated in months when mature egg capsules became available in the local habitat. The first culture was initiated in October 1984 and the second in July 1985. Capsules were collected by a diver at 3–5 m, from the surfaces of subtidal rocks near the mouth of Herradura Bay (30°S); capsules containing mature larvae were chocolate brown in color. Capsules were maintained in unfiltered, aerated seawater, which was changed daily, at ambient temperatures near 16°C until hatching was observed. As these cultures involved trial and error in handling the larvae, we describe only the methods from the second culture which was more successful.

About 10^5 actively swimming veligers were collected on a 100-μm aperture nylon screen (Nytex Co.) within 16 h of their emergence from the capsules. The larvae were washed with 1-μm filtered, UV treated seawater, and distributed evenly by visual estimate into 10 10-L plastic pails. The water was renewed every other day. To avoid breakage of the fragile larval shells, the larvae were always caught on the 100-μm screen without removing it from the water (D'Asaro, 1965). Culture water was treated with 25 mg/L chloramphenicol (Merck Co.) during the first 10 water changes in an attempt to eliminate bacterial infections that might have been acquired within the capsule. After the early water changes, antibiotic treatment was administered as needed when microscopic examination showed incipient bacterial infections of the larvae.

A number of empirical trials were made with early larvae to determine acceptable temperature, food, and larval density; larval survival, growth, and behavior were used to evaluate the success of these trials. Larvae were offered monospecific cultures of microalgae that were available from our bivalve hatchery production system. These included *Tetraselmis* sp., *Pavlova* sp., *Chaetoceros* sp., *Isochrysis galbana* (Tahitian strain), and a *Pseudoisochrysis* sp. Advanced larvae were given small amounts of mixed algae of the above species in an attempt to vary the nutritive sources in addition to the daily monospecific food ration found to be best for early larvae.

Shell fouling of the larvae by bacteria and stalked protozoa sometimes mechanically interfered with larval swimming and contributed to a deterioration in water quality. Also, free-living protozoa and copepods occasionally appeared as contaminants in the cultures. These problems were treated by administering 1-min tap-water rinses to the larvae at the time of water change, usually eliminating the contaminants without observable effects on the larvae.

Larvae were routinely observed in a 25-mL plankton chamber using an inverted microscope, and were measured with a calibrated ocular micrometer. Shell length in this report refers to the major length from the tip of the siphonal canal to the apex of the shell as seen in silhouette. After metamorphosis, shell length was measured using the ocular micrometer in a stereo microscope, and later with a ruler, estimating to the nearest 0.5 mm. Calipers were not used owing to the risk of breaking the fragile shells. Some observations of shells and radulae were made using a JEOL Corp. model JSM T300 scanning electron microscope (SEM).

The single laboratory cultured postlarva that survived past metamorphosis in November 1985 was maintained in an aerated culture pail with daily changes of ambient seawater at room temperature of about 16–18°C. Initially the specimen was kept on a scallop shell that was collected from the local intertidal zone and was lightly fouled with microbial slime films, small polychaetes, barnacles, and bryozoans. At about 8 mm in length, it was transferred to a similarly encrusted stone collected from the low intertidal zone in the bay, upon which had been found a naturally recruited loco of about the same size. At about 12 mm in length, juveniles of *Semimytilus algosus* (Gould) were added to the system as prey.

Recovery of naturally occurring larvae from plankton was accomplished by towing a buoyed-frame neuston net, 2 m in length, with 600-μm mesh openings. The mouth of the net was rectangular, measuring 40 cm high by 80 cm wide, and was floated to sample the top 20 cm of the sea surface. One-kilometer hauls were made between December 1986 and March 1987, in and around the mouth of Herradura Bay. Loco veligers were recognized by their similarity to laboratory reared larvae, and were easily separated from other plankton by their tendency to fall to the bottoms of the collecting vessels and adhere firmly in place. Larvae were handled with a small camel's hair brush to avoid breaking their shells. Veligers so collected were introduced into a laboratory aquarium containing naturally encrusted stones from the intertidal zone and a constant flow of ambient seawater. The effluent pipe was screened with 1-mm mesh so as not to lose swimming veligers. These larvae were observed daily for evidence of metamorphosis and those passing metamorphosis were transferred to a rearing system where they were observed and measured periodically. Natural substrates used in setting and rearing were lightly populated by microbial slime films, crustose red, green, and brown algae, as well as by small barnacles, bryozoans, polychaetes, and sponges. Large invertebrates were eliminated, leaving some clean surfaces on the stones. Juveniles of *Semimytilus algosus* were added to the system as prey.

RESULTS

Of the many thousands of larvae placed in culture during two successive years, few larvae survived the experimental period to pass metamorphosis. Two larvae from the 1984

culture and five larvae from the 1985 culture passed metamorphosis; all other larvae died during the course of the cultures. Figure 1 plots the sizes of the largest larvae produced in the cultures over time periods lasting from 111 to 124 days. Of the five postlarvae produced in the 1985 culture, only one survived more than a few days and was raised to a size in excess of 20 mm (Figure 6).

Sources of Mortality

The veligers suffered chronic mortality punctuated by irregular mass mortalities at all stages of their development. Microbial diseases often appeared in the cultures, with at least four types of infection clearly definable. The first of these was internal necrosis of early larvae by a purple-pigmented microorganism that we believe, based on unpublished data, to be a bacterium contracted during the capsular developmental phase. A second type of infection was produced by a finely filamentous microorganism, extensively investing the mantle edge of the larvae, causing debilitation and death. Larvae infected in this manner failed to respond to antibiotic treatment, suggesting that the infection was fungal. A third type of infection included a green-pigmented microorganism that infected the basal region of the compound velar cilia, causing piecemeal loss of ciliary tufts. This infection could be arrested by the addition of chloramphenicol to the culture water; most larvae infected in this manner recuperated and regenerated the lost cilia. A fourth problem was attack of the larvae by a ciliate protozoan (*Tetrahymena* sp.), an occasional parasite that is capable of invading the larval digestive gland causing death of the host. This disease may be the primary cause of chronic mortality in cultures of *Concholepas concholepas* at all stages, and has also been the cause of mass mortalities of scallop postlarvae in our hatchery (unpublished data). No effective control measures have been found for this disease in the loco cultures. Other losses of larvae may be due to shell breakage during handling, although larvae do have limited capacity to repair damage to the leading shell edge and siphonal canal.

The following is a sequential account of events observed in our cultures, based on observation of the largest larvae recoverable at each time.

Early Larvae

Eclosion from capsules occurred slowly over several days. Most larvae swim actively in the water column, rising to the surface in ambient light directed from above. Some larvae, perhaps those not fully developed, settle to the bottoms of the eclosion pails. At this stage the protoconch measures 240–260 μm, and is semitransparent with tuberculate ornamentation (Figure 2A). The velum consists of two round lobes, each about 150 μm in diameter (Figure 2B). The head region between the velar lobes has eyespots on either side of the mouth (Figure 2C) and one short cephalic tentacle that is anteroventral to the right eyespot and has four apical sensory bristles. A pair of statocysts is visible posterior to the eyespots. At hatching the foot does not extend beyond the posterior border of the protoconch, is immobile, and has a few short sensory bristles at its posterior extremity. At hatching the larval gut retains a small amount of vitelline material which is utilized in a few days. Larvae begin feeding in 24–48 h, as evidenced by the appearance of microalgal food in the digestive tract. If food is withheld after the larvae begin feeding, die-off begins after 3 days with complete mortality after 7 days. Larval kidneys emerge from the mantle cavity and are lost at about 24 h after hatching. Shell growth begins soon after the initiation of feeding, appearing as successive increments on the protoconch.

Among the five species of microalgae offered to replicate samples of larvae in several trials throughout the culture period, *Isochrysis galbana* (Tahitian strain) was the most acceptable, as evidenced by digestion of the algal cells and the survival and growth of the larvae. Excessive numbers of microalgae in the water induce the veligers to produce mucus, which comes away from the larvae in thin, algal-laden strands. This material settles, producing undesirable organic contamination in the culture vessels. Acceptable initial culture conditions include one larva and about 2×10^5 microalgal cells per mL of culture water. As the larvae grow, the food ration is increased according to the larval capacity to ingest the algae without producing mucus strands.

The veligers appear to be positively phototactic throughout the entire culture period. When placed in cylindrical plankton chambers for observation with an inverted microscope they swim upward toward the light source and drop quickly to the bottom when the light is extinguished.

One to Three Weeks

By the end of the first week, a dorsocentral beak begins to form on the shell over the cephalic region and the siphonal canal develops on the left side of the shell. After about 10 days the shell begins to darken, and by three weeks it is dark amber-brown in color. Shell color is due to a periostracum that can be dissolved away with 0.1 N NaOH. At 10 days, black chromatophores are scattered over the dorsal surface of the foot, and the foot begins to show its first weak contractions. A few sensory bristles appear around the margin of the foot.

At about three weeks, a mantle tentacle appears inside the right mantle cavity, barely visible inside the shell edge. The velum has doubled its original size, and begins to show lateral indentations. The outer margin of the velum develops brown pigmentation demarcating the line of origin of the locomotory (compound) cilia.

Four to Seven Weeks

By four weeks the largest larvae have completed the first shell revolution around the protoconch, and measure about

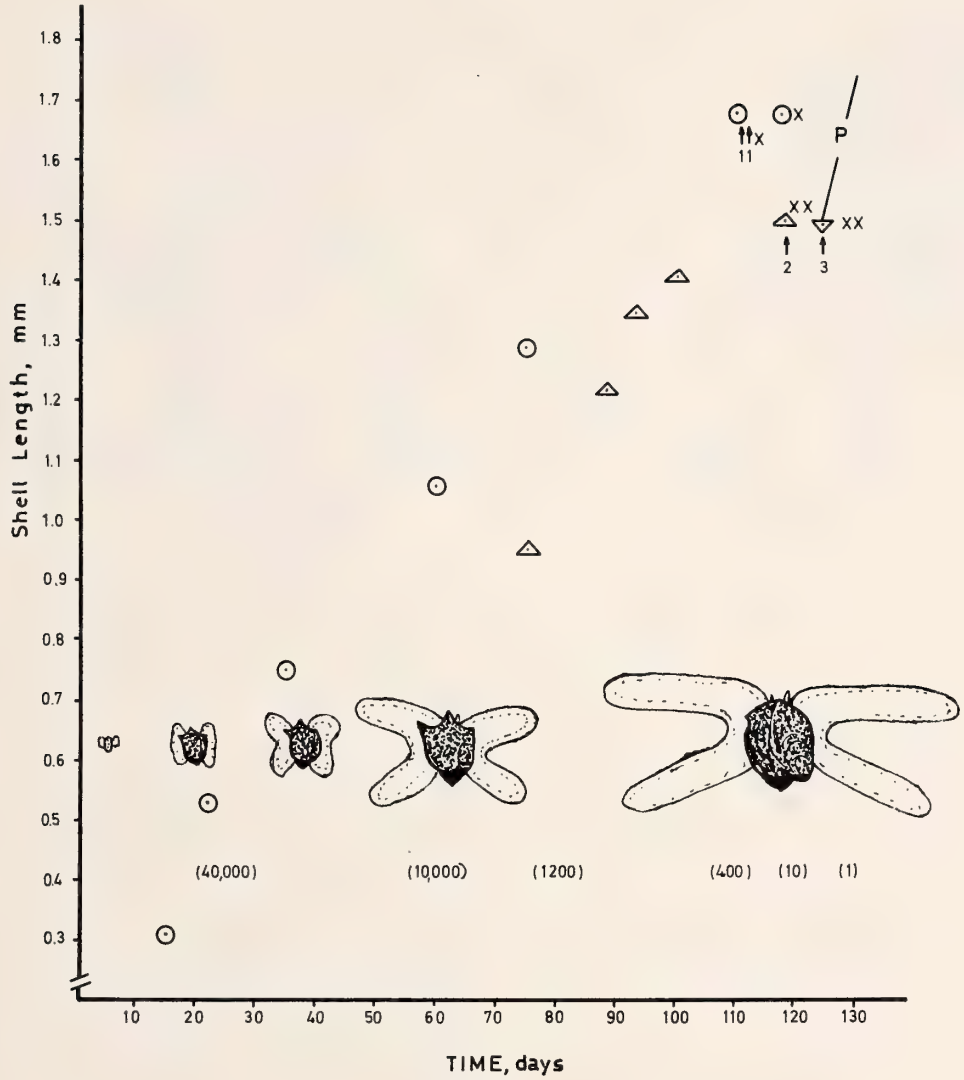


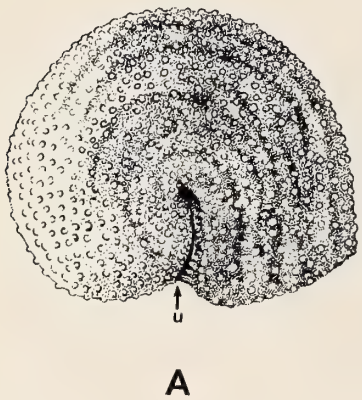
Figure 1

Sizes of largest individual veligers of *Concholepas concholepas* occurring in cultures initiated in October 1984 (circles) and July 1985 (triangles). Dorsal silhouette views of larvae show relative sizes of the larvae with time and development of the velum. Numbers in parentheses indicate approximate number of larvae surviving with time during the 1985 culture. Key: arrows, day of metamorphosis and number of specimens passing metamorphosis; X, death of a metamorphosed specimen; P, postlarval growth of single survivor, also plotted in Figure 6.

650 μm. The beak, with its central beak line, and the siphonal canal become prominent shell features (Figure 3). The shell becomes ornamented with radial lines (now coalescing from what began as lines of tubercles). The radial lines may act as reinforcement for the otherwise fragile shell. The velum has begun to elongate into four lobes, giving the veliger a "butterfly" appearance (Figure 3B). The velum remains unpigmented except for the outer margin. The single cephalic tentacle has begun to elongate and develop numerous sensory bristles.

The veligers swim freely in the culture pails at this stage, with no definable behavior pattern evident. The massing of larvae on the bottoms of the pails is often, although not always, a sign of developing disease or nutritional problems for a given group of larvae.

A notable development in the life of this veliger occurs beginning at 3–4 weeks with the appearance of a byssal thread issuing ventrally from a small gland at the extreme tip of the foot (Figure 3B). The byssal thread is about 1 μm in thickness and may extend for several centimetres. Larvae become capable of using the byssal thread for flotation, and are sometimes observed suspended in undis-



Figures 2A, B

External aspects of newly eclosed veliger larvae of *Concholepas concholepas,* shell length 260 μm. A. Right lateral view (shell only): u, umbilicus at center. B. Dorsal view: rt, right cephalic tentacle; lc, locomotory cilia.

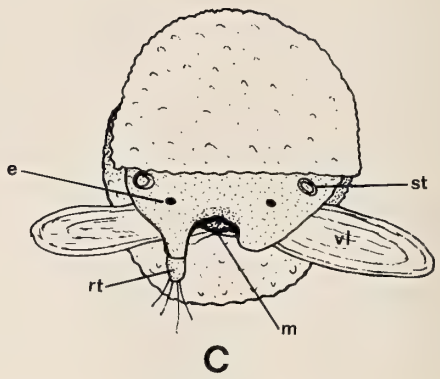


Figure 2C

Anterior view (locomotory cilia excluded): e, eyespot; st, statocyst; rt, right cephalic tentacle; vl, velar lobe; m, larval mouth.

turbed culture water with the thread adhering to the water surface film. These larvae could be gathered by inserting a dissecting needle through the air-water interface and catching the threads; threads were strong enough that individuals could be lifted from the water. Thread production could be induced in freely swimming larvae by short vigorous agitation of the culture water.

At about 40 days, the primordium of the second cephalic tentacle appears on the left side of the head region. The shell measures about 800 μm and has a pronounced beak. The four velar lobes become horizontally elongate and can measure a total width of 1350 μm when extended. The chromatophores on the foot become more numerous and diffuse, producing dark gray coloration; the foot increases its contractile movements. The propodial mucus gland appears as a horizontal slit across the anterior of the propodium, a structure that is now beginning to elongate and show independent movement. The secretion of a purple dye, typical of adult locos, is first observed at about 50 days as pigment granules deposited on the dorsum of the larval operculum.

Replicate cultures run between day 20 and 50 under the same conditions except for larval densities, showed significantly ($P = 0.95$) better growth of the larvae when maintained at densities of 250/L when compared with those at densities of 500 or 1000 larvae/L. Maximum shell length attained in these tests was 770 μm with 250 larvae/L, 624 μm with 500 larvae/L, and 562 μm with 1000 larvae/L. Individuals from a replicate culture with 250 larvae/L kept at 13–14°C were significantly ($P = 0.95$) smaller than those of the other groups maintained at 16–18°C; the maximum size recorded for this group was 580 μm. Unlike the other cultures, the cooler replicate experienced almost complete mortality near the end of the test period. Overall, larval densities had to be markedly decreased as the larvae grew in size, as they increasingly showed a tendency to become entangled with byssal threads or mucus strands. Nearing metamorphosis, the larval density had to be kept to 5–10 larvae/L.

Eight Weeks

The shell length measures 950–1000 μm, with about 20 μm added daily to the leading shell edge. The beak and siphonal canal continue to be prominent features of the shell. Larvae are capable of crawling on the foot for periods of up to 1 min during observations with the inverted microscope.

At 65 days, the extended foot measures about 950 μm, of which the propodium occupies about 200 μm. The propodium is about 200 μm in breadth when extended, and becomes active in dislodging mucus and algal debris from the velum and shell margin.

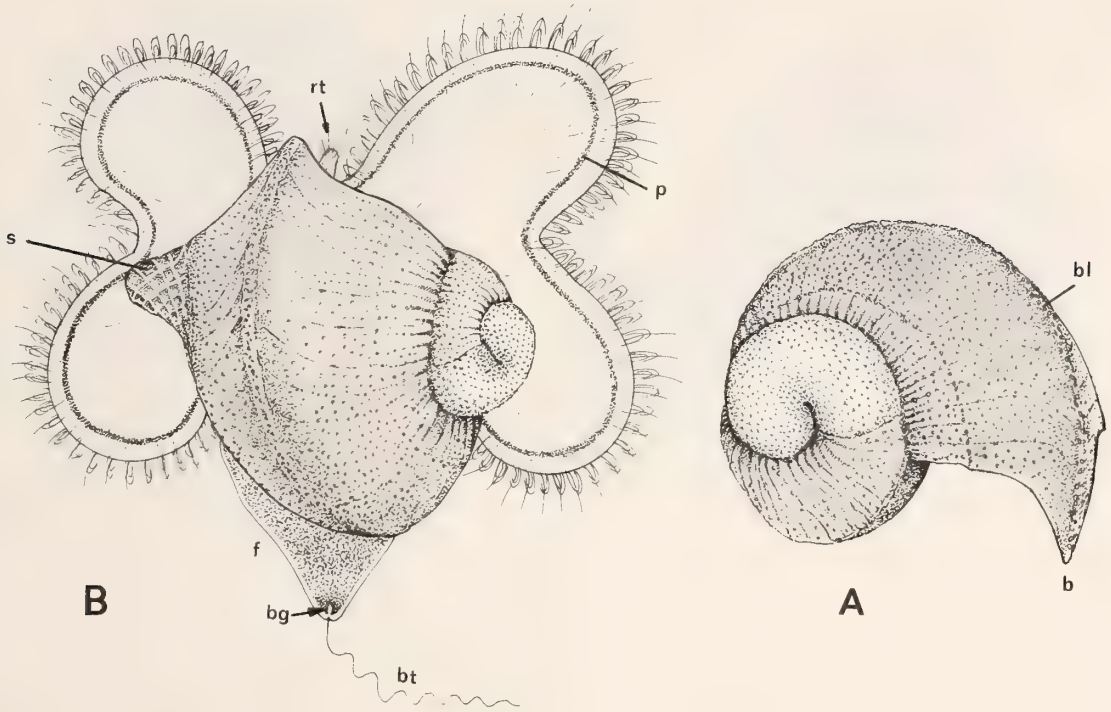


Figure 3

External aspects of one-month-old veliger larvae of *Concholepas concholepas,* shell length 650 μm. A. Right lateral view (shell only): b, beak; bl, beak line (crest). B. Dorsal view: bg, byssal gland; bt, byssal thread; f, foot; s, siphonal canal; rt, right cephalic tentacle; p, pigment.

Ten Weeks

Advanced larvae measure 1000–1200 μm in shell length, with a total velar extension of about 3200 μm. The right cephalic tentacle now measures about 260 μm in length, the left tentacle is about two-thirds this length, and the eyes are now located in the tentacle bases. The head and foot are now black, but the mantle edge, tentacle tips, and velum show little or no pigmentation. Veligers are capable of crawling on the foot for 3 min before they fall over. The operculum saddles the foot, is about 400 μm wide, and is stained purple.

At this stage larvae rarely swim, and are typically seen hanging by their byssal threads equidistant from one another in the culture water. The velum remains open and actively filtering. If released from the byssal threads, larvae drop to the bottom of the pail, but soon rise again in the water column. If they encounter the walls of the pail, they "push off" with a clapping motion of the velar lobes.

Twelve Weeks

The left tentacle reaches about three-quarters the length of the right tentacle. Shell growth has slowed, with largest veligers measuring 1400 μm (Figure 4). The gaps on either side of the beak have filled with shell, and the remnant of the beak is only a small projection.

Fourteen Weeks

Between 90 and 110 days, shell growth stops after completing 2.5 revolutions around the protoconch. Although early observations had suggested that ornamentation lines reflected daily growth increments, these "daily growth lines" could not be correlated with the known number of days in culture of the larvae. Using the SEM, what appeared to be true daily growth increments were demarcated by fine sutures in the shell. The cephalic tentacles are approximately equal in length, although the left tentacle tends to remain shorter than the right. The eyes project dorsolaterally near the base of each tentacle. A conical mentum, indicative of the site of the future opening of the postlarval mouth, is evident between the tentacles (Figure 4B).

The major event at this stage, indicating the termination of larval shell growth, was the production of an upturned lip around the leading edge of the shell (Figure 5). On two successive days metamorphosis was observed 24 h after the formation of the lip in each of two larvae from the culture initiated in October 1984 (Figure 1). Other lipped larvae from culture, as well as comparable larvae captured at sea, failed to undergo metamorphosis for days or weeks without further growth of the shell when maintained in clean culture vessels with microalgal food.

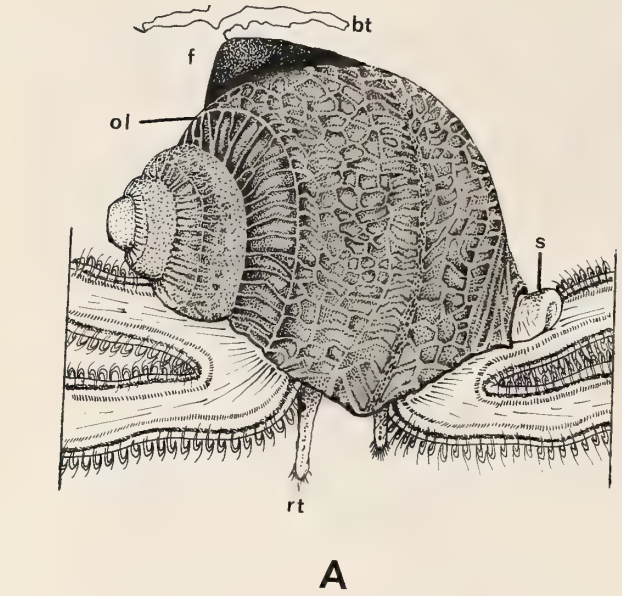
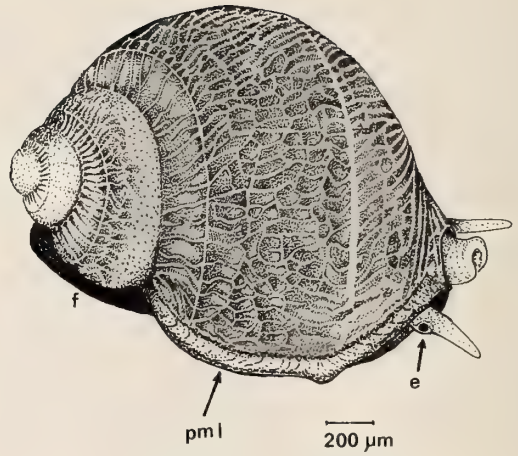


Figure 4

External aspects of three-month-old veliger larvae of *Concholepas concholepas*, shell length 1400 µm. A. Anterodorsal view: rt, right cephalic tentacle; s, siphon; ol, ornamentation lines; f, foot; bt, byssal thread. B. Anterior view of cephalic region (locomotory cilia omitted): SH, shell; s, siphon; me, mantle edge; e, eye; vl, velar lobe; rt, right cephalic tentacle; mt, mentum; m, larval mouth; po, post oral ciliary band; fg, food groove; pmg, propodial mucus gland; p, propodium; op, operculum.

The lipped shells of seven larvae from culture that passed metamorphosis measured between 1350 and 1690 µm in shell length, with velar extensions of up to 6500 µm. Thirty-one lipped larvae captured at sea measured between 1590 and 1830 µm ($\bar{x}$ = 1686; SD = 77).



Postlarval *Concholepas concholepas* prior to appearance of teleoconch, shell length 1690 µm: pml, premetamorphic lip; e, eye; f, foot.

Behavior Related to Settling and Metamorphosis

Development of a new behavior pattern becomes apparent after lip formation on the shell, preceding metamorphosis. The veliger acquires the capability of quick attachment to surfaces with which it comes in contact by the use of the suckerlike action of the (cupped) propodium. This behavior was first noted when attempting a routine transfer of lipped larvae with a glass pipette, to which they stuck immediately and with great tenacity.

At the lipped stage, veligers are capable of continuous crawling; we observed two of these veligers to settle on a natural substrate over which they crawled for periods of 24 h, after which they returned to a swimming existence. One veliger, accidentally left emersed for 8 h, returned to its swimming existence when returned to the water, and later passed metamorphosis. A further behavioral adaptation observed in lipped larvae may be referred to as "bubble capture." When strongly agitated by a jet of seawater from a hose, each veliger was observed to capture an air bubble using the foot, thus permitting it to float after loss of the byssal thread, and with the velum retracted. When left in calm water, each veliger released its bubble and resumed normal activity. This behavior was repeatedly elicited with dozens of larvae on different days.

Metamorphosis and Early Growth

Detailed observations of metamorphosis could not be made owing to the few larvae available and the unpredictability of the onset of metamorphosis. Of the total of seven larvae from the two laboratory cultures that passed metamorphosis, three died owing to accidents in handling, three failed to accept food and died without further growth in 3 to 7 days, and one survived and grew to juvenile size. The surviving postlarva was cryptic and difficult to find

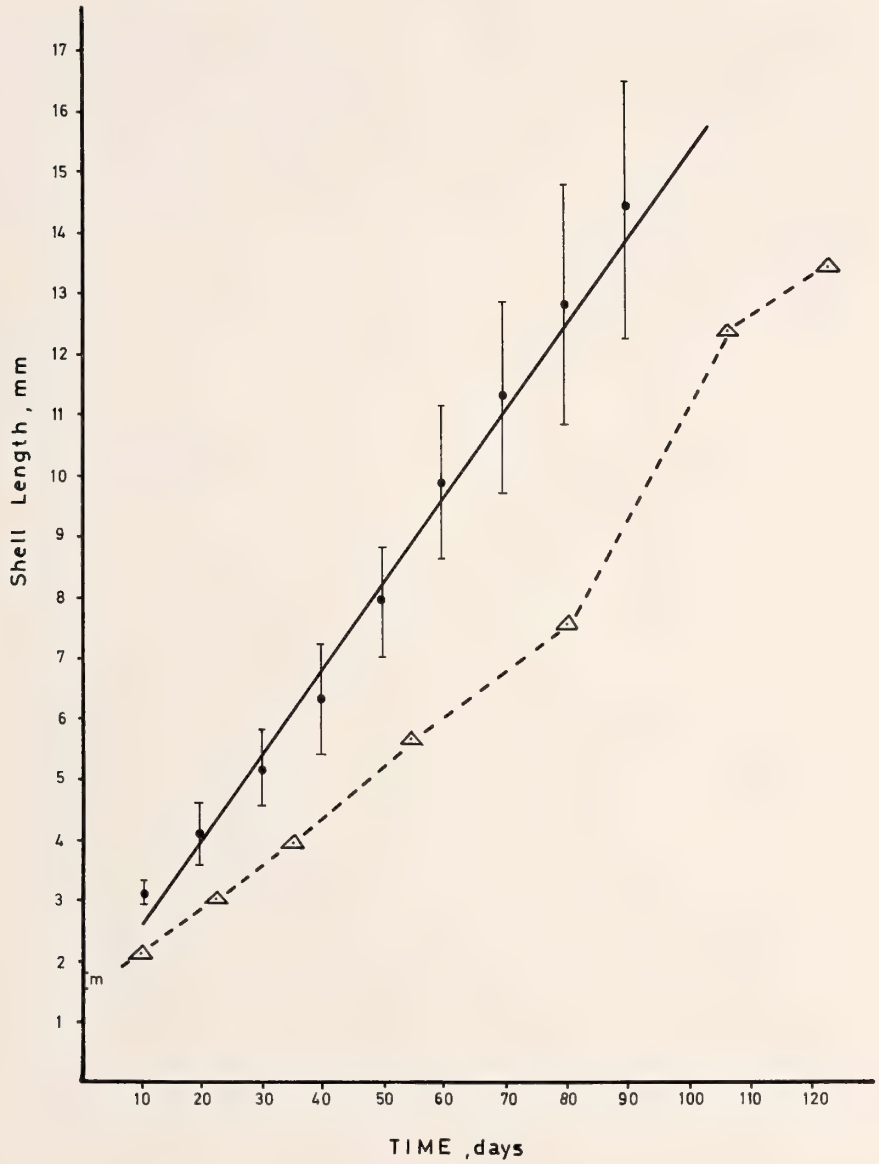


Figure 6

Growth after metamorphosis in the laboratory of 11 locos captured at sea as pre-metamorphic veligers (dots) ± 1 SD ($L_t = 1.16 + 0.143t$; $r = 0.98$). The growth of the single loco that survived through metamorphosis in laboratory culture is shown by the dotted line. m, sizes of specimens at metamorphosis.

while on its natural substrate. The first deposition of teleoconch material was observed at about 24 h post-metamorphosis as an extension of the siphonal canal. At about 48 h, the teleoconch became visible as a white ring around the shell margin. Teleoconch material deposited in the first few days was unpigmented, deposited in marked daily increments, and showed rugosity typical of advanced shells of *Concholepas concholepas*. A trunklike proboscis developed within 48 h of metamorphosis. This specimen grew to a size of 13.5 mm in the first four months post-metamorphosis (Figure 6). The first invertebrate prey taken by this specimen is unknown, although the specimen rasped the substrate at a very early stage, and later grazed on microalgae from the walls of the culture pail. Even after it began active predation on *Semimytilus algosus* it continued to graze clean 1–2 cm circular areas in a film of diatoms and bluegreen algae that had accumulated on the walls of the pail.

About 60 lipped larvae were captured at sea, half of which passed metamorphosis in the laboratory; 11 of these

survived the postlarval phase and were cultured to larger sizes (Figure 6). These veligers passed metamorphosis sporadically, rather than *en masse,* over periods of several days after their capture. Subsamples of this group failed to pass metamorphosis over a 48-h period when held in clean culture pails with aeration. Crawling veligers and postlarvae became negatively phototactic and were observed with difficulty on natural substrates owing to their small size, cryptic habits, and dark coloration. Remarkably, in a few days after metamorphosis, most of the black pigmentation disappeared from the head and foot, which assumed a whitish translucent color. Gray pigmentation was slowly regained by these structures, beginning about two months after metamorphosis.

Of all the crawling veligers observed, none was observed to possess a partially resorbed velum, suggesting that the loss of the velum is abrupt, possibly by swallowing (FRETTER, 1967). Newly metamorphosed postlarvae are found on the cleanest available parts of the substrate, including unpopulated surfaces, barnacle shells, and calcareous algae. They possess a well-developed radula at metamorphosis, of which the rachidian teeth have a morphology distinct from those of adult *Concholepas concholepas* (Figure 7). Postlarvae rasp microbial films from both culture pails and natural substrates, leaving cleaned areas of several square millimetres daily. The digestive tract of a sacrificed 3-mm long postlarva reared on a natural substrate contained great numbers of bacteria, as well as some diatoms and a few fragments of fleshy encrusting red and brown algae.

The 11 specimens maintained in culture grew to 11–19 mm in length during the first 90 days, with a mean growth rate of 0.143 mm/day (Figure 6). They remained on a home range of about 10 × 20 cm on the underside of a stone during the day, and foraged over the whole stone at night. Upon reaching a few millimetres in size they began to perforate, paralyze, and consume animal prey.

DISCUSSION

The rearing of long-lived planktotrophic veliger larvae poses serious technical problems, as mentioned by D'ASARO (1965) in his study of *Strombus gigas.* Although there were similarities between the present study and that of D'Asaro, the rearing of *Concholepas concholepas* was even more problematical owing to the unusual longevity of these larvae. Personal communication with workers developing commercial cultures of *S. gigas* under proprietary conditions has suggested that the time to maturity of these larvae became progressively reduced as optimal feeding and handling methods were discovered. Similar advances may be expected in the culture of locos. The high levels of mortality in our cultures were disturbing, and reflect the present lack of knowledge concerning nutritional and environmental requirements of loco veligers. These larvae may indeed change food requirements as they grow and develop new organ systems (D'ASARO, 1965). Disease problems may be no more than a response to stress imposed by presently suboptimal culture conditions.

In the past, Castilla and co-workers (unpublished data) recovered molluscan larvae in vertical plankton hauls not far from our laboratory, but were unable to confirm the presence of advanced loco larvae in their samples owing to the unavailability of authentic reference specimens. Our experience with larvae in laboratory cultures allows the immediate recognition of loco larvae captured at sea. Our repeated collection of advanced veliger larvae in the surface plankton confirms observations made in the laboratory that these larvae tend to rise to the surface of the water column. On days when we captured naturally occurring loco larvae at the sea surface, hauls made with the same net towed at 2-m depth over the same transect captured none of these larvae. Metamorphosis and growth of field-captured larvae in the laboratory duplicated in a few days a result that had taken months to achieve by way of the time-consuming laboratory cultures.

Larval Strategies

The present laboratory and field observations suggest some of the evolved mechanisms whereby *Concholepas concholepas* has survived and become widely distributed, and permits hypothetical reconstruction of the natural history of the larval phase of the life cycle. Larvae may require up to four months to reach the lipped form, ready for metamorphosis. Lipped larvae may survive for many more weeks, suspended by the byssal thread and feeding while drifting in oceanic currents in a manner similar to that described by SIGURDSSON *et al.* (1976) for plantigrade bivalve larvae. (KENSLEY [1985] discovered a relict fossil population of locos in southwest Africa which he attributed to the possible long distance dispersal of larvae by the West Wind Drift.) Larvae may maintain themselves near the water surface by velar swimming governed by their positive phototaxis. They may thus be maintained near the coastline by surface circulation driven by prevailing onshore winds active during the daytime. Byssal threads inserted in the air-sea interface may tow larvae along the surface when acted upon by these winds. Upon arrival at the shore, larvae tossed by the surf may effect "bubble capture," maintaining themselves in the neuston to be carried ashore with the surface slick or in sea foam. Upon being cast ashore, larvae quickly settle on the rocks using the propodium, seek a protected spatial niche, metamorphose, and begin feeding on microbial films. They become cryptic inhabitants of the rocky shore infauna until they have produced a resistant shell and can begin active feeding on invertebrates.

All 60 larvae caught by us at sea during a two-month period were competent for metamorphosis (lipped). These may have been the last individuals representing the reproductive cohort hatched during 1986, assuming that the majority of larvae of that year class had recruited to the plankton by August (CASTILLA, 1982). The early growth

of postlarval locos (Figure 6) appears to be linear during the first few months of life, and may be continuous with the growth curve obtained by GUISADO & CASTILLA (1983) for naturally occurring populations ranging in size from 11 to 57 mm. We do not know what factors induce metamorphosis in loco veligers, although chemosensory recognition of suitable substrates probably plays an important role (MORSE *et al.*, 1980).

Observation of algal feeding by juvenile locos is not inconsistent with known omnivorous feeding patterns observed in life histories of other juvenile muricids (M. R. Carriker, personal communication), but it is remarkable that algal feeding did not cease even after the young locos had begun to feed actively on mussels. Also remarkable is the finding that the radular teeth of the postlarva were distinct from those of the adult (Figure 7).

Prospects for Mass Culture

The limited knowledge presently available from our laboratory cultures of *Concholepas concholepas* suggests that mass commercial culture of this species is infeasible in the near future. Larval locos are simply not suitable for the presently used techniques of tank culture. Possession of a large, fragile, and efficient velum, as well as a highly specific mechanism for flotation (byssal thread), has adapted this species to a solitary drifting existence in oceanic waters. A widely separated distribution at the sea surface was demonstrated during our plankton hauls, where the net had to be towed several kilometres to obtain a very few larvae. On our most successful day in January 1986 we obtained a total of 47 larvae from seven separate 1-km hauls. Implications of this mode of life for hatchery design include maximization of culture volume per larva, continuous feeding with dilute suspensions of microalgae, and maintenance of high water quality for extended periods of culture. If such conditions are not maintained, larvae become entangled with byssal threads or mucus strands, fall to the tank bottom, and are subject to microbial attack.

The above-mentioned hatchery requirements are uneconomical compared with methodology used in mass rearing of bivalve larvae (DISALVO *et al.*, 1984) or lecithotrophic gastropod larvae (OWEN *et al.*, 1984), which can be maintained at high densities and pass metamorphosis in a few days or weeks. Mass culture of the loco might be based on the capture of lipped veligers at sea, with transfer to hatchery settling and rearing systems. Presently, such development is limited by the lack of knowledge of season and geographic location of larval concentrations off the coastline.

Resource Management

If culture seems a distant possibility, then preservation of the resource lies now in the correct management of remaining natural stocks. Such management has been hindered by logistical difficulties in the estimation of population parameters. The procedure of capturing pre-metamorphic larvae at sea provides a new method for the indirect monitoring of the reproductive success of the remaining stocks of locos. This technique can be made at least semi-quantitative by the establishment of standard transects to be monitored routinely throughout the year, and calculating the number of competent larvae per km^2 of sea surface. Yearly counts of competent larvae near shore could provide information on long-term trends in the reproductive success of the loco in the face of continued harvesting pressure. The method proposed is unsophisticated and inexpensive compared with diver surveys of loco populations and with shoreside censuses of fishery success, which are subject to many sources of bias. The measurement proposed would not, however, predict actual recruitment to the population, which should be measured by other means and then correlated with larval counts.

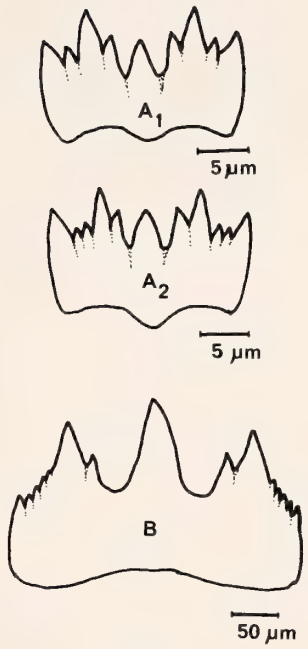


Figure 7

Rachidian teeth from a postlarval *Concholepas concholepas*. A_1 from anterior teeth; A_2 from posterior teeth. Adult loco rachidian tooth (B) presented for comparison of form.

ACKNOWLEDGMENTS

This research was sponsored by the Direccion de Investigaciones, Universidad del Norte, Antofagasta. I am grateful for helpful correspondence from Dr. M. R. Carriker, technical aid and suggestions from E. Martinez, E. Lara, and E. Montes, and critical reading of the manuscript by Dr. Matias Wolff. Drawings of loco larvae were executed by Mr. Marco Leon, and I thank Mrs. Gilda Bellolio for

meticulous dissection of the larval radula and operation of the scanning electron microscope. Support for fieldwork was provided by the Chilean Government Corporation for the Promotion of Development (CORFO).

LITERATURE CITED

CASTILLA, J. C. 1982. Pesqueria de moluscos gastropodos en Chile; *Concholepas concholepas,* un caso de estudio. Monografias Biologicas 2:199–212.

CASTILLA, J. C., C. GUISADO & J. CANCINO. 1979. Aspectos ecologicos y conductuales relacionado con la alimentacion de *Concholepas concholepas* (Mollusca: Gastropoda: Muricidae). Biol. Pesq. 12:99–114.

CASTILLA, J. C. & J. JEREZ. 1986. Artisanal fishery and development of a data base for managing the loco, *Concholepas concholepas,* resource in Chile. Pp. 133–139. *In:* G. S. Jamieson & N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. No. 92.

D'ASARO, C. N. 1965. Organogenesis, development, and metamorphosis in the queen conch, *Strombus gigas,* with notes on breeding habits. Bull. Mar. Sci. Gulf Carib. 15:359–416.

DISALVO, L. H., E. ALARCON, E. MARTINEZ & E. URIBE. 1984. Progress in mass culture of *Chlamys* (*Argopecten*) *purpurata* Lamarck (1819) with notes on its natural history. Revista Chilena de Historia Natural 57:33–45.

F.A.O. (United Nations). 1981. Yearbook of fishery statistics. Catches and landings. F.A.O., Fish. Ser.; Stat. Ser. No. 50.

FRETTER, V. 1967. The prosobranch veliger. Proc. Malacol. Soc. Lond. 37:357–366.

GEAGHAN, J. & J. C. CASTILLA. 1986. Use of catch and effort data for parameter estimates for the loco (*Concholepas concholepas*) fishery in central Chile. Pp. 168–174. *In:* G. S. Jamieson & N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. No. 92.

GUISADO, C. & J. C. CASTILLA. 1983. Aspects of the ecology and growth of an intertidal juvenile population of *Concholepas concholepas* (Mollusca: Gastropoda: Muricidae) at Las Cruces, Chile. Mar. Biol. 78:99–103.

KENSLEY, B. 1985. The fossil occurrence in southern Africa of the South American intertidal mollusc *Concholepas concholepas.* Ann. S. Afr. Mus. 97:1–7.

MORSE, D. E., M. TEGNER, H. DUNCAN, N. HOOKER, G. TREVELYAN & A. CAMERON. 1980. Induction of settling and metamorphosis of planktonic molluscan (*Haliotis*) larvae. III: signaling by metabolites of intact algae is dependent on contact. Pp. 67–86. *In:* D. Müller-Schwarze & R. M. Silverstein (eds.), Chemical signals. Plenum: New York.

OWEN, B., L. H. DISALVO, E. EBERT & E. FONCK. 1984. Culture of the California red abalone *Haliotis rufescens* Swainson (1822) in Chile. Veliger 27:101–105.

SERNAP. 1985. Anuario de estadistica en pesca 1984. Servicio Nacional de Pesca. Santiago, Chile.

SIGURDSSON, J. B., C. W. TITMAN & P. A. DAVIES. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. Nature 262:386–387.

STUARDO, J. 1979. Sobre la clasificacion, distribucion, y variacion de *Concholepas concholepas* (Bruguière, 1789): un estudio de taxonomia beta. Biol. Pesq. 12:99–114.

NOTE ADDED IN PROOF

On 21 September 1987, 24 lipped veligers ($\bar{x}$ = 1780 μm, SD = 100 μm) were captured in a surface plankton haul about 2 km seaward of the mouth of Herradura Bay. These larvae were returned to the laboratory setting system containing a natural substrate as described in the text, with a continuous flow of seawater of 10 L/min at 15°C. This flow rate rate caused agitation within the system, and circulation of the veligers over the substrate. Within 16 h (overnight) 22 of these veligers had passed metamorphosis, settling both on the substrate and walls of the aquarium. This was taken as evidence that these larvae could pass metamorphosis *en masse* in the presence of turbulent water.

The Veliger 30(4):369–371 (April 1, 1988)

THE VELIGER

Spawning and Larval Development of the Trochid Gastropod *Calliostoma ligatum* (Gould, 1849)

by

ALAN R. HOLYOAK*

Department of Zoology, 574 WIDB, Brigham Young University, Provo, Utah 84602, U.S.A.

Abstract. Spawning and larval development through metamorphosis were observed in the trochid gastropod *Calliostoma ligatum*. Gametes were broadcast into the water column, sperm in white puffs and eggs in mucous strings. Larvae hatched as swimming veligers after 6 days, stayed in the water column for 3 to 4 days, and metamorphosed after 12 days. Broadcast spawning and planktic larvae indicate a more primitive reproductive strategy in *C. ligatum* than in other *Calliostoma* species which attach to substrata eggs from which hatch metamorphosed snails.

INTRODUCTION

Reproduction in *Calliostoma ligatum* (Gould, 1849), a common and conspicuous member of intertidal and subtidal communities along the Pacific coast of North America, has not been studied in detail. Information concerning the reproductive biology of this snail is limited to a brief report by HUNT (1980) on the eggs and their release. Developmental studies have been made on two other *Calliostoma* species: *C. zizyphinum* (Linnaeus) (LEBOUR, 1936; CROFTS, 1955) and *C. papillosum* (Da Costa) (ROBERT, 1902).

This paper presents a description of spawning and development through metamorphosis for *Calliostoma ligatum* collected in the San Juan Islands, Washington, U.S.A., in the winter and early spring of 1985. A comparison between the development of *C. ligatum* and other *Calliostoma* species is also made.

MATERIALS AND METHODS

Ten adults of *Calliostoma ligatum* were put in 800 mL of filtered seawater and placed in direct sunlight. When the water warmed, the snails began to release gametes.

Once spawning had commenced males and females were segregated by sex, rinsed to remove gametes, and put into 800 mL of 10–15°C filtered seawater. Both sexes continued to spawn after rinsing and transfer.

Eggs were pipetted from the bottom of the beaker and from the water column as they were released, transferred to 800 mL of fresh filtered seawater, and refrigerated until sperm were collected.

Sperm (3–5 mL) were collected as they were ejaculated and mixed with 100 mL of filtered seawater. This sperm solution was used immediately to fertilize previously collected eggs.

Approximately 100 eggs, or enough to nearly cover the bottom of a beaker, were pipetted into 800 mL of filtered seawater. Fertilization was accomplished by adding 2–3 mL of sperm solution to the eggs and gently agitating the gamete mixture for a few minutes. Fertilized eggs were rinsed to remove excess sperm. Beakers containing fertilized eggs were placed in a running seawater table and maintained at 7–9°C during development.

Cultures were periodically agitated, especially during early developmental stages. The water was changed each 2–3 h with freshly filtered seawater for the first day, and daily thereafter. No food was given to hatched larvae.

RESULTS

Spawning was first observed on 23 February 1985 with subsequent spawnings occurring through mid-April (Table 1). Spawning occurred during all lunar phases and included late morning and early evening hours. During all spawns the water temperature was at least 10°C.

Snails of both sexes moved to the air-water interface before releasing gametes.

Sperm were released as a milky white substance. No

* Current address: Institute of Marine Sciences, University of California, Santa Cruz, California 95064, U.S.A.

Table 1

Date, time of day, water temperature, and lunar phase during five spawnings of *Calliostoma ligatum*.

Date (1985)	Time	Water temp. (°C)	Lunar phase
23 Feb.	1700	10	New–1st Quarter
27 Feb.	1139	16	1st Quarter
1 Mar.	1815	11	1st Quarter–Full
9 Mar.	1915	10	Full
13 Apr.	1544	15	Last Quarter

size measurements of sperm were obtained. Cursory observations confirmed, however, that sperm were released individually and not in packets and that they were very active. Sperm release lasted 10–45 min.

Eggs were sheathed in mucous strands as they were spawned. These strands were 1–3 mm wide, held 1–4 eggs across the strand, and contained 10–90 eggs. Many pulses of eggs were released per spawn. Female spawns lasted 39–60 min and individual females released more than 1500 eggs. Eggs were not secured to any surface by adults but drifted to the bottom. The light green, granular eggs were opaque and 225 μm in diameter. The egg was separated from a gelatinous coat by a 20-μm wide space. The gelatinous coat was 30 μm in width and a frilly chorion 215 μm wide bordered that coat. An egg with its associated structures had a diameter of 750 μm (Figure 1A).

Fertilization and Development

Upon sperm penetration, the space between the egg and surrounding gelatinous coat increased from 20 to 50 μm and the gelatinous coat increased from 30 to nearly 100 μm in width (Figure 1B).

Development proceeded in a spiral cleavage pattern. The first two cleavages were meridional, equal, and holoblastic. The third cleavage was equatorial and unequal. Subsequent cleavages and differential cell divisions resulted in morula and then gastrula stages. For the timing of development see Table 2.

Gastrulae produced cilia at one end and ciliary beating caused spinning and rotation within the gelatinous coat. These cilia later formed the prototroch of the trochophore larvae (Figure 1C).

The shell gland and foot rudiment appeared during the trochophore stage. Shell secretion soon followed with the first sign of the larval shell being a shiny spot on one side of the trochophore. On the opposite side of the larva, the foot fold was becoming more prominent. Larvae soon thereafter became veligers (Figure 1D).

As prehatched veligers, larvae continued to secrete shell material and enlarge a now bilobate velum. The operculum formed during this stage, the digestive gland was visible,

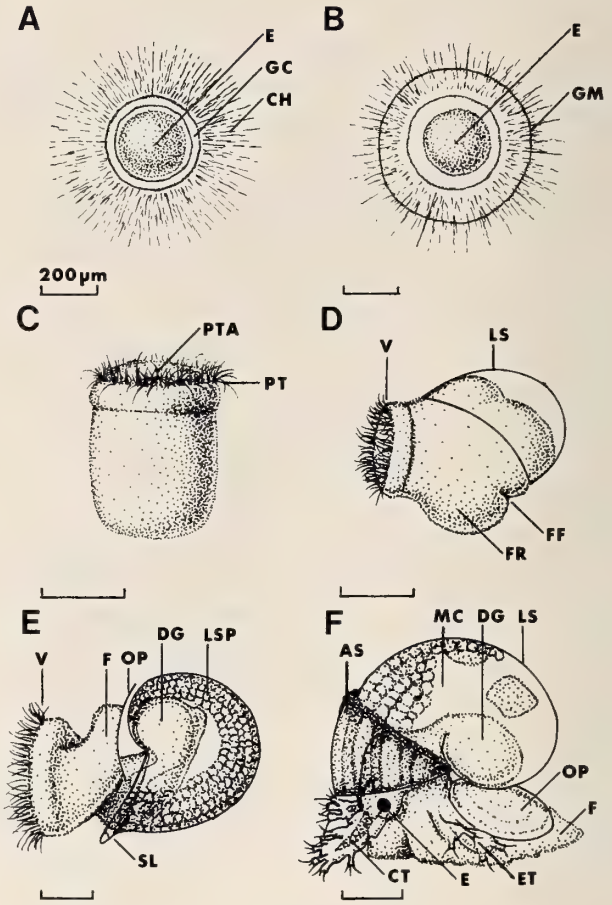


Figure 1

Developmental stages of *Calliostoma ligatum*. All scale bars represent 200 μm. A. Unfertilized egg: E, egg; GC, gelatinous coat; CH, chorion. B. Fertilized egg: E, egg; GM, gelatinous coat membrane. C. Trochophore: PTA, pretrochal area; PT, prototroch. D. Early veliger: V, velum; LS, larval shell; FF, foot fold; FR, foot rudiment. E. Prehatching veliger with torsion nearly completed: V, velum; F, foot; OP, operculum; DG, digestive gland; LSP, larval shell pattern (which covers the entire shell); SL, shell lip. F. Metamorphosed snail: AS, adult shell; MC, mantle cavity; DG, digestive gland; LS, larval shell; OP, operculum; F, foot; ET, epipodial tentacles; E, eyespot; CT, cephalic tentacle.

and larval shells had a honeycomb pattern and a lip. Torsion was also accomplished before hatching. At hatching the larval shell had 1¼ whorls (Figure 1E).

Calliostoma ligatum hatched as a swimming veliger after 6 days and spent 3–4 days in the water column. Individuals then went to the bottom where they spent 3–4 days crawling and swimming before metamorphosis occurred. During this swimming-crawling stage epipodial tentacles formed and the foot became mottled. At metamorphosis the velum was sloughed off, cephalic tentacles and eyes became readi-

Table 2

Timetable of the development of *Calliostoma ligatum*. Times are mean values for five cultures at 7–9°C.

Time	Stage
0 h	Fertilization
3.7 h	1st cleavage
5.8 h	2nd cleavage
7.4 h	3rd cleavage
1.8 day	Ciliated gastrula
2.1 day	Trochophore
2.4 day	Shell visible
2.6 day	Foot fold visible
3.1 day	Veliger
3.5 day	Shell pattern visible
4–5.5 day	Torsion
6 day	Hatching
9.5 day	Swimming-crawling
12.2 day	Metamorphosis

ly visible, and secretion of the adult shell was begun (Figure 1F).

Approximately 90% of fertilized eggs reached metamorphosis.

DISCUSSION

Spawning in *Calliostoma ligatum* depends on neither lunar phase nor on time of day since spawning occurred during all lunar phases and times of day as shown in Table 1. Elevated water temperature appears to be a primary factor in inducing spawning.

When *Calliostoma ligatum* spawns it broadcasts gametes into the water column. Broadcast spawning is unknown for other species within this genus. Two other *Calliostoma* species produce egg masses or at least attach an egg-bearing mucous string to the bottom (Robert, 1902; Lebour, 1937). *Calliostoma ligatum* falls between the spawning strategies of (1) eggs set free singly into the plankton, and (2) eggs laid in gelatinous layers (Purchon, 1977) by releasing eggs in a mucous string. In the laboratory, mucus integrity broke down and eggs were released into the water column. It is doubtful that developing larvae would be held in place by mucus in the field.

The eggs of *Calliostoma ligatum* obtained here are similar to those described by Hunt (1980) with the exception of egg size. Hunt reported eggs being 29–30 μm in diameter, certainly an error. Eggs in the present study were approximately 225 μm in diameter, a size comparable to egg sizes of *C. zizyphinum* (280 μm) and *C. papillosum* (170 μm) (Lebour, 1937).

The development of *Calliostoma ligatum* differs from other *Calliostoma* species that have been described. Other *Calliostoma* species bypass a planktic larval stage and hatch as metamorphosed snails (Lebour, 1937) while larvae of *C. ligatum* hatch as swimming veligers.

Swimming veligers of *Calliostoma ligatum* go to the bottom and swim and crawl for 3 to 4 days before metamorphosis. It is possible that the duration of the swimming-crawling stage would be shortened in the presence of a favorable substrate as has been suggested for other species (Scheltema, 1961; Fretter & Manly, 1977). The ability to prolong the swimming-crawling stage is advantageous as it allows larvae the time to search for favored habitats (Pechenik, 1980). Since clean glass is most likely not an ideal substrate, larvae in this study show that they will eventually metamorphose even if an ideal substrate is not present.

In conclusion, broadcasting gametes and hatching as planktic larvae places the developmental pattern of *Calliostoma ligatum* closer to the primitive gastropod pattern than that of other *Calliostoma* species whose development is known.

ACKNOWLEDGMENTS

I thank M. Strathmann, B. Bingham, Dr. L. Cameron, and Dr. L. F. Braithwaite for providing helpful suggestions pertaining to this project and to B. Bingham for his willingness to act as a diving partner. I also thank two anonymous reviewers for their helpful comments. Dr. A. O. D. Willows provided research facilities at the Friday Harbor Laboratories. Support for this project came from research funds allocated by the Department of Zoology, Brigham Young University, and from a student research award from the Associated Students of Brigham Young University.

LITERATURE CITED

Crofts, D. R. 1955. Muscle morphogenesis in primitive gastropods and its relation to torsion. Proc. Zool. Soc. Lond. 125:711–750.

Fretter, V. & R. Manly. 1977. Algal associations of *Tricolia pullus*, *Lacuna vincta* and *Certhopsis tuberculatis* (Gastropoda) with special reference to the settlement of their larvae. Jour. Moll. Stud. 57:999–1017.

Hunt, D. E. 1980. Observations on spawning in *Calliostoma ligatum* (Gould, 1849). Veliger 22:292.

Lebour, M. V. 1936. Notes on eggs and larvae of some Plymouth prosobranchs. Jour. Mar. Biol. Assoc. U.K. 20:547–565.

Lebour, M. V. 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. Jour. Mar. Biol. Assoc. U.K. 22:105–166.

Pechenik, J. A. 1980. Growth and energy balance during the larval lives of three prosobranch gastropods. Jour. Exp. Mar. Biol. Ecol. 44:1–28.

Purchon, R. D. 1977. The biology of the Mollusca. Pergamon Press: Oxford. 560 pp.

Robert, A. 1902. Recherches sur le developpement des troches. Arch. Zool. Exp. Gen., 3rd Ser. 10:269–538.

Scheltema, R. S. 1961. Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. Biol. Bull. 121:92–109.

The Veliger 30(4):372–376 (April 1, 1988)

THE VELIGER

Individual Movement Patterns of the Minute Land Snail *Punctum pygmaeum* (Draparnaud) (Pulmonata: Endodontidae)

by

ANETTE BAUR AND BRUNO BAUR

Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden

Abstract. Movement patterns of the minute land snail *Punctum pygmaeum* were studied in boxes provided with natural substrate. Experiments were conducted with different snail densities and box sizes, but at constant temperature and humidity. The mean displacement per 12 h averaged 47 mm and was significantly influenced by snail size, but not by box size or snail density. *Punctum pygmaeum* moved equal distances at night and during the day. Snails kept in groups showed aggregative behavior. The adaptive significance of this behavior is discussed.

INTRODUCTION

Movement patterns, and especially distances covered, have important consequences in determining population size and genetic structure (*cf.* DOBZHANSKY & WRIGHT, 1943). Studies of individual movement patterns in terrestrial gastropods have been concerned mainly with nocturnal activity and with homing and trail following of large-sized species (*e.g., Helix pomatia* Linné [EDELSTAM & PALMER, 1950], *Euglandina rosea* (Férussac) [COOK, 1985], *Limax maximus* Linné [GELPERIN, 1974], *Limax pseudoflavus* (Evans) [COOK, 1980]). Little attention has been directed to movements of minute snail species living in leaf litter (but see BOAG, 1985). In this paper we report on individual movement patterns of *Punctum pygmaeum* (Draparnaud), the smallest among European land snails.

Punctum pygmaeum occurs in a wide variety of moderately moist habitats, especially in leaf litter of deciduous forests (KERNEY & CAMERON, 1979). It is one of the most abundant land snails in Europe, reaching densities of 173 snails/m^2 (PHILLIPSON & ABEL, 1983). However, little is known about its life history. Like other endodontoids, *P. pygmaeum* exhibits indeterminate shell growth (*cf.* SOLEM, 1976). It can reproduce in the absence of a mate (BAUR, 1987).

Several hypotheses have been proposed to explain observed movement patterns. Distances traveled have been assumed to depend on snail density (GREENWOOD, 1974; OOSTERHOFF, 1977), and they have also been found to correlate with individual shell size (*e.g., Helminthoglypta arrosa* Binney [VAN DER LAAN, 1971], *Arion ater* (Linné) [HAMILTON & WELLINGTON, 1981], *Monadenia hillebrandi mariposa* Smith [SZLAVECZ, 1986]). As a result of the mainly nocturnal activity of land snails, distances traveled at night may exceed those covered during the day (*e.g., Helix aspersa* Müller [BAILEY, 1975], *Helix lucorum* Linné [BAILEY & LAZARIDOU-DIMITRIADOU, 1986]). Our experiments were conducted to determine whether distances moved by *Punctum pygmaeum* are affected by the size of experimental containers, snail density, snail size and (or) time of day. In addition, the spatial distribution of snails was tested for deviation from randomness.

MATERIALS AND METHODS

Specimens of *Punctum pygmaeum* were collected in an aspen (*Populus tremula*) and birch (*Betula* spp.) dominated part of the forest Nåsten 5 km SW of Uppsala in central Sweden (59°50′N, 17°40′E) in September 1986. The snails were maintained singly on decaying leaves of aspen in 50 × 10 mm petri dishes lined with moist paper towel in natural daylight at 20–22°C and 90–100% relative humidity. The size of the snails (shell breadth) was measured to the nearest 0.02 mm using a binocular microscope with a stage micrometer.

Experimental Design

Movement patterns of *Punctum pygmaeum* on their natural substrate were recorded. For this purpose the bottom of transparent plastic boxes was lined with moist paper towel covered by a single layer of decaying leaves of aspen.

Since the movements of snails may be constrained by the size of the container, two different box sizes were used during the experiments: 12.5 × 9 × 7 cm (small box) and 24.7 × 18 × 7 cm (large box).

To test whether snail density influences movement patterns, experiments were conducted with one or four snails in each test box. To follow individual behavior, snails were marked on the shell with minute dots of correction fluid ("Tipp-Ex"). The experiments were conducted under natural light conditions at 20–22°C. Humidity in the boxes ranged between 90 and 100%. Snails were randomly assigned to different box sizes and snail densities. Each snail was tested only once, with each test trial lasting 10 days. Position recordings were made twice a day (0900 and 2100 h). Consequently, 21 positions and 20 displacements were recorded for each snail. We define movement frequency as the percent of all displacements where the snails moved 3 mm or more.

Individual movement patterns were recorded for 48 snails. Forty-one of these were collected in the field, and seven were born in the laboratory.

Statistical Analysis

Data analysis was performed using the SAS program package (SAS Institute, Inc., 1985). A Mann-Whitney *U*-test was applied to test whether snails raised in the laboratory differed in behavior from those collected in the field. The influences of box size, snail density, time of day, and snail size on the distances covered (logarithmic transformed) were evaluated by analysis of variance (ANOVA). For this analysis snail size was divided into three size classes. The directions of successive displacements were tested for independence using χ^2-test (Batschelet, 1981). The null hypothesis of this test states randomness in the directions of successive displacements. A runs-test (Sokal & Rohlf, 1969:624) was applied to test whether the snails' behavior showed periodic sequences of activity. Nearest neighbor distances were calculated for all observations to determine whether snails tested in groups of four showed aggregative behavior (Clark & Evans, 1954). These distances were compared with simulated ones (100 runs for each box size) using *t*-tests.

Simulated values, based on the assumption of random dispersion, were obtained by calculating distances between randomized snail positions.

RESULTS

Displacement

In terms of mean displacement and frequency of movement, snails raised in the laboratory did not differ from similar-sized ones collected in the field (Mann-Whitney *U*-test, both cases $P > 0.1$). Consequently data of both groups were pooled for further analyses.

The mean displacements of the snails are summarized in Figure 1. Since the individuals were not continuously observed, the values recorded represent minimum distances traveled over each 12-h period. Mean minimal distances averaged 47 mm with a range of 3 to 95 mm. This high variability among individuals can be explained partly by size, which significantly influenced displacement (Table 1), with larger individuals on average traveling greater distances (Figure 2). In contrast, box size, snail density, and time of day had no significant effect on mean displacement (Table 1). These results indicate that *Punctum pygmaeum* kept singly or in groups of four in each box size traveled similar distances within 12 h. However, the interaction of snail size and density was significant (Table 1).

Table 1

Analysis of variance of the minimal distance traveled by *Punctum pygmaeum* in 12 h.

Source of variation	d.f.	SS	*F*-value	*P*
Model	14	32.99	5.02	<0.0001
Error	963	451.79		
Snail size (S)	2	16.99	18.11	<0.0001
Density (D)	1	0.57	1.21	0.2719
Box size (B)	1	0.14	0.31	0.5799
Time of day (T)	1	0.12	0.26	0.6122
S × D	2	12.73	13.57	<0.0001
S × B	2	0.74	0.79	0.4553
S × T	2	0.12	0.13	0.8753
B × D	1	0.22	0.46	0.4986
B × T	1	1.33	2.84	0.0922
D × T	1	0.02	0.05	0.8225

Representative displacement tracks of two *Punctum pygmaeum* kept singly in large boxes are illustrated in Figure 3. In general, the direction of a given displacement was independent of the direction of the preceding displacement (χ^2-test, all snails $P > 0.2$, but one $P < 0.01$).

Timing of Activity

The frequencies of movement for the snails are summarized in Figure 4. Nineteen of the 48 *Punctum pygmaeum* were active during 19 or more 12-h periods, while 16 snails were active during 10–17 periods. The latter snails, however, showed active sequences of 4–6 consecutive periods interrupted by pauses of 1–3 periods (runs-test in 12 snails $P < 0.01$, in four snails $P < 0.05$). The remaining 13 snails were irregularly active with no distinct pattern.

Aggregative Behavior

Significant aggregations of *Punctum pygmaeum* during the whole experiment were observed in three of four small boxes and in two of three large boxes (Table 2). Analysis of the snails' positions indicates that in some boxes snails rested on only a few selected leaves, while in others they

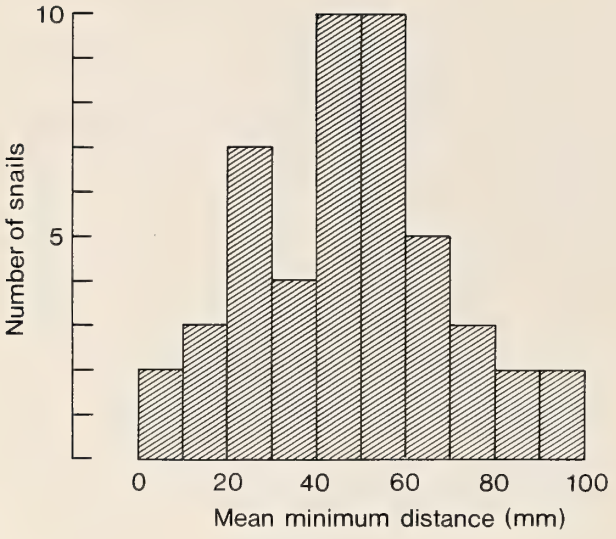


Figure 1

Distribution of mean displacements for *Punctum pygmaeum*. Each value represents the mean of 20 displacements of an individual snail during 12 h.

showed no preference for any particular leaf. Similar patterns of leaf preference were observed for boxes containing only one snail.

DISCUSSION

Displacement

Our results showed that individuals of *Punctum pygmaeum* moved approximately 5 cm in 12 h. However, in the course of a single 12-h period, a snail may actually travel farther than recorded here. In a pilot experiment, we monitored the actual tracks of individual *Punctum pygmaeum* creeping on wet paper towels. Stressed by the artificial light of a 40-W bulb, individual snails moved between 282 and 480 mm within 40 min (mean for 16 individuals = 407 mm), which corresponded to 6–66% of their resultant displacement (mean = 29%). Thus, one may assume that the average distance traveled is about three times the minimum displacement distance recorded here. On the other hand, the natural habitat of *Punctum pygmaeum* consists of a multiple layer of leaves and, consequently, distances traveled may result in shorter horizontal displacements. Distances covered may also be influenced by microclimatic factors. In our experiments the snails were kept under constant temperature and humidity, as seldom prevail in the field. Undoubtedly, heterogeneity in microclimate and substrate will influence snail movements under natural conditions.

The positive correlation found between shell size and distance traveled in *Punctum pygmaeum* is paralleled in other snail species (*e.g., Helminthoglypta arrosa* [VAN DER LAAN, 1971], *Arion ater* [HAMILTON & WELLINGTON, 1981], *Monadenia hillebrandi mariposa* [SZLAVECZ, 1986]). However, it seems not to be a general feature of terrestrial gastropods. For instance, no difference in distances covered between adults and half-grown juveniles was observed in *Cerion bendalli* (WOODRUFF & GOULD, 1980), *Ariolimax columbianus* (Gould) (HAMILTON & WELLINGTON, 1981) and *Arianta arbustorum* (Linné) (BAUR, 1984, 1986). In addition to size effects, the high variability in terms of distances traveled in *Punctum pygmaeum* may result from physiological and (or) genetic differences between individuals. Similar individual variation in mobility has been described for *Helix pomatia* Linné (LOMNICKI, 1969) and *Arianta arbustorum* (BAUR & GOSTELI, 1986).

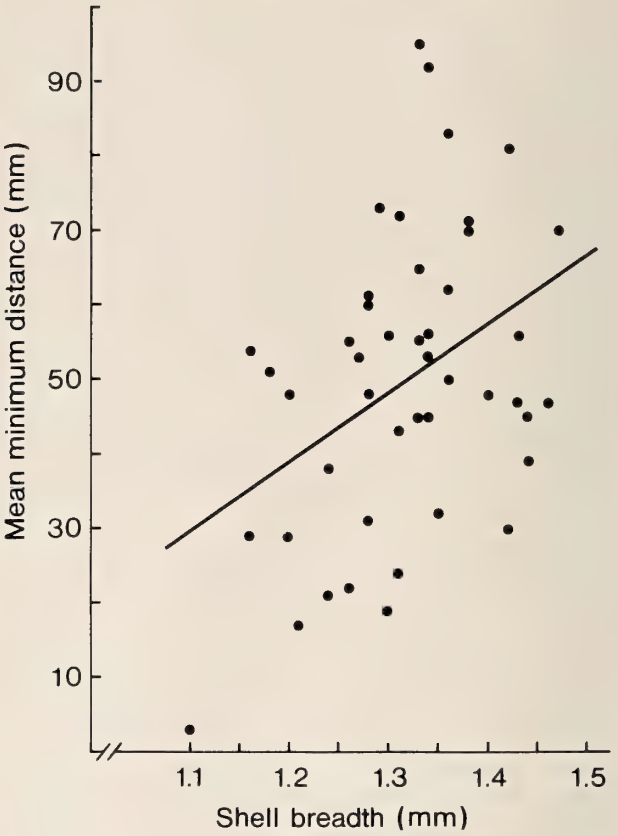


Figure 2

Relationship between mean displacement (y) and shell size (x) of *Punctum pygmaeum* ($y = 92.4x - 71.7$; $r = 0.49$, $n = 45$, $P < 0.01$).

In our experiments *Punctum pygmaeum* was kept at densities ranging from 22 snails/m^2 (one snail in a large box) to 356 snails/m^2 (four snails in a small box), while the actual density of the original population was estimated at 63 ± 38 snails/m^2 (mean ± SE) in September 1985 (unpublished results). However, we failed to find any influence of snail density on displacements. In the literature both density-dependent dispersal (*e.g., Cepaea nemoralis* (Linné) [GREENWOOD, 1974; OOSTERHOFF, 1977], *Arion ater* [HAMILTON & WELLINGTON, 1981]) and density-in-

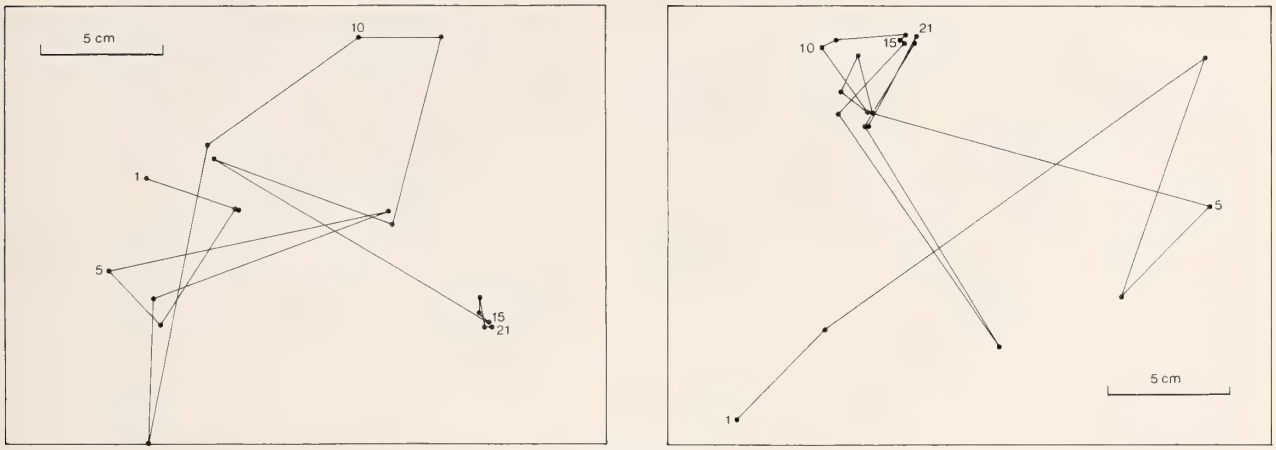


Figure 3

Representative displacement tracks of two individuals of *Punctum pygmaeum* kept singly in large boxes during 21 periods of 12 h. Numbers indicate the sequence of the snails' positions.

dependent dispersal (*e.g., Ariolimax columbianus* [HAMILTON & WELLINGTON, 1981]) have been claimed to occur.

Timing of Activity

In contrast to other studies of gastropods (BAILEY, 1975; BAILEY & LAZARIDOU-DIMITRIADOU, 1986; ROLLO, 1982; WAREING & BAILEY, 1985), no distinct differences in activity between day and night were found in *Punctum pygmaeum*. In *Helix aspersa,* for example, 76–92% of the total activity was observed to take place during the night, with daytime activity being confined to periods of rainfall (BAILEY, 1975). The apparent lack of a circadian rhythm observed in *Punctum pygmaeum* can be an artifact of the experimental set-up (natural daylight, but constant temperature and humidity), or a trait characteristic of snails inhabiting leaf litter. The latter suggestion is supported by findings of BOAG (1985), who described humidity as the major factor influencing activity of the litter-dwelling snails *Discus cronkhitei* (Newcomb), *Euconulus fulvus* (Müller), *Vertigo gouldi* (Binney), and *Vertigo modesta* (Say), while light conditions *per se* appeared to play a minor role. Furthermore, snails with distinctly nocturnal activity and diurnal inactivity, such as *Achatina fulica* (Linné), have been shown to retain a circadian rhythm even when kept under constant high humidity in the laboratory (CHASE *et al.,* 1980).

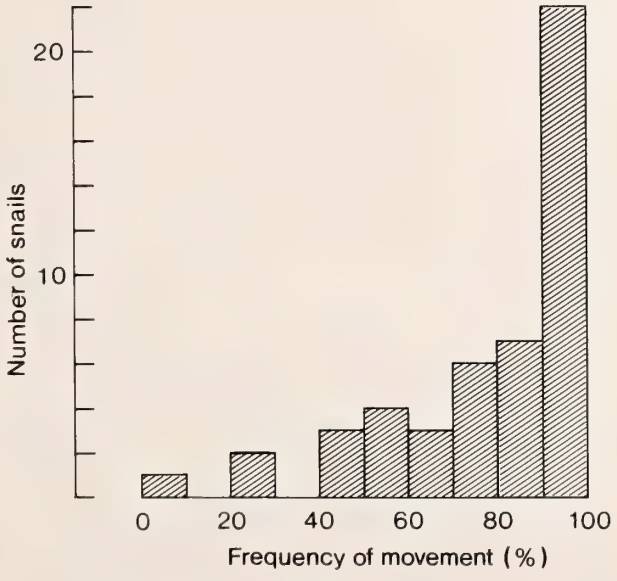


Figure 4

Distribution of movement frequencies for *Punctum pygmaeum.*

Table 2

Aggregative behavior of *Punctum pygmaeum.* The snails' dispersion is clumped if the observed nearest neighbor distances are significantly smaller than the simulated nearest neighbor distances (based on randomized snail positions). Distances are given in mm.

Experiment	Observed nearest neighbor distance Mean	(SD)	Simulated nearest neighbor distance Mean	(SD)	*t*-value	*P*
Small boxes:						
I	26.6	(10.2)	35.4	(10.9)	3.44	<0.001
II	32.3	(11.6)	35.4	(10.9)	1.25	N.S.
III	28.1	(9.5)	35.4	(10.9)	2.88	<0.01
IV	28.4	(8.4)	35.4	(10.9)	2.82	<0.01
Large boxes:						
I	44.9	(17.7)	65.1	(22.0)	3.95	<0.001
II	64.2	(24.7)	65.1	(22.0)	0.17	N.S.
III	48.9	(17.3)	65.1	(22.0)	3.18	<0.01

N.S. = not significant.

Aggregative Behavior

Punctum pygmaeum tended to aggregate. This behavior might depend upon signals emanating from the animals themselves, such as pheromones in mucus trails (*cf.* CROLL, 1983). In fact, *P. pygmaeum* clustered significantly above chance level when kept in plastic boxes without environmental stimuli capable of biasing particular locations (unpublished results). However, observations that aggregations are restricted to particular leaves in some boxes and not in others, and that snails kept singly tended to rest on some leaves more often than others, point to the effect of additional environmental stimuli. Under natural conditions, local concentrations of food (leaves with a high palatability) and high moisture may attract snails. In addition, the following of mucus trails might contribute to grouping behavior.

Aggregation is known to occur in several other gastropod species, but its adaptive significance does not appear to be the same in every case. In some species aggregative behavior may be part of reproductive activities (KUPFERMANN & CAREW, 1974), while in others it may protect snails from predation and reduce net water loss by decreasing the total surface-volume ratio (CHASE *et al.*, 1980; COOK, 1981). The adaptive advantage of aggregative behavior in *Punctum pygmaeum* is unknown.

ACKNOWLEDGMENTS

Financial support was received from the Swiss National Science Foundation and the Ahlstrand Foundation. We thank Heidi Dobson, Staffan Ulfstrand, and an anonymous reviewer for comments on the manuscript.

LITERATURE CITED

BAILEY, S. E. R. 1975. The seasonal and daily patterns of locomotor activity in the snail *Helix aspersa* Müller, and their relation to environmental variables. Proc. Malacol. Soc. Lond. 41:415–428.

BAILEY, S. E. R. & M. LAZARIDOU-DIMITRIADOU. 1986. Circadian components in the daily activity of *Helix lucorum* L. from northern Greece. Jour. Moll. Stud. 52:190–192.

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press: London. 371 pp.

BAUR, B. 1984. Dispersion, Bestandesdichte und Diffusion bei *Arianta arbustorum* (L.) (Mollusca, Pulmonata). Ph.D. Thesis, Zurich Univ. 89 pp.

BAUR, B. 1986. Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). Holarct. Ecol. 9:117–125.

BAUR, B. 1987. The minute land snail *Punctum pygmaeum* (Draparnaud) can reproduce in the absence of a mate. Jour. Moll. Stud. 53:112–113.

BAUR, B. & M. GOSTELI. 1986. Between and within population differences in geotactic response in the land snail *Arianta arbustorum* (L.) (Helicidae). Behaviour 97:147–160.

BOAG, D. A. 1985. Microdistribution of three genera of small terrestrial snails (Stylommatophora: Pulmonata). Can. Jour. Zool. 63:1089–1095.

CHASE, R., R. P. CROLL & L. L. ZEICHNER. 1980. Aggregation in snails, *Achatina fulica*. Behav. Neural Biol. 30:218–230.

CLARK, P. J. & F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453.

COOK, A. 1980. Field studies of homing in the pulmonate slug *Limax pseudoflavus* (Evans). Jour. Moll. Stud. 46:100–105.

COOK, A. 1981. Huddling and the control of water loss by the slug *Limax pseudoflavus* Evans. Anim. Behav. 29:289–298.

COOK, A. 1985. Functional aspects of trail following by the carnivorous snail *Euglandina rosea*. Malacologia 26:173–181.

CROLL, R. P. 1983. Gastropod chemoreception. Biol. Rev. 58: 293–319.

DOBZHANSKY, T. & S. WRIGHT. 1943. Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. Genetics 28:304–340.

EDELSTAM, C. & C. PALMER. 1950. Homing behaviour in gastropods. Oikos 2:259–270.

GELPERIN, A. 1974. Olfactory basis of homing behavior in the giant garden slug, *Limax maximus*. Proc. Natl. Acad. Sci. USA 71:966–970.

GREENWOOD, J. J. D. 1974. Effective population numbers in the snail *Cepaea nemoralis*. Evolution 28:513–526.

HAMILTON, P. A. & W. G. WELLINGTON. 1981. The effects of food and density on the movement of *Arion ater* and *Ariolimax columbianus* (Pulmonata: Stylommatophora) between habitats. Res. Popul. Ecol. 23:299–308.

KERNEY, M. P. & R. A. D. CAMERON. 1979. A field guide to the land snails of Britain and north-west Europe. Collins: London. 288 pp.

KUPFERMANN, I. & T. J. CAREW. 1974. Behavior patterns of *Aplysia californica* in its natural environment. Behav. Biol. 12:317–337.

LOMNICKI, A. 1969. Individual differences among adult members of a snail population. Nature 223:1073–1074.

OOSTERHOFF, L. M. 1977. Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). Neth. Jour. Zool. 27:1–132.

PHILLIPSON, J. & R. ABEL. 1983. Snail numbers, biomass and respiratory metabolism in a beech woodland—Wytham Woods, Oxford. Oecologia 57:333–338.

ROLLO, C. D. 1982. The regulation of activity in populations of the terrestrial slug *Limax maximus* (Gastropoda; Limacidae). Res. Popul. Ecol. 24:1–32.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics. 1985 edition. SAS Inst. Inc.: Cary, North Carolina.

SOKAL, R. R. & F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co.: San Francisco. 776 pp.

SOLEM, A. 1976. Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra). Part I. Family Endodontidae. Field Museum of Natural History: Chicago, Illinois. 508 pp.

SZLAVECZ, K. 1986. Food selection and nocturnal behavior of the land snail *Monadenia hillebrandi mariposa* A. G. Smith (Pulmonata: Helminthoglyptidae). Veliger 29:183–190.

VAN DER LAAN, K. L. 1971. The population ecology of the terrestrial snail, *Helminthoglypta arrosa* Binney (Pulmonata: Helicidae). Ph.D. Thesis, Univ. Calif., Berkeley. 235 pp.

WAREING, D. R. & S. E. R. BAILEY. 1985. The effects of steady and cycling temperatures on the activity of the slug *Deroceras reticulatum*. Jour. Moll. Stud. 51:257–266.

WOODRUFF, D. S. & S. J. GOULD. 1980. Geographic differentiation and speciation in *Cerion*—a preliminary discussion of patterns and processes. Biol. Jour. Linn. Soc. 14:389–416.

The Veliger 30(4):377–383 (April 1, 1988)

THE VELIGER

The Gastropods in the Streams and Rivers of Five Fiji Islands: Vanua Levu, Ovalau, Gau, Kadavu, and Taveuni

by

A. HAYNES

School of Pure and Applied Sciences, University of the South Pacific,
P.O. Box 1168, Suva, Fiji

Abstract. Streams and rivers on the islands of Vanua Levu, Ovalau, Gau, Kadavu, and Taveuni, Fiji, were investigated for gastropods, water conductivity, water hardness, temperature, substrate, and current speed during 1983 and 1984. As at other Indo-Pacific islands there was a diverse and abundant lotic gastropod fauna. Twenty-six species were collected on Vanua Levu and 13–16 species were found in each torrential stream studied on the other four islands. Upstream, above the influence of the tide, both the longitudinal and horizontal distributions of gastropods appeared to be mainly dependent on the water speed and type of substrate. A suspected new species of *Acochlidium* (Opisthobranchia) was discovered on the island of Vanua Levu.

INTRODUCTION

Land and freshwater mollusks were first collected by Graeffe from the Fiji islands of Viti Levu, Ovalau, Motiriki, Ngara, Kadavu, Vanua Balavu, Mago, Kanacea, and Cikobia-i-lau, and were described by MOUSSON in 1870. More recently the freshwater gastropods on Viti Levu have been investigated by STARMÜHLNER (1976) and HAYNES (1985) but nothing has been written about gastropods on the other islands since 1870.

This investigation was aimed at finding what freshwater gastropods were present on the high islands of Vanua Levu, Ovalau, Gau, Kadavu, and Taveuni. Physical factors and water chemistry were also measured in order to see how much these factors contributed to the distributions of the gastropods.

STUDY AREA

The islands investigated are shown in Figure 1. Vanua Levu, the second largest island of the group, rises about 1000 m above sea level and has extensive areas on the northern side where sugar cane is grown, while on the wetter southern side there are many coconut plantations.

The four smaller volcanic islands (Ovalau, Gau, Kadavu, and Taveuni) rise steeply to an altitude of 400–500 m. Their high central regions are covered mainly in rain forest, while there are many villages and village gardens containing dalo (*Colocasis esculenta*), cassava (*Manihot esculenta*), paw paw (*Carica papaya*), banana (*Musa paradisiaca*), and yoqona (*Piper methysticum*) in the coastal areas. Some coconut plantations are found on Ovalau and Taveuni. The torrential streams on these islands are liable to sudden flooding and occasionally they become dry in their lower courses. The substrate of the streams is composed of large rocks and boulders so that the water flows in a series of short waterfalls, pools, and white cascades. Macrophytes were absent except 300–400 m upstream from the mouth at the sides of Naivika Creek, Taveuni, where watercress (*Nasturtium officinale*) grew.

All five islands were formed from volcanic eruptions in Miocene and late Pliocene times while Taveuni is the site of the most recent (1200 AD) volcanic activity in the Fiji group (RICKARD, 1966; IBBOTSON, 1961; WOODROW, 1980).

MATERIALS AND METHODS

Vanua Levu

Gastropods were collected from rivers and streams in October 1983. The stations, 1–10 on the map (Figure 1), were chosen to be as representative as possible while still being accessible by road.

The substrate at each station was searched for 30 min for gastropods. The leaf litter, plants, wood, and upper and lower surfaces of stones and boulders were inspected

Figure 1

A map of the main islands of Fiji showing the localities of the sampling stations on Vanua Levu and the positions of the streams that were sampled on Ovalau, Gau, Kadavu, and Taveuni.

and the sand and gravel were sieved. Samples of each species at all the stations were taken to the laboratory and identified according to RIECH (1937), STARMÜHLNER (1970, 1976), and HAYNES (1984).

The substrate, water speed, and temperature were noted and water samples were taken at most stations. The water samples were analyzed for conductivity (μS) and hardness (mg $CaCO_3$/L) by the Institute of Natural Resources, University of the South Pacific.

Ovalau, Gau, Kadavu, and Taveuni

Physical parameters were noted and water samples and gastropods were collected in 1983–1984 by the methods described above. A stream on each island was sampled from the mouth to 2000 m inland at four stations (three stations on Kadavu). The streams sampled were Rukuruku Creek, Ovalau; Navure Creek, Gau; Nubulevu Creek, Kadavu; and Naivika Creek, Taveuni (Figure 1).

Several of each species of gastropod were dissected and the contents of the guts were examined to find what food they had been eating.

RESULTS

Specimens of the prosobranchs collected in this survey were deposited in the Los Angeles County Museum of Natural History and duplicate specimens are available at the School

of Pure and Applied Sciences, University of the South Pacific, Suva, while specimens of the suspected new species of *Acochlidium* were sent to the Vienna Natural History Museum.

Vanua Levu

The physical and chemical conditions and gastropods present at each station are shown in Table 1. The nomenclature of STARMÜHLNER (1970, 1976) has been used where possible. A total of 26 species of gastropods was found on Vanua Levu, and all except two were prosobranchs. These exceptions were *Physastra nasuta* (LACM 83-135.1) (Pulmonata, Planorbiidae) and *Acochlidium* sp. (Opisthobranchia, Acochlididae). Of the Prosobranchia, 12 (*Neritina pulligera* [LACM 84-174.1], *N. squamipicta* [LACM 83-139.1], *N. auriculata* [LACM 84-170.1], *N. turtoni* [LACM 83-140.1], *N. canalis* [LACM 84-171.1], *N. petiti* [LACM 84-173.2], *N. porcata* [LACM 84-168.1], *Neritilia rubida* [LACM 83-136.1], *Clithon diadema* [LACM 83-142.1], *C. olivaceus* [LACM 83-145.1], *C. pritchardi* [as *C. corona* in HAYNES, 1984] [LACM 83-143.1], *C. oualaniensis* [LACM 84-172.1]) belong to Neritidae, 8 (*Melanoides tuberculata* [LACM 83-141.1], *M. lutosa* [LACM 83-145.2], *M. plicaria* [LACM 83-137.1], *M. aspirans* [LACM 83-138.1], *Thiara bellicosa* [LACM 83-142.3], *T. scabra, T. terpsichore* [LACM 83-142.2], *T. amarula* [LACM 83-144.1]) belong to Thiaridae, and 4 (*Septaria lineata* [LACM 83-142.4], *S. suffreni* [LACM 84-174.3], *S. porcellana* [LACM 84-173.3], *S. sanguisuga* [as *S. borbonica* in HAYNES, 1984] [LACM 84-174.2]) belong to Septariidae (Neritacea).

Physastra nasuta was found only on the northern side of the island (Stations 1–4, Figure 1), while *Acochlidium* sp. was discovered only at Station 6. Station 6 was also where the greatest number of species (11) were found. In general more species (6–11) were present in the rivers and streams on the steeper southern coast compared with those (3–6) on the flatter more cultivated northern coast (Figure 1).

The values for total ions (916 μS) and hardness (252 mg $CaCO_3$/L) were higher at Station 3 than at any other station, probably because of nearby limestone rock (RICKARD, 1966). At this station a green sponge encrusted boulders and stones. In the Dreketi-Seaqaqa river system (Stations 1–4) the temperature (30, 28, 28, 27°C) decreased as the distance from the sea increased (3, 6, 26, 33 km) (Table 1).

The temperatures at Stations 8 and 9 were lower than at other stations probably because measurements were taken earlier in the morning.

In the Dreketi-Seaqaqa river system (Stations 1–4) at Stations 1, 3, and 4, where the current was between 20 and 40 cm/sec, the gastropods *Physastra nasuta, Melanoides tuberculata,* and *Neritina pulligera* were found (Table 1). The inland or high altitude species *Melanoides lutosa* appeared at Station 3 (26 km upstream) and was also present at Station 4. *Septaria porcellana* and *S. suffreni* were present on the boulders at Station 3 but had not reached the stream at Station 4. The Dreketi River, where Station 2 was located, was wide and deep and the current slow; consequently, three different gastropods, *Thiara bellicosa, Neritilia rubida,* and *Clithon diadema,* were found at this station (Table 1).

Ovalau, Gau, Kadavu, and Taveuni

The physical and chemical conditions that existed and the gastropods that were present in the four sampled streams are recorded in Table 2. The number of species in each stream was approximately the same. There were 16 species in Rukuruku Creek, Ovalau, 15 in Navure Creek, Gau, 15 in Nubulevu Creek, Kadavu, and only 14 in Naiviki Creek, Taveuni, where the calcium content of the water was low (9 mg $CaCO_3$/L).

Generally the same gastropods were found in the streams of the four islands. From the mouth to 20 m upstream, only species that are able to live in brackish water were present (Table 2). Further upstream (300–400 m) in fairly swift currents, some of these species persisted, *e.g., Clithon oualaniensis, C. diadema, C. pritchardi,* and *Septaria porcellana.* Of these, however, only *C. pritchardi* and *S. porcellana* were found 1500 m or more upstream (Table 2). These higher, steeper parts of the streams were rich in gastropod species (5–11 species) and in numbers of individuals (up to 125/m^2). *Melanoides tuberculata* and *M. lutosa* were usually found in quieter parts of the stream, while species such as *Clithon olivaceus, C. pritchardi, Neritina variegata* (LACM 84-169.1), and *N. canalis* were found on the sides or on the under surface of rocks; the limpets *Septaria* spp. were able to live on the upper surfaces as well as the sides of rocks (Figure 2).

The course of Rukuruku Creek rose less steeply for the first 500 m than did that of the other three streams. Consequently there was greater diversity of gastropod species at 300–400 m upstream, because those favoring a less swift current (*e.g., Thiara amarula* and *Neritina squamipicta*) were able to survive.

When the stomachs of the various gastropod species were examined they were found to contain mainly unicellular green algae, diatoms, and filamentous cyanobacteria. Periphyton scraped from stones on which gastropods had been found contained similar microphytes.

In the torrential streams investigated, gastropods were the dominant benthic invertebrates. Insect larvae were absent from most parts of the streams. Prawns and fish were present in all streams, especially in pools below cascades.

The temperature, hardness, and total ions in the water of Rukuruku Creek, Ovalau, and Navure Creek, Gau, were similar (Table 2) but the water of Nubulevu Creek, Kadavu, had a slightly higher value for total ions (160 compared with 122 and 147 μS) and was less hard (20 mg $CaCO_3$/L compared with 56 and 52). Naivika Creek, Taveuni, was low in calcium ions (9 mg $CaCO_3$/L) and total ions (36.1 μS). The temperature was significantly

Table 1

The physical conditions, results of water analysis, and gastropods present at the sampling stations on the island of Vanua Levu. ND = not determined.

Station	River & map reference, 1:250,000, Vanua Levu	Substrate	Distance from sea	Water speed (cm/sec)	Temperature (°C)	Total ions (μS)	Hardness (mg $CaCO_3$/L)	Gastropods present
1	Creek into Dreketi R.: YG0365	stones	3 km	30–40	30	144.6	56	*Physastra nasuta* (Morelet), *Melanoides tuberculata* (Müller), *Neritina pulligera* (Linné)
2	Dreketi R. 2 km east of Nabavati: YG0866	sand & stones	6 km	10	28	141.4	40	*Thiara bellicosa* (Hinds), *Neritilia rubida* (Pease), *Clithon diadema* (Récluz)
3	Seaqaqa R. near Naravuka turnoff: YG2462	stones & boulders	26 km	30	28	915	252	*Physastra nasuta, Melanoides lutosa* (Gould), *M. tuberculata, Neritina pulligera, Septaria porcellana* (Linné), *S. suffreni* (Récluz)
4	Stream into Seaqaqa R. at Salvou: YG2963	stones, boulders & rocks	33 km	20–30	27	ND	ND	*Physastra nasuta, Melanoides tuberculata, M. lutosa, Neritina pulligera*
5	Stream at Nabalebale: YG4156	gravel & stones	8 km	50–60	28	111.1	36	*Melanoides tuberculata, M. plicaria* (Born), *M. aspirans* (Hinds), *Thiara terpsichore* (Gould), *Clithon olivaceus* (Récluz), *C. pritchardi* (Dohrn), *Neritina pulligera, Septaria porcellana, S. suffreni*
6	Nasekawa R. at Venivesi: YG4355	stones	7 km	10–30	29	123.7	40	*Melanoides tuberculata, M. aspirans, Clithon olivaceus, Neritina canalis* Sowerby, *N. petiti* Récluz, *N. porcata* Gould, *Septaria sanguisuga* (Reeve), *S. porcellana*
7	Nakelikosa Ck.: YG5342	gravel & rocks	20 m	10	28	697	136	*Melanoides aspirans, Clithon pritchardi, Neritina auriculata* Lamarck, *N. squamipicta*
8	Creek on Hibiscus Hwy.: YG8848	sand & rocks	500 m	10	22	292	64	*Melanoides tuberculata, Clithon pritchardi, C. diadema, Neritina turtoni* (Récluz), *N. auriculata, N. squamipicta, Septaria porcellana, S. lineata*
9	Bagasau Ck.: YG9252	rocks & boulders	2 km	0–50	25	287	100	*Melanoides tuberculata, M. aspirans, Clithon olivaceus, Neritina canalis* Sowerby, *N. petiti* Récluz, *N. porcata, Septaria sanguisuga, S. porcellana*
10	Buca Ck.: ZG0457	gravel, rocks & wood	50 m	0–20	28	257	72	*Thiara terpsichore, T. bellicosa, Clithon diadema, Clithon oualaniensis* (Lesson), *Septaria lineata, S. porcellana*

Table 2

The physical conditions, results of water analysis, and gastropods present at four (three on Kadavu) sampling stations in a stream on each of the islands of Ovalau, Gau, Kadavu, and Taveuni. ND = not determined.

	Rukuruku Ck. Ovalau	Navure Ck. Gau	Nubulevu Ck. Kadavu	Naivika Ck. Taveuni
Mouth–20 m upstream				
Current speed (cm/sec)	0–10	0–10	0–10	0–10
Temperature (°C)	26	27	27	22
Hardness (mg $CaCO_3$/L)	190	180	110	330
Conductivity (μS)	2100	1330	1820	6280
Species	*Clithon rarispina* (Mousson), *C. pritchardi, C. diadema, C. oualaniensis*	*Clithon diadema, C. oualaniensis*	*Clithon pritchardi, Neritina auriculata*	*Clithon diadema, C. oualaniensis, C. pritchardi, Neritina auriculata, Septaria porcellana*
300–400 m upstream				
Current speed (cm/sec)	0–50	30–40	0–40	20–30
Temperature (°C)	25.5	26	26	22
Hardness (mg $CaCO_3$/L)	56	52	20	19.67
Conductivity (μS)	147.1	122	160	66.7
Species	*Clithon oualaniensis, C. diadema, C. pritchardi, Neritina pulligera, N. canalis, N. squamipicta, Melanoides aspirans, M. plicaria, M. tuberculata, Thiara amarula* (Linné), *Septaria porcellana*	*Clithon diadema, C. pritchardi, Neritina turrita* (Gmelin), *Melanoides aspirans*	*Clithon pritchardi, C. olivaceus, Neritina petiti, N. porcata, Septaria macrocephala* (Guillon), *S. porcellana*	*Neritina canalis, N. variegata* (Lesson), *Melanoides aspirans, M. tuberculata, S. porcellana*
1000–1100 m upstream				
Current speed (cm/sec)	0–100	0–80	0–100	50–100
Temperature (°C)	25	25	26	22
Hardness (mg $CaCO_3$/L)	58	55	20	9
Conductivity (μS)	149.8	134	159	36.1
Species	*Clithon olivaceus, Melanoides lutosa, M. tuberculata, Septaria porcellana, S. suffreni*	*Clithon olivaceus, C. pritchardi, Neritina variegata, N. canalis, N. petiti, N. macgillvrayi* (Reeve), *Melanoides aspirans, Septaria porcellana, S. sanguisuga, S. suffreni*	*Clithon olivaceus, C. pritchardi, Neritina variegata, N. canalis, N. pulligera, Melanoides arthurii* (Brott), *M. tuberculata, Septaria porcellana, S. suffreni, S. macrocephala, S. sanguisuga*	*Clithon olivaceus, Neritina variegata, Melanoides arthurii, M. tuberculata, Septaria suffreni, S. porcellana, S. macrocephala, S. sanguisuga*
2000 m upstream (side stream)				
Current speed (cm/sec)	20–40	40–60	ND	50–100
Temperature (°C)	25	ND	ND	21
Hardness (mg $CaCO_3$/L)	60	ND	ND	9.0
Conductivity (μS)	152.3	ND	ND	36.1
Species	*Clithon olivaceus, Melanoides lutosa, M. tuberculata*	*Clithon olivaceus, Neritina pulligera, N. petiti, N. canalis, N. variegata, N. porcata, Septaria porcellana, S. suffreni, S. sanguisuga*	ND ND	*Clithon olivaceus, Neritina variegata, Septaria porcellana*

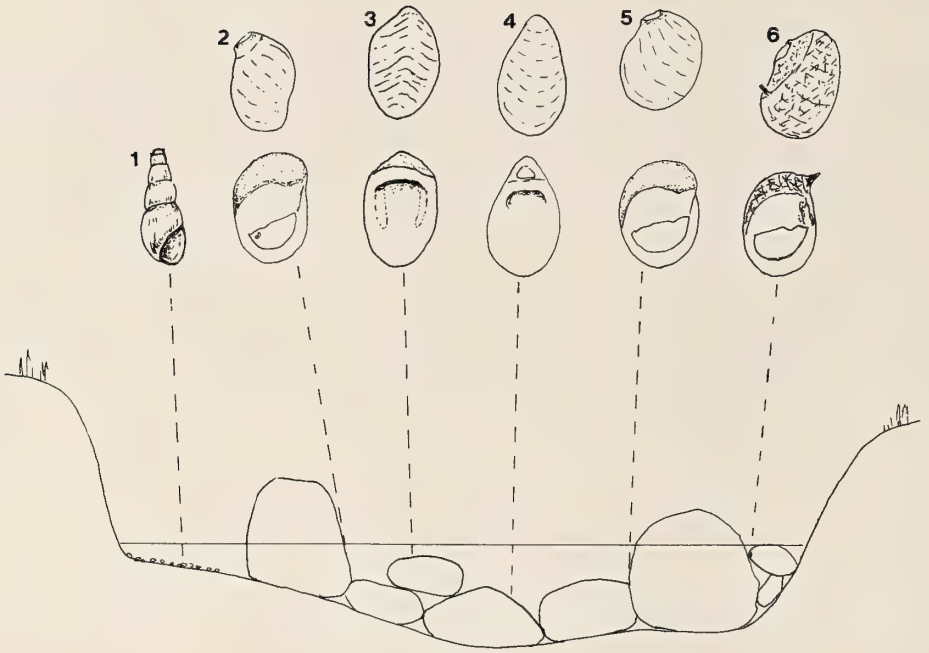


Figure 2

The distribution of gastropods across a Fijian torrential stream showing the different habitats of the various shell types. 1, *Melanoides lutosa*; 2, *Neritina variegata*; 3, *Septaria porcellana*, 4. *S. sanguisuga*; 5, *Clithon olivaceus*; 6, *C. pritchardi*.

lower (21–22°C) than that of the other three streams (25–27°C) ($P < 0.01$). Above the brackish water region of the streams there was little difference in the chemical composition along the length of each stream.

DISCUSSION

Twenty-six species of gastropods were found on Vanua Levu at 10 stations compared with 32 species from 47 stations on Viti Levu (HAYNES, 1985). Species present on Viti Levu but not found on Vanua Levu were *Planorbarius corneus, Ferrissia noumeensis, Gyraulus montrouzieri, Assiminea crosseana, Melanoides arthurii, Fluviopupa pupoidea,* and *Fijidoma maculata.* The endemic species *Fluviopupa pupoidea* Pilsbry and *Fijidoma maculata* (Mousson), which are found in the headwaters of the rivers of Viti Levu, were not found on any of the five islands. These two species may be remnants of an old fauna that has survived only on the geologically older Viti Levu (LADD, 1934).

Some species (*Clithon olivaceus, Neritina variegata, Septaria macrocephala* [LACM 84-169.3], and *S. sanguisuga*) were absent from all collecting stations on Viti Levu (HAYNES, 1985) but were present on the four smaller islands. *Clithon olivaceus* and *S. sanguisuga* were also found on Vanua Levu. It is difficult to judge whether these species have always been absent from streams on Viti Levu or whether they have recently disappeared because logging operations have increased the turbidity of the water. Several *Thiara* spp. (*e.g., Thiara bellicosa* and *T. terpsichore*) were found on Vanua Levu and Viti Levu (HAYNES, 1985) but not in the torrential streams. This was probably because they have failed to become established in the swift currents of these streams.

The small (10–15 mm long) shell-less opisthobranch *Acochlidium* sp. was found only at Station 6 on Vanua Levu. It is thought to be an undescribed species and specimens have been sent to E. Wawra, Naturhistorisches Museum Wien. It is somewhat similar to *Acochlidium bayerfehlmanni* Wawra from the Palau Islands (WAWRA, 1980) and *Acochlidium sutteri* Wawra from Sumba, Indonesia (WAWRA, 1979).

A feature of many streams in Fiji is the richness and abundance of gastropod species. In contrast, islands in the Caribbean region appear to have many more rheolite insect species than gastropod species. HARRISON & RANKIN (1976) found 14 insect species and no gastropod species in high-level streams (290–488 m altitude) on St. Vincent (Lesser Antilles) and 15 insect species and 3 gastropod species in low-level streams (8–274 m altitude). STARMÜHLNER & THEREZIEN (1983) found only one lotic gastropod species (*Neritina punctulata*) but over 20 species of insects in streams on Guadeloupe, Dominica, and Martinique.

However, other islands in the Indo-Pacific region appear to have a rich gastropod fauna similar to that found in the Fiji Islands. STARMÜHLNER (1982) described 16

gastropod species in running water on Andaman Island, Indian Ocean. These include *Melanoides tuberculata, M. plicaria, Thiara scabra, Neritina pulligera, N. variegata, N. squamipicta, Septaria porcellana,* and *Neritilia rubida,* which are also present in Fijian streams and rivers. The mountain streams of New Caledonia had at least 16 species of gastropods and those of Sri Lanka 13 gastropod species (STARMÜHLNER, 1979).

Likely predators in the slower streams and rivers of Vanua Levu were odonatid nymphs, coleopterid larvae, leeches, fishes, and cane toads (*Bufo marinus*) but in the torrential streams, because of the scarcity of rheolite insects, the only obvious predators were fish species.

Thiarid species (*Melanoides* spp. and *Thiara* spp.) are viviparous, and almost all are exclusively parthenogenetic, although a few dioecious populations have been found (DAVIS, 1971). Those species (*e.g., Melanoides tuberculata* and *M. lutosa*) that live far inland give birth to juvenile adults, while species (*e.g., M. aspirans* and *M. plicaria*) that inhabit tidal regions release veligers into the water (STARMÜHLNER, 1976).

The neritid snails (*Neritina* spp., *Clithon* spp., and *Septaria* spp.) are dioecious. After copulation the females lay eggs in egg cases that they cement to stones, boulders, and often to shells of other gastropods. It is not known for most species whether the young hatch as veligers or as juvenile snails. GOVINDAN & NATARAJAN (1972) reported that eggs of the lowland Indian species *Neritina layardi* (Lesson) hatched as veligers after 20–22 days and those of *Septaria tesselata* (=*S. lineata* Lamarck) hatched as veligers after 14–15 days. FORD (1979) reported that the eggs of the Hawaiian torrential stream species *Neritina granosa* Sowerby also hatched as veligers. Ford believed that after hatching the veligers of *N. granosa* were swept out to sea and later settled at the mouth of rivers or streams. FORD (1979) observed long chains of up to 80 young snails (less than 5 mm high) moving upstream. No such phenomenon has been observed in Fiji streams but small juveniles (1.5–2.0 mm high) have been found clinging to the shells of adult *Septaria* spp. and *Clithon* spp. 2 km upstream from the mouth. These species likely either hatch as juvenile snails or as veligers that settle in freshwater.

Certain species (*e.g., Neritina auriculata, N. turrita,* and *Clithon diadema*) were confined to brackish or tidal regions where total ions were high. Above the influence of the tide, the water speed, and consequently the nature of the substrate, appeared to determine the distribution of gastropods both along and across the stream. However, it is possible that the absence of *Neritina pulligera* and *Neritina petiti* from Naivika Creek, Taveuni, was caused by low amounts of dissolved ions in the water.

ACKNOWLEDGMENT

I thank the Research Committee of the University of the South Pacific for a grant that made this work possible.

LITERATURE CITED

DAVIS, G. M. 1971. Systematic studies of *Brotia costula episcopalis,* first intermediate host of *Paragonimus westermani* in Malaysia. Proc. Acad. Natur. Sci. Phila. 123:53–66.

FORD, J. I. 1979. Biology of a Hawaiian fluvial gastropod *Neritina granosa* Sowerby (Prosobranchia: Neritidae). M.S. Thesis, University of Hawaii.

GOVINDAN, K. & R. NATARAJAN. 1972. Studies on Neritidae (Neritacea: Prosobranchia) from peninsular India. Proc. Indian Acad. Sci. 38B:225–239.

HARRISON, A. D. & J. J. RANKIN. 1976. Hydrobiological studies of eastern Lesser Antillean islands 2. St. Vincent: freshwater fauna—its distribution, tropical river zonation and biogeography. Arch. Hydrobiol. 2/3(Suppl. 50):275–311.

HAYNES, A. 1984. Guide to the brackish and fresh water gastropods of Fiji. Institute of Natural Resources, University of the South Pacific, Suva. 39 pp.

HAYNES, A. 1985. The ecology and local distribution of non-marine aquatic gastropods in Viti Levu, Fiji. Veliger 28(2): 204–210.

IBBOTSON, P. 1961. The geology of Ovalau, Motiriki and Naingani. Geol. Surv. Dept., Suva, Fiji, Bull. 9:1–7.

LADD, H. S. 1934. Geology of Viti Levu, Fiji. Bernice P. Bishop Mus. Bull. 119:1–263.

MOUSSON, A. 1870. Faune malacologique terrestre et fluviatile des isles Viti, d'après les envois de M. le Dr. Edouard Graeffe. Jour. Conchol. 18(2):109–135, 179–236.

RICKARD, M. J. 1966. Reconnaissance geology of Vanua Levu. Geol. Surv. Fiji, Mem. 2:1–81.

RIECH, E. 1937. Systematiche, anatomische, ökologische und tiergeographische Unterschungen über die susswassermollusken Papuasiens und Melanesiens. Arch. Naturgesch. (N.F.) 6(36):40–101.

STARMÜHLNER, F. 1970. Die mollusken der Neukaledonischen binnengewasser. Cah. ORSTOM Ser. Hydrobiol. 4(3/4): 3–127.

STARMÜHLNER, F. 1976. Beitrage zur Kenntnis der Susswasser-Gastropoden pazifischer Inseln. Ann. Naturhist. Mus. Wien 80:473–656.

STARMÜHLNER, F. 1979. Distribution of freshwater molluscs in mountain streams of tropical Indo-Pacific Islands (Madagascar, Ceylon, New Caledonia). Malacologia 18:245–255.

STARMÜHLNER, F. 1982. Occurrence, distribution and geographical range of the freshwater gastropods of the Andaman Islands. Malacologia 22(1/2):455–462.

STARMÜHLNER, F. & Y. THEREZIEN. 1983. Résultats de la mission hydrobiologique Austro-Francaise de 1979 aux Iles de la Guadeloupe, de la Dominique et de la Martinique. Ann. Naturhist. Mus. Wien Part 1A, 85/B:171–218; Part 1B, 85/B:219–262.

WAWRA, E. 1979. *Acochlidium sutteri* nov. spec. (Gastropoda, Opisthobranchia, Acochlidiacea) von Sumba, Indonesien. Ann. Naturhist. Mus. Wien 82:595–604.

WAWRA, E. 1980. *Acochlidium bayerfehlmanni* spec. nov. (Gastropoda: Opisthobranchia: Acochlidiacea) from Palau Islands. Veliger 22(3):215–218.

WOODROW, P. J. 1980. Geology of Kandavu. Bull. 7:1–31. Ministry of Lands and Mineral Resources, Fiji Government.

The Veliger 30(4):384–386 (April 1, 1988)

THE VELIGER

New Molluscan Hosts for Two Shrimps and Two Crabs on the Coast of Baja California, with Some Remarks on Distribution

by

ERNESTO CAMPOS-GONZÁLEZ

Escuela Superior de Ciencias, Universidad Autónoma de Baja California,
Apartado Postal 2300, Ensenada, B.C., México

Abstract. *Astraea undosa* and *Hinnites giganteus* are recorded as new hosts for *Betaeus harfordi* and *Pinnotheres margarita* respectively. For the latter, a range extension is given to Bahía del Rosario, on the west coast of Baja California. *Atrina tuberculosa* is confirmed as a regular host for *Pontonia pinnae,* and *Protothaca grata* and *Tagelus affinis* as hosts for *Pinnotheres reticulatus.* The distributional data for *Pinnotheres reticulatus* in the Gulf of California are emended, and for *Pontonia pinnae* a range extension is given to Laguna de San Ignacio, on the west coast of Baja California Sur.

INTRODUCTION

Some species of decapod crustaceans commonly occur as symbionts of other invertebrates (PATTON, 1967). On the coasts of Baja California, some caridean shrimps and pinnotherid crabs are frequently collected inside, or on, their hosts (HART, 1964; SCHMITT *et al.,* 1973; WICKSTEN, 1983; CAMPOS-GONZÁLEZ, 1986). Recently, the author and some colleagues collected shrimps of the genera *Betaeus* and *Pontonia,* and two species of crabs, genus *Pinnotheres,* in hosts previously not recorded, or overlooked in the recent literature and now confirmed.

DESCRIPTIONS

ALPHEIDAE

Betaeus harfordi Kingsley, 1878

Distribution and hosts: Fort Bragg, Mendocino Co., California, U.S.A., to Bahía Magdalena, Baja California Sur, México; commensal in *Haliotis* spp. (CHACE & ABBOTT, 1980).

Material examined and new host: 1 male, 1 female, and 3 juveniles, Isla Cedros, Baja California, in the mantle cavity of *Astraea undosa* (Wood, 1828), 6 January 1987, Gabriel Jiménez-Beede, coll.

Remarks: The occurrence of *Betaeus harfordi* as a commensal of *Astraea undosa* is apparently rare, since the only hosts previously recorded are species of *Haliotis.* ACHE & DAVENPORT (1972) noted . . . . "Specifity experiments suggest that *B. harfordi* discriminates a chemical substance or complex of substances containing sufficient information for recognizing gastropods of the genus *Haliotis* from other gastropods . . . ." It is possible that *A. undosa* could be a temporary or occasional host, but more data are necessary to support this. GHISELIN *et al.* (1967) found that the amino acid composition of the shell matrix was similar in *Haliotis* and *Astraea.* It is possible that a putative "host factor" present in *Haliotis* may also be present in *A. undosa.* Laboratory experiments are necessary to resolve this question, and to determine whether preference is related not only to the recognition of a chemical substance, but also to morphology of these hosts.

PALAEMONIDAE

Pontonia pinnae Lockington, 1878

Distribution and hosts: Upper Gulf of California, to Panama; commensal in *Pinna rugosa* Sowerby, 1835 (WICKSTEN, 1983).

Material examined and new hosts: Dozens of males and females, Bahía de los Angeles, Baja California, commensal in *Pinna rugosa* and *Atrina tuberculosa* (Sowerby, 1835), summer 1986 and April 1987, Mario Nieves, Alma Rosa Murillo-Peralta & E. Campos-González, colls.; 8 females, and 1 male, Estero El Cordon, Laguna de San Ignacio, Baja California Sur, in "Callo de Hacha," 17 May 1987, Eulogio López, coll.

Remarks: WICKSTEN (1983), in her monograph of caridean shrimps of the Gulf of California, noted *Pinna rugosa* as the only host for *Pontonia pinnae*. However, LUKE (1977), in the catalog of crustacean decapods at the Scripps Institution of Oceanography, also cited this shrimp as occurring on *Atrina tuberculosa*. My record confirms Luke's data. Both *Pinna rugosa* and *A. tuberculosa* commonly harbor a sexual couple of *Pontonia pinnae* in the Bahía de los Angeles area.

PINNOTHERIDAE

Pinnotheres margarita Smith, 1869

Distribution and hosts: Bahía Kino, Sonora, México, to Panama Bay; commensal in *Pinctada mazatlanica* (Hanley, 1855), and *Argopecten circularis* (Sowerby, 1835) (CAMPOS-GONZÁLEZ & CAMPOY-FAVELA, in press).

Material examined and new hosts: 4 males and 30 ovigerous females, Estero El Cordon, Laguna de San Ignacio, Baja California Sur, in *Argopecten* (?) *aequisulcatus* (Carpenter, 1864), 17 May 1987, Eulogio López, coll.; 1 female, Agua Blanca, Bahía del Rosario, Baja California, in *Hinnites giganteus* (Gray, 1825), 4 April 1986, Alfredo Salas, coll.

Remarks: The females and males collected at Estero El Cordon agree with the description and variation previously noted (RATHBUN, 1918; WICKSTEN, 1982; CAMPOS-GONZÁLEZ & CAMPOY-FAVELA, in press). The female collected at Bahía del Rosario differed in two features: the carapace margins are arcuate, whereas they are subangular in the specimens from Estero El Cordon and from the Gulf of California, and the fine pubescence normally present in the body of this crab is lacking in this female.

Pinnotheres reticulatus Rathbun, 1918

Distribution and hosts: San Felipe, Baja California, to Costa Rica; hosts, *Polymesoda inflata* (Philippi, 1851), *Protothaca grata* (Say, 1831), and *Tagelus affinis* (C. B. Adams, 1852) (GLASSELL, 1935; GREEN, 1985).

Material examined: 22 females (2 ovigerous, 2 juveniles), 2 males, Laguna Percebú, about 23 km S of San Felipe, Baja California, in *Protothaca grata* and *Tagelus affinis*, summer 1986, E. Campos-González, coll.; 1 female, Puertecitos, km 72 road San Felipe–San Luis Gonzaga, in *P. grata*, August 1986, Gerardo Lopez & E. Campos-González, colls.

Remarks: Recently GREEN (1985) found that *Pinnotheres jamesi* Rathbun, 1923, is a junior synonym of *P. reticulatus* Rathbun, 1918. He noted that the distribution of this species is from off "San Josef Island" Isla San José, Baja California Sur, to Costa Rica, and recorded *Polymesoda inflata* as the only host known. This author, as well as SILAS & ALAGARSWAMI (1967) and SCHMITT *et al.* (1973), overlooked the distributional information and new host given by GLASSELL (1935) for this species. Glassell recorded *P. reticulatus* from San Felipe, Baja California, living in *Paphia grata* (=*Protothaca grata*) and *Tagelus affinis*. In the Laguna Percebú area, the prevalence of this pinnotherid in *Protothaca grata* is lower. About 1000 clams were dissected to obtain 20 specimens. Only females were found in this host; juveniles, males, and females were taken inside *T. affinis*. Additionally, I have sampled *Protothaca grata* in Campo Pescadores (about 2 km N of San Felipe), and Puertecitos, and found only 1 female in 3000 clams. In these places I did not find *T. affinis*, but the population of *Protothaca grata* is greater than at Laguna Percebú. It is possible that the presence of *T. affinis* ("primary host") is necessary for the subsequent infestation of *Protothaca grata* ("secondary host"). This phenomenon has been recorded for *Pinnixa littoralis* (PEARCE, 1966; GARTH & ABBOTT, 1980).

ACKNOWLEDGMENTS

My great appreciation is due to Gabriel Jiménez-Beede (Escuela Superior de Ciencias, U.A.B.C.), Alfredo Salas (Instituto de Investigaciones Oceanológicas, U.A.B.C.), and Rubén Ríos (Centro de Investigación Científica y de Educación Superior de Ensenada) for sending me part of the material recorded. I acknowledge my students, José R. Campoy-Favela, Gerardo López, Patricia Alemán-Díaz, Alma Rosa Murillo-Peralta, and Sara Terui-García, for the invaluable effort and support in my investigations on commensal crustaceans. I am also indebted to Dr. Meredith Gould (Escuela Superior de Ciencias) and two anonymous reviewers for their comments and criticism of the manuscript. This work was supported in part by the project 038-UABC of the Escuela Superior de Ciencias, Universidad Autónoma de Baja California.

LITERATURE CITED

ACHE, B. W. & D. DAVENPORT. 1972. The sensory basis of host recognition on symbiotic shrimps, genus *Betaeus*. Biol. Bull. 143:94–111.

CAMPOS-GONZÁLEZ, E. 1986. Records and new host of pea crabs (Decapoda: Pinnotheridae) for Baja California, México. Veliger 29:238–239.

CAMPOS-GONZÁLEZ, E. & J. R. CAMPOY-FAVELA. In press. Morfología y distribución de dos cangrejos chicharo del Golfo de California (Crustacea, Pinnotheridae). Rev. Biol. Trop. (Costa Rica).

CHACE, F. A. & D. P. ABBOTT. 1980. Caridea: the shrimps. Pp. 567–576. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, California.

GARTH, J. S. & D. P. ABBOTT. 1980. Brachyura: the true crabs. Pp. 593–630. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, California.

GHISELIN, M. T., E. T. DEGENS, D. W. SPENCER & R. H. PARKER. 1967. A phylogenetic survey of molluscan shell matrix protein. Breviora 262:1–35.

GLASSELL, S. A. 1935. New or little known crabs from the

Pacific coast of Northern Mexico. Trans. San Diego Soc. Natur. Hist. 8:91–106.

Green, T. M. 1985. *Pinnotheres jamesi* synonymized with *P. reticulatus* (Decapoda: Brachyura). Proc. Biol. Soc. Wash. 98:611–614.

Hart, J. F. L. 1964. Shrimps of the genus *Betaeus* on the Pacific coast of North America with descriptions of three new species. Proc. U.S. Natl. Mus. 115:431–466.

Luke, S. R. 1977. Catalog of the benthic invertebrate collection. I. Decapod Crustacea and Stomatopoda. Scripps Inst. Oceanogr. Ref. No. 77-9. 72 pp.

Patton, W. K. 1967. Commensal Crustacea. Proc. Symp. on Crustacea, Mar. Biol. Assoc. India 2:1228–1243.

Pearce, J. B. 1966. On *Pinnixa faba* and *Pinnixa littoralis* (Decapoda, Pinnotheridae) symbiotic with the clam *Tresus capax* (Pelecypoda: Mactridae). Pp. 565–589. *In:* H. Barnes (ed.), Some contemporary studies in marine science. Allen & Unwin: London.

Rathbun, M. J. 1918. The grapsoid crabs of America. Bull. U.S. Natl. Mus. 97:1–461.

Rathbun, M. J. 1923. The brachyuran crabs collected by the U.S. Fisheries steamer "Albatross" in 1911, chiefly on the west coast of Mexico. Bull. Amer. Mus. Natur. Hist. 48: 619–637.

Schmitt, W. L., J. C. McCain & E. S. Davidson. 1973. Decapoda I. Brachyura I. Family Pinnotheridae. *In:* H. E. Gruner & L. B. Holthuis (eds.), Crustaceorum catalogus. W. Junk. B.V.: Den Haag. 160 pp.

Silas, E. G. & K. Alagarswami. 1967. On an instance of parasitization by the pea-crab (*Pinnotheres* sp.) on the black water clam (*Meretrix casta* (Chemnitz)) from India, with a review of the work on the systematics, ecology, biology and ethology of pea-crabs of the genus *Pinnotheres* Latreille. Proc. Symp. on Crustacea, Mar. Biol. Assoc. India 2:1161–1227.

Wicksten, M. K. 1982. New records of pinnotherid crabs from the Gulf of California (Brachyura: Pinnotheridae). Proc. Biol. Soc. Wash. 95:354–357.

Wicksten, M. K. 1983. A monograph on the shallow water caridean shrimps of the Gulf of California, Mexico. Allan Hancock Monogr. Mar. Biol. 13:1–59.

The Veliger 30(4):387–394 (April 1, 1988)

THE VELIGER

Systematics of the Scurriini (New Tribe) of the Northeastern Pacific Ocean (Patellogastropoda: Lottiidae)

by

DAVID R. LINDBERG

Museum of Paleontology, University of California, Berkeley, California 94720, U.S.A.

Abstract. **Scurriini**, a new tribe of the subfamily Lottiinae Gary, 1840, is proposed for the lottiids of the Peruvian molluscan province in the southeastern Pacific (*Scurria* Gray, 1847, species) and *Notoacmea insessa* (Hinds, 1842) of the Californian and Oregonian molluscan provinces in the northeastern Pacific. ***Discurria*** new genus is proposed for *N. insessa* and the new, early Pleistocene species ***Discurria radiata*** from southern California. Recognition of the relationship between the genera *Scurria* and ***Discurria*** provides another example of a taxon shared by these two disjunct nearshore marine regions. The pattern of fossil and Holocene distributions of *Scurria* and *Lottia* Sowerby, 1834, in the eastern Pacific Ocean and Caribbean Sea suggests that migration and later radiations in the family Lottiidae have proceeded from south to north. This direction is unlike that of many other northeastern Pacific molluscan taxa that appear to have originated in the northwestern Pacific and migrated into the northeastern Pacific (west to east).

INTRODUCTION

Discontinuous spatial distributions of marine organisms are striking and important features in historical biogeography. Divisions in the distributions of nearshore marine molluscan taxa usually reflect prominent geological features or areas of geologically recent perturbations (*e.g.*, the Isthmus of Panama between the tropical eastern Pacific and the Caribbean Sea and the Wisconsian Glacial Period prohibiting exchange between the North Pacific and North Atlantic respectively).

While the absolute time of the event that divided a taxon can be used to estimate evolutionary or migratory rates, the pattern that emerges from any analysis is, to a large extent, dependent on the recognition of phylogenetic relationships between members of the fragmented fauna and flora (Nelson & Platnick, 1981; Wiley, 1981). When a clade has been divided relatively recently, the subclades tend to be more similar at lower taxonomic levels (*e.g.*, subspecies, species, subgenera) than clades that were separated earlier. For example, 92 species in 48 shared genera (about 2:1) occur in both the North Pacific Ocean and North Atlantic Ocean, separated by the Pleistocene glaciations of Arctic Canada during the last 0.150 Myr (data from Durham & MacNeil, 1967:330), while only 56 species in 205 shared genera (about 1:4) are in common between the tropical eastern Pacific and Caribbean, separated by tectonic activity in Central America during the last 3.5 Myr (data from Vermeij, 1978:269).

The best documented cases of discontinuous distributions of marine molluscan taxa often involve east–west divisions (Durham & MacNeil, 1967; Vermeij, 1978: 242). However, one of the most intriguing discontinuous distributions occurs north to south—between the Californian and Peruvian molluscan provinces along the eastern Pacific margin.

The faunal and floral similarities between the Pacific coasts of temperate North and South America have been well documented in the terrestrial realm (Constance, 1963; Raven, 1963); Garth (1957), Marincovich (1973), White (1986) and others have pointed out relationships between taxa in the nearshore marine habitats. In a study of the marine mollusks of Iquique, Chile, Marincovich (1973) concluded that 49 intertidal genera out of a possible 68 (72%) were common to the Chilean and Californian provinces. However, Marincovich, like Garth before him, pointed out that further resolution of the pattern would require a better knowledge of the systematics of the faunas. This paper is a contribution towards that goal. Systematics follow Lindberg (1986b); see also Table 1.

Table 1

Classification of northeastern Pacific Lottiidae.

Classification	Nomenclatural discussion
Lottiidae Gray, 1840	Lindberg, 1986b
Patelloidinae Chapman & Gabriel, 1923	Oliver, 1926; Lindberg & Vermeij, 1985; Lindberg & Hickman, 1986
Lottiinae Gray, 1840	herein
Lottiini Lindberg, new tribe	herein
Lottia Sowerby, 1834	Lindberg, 1986b
Tectura Gray, 1940	Lindberg, 1986b
Scurriini Lindberg, new tribe	Thiem, 1917; herein
Scurria Gray, 1834	McLean, 1973; Christiaens, 1975b
Discurria Lindberg, new genus	herein

SYSTEMATICS

Order Patellogastropoda Lindberg, 1986a

Superfamily Acmaeacea Forbes, 1850

Family Lottiidae Gray, 1840

Shell composed of four to six shell layers. Innermost layer radial and/or complex crossed-lamellar followed by myostracum, optional radial crossed-lamellar layer, concentric crossed-lamellar layer, and prismatic layer(s). Radula three pairs of lateral teeth, marginal teeth two pairs, one pair, or lacking. Single gill in nuchal cavity typically present, but may be absent. Secondary gill in mantle groove present in some taxa.

Cretaceous to Holocene.

Subfamily Lottiinae Gray, 1840

Outer prismatic layer of shell consists of two layers; ventral portion fibrous prismatic, dorsal surface complex or simple prismatic. Marginal teeth one pair or lacking. Single gill in nuchal cavity present, and secondary gill in mantle groove present in some taxa.

Pliocene to Holocene.

Lottiini Lindberg, new tribe

Prismatic layer predominately fibrous with thin, outer layer of simple prismatic structure. Marginal teeth one pair or lacking. Looping of intestine typically simple with fewer than 3 loops. Secondary gill in mantle groove uncommon.

Distribution: [In the] Eastern Pacific: Alaska to Peru.

Age: Pliocene to Holocene.

Discussion: The *Lottiini* appear to be derived from the Scurriini by the conversion of the exterior complex prismatic layer to simple prismatic and the expansion of the fibrous prismatic shell layer (see discussion below).

Remarks: Two eastern Pacific genera are referred to this subfamily, *Lottia* Sowerby, 1834, and *Tectura* Gray, 1847. Members of this tribe predominate in the Aleutian, Oregonian, Californian, and Panamic molluscan provinces (60°N to 5°S).

Scurriini Lindberg, new tribe

"Scurriiden" Thiem, 1917:613.

Prismatic layer predominately complex prismatic with thin, inner layer of fibrous prismatic structure. Marginal teeth one pair or lacking. Looping of intestine moderately complex (<5 loops).

Distribution: Eastern Pacific [Disjunct]: Alaska to southern Baja California; Peru to Chile.

Age: Pliocene to Holocene.

Discussion: The shell structure of members of the **Scurriini** appears to be intermediate between the shell structure of the subfamilies Patelloidinae Chapman & Gabriel, 1923, and Lottiinae. In the Patelloidinae the outer shell layer is a single, uniform prismatic layer. In the Lottiinae the exterior prismatic shell layer consists of two layers, an inner fibrous layer and an outer complex or simple prismatic layer. The fibrous layer in the **Lottiini** is typically thick (about 60% of the prismatic layer) whereas in the **Scurriini** it is the thinnest shell layer (less than 20% of the prismatic layer). The shell structure of the **Scurriini** appears to be derived from that of the Patelloidinae by the differentiation of a fibrous prismatic shell structure from the ventral portion of the outer complex prismatic layer.

Remarks: Two eastern Pacific genera are referred to this subfamily, *Scurria* Gray, 1847, in the southern hemisphere and ***Discurria*** new genus in the northern hemisphere. Members of the genus *Scurria* form a diverse patellogastropod fauna in the Peruvian molluscan province (5°40′S to 42°S) (Marincovich, 1973). The new genus ***Discurria*** occurs between higher latitudes in the northern hemisphere (25°N to 60°N) and is monotypic in the Holocene of North America. Both genera have members that are associated with large intertidal kelps.

Thiem (1917) was the first to recognize the distinctness of the tribe **Scurriini**, and diagnosed the "Scurriiden" from the "Akmaeiden" primarily on gill and shell characters; he also documented shell structure differences. From his hierarchical arrangement and "Resultate für die Phylogenie" (translated and reproduced here as Table 2), it is clear that Thiem considered this taxon to represent a natural group at the familial level. He further divided the "Scurriiden" into two subfamily-level taxa, the "Scurriididen" and the "Scurriidinen," distinguishing them from one another by a suite of alimentary characters.

Thiem's nominal taxa "Scurriiden," "Scurriididen," and

"Scurriidinen" are vernacular names, and because they were published after 1900, the names cannot be latinized and recognized as dating from THIEM's (1917) publication [Article 11f (iii) (ICZN, 1985)]. In a review of the history of patellogastropod classification, CHRISTIAENS (1975a) referred to two of Thiem's three taxa as Scurriidae and Scurriinae; however, he did not use or discuss these names in his classification. Therefore, while Christiaens correctly latinized Thiem's names, he did not use them as valid names for taxa and provided no descriptions or definitions, and thus they remained unavailable [Article 11d (ii) (ICZN, 1985)].

Table 2

Systematics of the Scurriidae *sensu* THIEM (1917).

English translation of "Resultate für die Systematik."
A. Left neck gill in the nuchal cavity and true gill with lappets under the mantle edge, interrupted above the head. Radular formula 1·3·0·3·1; oral fringe around mouth; shell muscle segments 10–13 ..... Scurriiden
I. Posterior region of the intestinal coil with single loop of the small intestine ..... Scurriididen
Referred species: *Scurria viridula* (Lamarck, 1819), *S. zebrina* (Lesson, 1830), *S. coffea* (Reeve, 1855) [=*S. parasitica* (Orbigny, 1841)], *S. scabra chilensis* Thiem, 1917 [=*S. variabilis* (Sowerby, 1839)].
II. Posterior region of the intestinal coil with many loops of the small intestine. Furthermore: pharynxial salivary glands large and between the intestinal tract. Lappets on mantle edge much more numerous (as many as 10 per cm), almost a true gill type ..... Scurriidinen
Referred species: *S. scurra* (Lesson, 1830), *S. apicina chilensis* Thiem, 1917 [=*S. scurra*].

Discurria Lindberg, new genus

Type species: *Patella insessa* Hinds, 1842.

Shell: Profile medium to high; apex positioned in anterior one-third of shell. Anterior slope straight to convex, posterior slope convex. Radial and concentric sculpture present, typically weak. Exterior color brown with or without radial markings.

Radula: Lateral teeth unicuspid. Third lateral teeth lateral to second lateral teeth. Marginal teeth lacking. Ventral plates complex with strong anterior processes.

Animal: Left gill present in nuchal cavity.

Distribution: NORTHEASTERN PACIFIC: Alaska to southern Baja California.

Age: Pliocene to Holocene.

Etymology: *di-* (dis) apart + *scurria* (scurra) jester['s hat?]

Remarks: Monotypic in the Holocene, typically associated with the marine laminarian alga *Egregia*. Habitats more generalized in the late Neogene, occurring on hard substrata.

Discurria insessa (Hinds)

(Figures 1–3)

Patella insessa HINDS, 1842:82; pl. 6, fig. 3.

Shell (Figure 1): Profile high; apex positioned in the anterior one-third of shell. Anterior slope straight; posterior and lateral slopes convex. Lateral edges of shell parallel. Sculpture of fine riblets and concentric growth lines. Apex dark brown, with or without white markings; remainder of shell glossy brown. Interior of shell brown. Outcrops of shell layers along interior margin pronounced. Length, 5–20 mm.

Radula (Figure 2): Lateral teeth approximately equal in height; second and third lateral teeth broader than first lateral teeth. First lateral teeth closely set at anterior edge of ribbon segment, pointed distally, medial edge convex, lateral edges concave. Second lateral teeth broad, with straight cutting edge and pointed cusp displaced laterally; third lateral teeth not reduced, pointed distally, lateral edge concave, forming a lateral extension of tooth. Only the dorsal portions of the lateral teeth are heavily mineralized. Ventral plates subrectangular with broad, flat anterior processes. First lateral plates rectangular; second lateral plates with straight posterior edges and fused with laterally positioned third lateral plates. Third lateral plates semicircular in shape.

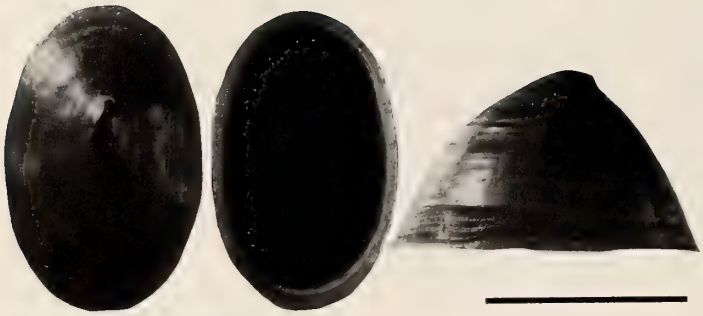
Animal: White except for brown pigmentation of dorsal mantle edge. Snout with encircling oral fringe.

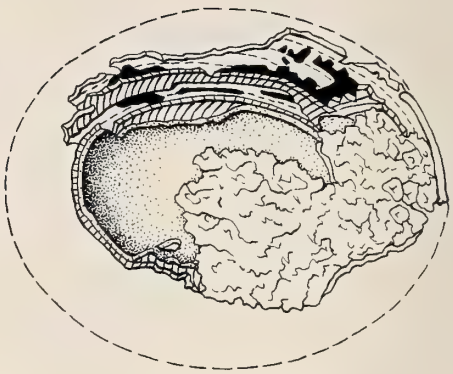
Distribution: ALASKA: Wrangell (56°20′N) to MEXICO: Baja California; Bahia Magdalena (24°30′N) (MCLEAN, 1966:108).

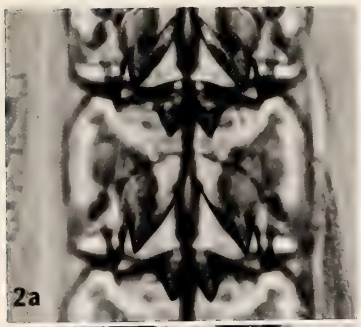
Age: Pliocene to Holocene.

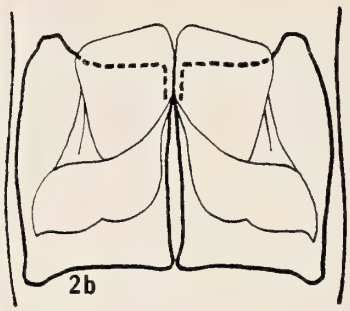
Remarks: The lustrous exterior surface of ***Discurria*** *insessa* has been commented on by DALL (1871) and almost every subsequent student of northeastern Pacific limpets. This surface, composed of complex prismatic crystals, and the convex medial edges of the radular lateral teeth distinguish ***D.*** *insessa* from all other North American species; both of these characters serve to unite ***D.*** *insessa* with the South American *Scurria*.

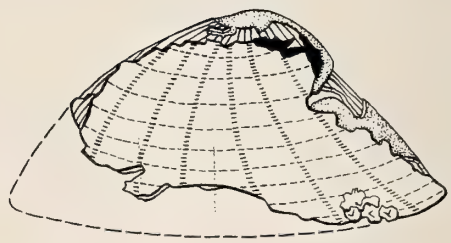
Discurria *insessa* has most recently been assigned to the genus *Notoacmea* in systematic accounts of the northeastern Pacific patellogastropod fauna (CARLTON & ROTH, 1975; MCLEAN, 1978; ABBOTT & HADERLIE, 1980; LINDBERG, 1981b). However, as early as 1871 DALL had pointed out similarities between ***D.*** *insessa* and members of the genus *Scurria* including: (1) the coloration patterns of young shells, (2) the outer, brown shell layers, and (3) the exterior sculpture. MACCLINTOCK (1967) further commented on the similar shell structure and protoconch morphologies of

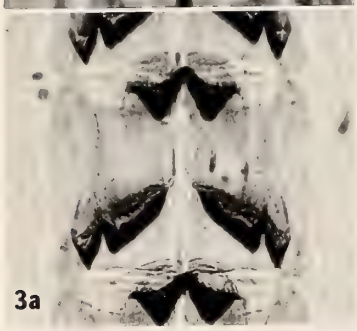


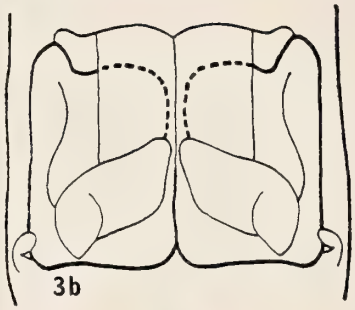


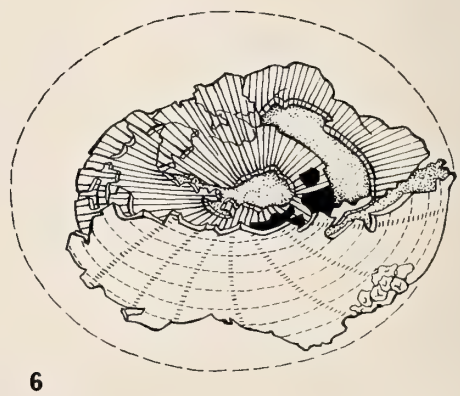


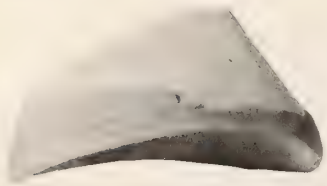


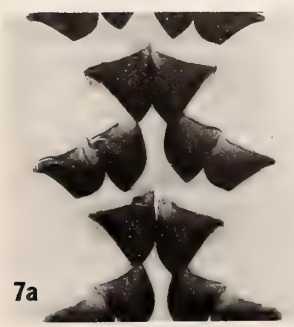


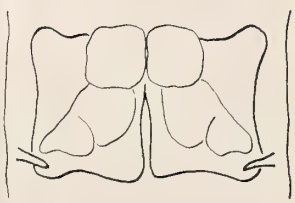


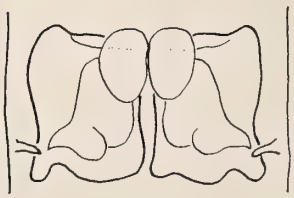












D. *insessa* and *Scurria scurra,* the type species of the genus *Scurria.* Neither worker commented on the shared characteristic radular lateral tooth shape (Figures 2, 3), and both gave too much phylogenetic significance to the presence of the secondary gill in *S. scurra.* It is now known that the secondary gill in members of the genus *Scurria* is variable in its development (McLean, 1973), and may be entirely lacking in some species. Moreover, secondary gills have arisen in many lottiid taxa and are poor indicators of phylogenetic relationships (Lindberg & McLean, 1981; Lindberg, 1983 and in press).

Discurria *insessa* is typically found on the stipes of the low intertidal laminarian alga *Egregia menziesii* (Turner) Areschoug, 1896. However, it also may occur on the shells of the mussel *Mytilus californianus* (Conrad, 1837) during the winter when the stipes of *Egregia* die back and are destroyed by winter surf. This has been observed along the rocky coast line of Santa Cruz County and on San Nicolas Island, Ventura County, California. At San Nicolas Island, what appeared to be the same individual limpets remained present on mussels (in fixed study quadrats) for up to four months before disappearing. It is not known whether these limpets subsequently returned to *Egregia* or died. Further study of this phenomenon is needed (also see Choat & Black, 1979).

The association of ***Discurria*** *insessa* with *Egregia* (and the resultant characteristic parallel lateral sides of the limpet) has not always been as fixed as it is in the Holocene. Some Pliocene and Pleistocene specimens of ***D.*** *insessa* have oval or highly irregular apertures that suggest that this species occurred on substrata other than *Egregia,* including rock and probably mussels (Figure 4).

Regardless of the apparent habitat plasticity seen in Neogene specimens of ***Discurria*** *insessa,* there is little doubt that its association with *Egregia* has been a strong selective force. The radular morphology of ***D.*** *insessa* suggests this association. The second lateral teeth with their broad, straight cutting edges are characteristic of patellogastropods that are associated with marine plants.

The recognition of a closer relationship between ***Discurria*** *insessa* and the Peruvian *Scurria* rather than with the North American Lottiinae necessitates reconsideration of ecological work that has been done with this species. For example, Choat & Black (1979) compared the life-history strategies of ***D.*** *insessa* and *Lottia digitalis* (Rathke, 1833). They reported that ***D.*** *insessa* has a higher growth rate, greater reproductive effort, and lower age of first reproduction than *L. digitalis.* From these findings, and because of the ephemeral habitat (the stipe of *Egregia* spp.) of ***D.*** *insessa,* Choat & Black (1979:43) concluded that "selective factors for the development of *A. insessa*'s life history may have been the life history characteristics of *Egregia.*" Their scenario is consistent with the data, but the different phylogenetic histories of ***D.*** *insessa* and *L. digitalis* complicate this interpretation. Are the differences in life-history characteristics of these two species the result of selection operating in different types of environments as proposed by Choat & Black, or are they different merely because different lineages of patellogastropods have different life-history characteristics? It is not possible to resolve this question from available data, but comparisons of life-history characteristics of ***D.*** *insessa* with other *Scurria* species in the Peruvian province could help to resolve this question.

Between clade comparisons can present problems in interpretation of patellogastropod biological and ecological literature (Lindberg, in preparation). Sometimes the data from previous studies needs to be reanalyzed in light of phylogenetic relationships, and future studies should be designed to recognize and make comparisons within phylogenetic units (*i.e.,* clades) first so that trends, constraints, *etc.,* can be recognized before between clade comparisons or generalizations are made.

Discurria radiata Lindberg, new species

(Figures 5, 6)

Acmaea sp.: Waterfall, 1929:checklist.

Shell (Figures 5, 6): Profile medium; apex position subcentral. Anterior slope concave, posterior slope convex. Lateral slopes straight. Reconstructed aperture oval.

←

Explanation of Figures 1 to 8

Figure 1. ***Discurria*** *insessa* Hinds, 1842. Holocene; Santa Cruz, Santa Cruz County, California. (UCMP Loc. E-756). Scale bar = 10 mm.

Figure 2. Radula of ***Discurria*** *insessa.* a. Lateral tooth morphology. b. Basal plate morphology.

Figure 3. Radula of *Scurria scurra* (Lesson, 1830). a. Lateral tooth morphology. b. Basal plate morphology.

Figure 4. ***Discurria*** *insessa* with irregular aperture. Pleistocene; San Nicolas Island, California; Terrace deposits (UCMP Loc. D-9614). Scale bar = 10 mm.

Figures 5 and 6. ***Discurria radiata*** new species. Holotype, UCMP Type No. 37530. Early Pleistocene; Saticoy, Ventura County, California; Saugus Formation (UCMP Loc. 7071). Figure 5: scale bar = 10 mm. Figure 6: solid light pattern = complex prismatic outer shell layer; solid dark = fibrous layer; hatched = concentric crossed-lamellar layer; stippled = radial crossed-lamellar layer; irregular, solid light pattern indicates the presence of matrix. Scale bar = 10 mm.

Figure 7. Radula of *Lottia mimica* Lindberg & McLean, 1981. Galápagos Islands. a. Lateral tooth morphology. b. Basal plate morphology.

Figure 8. Radula of *Lottia smithi* Lindberg & McLean, 1981. Galápagos Islands. a. Lateral tooth morphology. b. Basal plate morphology.

Sculpture of concentric growth lines. Exterior color tan with red-brown radial rays that gently curve from the apex to the shell margin. Interior of shell white.

Holotype dimensions: Length 12.0, width 8.6, height 6.2 mm.

Type locality: CALIFORNIA: Ventura County [Saticoy Quad]; Saugus Formation (34°18′N, 119°11′W). About 2 km [1.25 miles] N of mouth of unnamed canyon that lies 1.6 km [1 mile] E of Harmon Canyon, in creek bottom. Collector: L. N. Waterfall, December 1925 [Museum of Paleontology, University of California, Berkeley (UCMP) Loc. 7071].

Age: Early Pleistocene.

Type material: Holotype, UCMP Type No. 37530.

Etymology: *radius*- Latin noun, ray. Named for the red-brown radial rays that distinguish this species.

Discussion: Although based on a single specimen, ***Discurria radiata*** can be distinguished from other Pliocene, Pleistocene, and Holocene northeastern Pacific lottiid species by its shell structure, morphology and color pattern. Shell structure distinguishes ***D. radiata*** from all other Neogene and Holocene lottiids except ***Discurria*** *insessa.* Although the gross morphology of ***D. radiata*** resembles that of an oval ***D.*** *insessa,* the radiating red-brown rays are unique to ***D. radiata***; the only markings found on ***D.*** *insessa* consist of variable white markings around the apex.

Although less than 75% of the total shell and 50% of the exterior surface remains on the holotype, there is no doubt that it is distinct from ***Discurria*** *insessa.* Neogene specimens of ***D.*** *insessa* are identical to Holocene specimens in gross morphology and color except for some Pleistocene specimens that have oval or irregular apertures (Figure 4). The conservative morphology of ***D.*** *insessa* through the Pleistocene corresponds to the narrow range of variation present in Holocene specimens. Little morphological variation is common in limpets that are associated with marine algae and angiosperms (LINDBERG, 1982 and unpublished data). Thus, the morphological stability of ***D.*** *insessa* over the last 1.5–2 million years suggests that it has been associated with *Egregia* spp. for this same period of time. In contrast, the straight sides of ***D. radiata*** suggest an oval aperture and there is no hint of parallel lateral edges. The reconstructed gross morphology of ***D. radiata*** is that of a rock-dwelling species, not a marine plant species (Figure 6).

The broken and exfoliated shell of the holotype exposes all four major shell layers of ***Discurria radiata*** (Figure 6). The only shell layer not visible to the unaided eye is the myostracum. The relative thickness of the various shell layers is similar to that of ***D.*** *insessa.*

Remarks: The Saugus Formation was considered by WATERFALL (1929) to be either Late Pliocene or Early Pleistocene in age, and the associated fauna warm-water in character. VALENTINE (1961) suggested that the Plio-Pleistocene boundary in the western Ventura Basin was in the Pico Formation, which underlies the Saugus Formation. Thus, the type locality of ***Discurria radiata***, which is located in the western Ventura Basin, would be Early Pleistocene in age. Except for ***D. radiata***, the fauna at UCMP Loc. 7071 (WATERFALL, 1929:checklist) is composed entirely of extant species that occur today along the central and southern California coast; there are no species that suggest that thermal conditions were any different from those of today. The fauna includes such rocky intertidal and shallow subtidal gastropod species as *Acanthina spirata* (Blainville, 1832), *Margarites lirulata* (Carpenter, 1864), and *Ocenebra foveolata* (Hinds, 1844); soft-bottom taxa, including the bivalves *Tresus nuttalli* (Conrad, 1837), *Macoma nasuta* (Conrad, 1837), *Modiolus rectus* (Conrad, 1837), and the gastropods *Polinices reclusianus* (Deshayes, 1839) and *Olivella biplicata* (Sowerby, 1825) are also present. VALENTINE (1961) concluded that the fossil assemblage at UCMP Loc. 7017 represented the *Tellina bodegensis-Forreria belcheri* community, which he considered to indicate a shallow, inner subtidal, chiefly sand-bottom habitat between 0 and 30 m in depth. ***Discurria radiata*** was probably transported into this depositional environment.

DISCUSSION

The recognition of the distinctness and taxonomic affinity of an incomplete patellogastropod limpet that was collected 60 yr ago was possible because original shell material was present. The importance of shell structure in patellogastropod systematics has already been demonstrated (MACCLINTOCK, 1963, 1967; LINDBERG, 1976, 1978, 1979, 1981a, 1983; LINDBERG & MCLEAN, 1981; LINDBERG & HICKMAN, 1986). Moreover, shell-structure characters can be used for both fossil and Holocene specimens, and thus provide data for historical biogeography.

Californian and Peruvian Exchanges

The recognition of the relationship of ***Discurria*** *insessa* and ***D. radiata*** with the **Scurriini** of the Peruvian province provides another example of past faunal exchange between these two physically similar, but disjunct, molluscan provinces. Additional, previously unrecognized, northeastern Pacific rocky intertidal species that also appear to have immigrated from the southern hemisphere include: *Fissurella* (*Fissurella*) *volcano* Reeve, 1849, the single northeastern Pacific representative of a subgenus that is wholly restricted to the Peruvian province except for two outlying species (MCLEAN, 1984b), and *Fissurellidea bimaculata* (Dall, 1871), the only northeastern Pacific member of a southern hemisphere group that is distributed from South America to South Africa (MCLEAN, 1984a).

The genus ***Discurria*** first appears in the northeastern Pacific in the Pliocene of California at San Diego [UCMP Loc. 5092; San Diego Fm.] whereas *Fissurella s.s.* and

Fissurellidea first occur in the Early Pleistocene of southern California (GRANT & GALE, 1931). After these initial appearances, all three taxa quickly become common and abundant components in later Pleistocene faunas in southern and central California (GRANT & GALE, 1931; VALENTINE, 1961). It is also during the Pliocene that several northeastern Pacific taxa (*e.g., Chama* Linne, 1758; *Crenomytilus* Soot-Ryen, 1955; *Cryptomya* Conrad, 1848) first appear in the fossil record of northern Peru (T. DeVries, personal communication).

The above pattern of Holocene and fossil distributions and relationships suggests that during the Pliocene and Early Pleistocene the barriers (*e.g.,* temperature, current patterns) to faunal exchange between the temperate Californian and Peruvian provinces broke down more than once and taxa were able to move between the northern and southern temperate regions by crossing the intermediate tropical eastern Pacific. The movement of the Caribbean plate through the gap between North and South America (SYKES *et al.,* 1983), and the subsequent regional perturbations of temperature and currents in the marine environment (KEIGWIN, 1978, 1982) undoubtedly contributed to a changing regional setting across which the faunal exchanges were made.

Scurriini and the Evolution of the Lottiidae

While reviewing THIEM's (1917) monograph on the **Scurriini**, I realized that the endemic *Lottia* of the Galápagos Islands combine characters of both the **Scurriini** and the **Lottiini**. These endemic limpets have secondary gills with morphology similar to those in some members of the genus *Scurria,* but their shell structure is identical to that of *Lottia* species. Because secondary gills have arisen several times in different clades in the family Lottiidae (LINDBERG, in press), the presence of a secondary gill alone is not strong evidence for considering these species to be more closely related to the **Scurriini** than to the **Lottiini**. However, the lateral tooth morphology of the endemic Galápagos species (Figures 7, 8) has previously been seen only in members of the **Scurriini** (Figures 2, 3), and therefore, the Galápagos species may be more closely related to the **Scurriini** than previously thought.

The Galápagos endemics have characters that would place them in an intermediate position between the genera *Scurria* and *Lottia,* and they are known only from the Galápagos Islands, which places them directly between the centers of greatest diversity of both genera. If they are ancestral to **Lottiini**, their restriction to the Galápagos Islands, which have a depauperate Holocene patellogastropod fauna (LINDBERG & MCLEAN, 1981), would mean that the ancestral group survived in one of the only rocky intertidal faunas in the eastern Pacific Ocean without *Lottia* and *Tectura* species. Alternatively, they could represent a separate derivation from a different *Scurria* species.

The presence of the most primitive genus (*Scurria*) in the Peruvian province, the presence of possible intermediate species in the tropical eastern Pacific at the Galápagos Islands, and the derived genera *Lottia* and *Tectura* in the tropical eastern Pacific, Caribbean, and northeastern Pacific suggest that the direction of migration and later radiations of the Lottiinae may have been from south to north. This is in contrast to the common pattern of other molluscan groups that shows taxa originating in the northwestern Pacific and migrating into the eastern Pacific (MacNeil, 1965; Marincovich, 1984a, b).

ACKNOWLEDGMENTS

I thank E. V. Coan, M. G. Kellogg, and J. H. McLean for criticism of an early draft of the manuscript, T. DeVries for discussions of Neogene faunal exchanges between the Californian and Peruvian provinces, E. V. Coan for nomenclatural discussions, and M. E. Taylor for preparing Figure 6.

LITERATURE CITED

ABBOTT, D. P. & E. C. HADERLIE. 1980. Prosobranchia: marine snails. Pp. 230–307. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, California.

CARLTON, J. T. & B. ROTH. 1975. Phylum Mollusca: shelled gastropods. Pp. 467–515. *In:* R. I. Smith & J. T. Carlton (eds.), Light's manual: intertidal invertebrates of the central California coast. Univ. Calif. Press: Berkeley, California.

CHAPMAN, F. & C. J. GABRIEL. 1923. A revision and description of the Australian Tertiary Patellidae, Patelloididae, Cocculinidae, and Fissurellidae. Proc. Roy. Soc. Victoria 36: 22–40.

CHOAT, J. H. & R. BLACK. 1979. Life histories of limpets and the limpet-laminarian relationship. Jour. Exp. Mar. Biol. Ecol. 41:25–50.

CHRISTIAENS, J. 1975a. Revision provisoire des mollusques marins recents de la famille des Acmaeidae et description de deux nouveaux sous-genres: *Simplacmaea* nov. subgen. et *Collisellacmaea* nov. subgen. Inform. Soc. Belge Malacol. 4: 3–18.

CHRISTIAENS, J. 1975b. Revision provisoire des mollusques marins recents de la famille des Acmaeidae (seconde partie). Inform. Soc. Belge Malacol. 4:91–116.

CONSTANCE, L. 1963. Amphitropical relationships in the herbaceous flora of the Pacific coast of North and South America: a symposium. Introduction and historical review. Quart. Rev. Biol. 38:109–116.

DALL, W. H. 1871. On the limpets with special reference to the species of the west coast of America, and to a more natural classification of the group. Amer. Jour. Conch. 6:227–282.

DURHAM, J. W. & F. S. MACNEIL. 1967. Cenozoic migrations of marine invertebrates through the Bering Strait region. Pp. 326–349. *In:* D. M. Hopkins (ed.), The Bering land bridge. Stanford Univ. Press: Stanford, California.

FORBES, E. 1850. On the genera of British patellaceans. Rept. Brit. Assoc. Adv. Sci. (1849), Part 2:75–76.

GARTH, J. S. 1957. The Crustacea Decapoda Brachyura of Chile. Rept. Lund Univ. Chile Exped. 1948–49, 49:1–130.

GRANT, U. S., IV & H. R. GALE. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. San Diego Soc. Natur. Hist. Mem. 1:1–1036.

GRAY, J. E. 1840. Synopsis of the contents of the British Museum. 42nd ed. Woodfall & Son: London. 370 pp.

GRAY, J. E. 1847. A list of genera of Recent Mollusca, their synonyma and types. Proc. Zool. Soc. Lond. (1847):129–219.

HINDS, R. B. 1842. Descriptions of new shells. Ann. Mag. Natur. Hist. 10:81–84.

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE (ICZN). 1985. International Commission on Zoological Nomenclature (W. D. L. Ride & C. W. Sabrosky, Chairmen). 3rd ed. Univ. Calif. Press: Berkeley, California. 338 pp.

KEIGWIN, L. D., JR. 1978. Pliocene closing of the Isthmus of Panama, based on biostratigraphic evidence from nearby Pacific Ocean and Caribbean Sea cores. Geology 6:630–634.

KEIGWIN, L. D., JR. 1982. Isotopic paleoceanography of the Caribbean and east Pacific: role of Panama uplift in late Neogene time. Science 217:350–353.

LINDBERG, D. R. 1976. Cenozoic phylogeny and zoogeography of the Acmaeidae in the eastern Pacific. Ann. Rept. West. Soc. Malacol. 9:15–16.

LINDBERG, D. R. 1978. On the taxonomic affinities of *Collisella edmitchelli,* a Late Pleistocene limpet from San Nicolas Island, California. Bull. So. Calif. Acad. Sci. 77:65–70.

LINDBERG, D. R. 1979. *Problacmaea moskalevi* Golikov & Kussakin, a new addition to the eastern Pacific limpet fauna (Archaeogastropoda: Acmaeidae). Veliger 22(1):57–60.

LINDBERG, D. R. 1981a. Rhodopetalinae, a new subfamily of Acmaeidae from the boreal Pacific: anatomy and systematics. Malacologia 20:291–305.

LINDBERG, D. R. 1981b. Invertebrates of the San Francisco Bay estuary system: Mollusca, family Acmaeidae. The Boxwood Press: Pacific Grove, California. 122 pp.

LINDBERG, D. R. 1982. A multivariate study of morphological variation of the limpet *Notoacmea depicta* (Hinds) and its synonyms *Notoacmea gabatella* (Berry) and *Notoacmea lepisma* (Berry) (Gastropoda: Acmaeidae). Bull. So. Calif. Acad. Sci. 81(2):87–96.

LINDBERG, D. R. 1983. Anatomy, systematics, and evolution of brooding acmaeid limpets. Ph.D. Thesis, Biology, Univ. of Calif., Santa Cruz, California. 277 pp.

LINDBERG, D. R. 1986a. Radular evolution in the Patellogastropoda. Amer. Malacol. Bull. 4(1):115.

LINDBERG, D. R. 1986b. Name changes in the "Acmaeidae." Veliger 29(2):142–148.

LINDBERG, D. R. In press. The Patellogastropoda. Malacol. Rev., Supplement.

LINDBERG, D. R. & C. S. HICKMAN. 1986. A new giant anomalous limpet from the Oregon Eocene (Mollusca: Patellacea). Jour. Paleontol. 60:661–668.

LINDBERG, D. R. & J. H. MCLEAN. 1981. Tropical eastern Pacific limpets of the family Acmaeidae (Mollusca: Archaeogastropoda): generic criteria and descriptions of six new species from the mainland and the Galápagos Islands. Proc. Calif. Acad. Sci. 42:323–339.

LINDBERG, D. R. & G. J. VERMEIJ. 1985. *Patelloida chamorrorum* spec. nov.: a new member of the Tethyan *Patelloida profunda* group (Gastropoda: Acmaeidae). Veliger 27(4):411–417.

MACCLINTOCK, C. 1963. Reclassification of gastropod *Proscutum* Fischer based on muscle scars and shell structure. Jour. Paleontol. 37:141–156.

MACCLINTOCK, C. 1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). Peabody Mus. Natur. Hist. Yale Univ. 22:1–140.

MACNEIL, F. S. 1965. Evolution and distribution of the genus *Mya,* and tertiary migrations of Mollusca. U.S. Geol. Soc. Prof. Pap. 483-G:G1–G51.

MARINCOVICH, L., JR. 1973. Intertidal marine mollusks of Iquique, Chile. Natur. Hist. Mus. Los Angeles Co. Sci. Bull. 16:1–49.

MARINCOVICH, L., JR. 1984a. Neogene molluscan stages of the west coast of North America. Palaeogeo., Palaeoclimatol., Palaeoecol. 46:11–24.

MARINCOVICH, L., JR. 1984b. Eastern Pacific molluscan bioevents and their relation to Neogene planktonic datum planes. Pp. 69–73. *In:* N. Ikebe & R. Tsuchi (eds.), Pacific Neogene datum planes (Contributions to biostratigraphy and chronology). Univ. Tokyo Press: Tokyo.

MCLEAN, J. H. 1966. West American prosobranch Gastropoda: superfamilies Patellacea, Pleurotomariacea, Fissurellacea. Ph.D. Thesis, Biology, Stanford Univ., Stanford, California. 255 pp.

MCLEAN, J. H. 1973. Family Acmaeidae. Pp. 18–23. *In:* L. Marincovich, Jr., Intertidal marine mollusks of Iquique, Chile. Natur. Hist. Mus. Los Angeles Co. Sci. Bull. 16.

MCLEAN, J. H. 1978. Marine shells of southern California. Natur. Hist. Mus. Los Angeles Co., Sci. Ser. 24, Rev. Ed.: 1–104.

MCLEAN, J. H. 1984a. Shell reduction and loss in fissurellids: a review of genera and species in the *Fissurellidea* group. Amer. Malacol. Bull. 2:21–34.

MCLEAN, J. H. 1984b. Systematics of *Fissurella* in the Peruvian and Magellanic faunal provinces (Gastropoda: Prosobranchia). Natur. Hist. Mus. Los Angeles Co. Contrib. Sci. 354: 1–70.

NELSON, G. J. & N. I. PLATNICK. 1981. Cladistics and vicariance: patterns in comparative biology. Columbia Univ. Press: New York. 567 pp.

OLIVER, W. R. B. 1926. Australasian Patelloididae. Trans. Proc. New Zealand Inst. 56:547–582.

RAVEN, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. 38:151–177.

SOWERBY, G. B. 1825–1834. The genera of Recent and fossil shells. Vol. 2. London. Plates 127–262 and text; pages not numbered.

SYKES, L. R., W. R. MCCANN & A. L. KAFKA. 1982. Motion of Caribbean plate during the last 7 million years and implications for earlier Cenozoic movements. Jour. Geophy. Res. 87(B13):10656–10676.

THIEM, H. 1917. Beiträge zur Anatomie und Phylogenie der Docoglossen; II, Die Anatomie und Phylogenie der Monobranchen (Akmäiden und Scurriiden nach der Sammlung Plates. Jenaische Zeitschr. Naturw. 54:405–630.

VALENTINE, J. W. 1961. Paleoecologic molluscan geography of the California Pleistocene. Univ. Calif. Pub. Geol. Sci. 34:309–442.

VERMEIJ, G. J. 1978. Biogeography and adaptation. Harvard Univ. Press: Cambridge, Massachusetts. 332 pp.

WATERFALL, L. N. 1929. A contribution to the paleontology of the Fernando Group, Ventura County, California. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 18(3):71–92.

WHITE, B. N. 1986. The isthmian link, antitropicality and American biogeography: distributional history of the Atherinopsinae (Pisces: Atherinidae). Syst. Zool. 35(2):176–194.

WILEY, E. O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley & Sons: New York. 439 pp.

The Veliger 30(4):395–399 (April 1, 1988)

THE VELIGER

Anatomy and Zoogeography of *Glossodoris sedna* and *Chromodoris grahami* (Opisthobranchia: Nudibranchia) in the Tropical Western Atlantic and Caribbean

by

HANS BERTSCH

Biological Sciences, National University, 8 Executive Park Circle,
Irvine, California 92714, U.S.A.

Abstract. The eastern Pacific *Glossodoris sedna* is reported from the tropical western Atlantic Ocean, and the range of *Chromodoris grahami* is extended throughout the extremes of the Caribbean Sea. The anatomies of the specimens are described and compared with original and subsequent descriptions of these species.

The following records are significant range extensions for two species of Chromodorididae.

Glossodoris sedna (Marcus & Marcus, 1967)

(Figures 1–2, 5–9)

Synonymy and references: The synonymy and tropical eastern Pacific distribution of *Glossodoris sedna* have been summarized by BERTSCH (1978b) and RUDMAN (1984).

Material examined: Two specimens (Figures 1, 2), 65 mm long; 2 m depth, Tavenier Key, Florida (approx. 25°01′N, 80°30′W); *leg.* Barry Hamann, 7 June 1983. Specimen A, radula illustrated in Figure 9, is deposited in the collections of the Los Angeles County Museum of Natural History (Malacology), LACM 83-147. Specimen B, radula illustrated in the scanning electron micrographs of Figures 5–8, has been deposited in the collections of the California Academy of Sciences, Department of Invertebrate Zoology and Geology, CASIZ 064510.

Photographic records: One specimen, Biscayne Bay, Florida; photo by Bill Lyons. One specimen, Pennekamp State Park, off Key Largo, Florida; photo by Roy Manstan, published on the cover of *Sea Frontiers,* March–April 1980.

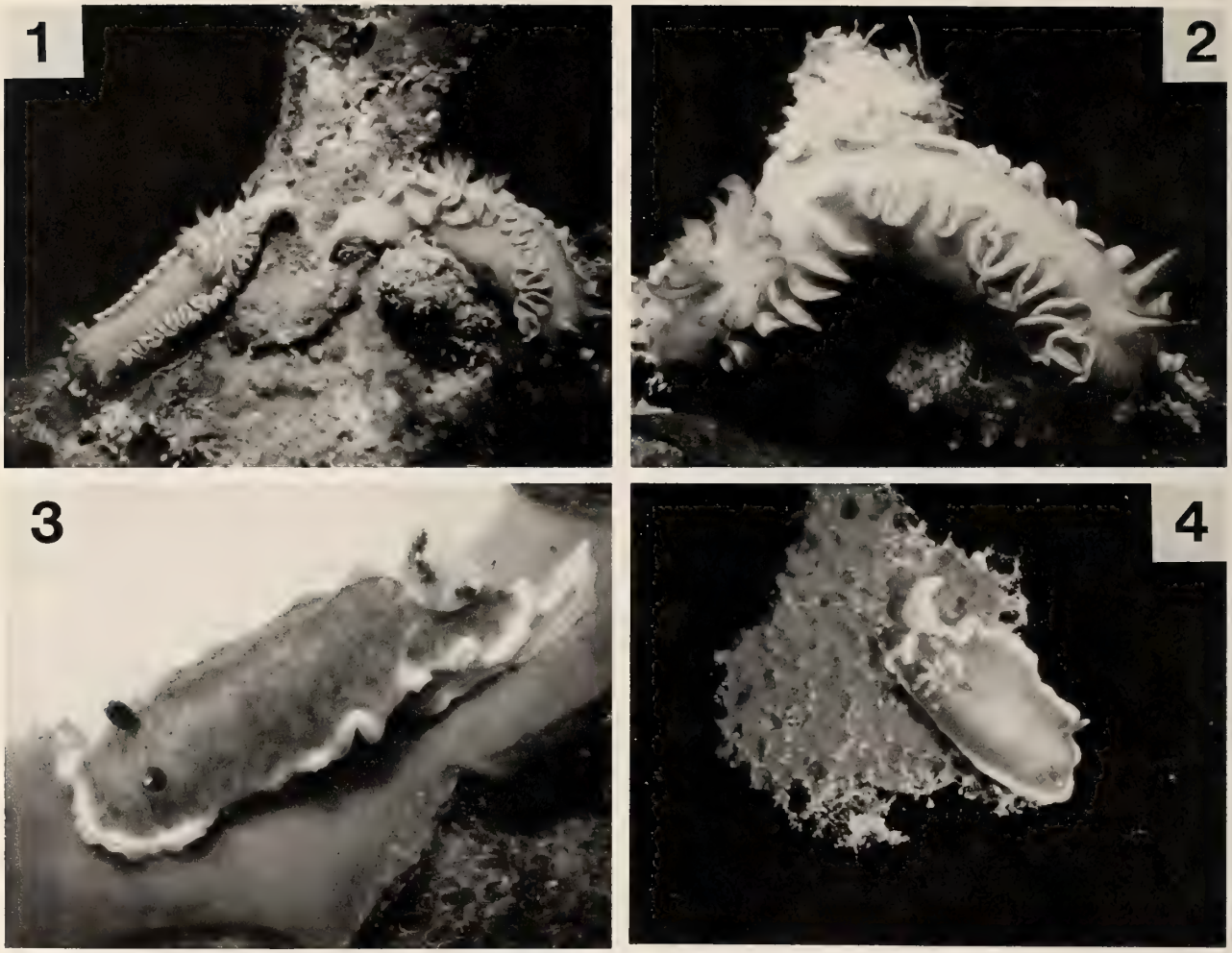
This is the first report of *Glossodoris sedna* in the tropical western Atlantic.

External morphology: The coloration of the animals was white (or a dirty gray white), with two marginal bands: an inner red and an outer yellow band. Identically colored bands were also on the underside of the ruffled mantle margin and around the base of the foot. Gills and rhinophores were tipped with pinkish red. There are prominent folds and crenulations of the mantle margin. These patterns are nearly identical with those seen in typical *Glossodoris sedna* from the Gulf of California.

The only differences in external morphology between the Caribbean and Gulf of California animals were the shade of whiteness and the amount of crenulations. The specimens collected at Tavenier Key (Figures 1, 2) are a light grayish white (not the pure white that is usually seen in eastern Pacific specimens); moreover, they have far more crenulations in the mantle margin (12 or more) than are usually present in eastern Pacific animals. The coloration is only a shading difference, easily variable by dietary differences; it is not a significant color difference (*e.g.,* blue vs. green or red vs. yellow). The crenulations are known to vary within and between individuals and species of *Glossodoris.* RUDMAN (1986:132, figs. 20F–H) illustrated three different individuals of *G. rufomarginata* (Bergh, 1905) with single, few, or many crenulations. The Florida animal illustrated in *Sea Frontiers* (MANSTAN, 1980) had fewer crenulations than the specimens from Tavenier Key, more closely matching the crenulation pattern shown in the original drawing of *G. sedna* (MARCUS & MARCUS, 1967:179, fig. 34).

Internal morphology: The reproductive system matched that described by MARCUS & MARCUS (1967:179–180). The morphology of the penis and vas deferens, and the arrangement and relative size of the vagina, insemination duct, bursa copulatrix and receptaculum seminis, are all identical.

The radular formula of specimen A from Tavenier Key



Explanation of Figures 1 to 4

Figures 1 and 2. Living animals of *Glossodoris sedna*, 65 mm long, collected at Tavenier Key, Florida. Photo by Jeff Hamann.

Figure 3. Living animal of *Chromodoris grahami* from Kingston Harbor, St. Vincent, 20 mm long. Photo by Jeff Hamann.

Figure 4. Living animal of *Chromodoris grahami* from La Parguera, Puerto Rico. Photo by C. E. Cutress.

was 133 (54.1.54). The innermost tooth in each half row had denticles on both sides of the cusp (2 on the inside and 3 or 4 on the outer face). The rest of the teeth in each half row had 4–6 small denticles on the outer side of each cusp, but the outermost 10 teeth lacked these accessory denticles on the cusp (Figure 9).

The radular formula of specimen B from Tavenier Keys (Figures 5–7) was 128 (49.1.49). The innermost lateral tooth of each half row had 3 or 4 inner and 4 or 5 outer denticles on the sides of the cusp (Figure 7). The outer lateral teeth had 6–8 denticles on the outer side of the cusp (Figure 6), except the outermost 19–21 teeth which were smooth (Figure 5). The jaw elements (Figure 8) are bifid; however some are trifid and there are several small accessory points on a few of the elements.

The holotype of *Glossodoris sedna* had a radular formula

→

Explanation of Figures 5 to 8

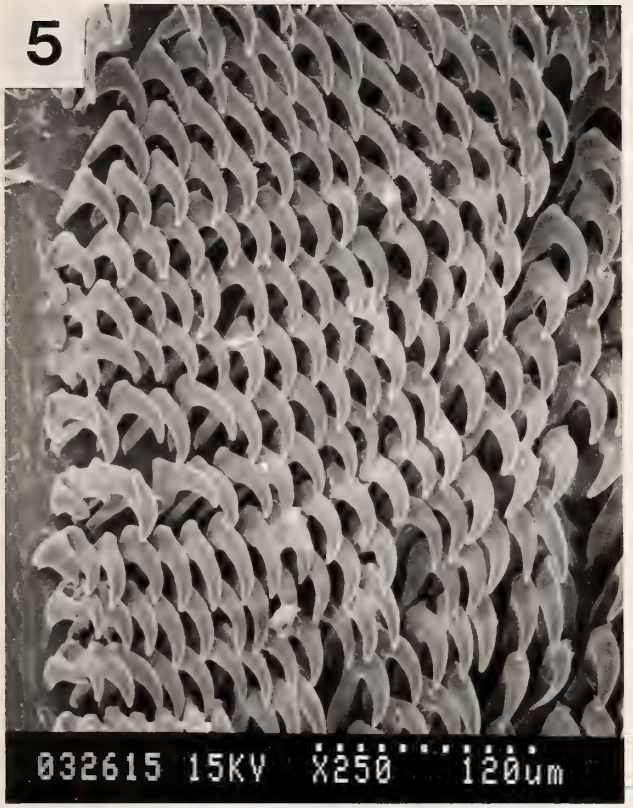
Scanning electron micrographs of the radula and jaws of *Glossodoris sedna*, specimen A, collected at Tavenier Key, Florida. SEMs by author.

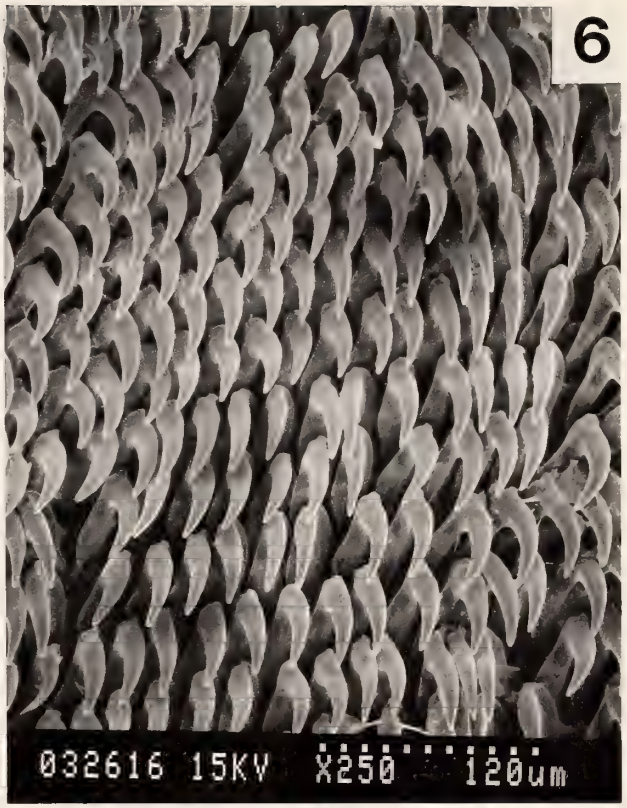
Figure 5. Outermost marginal teeth.

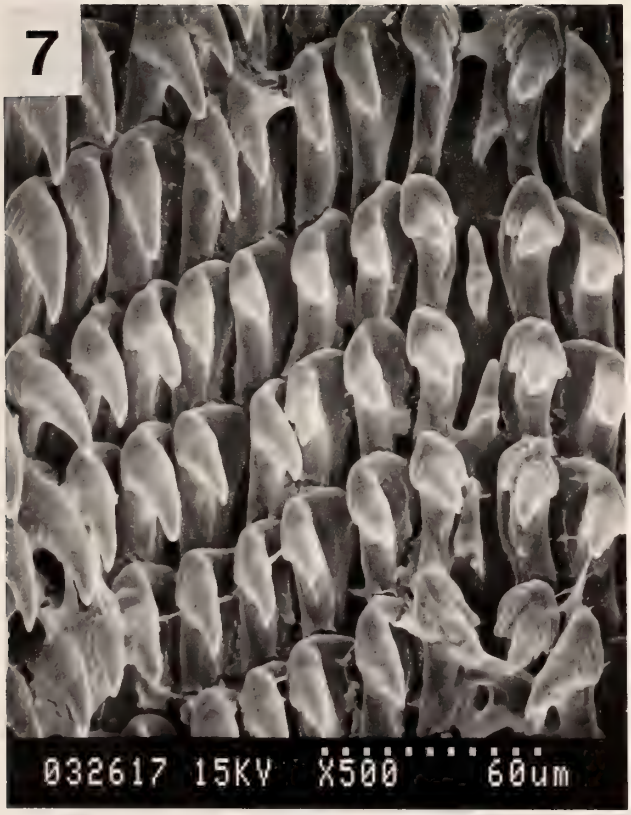
Figure 6. Teeth from center of half row.

Figure 7. Rachidian and innermost lateral teeth.

Figure 8. Bifid jaw elements.


5
032615 15KV X250 120um


6
032616 15KV X250 120um


7
032617 15KV X500 60um


8
032611 15KV X2.20K 13.6um

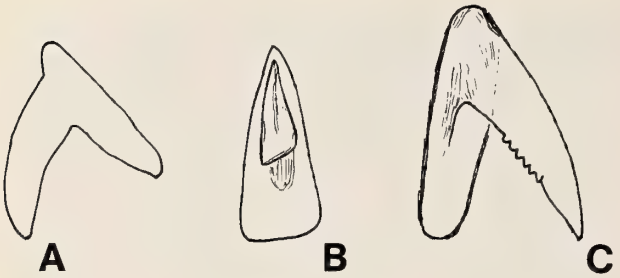


Figure 9

Sketches of radular teeth of *Glossodoris sedna,* specimen B, of Tavenier Key. A. Smooth outer marginal, posterior quarter of radula. B. Rachidian tooth. C. Denticulate lateral tooth from near the middle of the half row, one-third of the distance from the anteriormost end of radular ribbon.

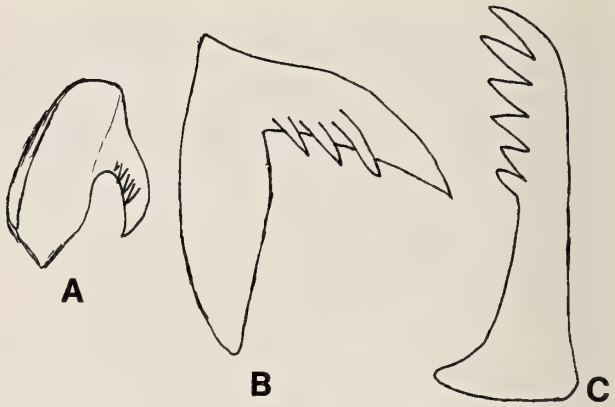


Figure 10

Sketches of radular teeth of *Chromodoris grahami,* specimen collected at Panama. A. Strongly curved innermost lateral tooth. B. Second lateral tooth, row 18. C. Elongate, pectinate condition of tooth from center of half row, tooth row 9.

of 130 (55.1.55); the innermost lateral tooth had 1 or 2 inner and about 5 outer denticles; the succeeding laterals had up to 7 denticles; and the outermost 25–35 teeth were smooth (Marcus & Marcus, 1967:180). The numerical counts of the Florida specimens closely match those of the holotype, and fall completely within the range of variation of the Gulf of California specimens described in the data and regression analyses of Bertsch (1978b:71–76). The tooth shapes illustrated in Figures 5–7 match well those illustrated by Bertsch (1978a:figs. 47–50).

The internal anatomy of the Florida animals is identical with that described for Gulf of California animals. The external anatomy is very similar (the only differences being a grayer body and more marginal ruffles). Given the overwhelming similarities, these differences are not sufficient to erect a new taxon. It is far more biologically reasonable to consider these west Atlantic specimens as *Glossodoris sedna,* with a slight variation of body tone and a tendency to more crenulations; this amount of morphological variation is certainly not unexpected and is consistent with the geographic separation and isolation of the population.

Zoogeography: This tropical eastern Pacific species is very common throughout the Gulf of California and along the Pacific coast of Mexico and Central America to the Galápagos (Bertsch, 1978b). Numerous other species of nudibranchs are known to occur in both the Pacific and Atlantic (Caribbean) coasts of the tropical Americas (*e.g.,* Bertsch, 1979; Gosliner & Bertsch, 1985). However, *Glossodoris sedna* is unique in that its known western Atlantic occurrences are only from the southern tip of Florida, not throughout the various islands of the Caribbean. Curiously, the three Florida localities are all within 75 km of each other.

Chromodoris grahami Thompson, 1980

(Figures 3, 4, 10)

Material examined: One specimen, 8 mm long, 4 mm wide; shallow subtidal, Iron Castle Point, Porto Bello, Panama (9°33′30″N, 79°40′45″W); *leg.* H. Bertsch, 22 September 1974. Deposited in the collections of the Los Angeles County Museum of Natural History (Malacology) LACM 74-104.

Photographic records: One specimen, 20 mm long; shallow water 1 m deep, Kingston Harbor, St. Vincent (approx. 13°9′N, 61°14′W); *leg.* Jeff Hamann, January 1987 (Figure 3).

One specimen, La Parguera, Puerto Rico (approx. 17°58′N, 67°03′W); *leg.* Charles E. Cutress, December 1983 (Figure 4).

Prior to this study, *Chromodoris grahami* had been reported in only its original description.

External morphology: The dorsal color of the animals found at St. Vincent (Figure 3) and at Puerto Rico (Figure 4, shown on a pinkish red sponge) was a cloudy salmon pink with three irregular rows of bright red spots. The color bands around the rims of the mantle and foot were different. The specimen from Puerto Rico had only a white band, whereas the St. Vincent animal had an outer yellow line encircling the notum, inside of which was a very thin red line, which in turn enclosed a broad white band. Thompson (1980) described only yellow and white marginal bands.

The animal from Panama was pinkish red with darker red spots irregularly placed over the dorsum, and a prominent whitish marginal band around the notum. The rhinophores and gills were also pinkish red, with tinges of white at the tips or edges. This specimen also did not have the yellow and white mantle margin bands reported by Thompson (1980). It exhibited an inner cream-white band and an outer translucent edge around the margin of the mantle.

These three specimens show a small range of variation from the coloration originally described in the mantle mar-

gin. However, common to all known *Chromodoris grahami* is the fairly broad white band encircling the animal, with a salmon-pink dorsal color mottled with three rows of bright red spots.

Internal morphology: The radular formula of the specimen from Panama was 39 (26–27.0.26–27), similar to the 36 (23.0.23) formula reported by THOMPSON (1980: 80). The innermost lateral tooth (Figure 10A) was strongly recurved (with 4 or 5 accessory denticles visible), while the outer laterals are more elongate (Figure 10B), approaching a pectinate condition (Figure 10C), as reported by THOMPSON (1980:80–81, fig. 5C).

Except for the slight variation in mantle margin coloration, these animals closely match the original description of *Chromodoris grahami*.

Zoogeography: The specimen from Panama represents a southern range extension of over 900 km, and the Puerto Rican and Lesser Antillean records are eastward range extensions of over 1000 and 1700 km respectively, from the only previously reported occurrence of *Chromodoris grahami* in Jamaica (approx. 18°N, 77°30′W). *Chromodoris grahami* is now known from four widely scattered Caribbean extremes (Panama, Jamaica, Puerto Rico, and St. Vincent). This species can be considered a shallow-water endemic throughout the Caribbean Sea.

ACKNOWLEDGMENTS

I thank Mr. Jeff Hamann, of El Cajon, California, for generously allowing me to use his and his family's collection data and his photographs; and Dr. Cutress for the use of his photo. A grant from the Smithsonian Tropical Research Institute enabled me to study and collect opisthobranchs in Panama; and Dr. Terrence Gosliner, of California Academy of Sciences, kindly provided me use of a scanning electron microscope.

LITERATURE CITED

BERTSCH, H. 1978a. The Chromodoridinae nudibranchs from the Pacific coast of America. Part II. The genus *Chromodoris*. Veliger 20(4):307–327.

BERTSCH, H. 1978b. The Chromodoridinae nudibranchs from the Pacific coast of America. Part III. The genera *Chromolaichma* and *Mexichromis*. Veliger 21(1):70–86.

BERTSCH, H. 1979. Tropical faunal affinities of opisthobranchs from the Panamic province (eastern Pacific). Nautilus 93(2–3):57–61.

GOSLINER, T. M. & H. BERTSCH. 1985. Records and morphology of *Lomanotus stauberi* Clark & Goetzfried, 1976, from the Panamic Pacific. Veliger 27(4):397–405.

MANSTAN, R. 1980. Cover photograph. Sea Frontiers 26(2).

MARCUS, EV. & ER. MARCUS. 1967. American opisthobranch mollusks. Univ. of Miami, Studies in Tropical Oceanography 6:viii + 256 pp.

RUDMAN, W. B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zool. Jour. Linn. Soc. 81(2/3):115–273.

RUDMAN, W. B. 1986. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: the genus *Glossodoris* Ehrenberg (= *Casella* H. & A. Adams). Zool. Jour. Linn. Soc. 86:101–184.

THOMPSON, T. E. 1980. Jamaican opisthobranch molluscs II. Jour. Moll. Stud. 46(1):74–99.

The Veliger 30(4):400–407 (April 1, 1988)

THE VELIGER

A New Fossil *Cypraea* (Gastropoda: Prosobranchia) from Southern Africa with Notes on the Alexandria Formation

by

WILLIAM R. LILTVED

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

AND

F. G. LE ROUX

Geological Survey, P.O. Box 1774, Port Elizabeth 6000, South Africa

Abstract. A new extinct species of *Cypraea, C.* ***zietsmani,*** is described from the Neogene of the Alexandria Formation from the eastern Cape Province of South Africa. It is compared with allied Recent and fossil taxa. The depositional environments and associated fauna are described.

INTRODUCTION

In June 1981, Ross Zietsman, of the Port Elizabeth City Engineers Department, collected a number of fossil gastropod and bivalve shells while excavating in the Neogene Alexandria Formation near Port Elizabeth, in the eastern Cape Province of South Africa. The collection included an undescribed species of *Cypraea.* Additional specimens pertaining to the new species were collected by the South African Geological Survey, during further investigation of the Alexandria Formation in 1985 and 1986. This paper describes the aforementioned taxon and gives a generalized summary of the Alexandria Formation and fauna associated with it.

DESCRIPTION

Cypraea ***zietsmani*** Liltved & Le Roux, sp. nov.

(Figures 1–3, 5 in part)

Shell large, 56–66 mm in length, depressed, pyriform. Margins broad, angularly rounded, corrugate, especially posteriorly, and deeply cut by wide posterior notch. Dorsal surface bears two heavily calcified tubercles in posterior one-third of shell, one on either side of medio-dorsal line. Less eroded shells possess a short dorsal sulcus between raised thickened ridges immediately adjacent to the medio-dorsal line. Sulcus situated on pronounced dorsal hump at one-third anteriorly. Hump slopes abruptly toward produced anterior terminal. Base heavily thickened, flattened, with distinct depression along columellar peristome. Margins reflected on either side, extending beyond lateral plane of body whorl in mature individuals. Aperture moderately narrow, slightly curved, constricted posteriorly by funicular callus. Medial portion of aperture evenly wide, becoming dilated anteriorly. Columellar peristome poorly defined owing to concave basal depression, edentate for most of its length, except for up to five coarse, uneven, rounded teeth situated above the fossula. Fossula flared, concave, edentate, with prominent terminal ridge extending concavely upward into flattened columellar flange, which borders the anterior siphonal canal. Labrum broad, widest posteriorly, becoming narrower anteriorly, with 15 to 20 coarse, evenly spaced, rounded teeth present along inner edge. Teeth extend as raised ridges to two-thirds of labral width. The type specimens are predominantly chalky white and lack any color. Under ultraviolet light, however, the raised transverse labral ridges are pigmented and the columellar portion of the base shows transverse bands and spots (Figure 3). Pigment spots are present on the margins within recessed portions of the posterior corrugations, and wide zig-zag markings are present anteriorly.

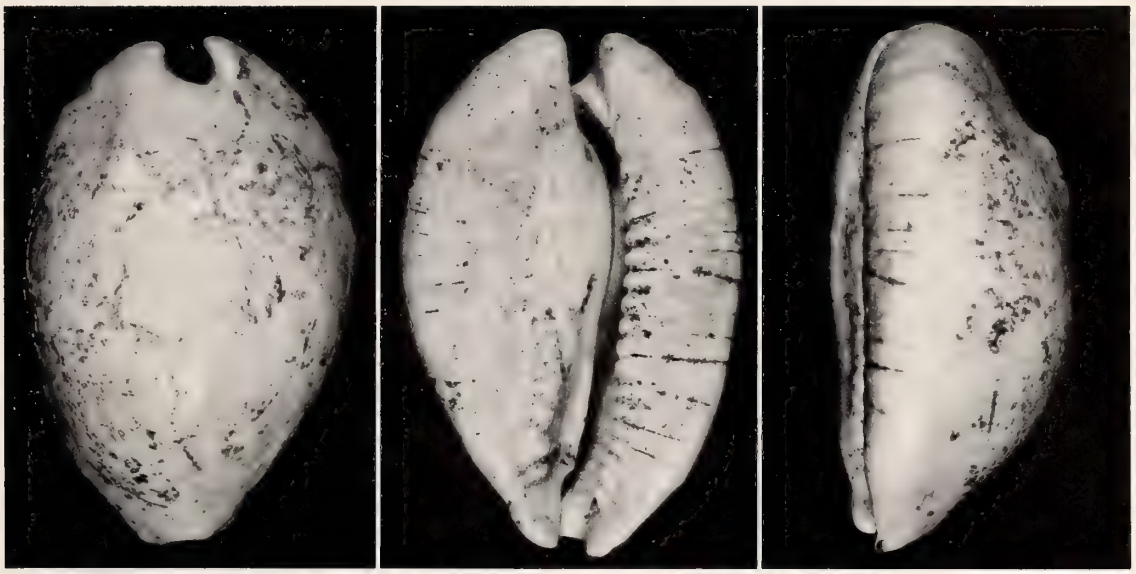


Figure 1

Cypraea ***zietsmani*** Liltved & Le Roux, sp. nov. Holotype shell, 58.6 mm long. Left, dorsal; middle, ventral; and right, lateral aspects.

Measurements:

	Length (mm)	Width (mm)	Height (mm)
Holotype (SAM-PQ 2573)	58.6	38.5	26.4
Paratype F (SAM-PQ 2574)	65.8	50.4	30.9
Paratype H (SAM-PQ 2575)	63.8	46.6	28.6
Paratype G (CASG-61612.01)	62.7	48.8	28.8
Paratype A (LR 263)	56.8	39.9	26.5
Paratype B (LR 270)	56.0	45.0	27.9
Paratype C (LR 265)	60.8	47.1	30.9
Paratype D (LR 271)	58.0	46.1	27.4
Paratype E (LR 267)	59.8	49.5	28.9

Type locality: Aloes Siding, 15 km north of Port Elizabeth (33°48′56″S, 25°37′49″E), eastern Cape Province, South Africa, Pliocene, Alexandria Formation, 44 m elevation, pebbly calcareous sandstone.

Type deposition: The holotype (SAM-PQ 2573), and two paratypes (SAM-PQ 2574, 2575) have been deposited in the South African Museum. The three aforementioned specimens were collected at the type locality by Ross Zietsman in June 1981. Five paratypes (LR 263, 265, 267, 270, 271) have been deposited in the collection of the Geological Survey, South Africa. These five paratypes were collected by the Geological Survey at St. George's Strand north of Port Elizabeth, in 1985 and 1986. One paratype (CASG-61612.01) has been deposited in the California Academy of Sciences. This specimen was collected at the type locality by Ross Zietsman in June 1981.

Discussion: *Cypraea* ***zietsmani*** sp. nov. conchologically most closely resembles the Recent species *C. fultoni* Sowerby, 1903, which occurs at depths exceeding 65 m off the coast of Natal, South Africa. The major difference in shell morphology between the two is that *C.* ***zietsmani*** invariably lacks the columellar dentition of *C. fultoni*. *Cypraea* ***zietsmani*** may possess up to five rounded teeth along the anteriormost portion of the columellar peristome immediately above the fossula, but otherwise is edentate. The columellar peristome of *C.* ***zietsmani*** is poorly defined owing to the innermost portion of the columellar basal area being recessed and relatively thin, whereas that of *C. fultoni* is heavily callused with a well-defined, toothed columellar peristome. All examined specimens of *C.* ***zietsmani*** possessed two pronounced, posteriorly situated dorsal tubercles. Some of the less eroded shells displayed a clear, short dorsal sulcus, situated anteriorly, between thickened ridges, immediately on either side of the medio-

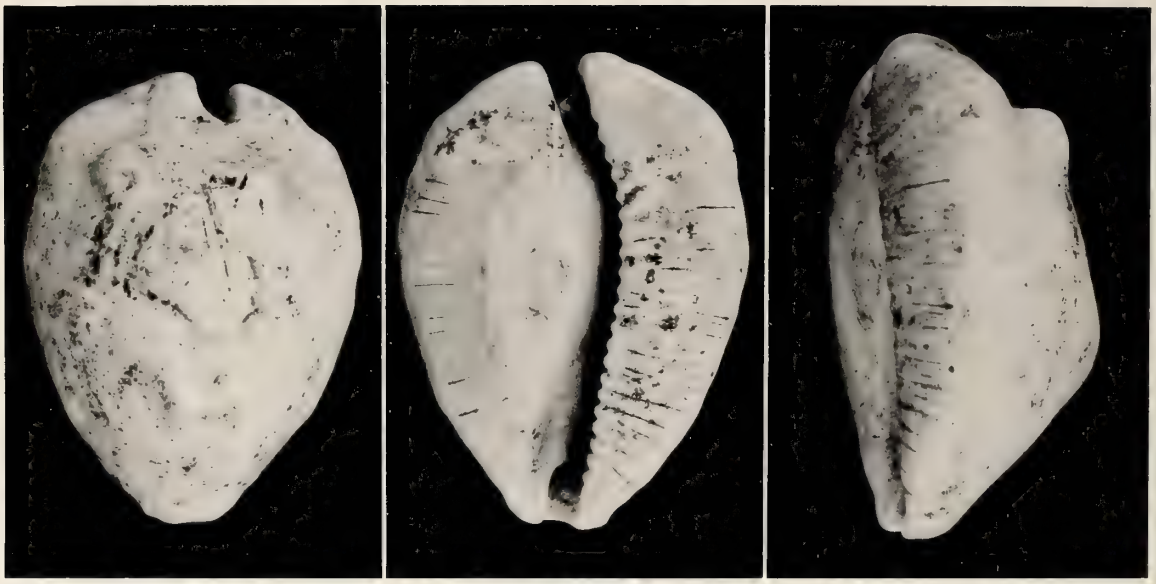


Figure 2

Cypraea ***zietsmani***. Shell from collection of Mrs. F. Ball, 60.5 mm long. Left, dorsal; middle, ventral; and right, lateral aspects.

dorsal line. Neither of these characters is present in *C. fultoni*. However, similar tubercules may be seen on the shells of extinct and extant congeners. *Cypraea mus* Linné, 1759, a living shallow-water species from Venezuela and Colombia, and ancestral species belonging to the *C. henekeni* Sowerby, 1850, complex (INGRAM 1947, 1948) from the Mio-Pliocene of South and Central America, exhibit similar dorsal tuberculations to those found on shells of *C.* ***zietsmani***. *Cypraea teulerei* Cazenavette, 1845, a recent, shallow-water species from the Gulf of Oman is also conchologically similar to *C. fultoni* and *C.* ***zietsmani***, but is virtually edentate and lacks any vestige of dorsal tuberculations. The three extant relic species, *C. fultoni, C. mus,* and *C. teuleri,* extinct species such as *C.* ***zietsmani***, and members of the *C. henekeni* complex (*C. andersoni* Ingram, 1947, *C. caroniensis* Maury, 1927, *C. cayapa* Pilsbry & Olsson, 1941, *C. grahami* Ingram, 1947, *C. henekeni* Sowerby, 1850, *C. isthmica* (Schilder, 1927), *C. merriami* Ingram, 1939, *C. nouelei* Maury, 1917, *C. projecta* Ingram, 1947, *C. quagga* (Schilder, 1939), *C. rugosa* Ingram, 1947, and *C. tuberae* Ingram, 1948) appear to be related. All of these species are characterized by being somewhat squat with a pronounced dorsal hump situated in the posterior one-third of the shell. The bases are typically flat and broad with centrally placed apertures. The margins are deeply cut posteriorly by a wide notch. The fossula terminates in a well-formed terminal ridge, and is normally devoid of denticles. Recent species are characterized by having a rather amorphous dorsal color pattern. Well preserved fossil material viewed under ultraviolet light shows remnants of a similar pattern.

PETUCH (1979) placed *Cypraea mus* and the *C. henekeni* complex in *Syphocypraea* Heilprin, 1887, on the basis of similar conchological morphology in the bulla stages of *C. mus, C. henekeni,* and *Cypraea* (*Syphocypraea*) *problematica* Heilprin, 1887, the type species of the genus. We place the members of the *C. henekeni* complex merely in *Cypraea,* not *Syphocypraea,* on the grounds that members of *Syphocypraea* possess a spiriform posterior canal and not the deeply cut posterior notch present within the *C. henekeni* complex. Shells of *S. problematica* have an elongate, ovoid shell, whereas those of the *C. henekeni* complex and *C. mus* tend to be more anteroposteriorly compressed, angular in

Figure 3

Cypraea ***zietsmani***. Paratype A shell, 56.8 mm long. Ventral aspect showing pigmented areas when exposed to ultraviolet light.

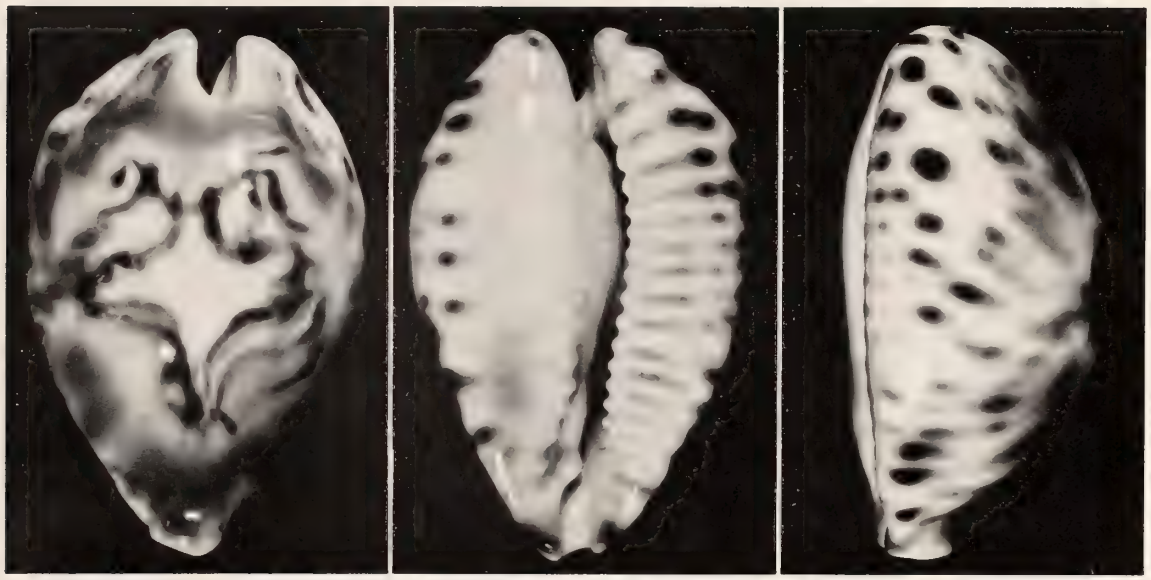


Figure 4

Cypraea fultoni Sowerby, 1903. Shell, 58.4 mm long. Left, dorsal; middle, ventral; and right, lateral aspects.

shape with an elevated dorsal hump. Based on conchological similarity, the affinities of the *C. henekeni-C. mus* complex appear to be with species placed in the *Cypraea* subgenus *Barycypraea* Schilder, 1927, which include *C. fultoni, C. teuleri,* and *C. **zietsmani**,* rather than with *Syphocypraea.*

One paratype of *Cypraea **zietsmani*** (Figure 5, in part) shows evidence of having been preyed upon by a molluscivorous fish. Shells of *C. fultoni* Sowerby, 1903 (Figure 4) and *C. broderipii* Sowerby, 1832 (Figure 5, in part), which are occasionally taken from stomachs of the musselcracker, *Cymatoceps nasutus* (Castelnau, 1861), caught

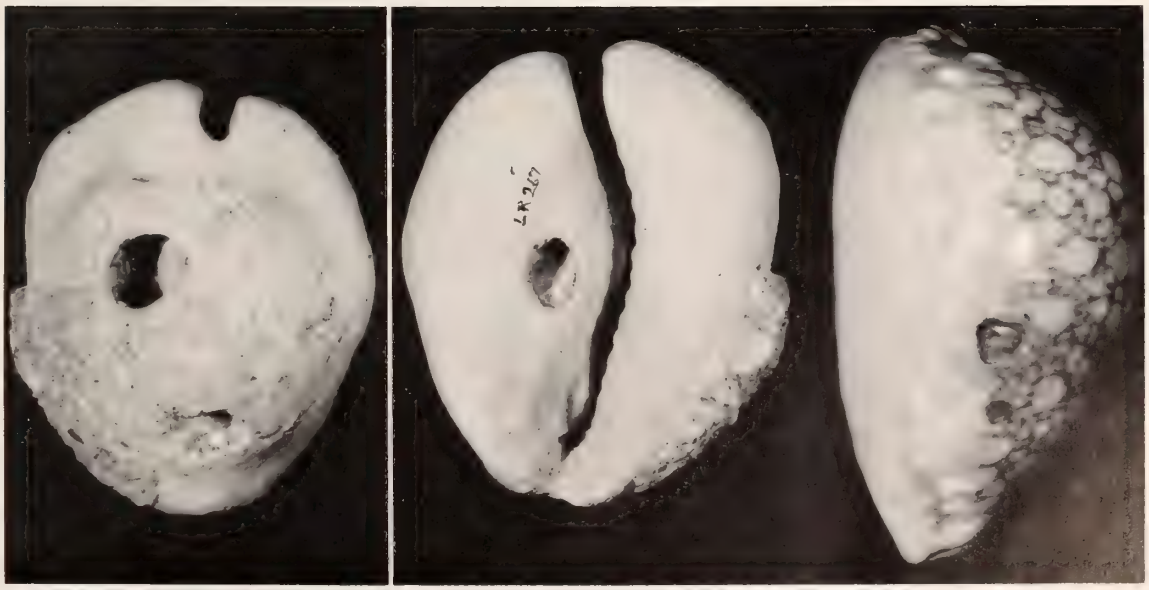


Figure 5

Left (dorsal) and middle (ventral): *Cypraea **zietsmani***, paratype E, 59.8 mm long, showing perforations caused by fish predation. Right, lateral: *Cypraea broderipii* Sowerby, 1832, 74.1 mm long, showing partially healed perforations due to predation by *Cymatoceps nasutus* (Castelnau, 1861).

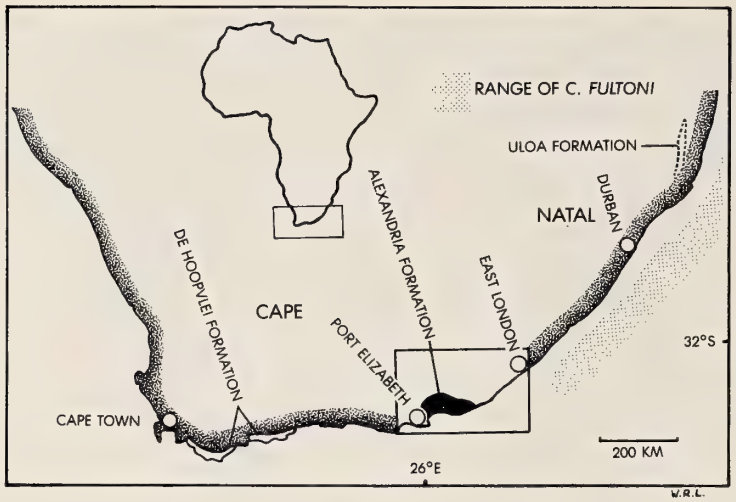


Figure 6

Index map showing areal extent of Alexandria Formation and its possible correlatives—the De Hoopvlei and Uloa formations. The range of *Cypraea fultoni* Sowerby, 1903, is shown by the shaded area. The area enclosed within the rectangle is shown in detail in Figure 7.

in deep water off Natal, occasionally bear round or ovoid perforations punched out by the powerful, toothed jaws. The holes are similar to those on the base and dorsum of paratype E. The interior of paratype F indicates that after death, the shell became the habitat of a bryozoan colony. The characteristically bored holes on the base of paratype H indicate that the shell became riddled by a clionid sponge afer death.

Etymology: The new species is named for Ross Zietsman of Port Elizabeth, South Africa, who collected the holotype and provided some of the type material used in this study.

PALEOECOLOGY

The Alexandria Formation represents a marine deposit of Neogene age. It unconformably overlies the Mesozoic Uitenhage Group or the Paleozoic Cape Supergroup as a veneer on a well-planed, dissected, and stepped seaward-sloping platform. Discontinuous outcrops of the formation occupy a narrow strip 20 to 40 km wide, between the Elands and Suur mountains in the south and the sea. The westernmost outcroup of the Alexandria formation is marked by an erosional cut-off in the vicinity of the Gamtoos River, while the eastern boundary is defined by the Kowie River (Figure 7). The northern limit of the formation roughly coincides with the 300-m contour, while southward it may pass below sea level onto the continental shelf, although it would seem more probable that post-Tertiary (marine) erosion has removed all but remnants of the Alexandria Formation in the offshore. The type area of the formation is situated east of the Sundays River in the vicinity of Colchester (Le Roux, in press b).

The age of the Alexandria Formation, as indicated by molluscan as well as foraminiferal assemblages, is Neogene (Siesser & Dingle, 1981), with stratification generally becoming more recent seawardly.

The formation consists essentially of alternating beds of whitish gray, fine to medium-grained, calcareous sandstone, subordinate shelly conglomerate and coquinite that contain rich assemblages of marine invertebrates (Le Roux, in press a). The formation is normally between 3 and 9 m thick. Sedimentary structures, corroborated by biogenic structures, fossil assemblages, and the physical condition of the shells, point to depositional environments ranging from shoreface and foreshore to lagoonal and/or estuarine.

The Alexandria Formation is correlated with the De Hoopvlei and Uloa formations (both Neogene) in the southwestern Cape Province and Natal (Le Roux, in press b), chiefly owing to lithological, paleontological and chronostratigraphical similarities (Figure 6).

Distribution and inferred habitat: Shells of *Cypraea* ***zietsmani*** were found at five localities on the lowest of three terraces. This terrace is tentatively regarded as being of Pliocene age.

(a) Aloes Siding (44 m elevation) northeast of Port Elizabeth (33°48′56″S, 25°37′49″E). At the type locality, specimens of *Cypraea* ***zietsmani*** were found in a trench, which has since been closed. The depositional environment, as inferred from outcrops in the immediate vicinity, is that of a beach. The locality is situated on one of a number of beach ridges that parallel the present-day shoreline. These beach ridges are taken to represent paleo-shorelines of a regressing sea during the Pliocene. Fossils at this locality

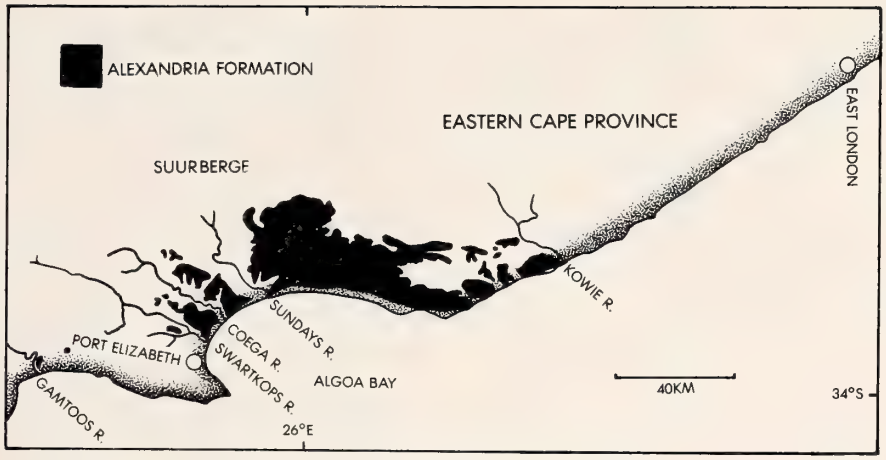


Figure 7

Distribution of Alexandria Formation (most of the formation is unexposed) (after Le Roux, in press b).

are rare owing to poor exposures, but shells of +*Glycymeris borgesi* (Cox, 1946), +*Melapium patersonae* Newton, 1913, *Marginella* sp., and *Conus* sp. were found on the surface.

(b) St. George's Strand (39 m elevation) northeast of Port Elizabeth, 33°49′22″S, 25°39′12″E). A foreshore (beach) depositional environment is inferred for the sequence exposed at this locality. Thin pebble-cobble beds alternate with coquina layers. A thin semiconsolidated sandstone bed yielded several *in situ Bullia digitalis* (Dillwyn, 1817) which are typical of a sandy beach environment. Fossils at this locality include the following (+ = extinct taxa).

	Inferred habitat preference
Gastropoda	
Amalda optima (Sowerby, 1892)	subtidal sand
Amalda obtusa (Swainson, 1825)	subtidal sand
Bullia digitalis (Dillwyn, 1817)	intertidal sandy beach
Conus sp.	reef/sand
Fusinus ocelliferus (Lamarck, 1816)	intertidal/subtidal, reef/sand
Heliacus cf. *trochoides* (Deshayes, 1830)	intertidal/subtidal, rocky shore
+*Pseudoliva* sp. nov. ?	sand
Siphonaria aspera Krauss, 1848	intertidal rocky shore
Thais capensis (Petit, 1852)	low neaptide downwards reef
Thais haemostoma (Linné, 1767)	intertidal/subtidal reef
Turritella carinifera Lamarck, 1822	intertidal/subtidal reef
+*Vasum* sp. nov. ?	subtidal reef
Bivalvia	
Crassatina capensis (Lamy, 1917)	subtidal sand
+*Glycymeris borgesi* (Cox, 1946)	subtidal sand
+*Notocallista schwarzi* (Newton, 1913)	subtidal sand
Perna perna (Linné, 1758)	intertidal/subtidal, rocky shore

(c) Coega (60 m elevation) northeast of Port Elizabeth (33°45′04″S, 25°40′06″E). Two *Cypraea* ***zietsmani*** specimens were found in a coquinite layer that had been deposited as a beach berm. The high wave energy that existed during the deposition of this shelly layer is suggested by the fragmented and worn nature of the fossil shells. Both specimens are worn and filled with comminuted shell fragments. Other fossils from this coquinite are the following.

	Inferred habitat preference
Gastropoda	
Bullia digitalis (Dillwyn, 1817)	intertidal sandy beach
Siliquaria cf. *wilmanae* (Tomlin, 1918)	subtidal rock
Bivalvia	
Arca noae (Linné, 1758)	subtidal reef
Barbatia foliata (Forsskål, 1775)	intertidal rocky shore
+*Cardium edgari* Newton, 1913	sand

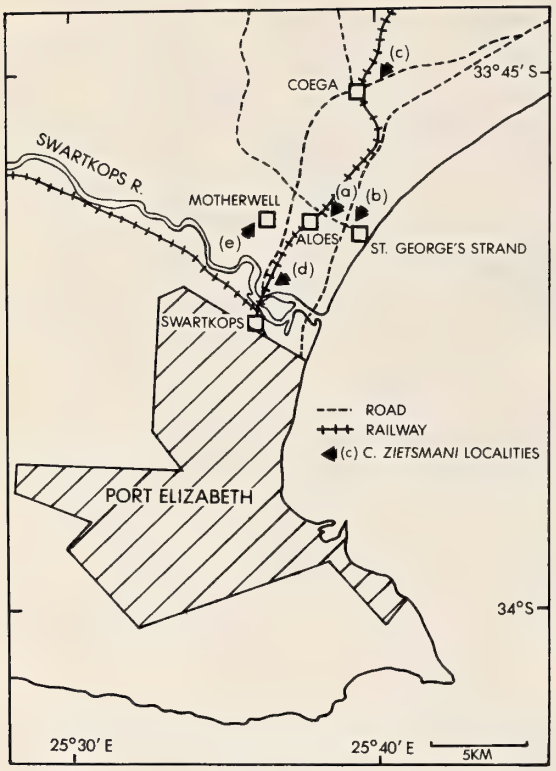


Figure 8

Localities of *Cypraea* ***zietsmani***.

Donax serra Dillwyn, 1817	intertidal sandy beach
+*Glycymeris borgesi* (Cox, 1946)	sand
Isognomon sp.	reef
Ostrea algoensis Sowerby, 1871	intertidal/estuarine rock
+*Pinctada* sp. nov. ?	reef
Scissodesma spengleri (Linné, 1767)	intertidal/subtidal sand
Anthozoa	
Balanophyllia sp.	reef
Echinoidea	
Echinodiscus sp.	lower intertidal to subtidal sand

(d) Railway cut 1 km north of Swartkops (43 m elevation) Port Elizabeth (33°50′15″S, 25°36′44″E). *Cypraea* ***zietsmani*** specimens were found in a fossiliferous, semi-consolidated conglomerate layer showing typical low-angle beach stratification as well as imbrication. A sandstone lens in this unit shows herringbone cross-bedding, which is also suggestive of a beach environment. The generally good physical condition of shells in this layer suggests only moderate wave energy during deposition. Fossils associated with *C.* ***zietsmani*** at this locality are the following.

	Inferred habitat preference
Brachiopoda	
Kraussina sp.	reef
Gastropoda	
Dendrofissurella scutellum (Gmelin, 1791)	intertidal rocky shore
+*Calyptraea kilburni* Kensley and Pether, 1986	reef
+*Clionella* sp. nov. ?	sandy reef
Diodora elevata (Dunker, 1846)	subtidal reef
Fissurellidea aperta (Sowerby, 1825)	intertidal/subtidal reef
Melapium elatum (Schubert and Wagner, 1829)	subtidal sand
Nucella squamosa (Lamarck, 1816)	subtidal reef
Turritella sanguinea Reeve, 1849	subtidal sand
+*Vasum* sp. nov. ?	subtidal reef
Bivalvia	
Barbatia obliquata (Gray, 1837)	intertidal rocky shore
+*Glycymeris borgesi* (Cox, 1946)	subtidal sand
G. cf. *queketti* (Sowerby, 1897)	subtidal
+*Pinctada* sp. nov. ?	subtidal reef
Scaphopoda	
Dentalium sp.	subtidal sand

(e) Trench at Motherwell, 3 km north of Swartkops (58 m elevation), Port Elizabeth (33°47′50″S, 25°36′22″E). Two specimens of *Cypraea* ***zietsmani*** were found in a fossiliferous pebbly coquinite, deposited as a beach berm. High wave energy during deposition is suggested by the fragmented nature of the shells. Fossils associated with this coquinite are the following.

	Inferred habitat preference
Gastropoda	
Bullia annulata (Lamarck, 1816)	subtidal sand
Melapium elatum (Schubert & Wagner, 1829)	subtidal sand
Bivalvia	
Ostrea atherstonei Newton, 1913	subtidal reef
Isognomon cf. *gaudichaudi* (d'Orbigny, 1842)	intertidal/subtidal reef

ACKNOWLEDGMENTS

We thank Terrence M. Gosliner of the California Academy of Sciences, San Francisco, and John Pether of the South African Museum, Cape Town, for giving valuable comment on this work, Mr. and Mrs. A. K. Ball of Jeffrey's Bay, South Africa, for providing photographs of their specimens of *Cypraea* ***zietsmani,*** and Patricia Dal Poroto of the California Academy of Sciences for typing the manuscript. The second author thanks the Chief Director of the Geological Survey of South Africa for permission to publish data collected by the Survey.

LITERATURE CITED

Bourdon, M. & P. Magnier. 1969. Notes on the Tertiary fossils at Birbury, Cape Province. Trans. Geol. Soc. S. Afr. 72(3):123–125.

Ingram, W. M. 1947. Fossil and Recent Cypraeidae of the western regions of the Americas. Bull. Amer. Paleo. 120:1–83.

Ingram, W. M. 1948. Fossils Cypraeidae from the Miocene of Florida and Colombia. Calif. Acad. Sci., 4th Ser., Proc. 6:125–133.

Le Roux, F. G. In press a. Tertiary macrofossils of the Alexandria Formation—a supplementary list. Ann. Geol. Surv. S. Afr. 21.

Le Roux, F. G. In press b. Lithostratigraphy of the Alexandria Formation. Stratigraphic Description and Amendments 1. South African Committee for Stratigraphy. Handbook 8 (2).

Petuch, E. J. 1979. A new species of *Syphocypraea* (Gastropoda: Cypraeidae) from northern South America with notes on the genus in the Caribbean. Bull. Mar. Sci. 29(2):216–225.

Siesser, W. G. & R. V. Dingle. 1981. Tertiary sea-level movements around southern Africa. Jour. Geol. 89:83–96.

The Veliger 30(4):408–411 (April 1, 1988)

THE VELIGER

Two New Species of Liotiinae (Gastropoda: Turbinidae) from the Philippine Islands

by

JAMES H. McLEAN

Los Angeles County Museum of Natural History, 900 Exposition Boulevard,
Los Angeles, California 90007, U.S.A.

Abstract. Two new gastropods of the turbinid subfamily Liotiinae are described: *Bathyliontia* ***glassi*** and *Pseudoliotina* ***springsteeni***. Both species have been collected recently in tangle nets off the Philippine Islands.

INTRODUCTION

A number of new or previously rare species have been taken in recent years by shell fishermen using tangle nets in the Philippine Islands, particularly in the Bohol Strait between Cebu and Bohol. Specimens of the same two new species in the turbinid subfamily Liotiinae have been received from Charles Glass of Santa Barbara, California, and Jim Springsteen of Melbourne, Australia. Because these species are now appearing in Philippine collections, they are described prior to completion of a world-wide review of the subfamily, for which I have been gathering materials and examining type specimens in various museums. Two other species, *Liotina peronii* (Kiener, 1839) and *Dentarene loculosa* (Gould, 1859), also have been taken by tangle nets in the Bohol Strait but are not treated here.

Much of the material coming from Philippine tangle net sources comes from either of two localities: off Punta Engano, Mactan Island, Cebu (10°18′N, 124°01′E) and off Balicasag Island, S of Panglao, Bohol (9°31′N, 123°40′E). These localities are at opposite ends of the Bohol Strait and are separated by a distance of approximately 100 km. Precise locality information for material from Philippine tangle nets is impossible to obtain, because the shell fishermen work the entire area and do not provide detailed localities (Jim Springsteen, personal communication). The type localities of the two species described here are given simply as the Bohol Strait. Maximum depth for the Bohol Strait is indicated as 190 fathoms on U.S. Hydrographic Chart no. 14429, from which the coordinates cited above were taken. After conversion to metres, the depth range is therefore approximately 200–350 m for this material.

Holotypes are deposited in the Los Angeles County Museum of Natural History (LACM); additional paratypes are deposited in the LACM, the U.S. National Museum of Natural History, Washington (USNM), and the Australian Museum, Sydney (AMS). Additional material in less perfect condition of the first described species has been recognized in the collections of the USNM and the Museum National d'Histoire Naturelle, Paris (MNHN).

Family Turbinidae Rafinesque, 1815

Subfamily Liotiinae H. & A. Adams, 1854

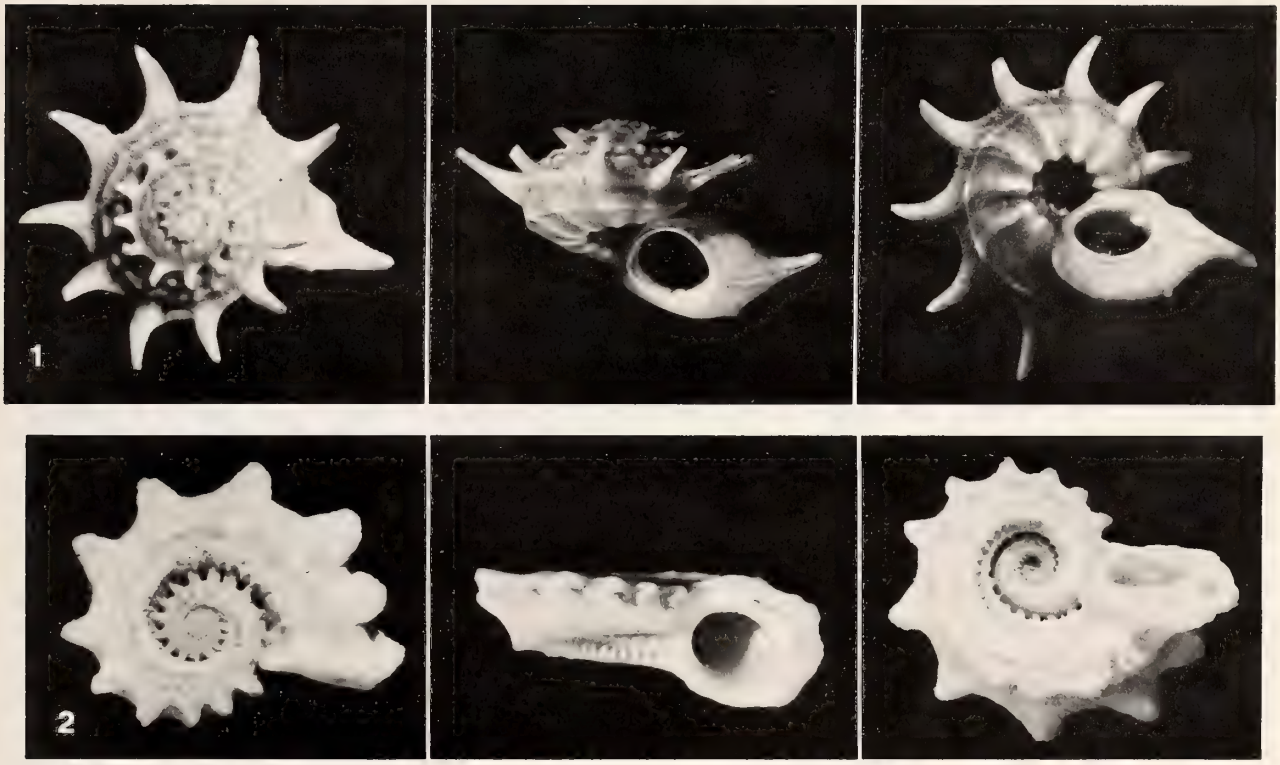
The subfamily is characterized by a turbiniform profile, nacreous interior, fine lamellar sculpture, an intritacalx in most genera, circular aperture, a multispiral operculum with calcareous beads, and a radula like that of other turbinid subfamilies.

Although previously treated by some authors as a full family, the Liotiinae have recently been ranked as a subfamily of Turbinidae (McLean, 1987).

Genus *Bathyliotina* Habe, 1961

Type species (original designation): *Liotia armata* A. Adams, 1861. Recent, Korea Strait.

Bathyliotina species are characterized by a broad umbilical opening, a spinose periphery, and greatly thickened final lip in which the aperture flares to its greatest extent, followed by deposition of lamellar layers that evenly decrease the diameter of the aperture to its final size. *Bathyliotina* is unique among liotiine genera in having the evenly decreasing lamellar layers forming the final expanded lip. *Liotina* Fischer, 1885, *Dentarene* Iredale, 1929, and *Austroliotia* Cotton, 1948, differ from *Bathyliotina* in having a greatly expanded lip followed by a constriction and then a secondary inflation to the final lip only slightly larger



Explanation of Figures 1 and 2

Figure 1. *Bathyliotina* ***glassi*** sp. nov. Holotype, LACM 2298. ×3.1.

Figure 2. *Pseudoliotina* ***springsteeni*** sp. nov. Holotype, LACM 2300. ×5.3.

than the diameter of the body whorl. Other differences are that *Liotina* has a broad cord bordering and narrowing the umbilicus, *Dentarene* has an umbilical ridge running into a twisted appendage of the inner lip, and *Austroliotia* Cotton, 1948, has a broadly open umbilicus not bordered by a major cord or a twisted ridge.

There are four previously described species of *Bathyliotina: B. armata* (A. Adams, 1861), *B. lamellosa* (Schepman, 1908), *B. schepmani* Habe, 1953, and *B. nakayasui* Habe, 1981. All occur offshore in the central Indo-Pacific.

Bathyliotina ***glassi*** McLean, sp. nov.

(Figure 1)

Description: Shell large for genus, depressed turbinate, yellowish white, maximum diameter 16.0 mm, whorls 4, periphery marked by pointed upturned spines, about 12 per whorl; aperture oblique, mature lip greatly expanded; shell surface marked by fine, sharp lamellar growth increments; lamellae sharp, not coalescing; intritacalx not evident. Protoconch diameter 200 μm, suture deeply impressed, first and second whorl rising above protoconch, third whorl descending, resulting in flat topped profile for early whorls. Early sculpture marked by strong axial lamellae and swellings at suture and periphery, those at periphery forming spines in final two whorls. Spines not sealed anteriorly, lamellae that form spines broadly spaced at periphery. Spiral sculpture of two nodulose cords between suture and periphery. Spiral sculpture on base of one cord near outer edge, an angular cord defining umbilicus, and another within umbilicus. Axial sculpture corresponding to spines, forming pronounced ribs close to umbilicus and forming crenulate border on cord defining umbilicus and cord within umbilicus. Lip descending below suture on final fifth of last whorl, flaring to full extent of last spine and marked by lamellar increments of decreasing breadth until lip reaches its final resting stage. Aperture circular, nacreous within. Operculum with numerous volutions, bearing sharply projecting beads. Dimensions of holotype: height 8.5, maximum diameter 16.0 mm.

Type locality: Bohol Strait, Philippines, 90–180 m (see Introduction).

Type material: 5 specimens: 4 specimens from Glass & Foster collection and 1 specimen from Springsteen collection. Holotype, LACM 2298; 2 paratypes LACM 2299 (height 7.4, diameter 14.5; height 7.0, diameter 13.9 mm); 1 paratype USNM 784761 (height 8.2, diameter 15.0 mm); 1 paratype AMS (height 8.6, diameter 15.0 mm).

Referred material: 13 specimens, Glass & Foster collection. The following dead shells in poor condition: 4 specimens MNHN, Musorstom Expedition II, sta. DG 32, off N side Mindoro Island, Philippines (13°40″N, 120°54″E), 192–220 m; 4 specimens (plus 2 juveniles) USNM 278563, Albatross sta. 5262, off Matacot Point, W side Luzon, Philippines, 208 m; 1 specimen (plus 3 juveniles) USNM 287574, Albatross sta. 5398, off Gigantangan Island, NW side Leyte, Philippines.

Remarks: *Bathyliotina* ***glassi*** is the only member of the genus having long peripheral spines. It most resembles *B. schepmani* Habe, 1953 (name based on "*Liotia* (*Arene*) *armata* var." *of* SCHEPMAN, 1908:35, pl. 3, fig. 1), from northeastern Borneo, which is smaller, more elevated, has some intritacalx, has shorter peripheral spines and a basal cord that is weakly spinose. *Bathyliotina* ***glassi*** is exceeded in size only by *B. nakayasui* HABE (1981:109, figs. 1–3), which has short peripheral spines and strong clathrate sculpture.

The holotype has been previously figured without an identification (GLASS, 1984).

Etymology: The species is named after Charles Glass, of Santa Barbara, California, former editor of the Conchologists of America Bulletin.

Genus *Pseudoliotina* Cossmann, 1925

Type species (original designation): *Liotia sensui* Vidal, 1921. Upper Cretaceous, Europe.

Pseudoliotina species are characterized by an extremely flat spire, presence of intritacalx, nearly planispiral coiling, forming an extremely broad umbilicus, and thickened final lip. The aperture has a terminal constriction that produces a secondary final lip following the major thickening, similar to that noted above for the genera *Liotina, Dentarene,* and *Austroliotia.*

Pseudoliotina has previously been treated (KEEN, 1960) as a synonym of *Cyclostrema* Marryat, 1818, but is here distinguished from that genus. Species of *Cyclostrema* are larger than those of *Pseudoliotina* and do not produce a thickened final lip. *Cyclostrema* is restricted to two species in the Caribbean faunal province: the type species *C. cancellatum* Marryat, 1818, and *C. tortuganum* Dall, 1927, both of which were reviewed by ABBOTT (1950).

Only three species have the characters of the aperture defined above: the fossil type species, the broadly distributed Indo-Pacific species *P. discoidea* (Reeve, 1843), and the following new species.

Pseudoliotina ***springsteeni*** McLean, sp. nov.

(Figure 2)

Description: Shell large for genus, discoidal, yellowish white, maximum diameter 10.5 mm, whorls 3.5, periphery marked by blunt double spines, 12 on final whorl; aperture only slightly oblique; mature lip thickened; whole surface of shell with fine, sharp lamellar growth increments, surface choked with intritacalx. Protoconch diameter 200 μm, suture deeply impressed, teleoconch whorls rising above and below protoconch to maintain discoidal profile, except on final fifth of whorl preceding lip, where suture descends, placing final aperture below position of previous whorls. Discoidal growth results in extremely broad umbilicus, revealing basal side of early whorls. Final whorl in contact with penultimate whorl only at tips of spines. Spiral sculpture of single, faint, mid-dorsal carination, and weak, double, peripheral cords that produce the tight, double spination; base with two cords, outermost cord nodose to correspond to spines; inner cord smooth; umbilical edge with two crisply crenulate cords; umbilical wall with two additional, finely fluted cords. Umbilical wall also with fine spiral threads not apparent on rest of shell. Lip thickened, buttressed behind by swollen spiral cords; final swelling of lip separated from flaring extent of lip by deep pits. Aperture circular, nacreous within. Operculum unknown. Dimensions of holotype: height 3.9, maximum diameter 10.5 mm.

Type locality: Bohol Strait, Philippines, 200–350 m (see Introduction).

Type material: 4 specimens from Springsteen collection. Holotype, LACM 2300, 1 immature paratype LACM 2301 (height 2.6, diameter 7.6 mm); 1 paratype USNM 784726 (height 4.0, diameter 10.8 mm); 1 paratype AMS (height 4.3, diameter 10.3 mm).

Referred material: 3 specimens (1 immature) Glass & Foster collection. No additional material is known; specimens have not been recognized in any museum collections.

Remarks: The sculpture of *Pseudoliotina* ***springsteeni*** is so intricate that no other species is remotely similar. *Pseudoliotina discoidea* (Reeve, 1843) is smaller and has sculpture of spiral cords with no peripheral spines. The type species also lacks the strong peripheral spines of *P.* ***springsteeni.***

Etymology: The name honors Jim Springsteen of Melbourne, Victoria, Australia, author of *Shells of the Philippines* (SPRINGSTEEN & LEOBRERA, 1986).

ACKNOWLEDGMENTS

I am grateful to Charles Glass and Robert Foster of Santa Barbara, California, and Jim Springsteen, of Melbourne, Victoria, Australia, for loan of material and donation of type material of the new species. I thank Philippe Bouchet of the Paris Museum, and Richard Houbrick of the U.S. National Museum, for the loan of additional material. Helpful commentary was provided by Carole S. Hickman, University of California, Berkeley.

LITERATURE CITED

Abbott, R. T. 1950. The genus *Cyclostrema* in the western Atlantic. Johnsonia 1(27):193–200.

Glass, C. 1984. Mystery shell. Conch. Amer. Bull. 12(1):18, fig. not numbered.

Habe, T. 1953. Addenda and corrigenda. Illustrated catalogue of Japanese shells, no. 25:213–215.

Habe, T. 1981. A new species of the genus *Bathyliotina* from off Formosa, South China Sea. Venus, Jap. Journ. Malacol. 40(2):109–110.

Keen, A. M. 1960. [Cenozoic Archaeogastropoda]. *In:* R. C. Moore (ed.), Treatise on invertebrate paleontology, Part I. (Mollusca 1). Geological Society of America and University of Kansas Press. xii + 351 pp.

McLean, J. H. 1987. Angariinae and Liotiinae—the primitive living trochaceans. Ann. Rept. Western Soc. Malacol. 19: 16.

Schepman, M. M. 1908. The Prosobranchia of the Siboga Expedition. Part 1. Rhipidoglossa and Docoglossa. Resultats des Explorations Zoologiques, Botaniques, Oceanographique et Geologique . . . a bord du Siboga. Monographie 49a, Livre 39:1–107, 9 pls.

Springsteen, F. J. & F. M. Leobrera. 1986. Shells of the Philippines. Carfel: Manila. 377 pp.

The Veliger 30(4):412–416 (April 1, 1988)

THE VELIGER

Six New Species of Terebridae (Mollusca: Gastropoda) from Panama and the Indo-West Pacific

by

TWILA BRATCHER

Los Angeles County Museum of Natural History, Malacology Section, Exposition Park, Los Angeles, California 90007, U.S.A.

Abstract. Six new species of Terebridae are described: *Terebra* ***rancheria***, Isla Rancheria, Gulf of Chiriqui, Panama; *T.* ***paucincisa***, Granc Récif South, New Caledonia; *T.* ***albocancellata***, Chesterfield-Bellona Plateau, Coral Sea; *T.* ***macleani***, East Cape, East London, South Africa; *Hastula* ***alboflava***, Sogod, Cebu, Philippine Islands; and *H.* ***colorata***, Lighthouse Beach, Western Australia.

Six new species of Terebridae have come to my attention too late to be included in the book *Living Terebras of the World* (Bratcher & Cernohorsky, 1986). To date 267 valid species have been described in the Terebridae, which has world-wide tropical and temperate zone distribution, with the majority of species living in the warmer waters of the tropics. They live in sand or sandy mud from the intertidal zone to a depth of about 1000 m.

It has been 15 yr since a new Panamic terebrid has been described. In 1986 Carol Skoglund brought to my attention one dredged off Isla Rancheria, a small islet near the large Coiba Island, which houses Panama's penal colony. Since then additional lots have been dredged in the same general area.

Seven lots of a new species of *Terebra* were among material collected by 250 dredge hauls made in New Caledonia. This material was sent for identification by Dr. Philippe Bouchet of the Muséum National d'Histoire Naturelle of Paris. Shortly after noting the new species, I received additional specimens of the same species collected in Fiji by Brian Parkinson.

Along with the New Caledonian material sent by Dr. Bouchet were some lots from the Chesterfield Islands, between New Caledonia and Queensland. These contained two lots of another new species.

Dr. Richard Kilburn of the Natal Museum in South Africa sent another new species dredged from the Agulhas Bank, an area that contains predominately endemic mollusks.

For the past 15 yr I have had specimens of an unusually shiny undescribed species of *Hastula* that are colored in clear pastels of pink, peach, lavender, yellow, and white. I have postponed describing the species until I could see a live-collected specimen or at least a good beach specimen. The species appears to be endemic to southwestern Australia. Both the Australian Museum at Sydney and the Western Australian Museum at Perth had many specimens of this species, but all were damaged. On a recent trip to Western Australia I failed to find anyone who had collected this species alive, but Wendy Anson kindly gave me some beach specimens in fine condition, of which the holotype is part.

Another new species of *Hastula* was brought to my attention by the Philippine collector Fernando Dayrit.

ABBREVIATIONS

Abbreviations have been used for a number of institutional collections cited in this paper, as follows.

AMNH—American Museum of Natural History, New York
AMS—Australian Museum, Sydney
ANSP—Academy of Natural Sciences of Philadelphia
BM(NH)—British Museum (Natural History), London
CAS—California Academy of Sciences, San Francisco
LACM—Los Angeles County Museum of Natural History
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge
MORG—Museu Oceanografico de Rio Grande, Brazil
NM—Natal Museum, South Africa
SDMNH—San Diego Museum of Natural History, San Diego
WAM—Western Australian Museum, Perth

TEREBRIDAE Mörch, 1852

Terebra Bruguière, 1789

Terebra ***rancheria*** Bratcher, sp. nov.

(Figures 6, 8)

Diagnosis: Small (maximum length 17 mm) *Terebra* with purplish black below the periphery of the body whorl, including the columella and siphonal fasciole.

Description: Shell small for the genus with 11 whorls of the teleoconch; protoconch of 1.5 pale mamillate whorls; outline of whorls almost straight; subsutural band flat, marked by deep punctations between ribs; axial ribs curved, indistinct, narrower than interspaces, 27 on penultimate whorl; spiral grooves weak, not crossing ribs, 4 rows on penultimate whorl; body whorl with broken spiral grooves coalescing into continuous grooves at periphery; aperture semi-elongate; columella straight; color grayish white with a few early whorls of dark amber and area beginning anterior to periphery of body whorl dark purple, including columella and siphonal fasciole.

Dimensions: Holotype 16.9 × 4.0 mm; paratypes from 12.5 × 3.1 mm to 15.6 × 3.4 mm.

Type locality: Off Isla Rancheria, Gulf of Chiriqui, Panama (7°38′N, 81°44′W), 3.5 m, white sand bottom with some broken shell.

Type material: Holotype LACM 2261; paratypes AMNH 222586 (1); ANSP (1); BM(NH) 1986259 (1); CA S(1); MORG 24.808 (1); SDMNH 29522 (1); USNM 859147 (1); Bratcher coll. (4); Koch coll. (4); Skoglund coll. (10).

Discussion: On most species of *Terebra* with dark stains on the anterior of the shell, the stain begins at the periphery of the body whorl. The stain on this species begins anterior to the periphery. Of the 26 specimens, the only variation is that several are slightly darker with lighter subsutural bands, and one lacks the dark purple anterior. It has a light brownish stain in that area.

The only species with which *Terebra* ***rancheria*** can be compared is *T. churea* Campbell, 1964, from which it differs by having a flatter outline, flatter subsutural band, fewer spiral grooves, and a blackish-purple anterior.

The name of the species is derived from Isla Rancheria, the type locality.

Terebra ***paucincisa*** Bratcher, sp. nov.

(Figure 4)

Diagnosis: A moderately small (maximum length 24 mm) *Terebra* with features somewhat resembling *T. nitida* Hinds, 1844, and *Duplicata raphanula* (Lamarck, 1822) with occasional spiral grooves and a paucispiral protoconch.

Description: Shell moderately small, slender, with 12 shiny whorls of the teleoconch; protoconch of 1.5 bulbous translucent whorls; outline of whorls slightly curved; subsutural band beginning on 4th whorl, defined by deep punctations between ribs; axial ribs narrower than interspaces, unbroken from suture to suture on early whorls and later becoming thickened slightly on subsutural band; spiral sculpture of occasional faint grooves between some ribs, 2 on penultimate whorl; body whorl with axial ribs becoming almost obsolete on final one-half of whorl; aperture elongate; columella with heavy parietal callus and with narrow brown line on inner edge; siphonal fasciole with sharp keel; color warm beige with brown nebulous streaks and a narrow light stripe on periphery of body whorl visible through aperture.

Dimensions: Holotype 19.7 × 4.0 mm; paratypes from 19.1 × 3.8 mm to 23.9 × 4.8 mm.

Type locality: Grand Récif South, New Caledonia, 22°37′S, 166°51′E, 17 m.

Type material: Holotype and 12 paratypes MNHNP; other paratypes AMNH 222587 (1); AMS C15234 (1); BM(NH) 1986260 (1); CAS (1); LACM 2260 (1); MCZ 296165 (1); USNM 859148 (1); Bratcher coll. (9); Parkinson coll. (6); Cernohorsky coll. (2).

Distribution: New Caledonia to Fiji and the Philippine Islands.

Discussion: The color varies from almost black to cream with a few darker or brownish blotches. Two individuals from Fiji and two from New Caledonia are grayish white with few brownish blotches and with the edge of the siphonal fasciole and inner lip outlined in gold. Many of the light-colored shells have a dark blotch on the dorsum of the body whorl. Most of the black specimens were found living in black volcanic sand in Fiji. The color of the protoconch varies from blackish brown on the holotype to translucent cream, some with an opaque dark stripe within. The axial ribs become more obsolete on some specimens than on others. The grooves are usually discontinuous, often very short and faint or almost missing.

This species bears some resemblance to both *Terebra nitida* and *Duplicaria raphanula,* both of which have larger shells with slender multi-whorled protoconchs in contrast to the short bulbous protoconch of this species. In addition, *D. raphanula* may be separated from this species by its more irregular axial ribs, which sometimes fade below the subsutural band. *Terebra nitida* has more widely spaced ribs than this species.

The name is derived from the Latin *paucus,* meaning "few," and *incise,* meaning "cut into."

Terebra ***albocancellata*** Bratcher, sp. nov.

(Figures 1, 9)

Diagnosis: A slender, dull-white Indo-Pacific *Terebra* with cancellate sculpture, small for the genus, maximum length 18.8 mm.


1
2
3
4
5
6
7
8
9
10

Description: A slender, small *Terebra* with teleoconch of 12 whorls; protoconch of 3.5 conical whorls; outline of whorls straight; subsutural band defined by groove cutting through riblets; axial riblets fine, narrow, numerous, slanting to right on subsutural band, curving to left on remainder of whorl, 34 on penultimate whorl; spiral threads, 5 on penultimate whorl, crossing riblets to form cancellate sculpture with small pustules forming at intersections; body whorl with cancellate sculpture continuing to siphonal fasciole; aperture semi-elongate; columella with heavy parietal callus; color dull white.

Dimensions: Holotype 18.8 × 3.4 mm; paratypes from 14.8 × 3.4 mm to 15.0 × 3.8 mm.

Type locality: Plateau Chesterfield-Bellona Chalcal, Coral Sea, 36°42′S, 158°59′E.

Type material: Holotype and 1 paratype MNHNP; 1 paratype Bratcher coll.

Distribution: Chesterfield Islands, Coral Sea (between New Caledonia and Queensland, Australia).

Discussion: Three specimens were dredged from two localities in the Chesterfield Islands. These show almost no variation. There is no other small white cancellate Indo-Pacific species with which this could be confused. An immature specimen of *Terebra conspersa* Hinds, 1844, bears a slight superficial resemblance, but does not have the spiral grooves crossing the axial ribs, and it does not have a parietal callus. Also *T. conspersa* is a warm beige with a few tiny brown dots and with a brownish stain anterior to the periphery of the body whorl in contrast to the white of *T. albocancellata.*

The name for this species is from the Latin *albus,* meaning "white," and *cancellatus,* meaning "lattice-like."

Terebra ***macleani*** Bratcher, sp. nov.

(Figures 3, 10)

Diagnosis: A moderately small *Terebra* with no subsutural band and sculpture of axial striae only.

Description: Shell of medium size for the genus (maximum length 22.8 mm) with no subsutural band and sculpture of axial striae only.

Description: Shell of moderate size for the genus with 9 dull-surfaced whorls of teleoconch; protoconch of 1.5 large mamillate pale amber whorls. Outline of whorls slightly convex; suture well marked; no subsutural band; axial sculpture of very fine crowded striae running from suture to suture; no spiral sculpture; body whorl elongate with axial striae unbroken from suture to siphonal fasciole; aperture quadrate; columella almost straight; operculum yellowish amber; color dull amber.

Dimensions: Holotype 22.8 × 5.1 mm; paratype 21.9 × 5.2 mm.

Type locality: E. Cape of East London, South Africa, 33°04.9′S, 27°54.0′E, muddy sand with lumps of black mud.

Type material: Holotype NM D473/3687; 1 paratype NM D4809/T3688.

Distribution: This species is known only from the type locality.

Discussion: Compared to this species, *Terebra albida* Gray, 1834, has a more inflated body whorl and a very weakly indicated subsutural groove. Also, the range appears to be confined to Victoria and Western Australia.

This species is named in honor of Dr. James McLean for his contributions to malacology.

Hastula ***alboflava*** Bratcher, sp. nov.

(Figures 2, 5)

Diagnosis: A yellow *Hastula* of moderate size for the genus (maximum length 27.3 mm) with a white subsutural band marked by color rather than sculpture and with ribs below the suture fading anteriorly.

Description: Shell of moderate size for the genus with 13 shiny whorls of teleoconch; protoconch of 1.25 bulbous whorls; outline of whorls straight; subsutural band defined only by a white band, no subsutural groove or punctations; axial ribs about equal to interspaces, running from suture to suture on early whorls, fading anteriorly on later whorls; no spiral sculpture; body whorl with ribs becoming obsolete below white subsutural band; aperture elongate; siphonal fasciole exceptionally large for size of shell; color golden yellow with white band below suture.

←

Explanation of Figures 1 to 10

Figure 1. *Terebra* ***albocancellata*** sp. nov., holotype, 18.8 × 3.4 mm.

Figure 2. *Hastula* ***alboflava,*** holotype, 24.8 × 4.9 mm.

Figure 3. *Terebra* ***macleani,*** holotype 22.8 × 5.1 mm.

Figure 4. *Terebra* ***paucincisa,*** holotype 19.9 × 4.0 mm.

Figure 5. Same shell as Figure 2, close-up of middle whorls.

Figure 6. Same shell as Figure 8, close-up of middle whorls.

Figure 7. *Hastula* ***colorata,*** holotype, 14.9 × 4.3 mm.

Figure 8. *Terebra* ***rancheria,*** holotype, 16.9 × 4.0 mm.

Figure 9. Same shell as Figure 1, close-up of middle whorls.

Figure 10. Same shell as Figure 3, close-up of middle whorls.

Dimensions: Holotype 24.8 × 4.9 mm; Paratypes from 16.3 × 3.4 mm to 27.3 × 5.4 mm.

Type locality: Off Sogod, Cebu, Philippine Islands, 15.5 m.

Type material: Holotype LACM 2262; paratypes AMNH 222588 (1); AMS C15235 (1); ANSP (1); BM(NH) 1986261 (1); CAS (1); MCZ 196166 (1); MORG 24.809 (1); NM 758/13690 (1); MNHNP (1); SDMNH 92523 (1); USNM 859149 (1); Bratcher coll. (4); Cernohorsky coll. (1); Dayrit coll. (41); Marquet coll. (1).

Distribution: Cebu, Philippine Islands.

Discussion: This species bears a resemblance to *Hastula albula* (Menke, 1843), which has a protoconch of 4.5 often blackish-purple conical whorls. The protoconch of *H.* ***alboflava*** has 1.25 bulbous whorls. *Hastula albula* is variable in color, usually in the same lot, while all 59 examined specimens of *H.* ***alboflava*** are golden yellow with a white subsutural band. Except for minimal differences in size, there is almost no intraspecific variation in the specimens examined.

The name of this species is from the Latin *albus,* meaning "white," and *flavus,* meaning "golden yellow," the colors of the shell.

Hastula ***colorata*** Bratcher, sp. nov.

(Figure 7)

Diagnosis: A shiny, small, bright pastel or white *Hastula* with no visible sculpture.

Description: Shell with glassy shine, 9 whorls in teleoconch; protoconch of 1.25 short bulbous, bright pink whorls, larger than following whorls; outline of whorls straight; no subsutural band or groove; no axial sculpture except for faint striae under extreme magnification; no spiral sculpture; body whorl with no sculpture; aperture quadrate; columella straight; color bright pink.

Dimensions: Holotype 14.9 × 4.3 mm; paratypes from 11.1 × 2.9 mm to 19.6 × 4.6 mm.

Type locality: Light House Beach, Augusta, Western Australia, 34°20′S, 115°10′E, beach.

Type material: Holotype WAM 514-86 (pink); paratypes AMNH 222984 (1 light pink); AMS C153006 (1 white); ANSP (1 lavender); BM(NH) 1986283 (1 pink); CAS (1 white); LACM 2263 (1 pink); MCZ 296167 (1 pale pink); MORG 24.810 (1 pale lavender); NM K175/T3689 (1 pale pink); SDMNH 92524 (1 light peach); USNM 859218 (1 purple); Anson coll. (2); Bratcher coll. (4); Buick coll. (1); Cernohorsky coll. (1); Marrow coll. (4).

Distribution: Southwest Australia.

Discussion: This is the only *Hastula* species that has been found in so many clear pastel colors: white, yellow, peach, rose lavender, and purple, all monochromatic. All 14 type specimens and many others examined in museums were beach specimens. As far as is known, no one has collected a live specimen.

This species differs from *Terebra albida* by being shiny, smaller, more slender, and by lacking the inflated body whorl. It also lacks the indication of a subsutural band found on *H. albida. Hastula* **colorata** does not resemble juvenile *H. albida* (W. Anson, personal communication).

The name is from the Latin *coloratus,* meaning "color or tinge," because of the many colors in which the species is found.

ACKNOWLEDGMENTS

I am greatly indebted to Wendy Anson, Donald Dan, Fernando Dayrit, Brian Parkinson, Carol and Paul Skoglund, and Thora Whitehead for the contribution of paratypes. I thank Dr. Philippe Bouchet, Museum National d'Histoire Naturelle, Paris, Dr. Richard Kilburn, Natal Museum, Ian Loch, Australian Museum, and Dr. Fred Wells, Western Australian Museum, for the loan of material from their institutions. Also for the loan of material for study I thank W. Buick and Max Marrow of Australia, Robert Koch of Arizona, and Jose Marquet of Belgium. I add my appreciation to Dr. James McLean for the critical reading of the manuscript.

LITERATURE CITED

Bratcher, T. & W. Cernohorsky. 1986. Living terebras of the world. American Malacologists, Inc.: Melbourne, Florida. 24 pp., 74 pls.

Campbell, G. B. 1964. New terebrid species from the eastern Pacific (Mollusca: Gastropoda). Veliger 5(3):101–103.

Gray, J. E. 1834. Enumeration of the species of the genus *Terebra.* Proc. Zool. Soc. Lond. Pt. 2:59–63.

Hinds, R. B. 1844. Description of new shells, collected during the voyage of the Sulphur, and in Mr. Cuming's late visit to the Philippines. Proc. Zool. Soc. Lond. (1843) Pt. 11: 149–168.

Lamarck, J. B. P. A. de M. 1822. Histoire naturelle des animaux sans vèrtebres. Mollusques. Paris. 7:1–711 (*Terebra,* pp. 283–291).

Menke, C. T. 1843. Molluscorum Novae Hollandiae. A. Hahn: Hanover. 46 pp.

The Veliger 30(4):417-420 (April 1, 1988)

THE VELIGER

Assignment to Genus *Naesiotus* (Albers, 1850) of Several Species Formerly Assigned to *Rabdotus* (Albers, 1850) (Gastropoda: Pulmonata: Bulimulidae)

by

JAMES E. HOFFMAN

Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

Abstract. The following species formerly assigned to *Rabdotus* are assigned to the genus *Naesiotus* on the basis of anatomical and conchological evidence: *Rabdotus nigromontanus* (Dall, 1897); *R. christenseni* Miller & Reeder, 1984; *R. milleri* Hoffman, 1987, of southern Arizona and Sonora, Mexico; and *R. pallidior* (Sowerby, 1833); *R. rimatus* (Pfeiffer, 1846); *R. excelsus* (Gould, 1853); *R. xantusi* (Binney, 1861); *R. spirifer* (Gabb, 1868); *R. gabbi* (Crosse and Fischer, 1872); *R. beldingi* (Cooper, 1892); *R. altus* (Dall, 1893); *R. montezuma* (Dall, 1893); *R. veseyianus* (Dall, 1893); *R. cosmicus* (Mabille, 1895); *R. dentifer* (Mabille, 1895); *R. ceralboensis* (Hanna, 1923); *R. chamberlini* (Hanna, 1923); *R. hannai* (Pilsbry, 1927); *R. gigantensis* Christensen & Miller, 1977; and *R. laevapex* Christensen & Miller, 1977, from Baja California, Mexico.

While working on the zoogeography and interrelationships of several land snail species that had been placed in the genus *Rabdotus* Albers, 1850, I found that some of them more closely matched the diagnosis of *Naesiotus* Albers, 1850, according to BREURE (1979). These species were from southern Arizona, and from Sonora and Sinaloa, Mexico. I also found that a number of species from Baja California, Mexico, seemed, from drawings of their reproductive anatomy (CHRISTENSEN, 1978), to be in the genus *Naesiotus*.

The diagnostic points of difference between *Rabdotus* and *Naesiotus* lie in the reproductive anatomy and embryonic whorls of the shell. In the reproductive tract of *Rabdotus,* the vagina and penis are typically short (Figure 1), the glandular part of the penis consists largely of "pouches" (BREURE, 1979), and the spermathecal duct becomes broad midway along its length and has ridges within its lumen (CHRISTENSEN, 1978; Hoffman, unpublished data). In the reproductive tract of *Naesiotus,* the vagina and penis are typically longer (Figure 1), the glandular portion of the penis consists largely of tubules, and the spermathecal duct is uniformly narrow and cylindrical, lacking internal ridges (HOFFMAN, 1987; BREURE, 1979; BREURE & COPPOIS, 1978; CHRISTENSEN, 1978). The embryonic whorls of the shells of both genera have axial riblets, but the embryonic whorls of *Naesiotus* have very fine spiral threads in the interstices between the riblets, while *Rabdotus* lacks them (BREURE, 1979; BREURE & COPPOIS, 1978) (Figure 2).

While trying to deduce the relationships and geographical source of a complex of snails including *Rabdotus nigromontanus* (Dall, 1897), *R. christenseni* Miller & Reeder, 1984, and *R. milleri* Hoffman, 1987, I concluded that they had all of the characteristics of *Naesiotus*. By comparing reproductive anatomies and apical sculptures of other bulimulid snails that occur in northern Mexico and the southwestern United States, I found that all, with the exception of some of those in Baja California, were of the *Rabdotus* type. Within Baja California, snails listed by CHRISTENSEN (1978) as subgenus *Leptobyrsus* have, in the cases when they were obtainable, reproductive anatomies typical of *Naesiotus*. In most cases the embryonic sculptures also contained the spiral threads (Table 1). I, therefore, place the three species mentioned above as well as those in Table 1 in the genus *Naesiotus*. I was unable to obtain either the reproductive anatomy or shells of *R. ceralboensis* (Hanna, 1923); *R. chamberlini* (Hanna, 1923) lacks all shell sculp-

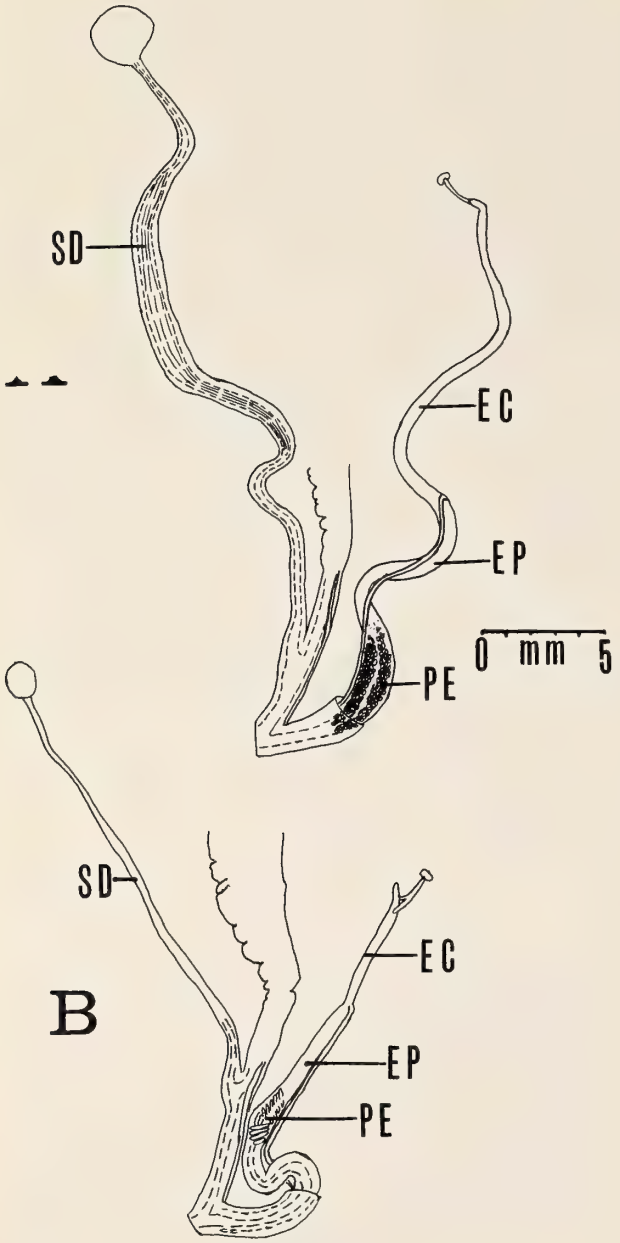


Figure 1

A. Genitalia of *Rabdotus baileyi* (Dall, 1893), J. E. Hoffman Collection No. 54A. B. Genitalia of *Naesiotus nigromontanus,* J. E. Hoffman Collection No. 52A: EC, epiphallic cecum; EP, epiphallus; PE, penis; SD, spermathecal duct.

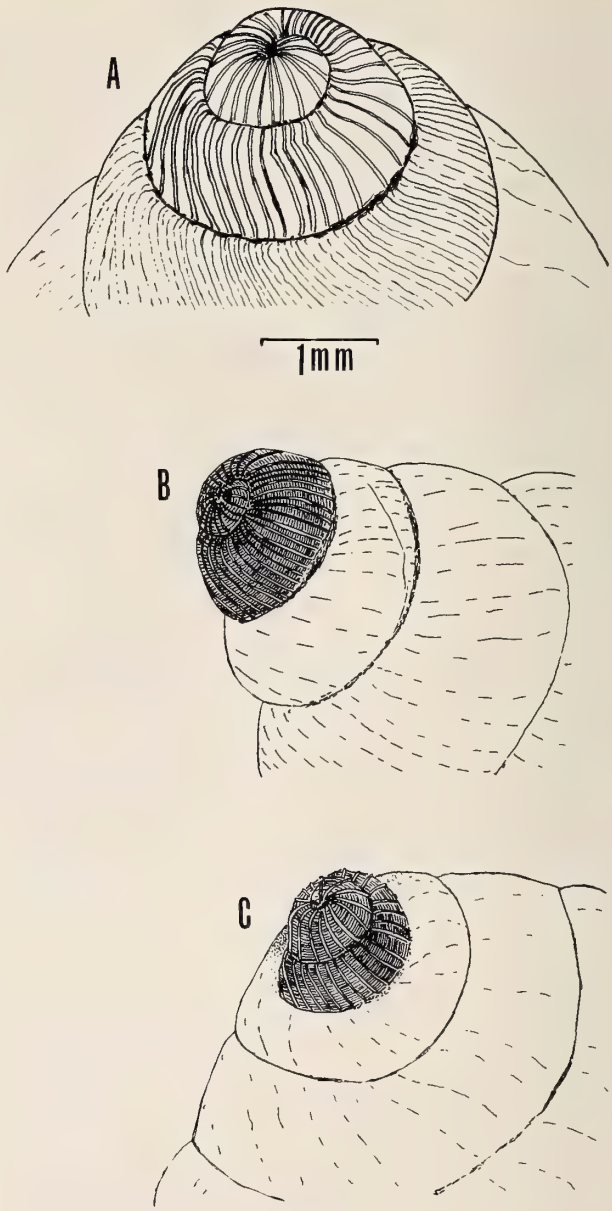


Figure 2

A. Apex of the shell of *Rabdotus baileyi* from Sonora, Mexico, J. E. Hoffman Collection No. 10. B. Apex of the shell of *Naesiotus christenseni* from Arizona, W. B. Miller Collection No. 7216. C. Apex of the shell of *Naesiotus tanneri* from Isla. Sta. Cruz, Ecuador, J. E. Hoffman Collection No. 250.

ture, and its reproductive anatomy was also unavailable. However, because of traits that the latter two species have in common with other snails that Christensen placed in *Leptobyrsus,* I tentatively place them in *Naesiotus.* Species listed by CHRISTENSEN (1978) as belonging to subgenera *Plicolumna* and *Rabdotus s.s.,* on the other hand, have typical *Rabdotus* characteristics.

Previously, *Naesiotus* was thought to be limited to South America, with its northern limit in Ecuador. These changes in assignment, of course, greatly increase the range of *Naesiotus* and indicate that the genus has a disjunct dis-

Figure 3

Proposed distribution of the genus *Naesiotus*.

tribution (Figure 3). Disjunct distributions are not rare, either among the Bulimulidae or land snails in general. In fact the "new" distribution of *Naesiotus* almost matches the disjunct distribution of *Bulimulus* Leach, 1815, a closely related genus, as well as that of the two subfamilies of Helminthoglyptidae: the Helminthoglyptinae of western North America and the Epiphragmaphorinae of western South America. Possible explanations for this disjunct pattern might be that snails near the center of a large range have died out, or plate tectonics may have been involved. The alternative possibility of convergent evolution seems unlikely because of the diverse nature of the traits involved.

Table 1

Reproductive traits and embryonic sculpture in Baja California snails assigned to the genus *Naesiotus*.

Species	Embryonic Sculpture riblets	threads	*Naesiotus* type repro. anatomy
gigantensis Christensen & Miller, 1977	yes	yes	not available
dentifer (Mabille, 1895)	yes	yes	not available
gabbi (Crosse & Fischer, 1872)	yes	yes	yes
hannai (Pilsbry, 1927)	yes	yes	yes
spirifer (Gabb, 1868)	shell unavail.		yes
rimatus (Pfeiffer, 1846)	yes	yes	yes
veseyianus (Dall, 1893)	shell unavail.		yes
excelsus (Gould, 1853)	yes	no*	yes
pallidior (Sowerby, 1833)	yes	yes	yes
harribaueri (Jacobson, 1958)	yes	no	yes
cosmicus (Mabille, 1895)	yes	yes	yes
montezuma (Dall, 1893)	yes	no	yes
beldingi (Cooper, 1892)	yes	yes	yes
altus (Dall, 1893)	shell unavail.		probably
laevapex Christensen & Miller, 1977	no	no	yes
xantusi (Binney, 1861)	yes	yes	yes

* Threads may have been missed owing to very weak embryonic sculpture in this species.

ACKNOWLEDGMENTS

I am deeply indebted to Walter B. Miller for the loan for his specimens, especially those from Baja California, Mexico, and for much helpful discussion and advice. In addition, I wish to thank Robert Van Syoc and the California Academy of Sciences for the loan of specimens of *Naesiotus* from the Galápagos Islands.

LITERATURE CITED

Breure, A. S. H. 1979. Systematics, phylogeny and zoogeography of Bulimulinae (Mollusca). Zool. Verh. Leiden 168: 1–215.

Breure, A. S. H. & G. Coppois. 1978. Notes on the genus *Naesiotus* Albers, 1850 (Mollusca, Gastropoda, Bulimulidae). Neth. Jour. Zool. 28(2):161–192.

Christensen, C. C. 1978. A revision of the genus *Rabdotus* (Pulmonata: Bulimulidae) in Baja California, Mexico. Ph.D. Dissertation, E9791, Univ. of Arizona, Tucson, Arizona. i–xiv + 354 pp.

Hoffman, J. E. 1987. A new species of *Rabdotus* (Gastropoda: Pulmonata: Bulimulidae) from Sonora, with a description of the reproductive anatomy of *Rabdotus nigromontanus*. Veliger 29:419–423.

Miller, W. B. & R. L. Reeder. 1984. A new species of *Rabdotus* (Gastropoda: Pulmonata: Bulimulidae) from Arizona. Bull. S. Calif. Acad. Sci. 83(2):106–109.

The Veliger 30(4):421–426 (April 1, 1988)

THE VELIGER

NOTES, INFORMATION & NEWS

Mexichromis tura: Range Extension of a Rarely Observed Nudibranch

by
Alex Kerstitch
10700 E. Calle Vaqueros,
Tucson, Arizona 85749, U.S.A.
and
Hans Bertsch
Biological Sciences, National University,
8 Executive Circle,
Irvine, California 92714, U.S.A.

Only nine specimens of the Chromodorididae species *Mexichromis tura* (Marcus & Marcus, 1967) have been recorded. The holotype specimen was collected at Deale Beach, Ft. Kobbe Beach, Panama (8°48′N, 79°55′W). BERTSCH *et al.* (1973) reported four specimens from Sayulita, Nayarit, Mexico (21°15′N, 105°15′W). BERTSCH (1978) cited three specimens from La Cruz, Nayarit (21°30′N, 105°16′W) and one specimen from La Paz, Baja California Sur (24°11′N, 110°23′W).

Because of the apparent rarity of this species in collections, our greater than 400 km northward range extension is noteworthy. On 24 June 1987, four specimens (one measuring 12 mm long) of *Mexichromis tura* were observed by A. Kerstitch at Bahía San Carlos, Sonora, Mexico (27°55′N, 111°04′W), in 20 m depth. These specimens represent the first collection of this species in the eastern and central Gulf of California and from the shores of Sonora.

Figure 1

Mexichromis tura collected at San Carlos; photo by Alex Kerstitch.

The mantle margin of the animal illustrated (Figure 1) was rimmed with three encircling bands: an outermost yellow, a middle black, and an innermost powder blue. The black dorsum had numerous yellow spots; the periphery of the dorsum had larger, whitish streaks and splashes. The gills were white, with black tips. The rhinophores were completely black.

Literature Cited

BERTSCH, H. 1978. The Chromodoridinae nudibranchs from the Pacific coast of America.—Part III. The genera *Chromolaichma* and *Mexichromis*. Veliger 21(1):70–86.

BERTSCH, H., A. J. FERREIRA, W. M. FARMER & T. L. HAYES. 1973. The genera *Chromodoris* and *Felimida* (Nudibranchia: Chromodorididae) in tropical west America: distributional data, description of a new species, and scanning electron microscopic studies of radulae. Veliger 15(4):287–294.

MARCUS, EV. DU BOIS-REYMOND & ER. MARCUS. 1967. American opisthobranch mollusks. Stud. Trop. Ocean. (Univ. Miami Inst. Mar. Sci., Miami, Florida), No. 6:viii + 256 pp.

New Record of the Coral Clam *Coralliophaga coralliophaga* (Gmelin, 1791) (Bivalvia: Trapezidae) in the Mediterranean Sea

by
Carmen Salas
Dept. Zoología, Facultad de Ciencias,
Universidad de Málaga, 29071-Málaga, Spain
Agustín Barrajon
C/Nuzas, Bl. 7-5°-A, 29010-Málaga, Spain
and
Francisco Carpena
C/Nuzas, Bl. 7-6°A, 29010-Málaga, Spain

The family Trapezidae Lamy, 1920, contains three living genera, species of which live on coral bottoms: *Trapezium* Mühlfeld, 1811, distributed along Madagascar, the Indo-Pacific and Japan; *Coralliophaga* Blainville, 1824, which is present in the Mediterranean, Atlantic and Indo-Pacific; and *Isorropodon* Sturany, 1854, from the deep sea in the eastern Mediterranean (FRANC, 1960).

Up to now, only two species of this family have been recorded in the Mediterranean (PIANI, 1980): *Coralliophaga lithophagella* (Lamarck, 1819), a species with a wide geographical distribution—Atlantic (Britain to Senegal and the Azores) and Mediterranean (NORDSIECK, 1969)—and *Isorropodon perplexum* (Lamarck, 1819), the only species

in this genus, found at 2420 m depth, off Alexandria (Egypt) (KEEN, 1969).

During 1984 and 1985, the Spanish Institute of Oceanography (I.E.O.) carried out several expeditions to study the biocoenoses of the red coral bottoms in the Alboran Sea, between about 50 and 200 m. Within the bivalve taxocoenoses from the expeditions of 1984, only *Coralliophaga lithophagella* was collected (SALAS & SIERRA, 1986). However in March 1985, we found one specimen of *C. coralliophaga* (Gmelin, 1791) inside red coral stones from around Alboran Island (35°54'–35°52'N, 3°09'–3°05'W), which had some remains of the red coral *Corallium rubrum* (Linnaeus, 1758). This specimen was collected dead; a small drill hole was present in the valve. We were able to confirm the identification by comparing it with three lots of *Coralliophaga coralliophaga* from the National Museum of Natural History (NMNH), Smithsonian Institution (Washington).

According to ABBOTT (1974), *Coralliophaga coralliophaga* occurs in America from North Carolina to Texas and in the West Indies, Bermuda, and Brazil. The lots in the NMNH are from the Indo-Pacific area—Caroline Islands (USNM 634489; USNM 634506), Gilbert Islands (USNM 608983), Red Sea (USNM 608869)—and Japan (USNM 345022). They have always been found in coral reefs.

MORRIS (1984) does not note this species in the Red Sea, listing only two species of *Trapezium*: *T. oblongum* (Linnaeus, 1758) and *T. bicarinatum* (Schumacher, 1817).

Coralliophaga coralliophaga is elongate, with the umbones at the anterior end. The shell is yellowish white and finely sculptured, with radial threads and concentric lamellations at the posterior end. This is an uncommon species, which lives in the burrows of other rock-boring mollusks. It ranges in size from about 1 to 5 cm (ABBOTT, 1974). The hinge of this species has two parallel, slender cardinals and one posterior lateral in each valve. The two muscle scars are unequal, with the posterior being larger and more elongate. There is a large pallial line, and a small pallial sinus.

In our 7-mm long shell, the lateral teeth are very weak, like a lateral ridge, and radial sculpture is absent.

Coralliophaga lithophagella differs from *C. coralliophaga* by: (a) the outline of the shell, which in the former is higher, trapezoidal, and without radial sculpture; (b) the hinge, which bears the two cardinal teeth (in each valve) which are larger and divergent (there are no lateral teeth); and (c) the pallial sinus is less deep and it is posteriorly closed by the pallial line.

Acknowledgments

We express our appreciation to the Spanish Institute of Oceanography (I.E.O.) and to Dr. J. Templado for sending us the bivalve material from the Red-Coral Expeditions in the Alboran Sea. Also, we are grateful to Miss Diane Bohmhauer, Museum Specialist (Mollusks) of the Smithsonian Institution (NMNH), for sending us the lots of *Coralliophaga coralliophaga* and indicating the geographic distribution of the Smithsonian collections of this species.

Literature Cited

ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold Co.: New York. 663 pp., 24 color pls.

FRANC, A. 1960. Classe des Bivalves. Pp. 1845–2164. *In:* P. P. Grasse, Traité de zoologie, T.V (II). Ed. Masson & Cie. 2164 pp.

KEEN, M. A. 1969. Family Trapeziidae, Lamy 1920. Pp. N655–N657, fig. E132. *In:* R. C. Moore (ed.), Treatise on invertebrate paleontology, L. C. Cox *et al.*, Part N (Bivalvia) 2: 491–952. Geol. Soc. Amer. & Univ. Kansas: Lawrence, Kansas.

MORRIS, S. 1984. Bivalves. Pls. 38–49. *In:* D. Sharabati (ed.), Red Sea shells. KPI Limited Routletge & Kegan Paul Plc: London.

NORDSIECK, F. 1969. Die europäischen Meeresmascheln (Bivalvia) von Eismeer bis Kapverden Mittelmeer und Schwarzes Meer. Gustav Fischer Verlag Ed.: Stuttgart. 256 pp.; 25 pls.

PIANI, P. 1980. Catalogo dei Molluschi Conchiferi viventi nel Mediterraneo. Boll. Malacol., Milano 16(5/6):113–224.

SALAS, C. & A. SIERRA. 1986. Contribution to the knowledge of the molluscs bivalves from the red coral bottoms of the Alboran Island (Spain). Iberus 6(II):189–200; 1 pl.

Harpidae Bronn, 1849 (Gastropoda): Conserved by ICZN

by

William K. Emerson
Department of Invertebrates,
American Museum of Natural History,
New York, New York 10024, U.S.A.
and
Roger N. Hughes
School of Animal Biology,
University College of North Wales,
Bangor, Gwynedd LL57 2 UW, U.K.

In a recent paper on the anatomy and taxonomy of the gastropod genera *Harpa* and *Morum*, we (HUGHES & EMERSON, 1987:357) accepted RAVEN's (1985) proposal to use Harpaidae as an emended name to replace Harpidae Bronn, 1849 (type genus *Harpa* Röding, 1798), not Harpidae Hawle & Corda, 1847 (type genus *Harpes* Goldfuss, 1839, in Trilobita). We noted that final acceptance of the emended name Harpaidae would have to await action by the International Commission on Zoological Nomenclature to remove the homonymy. Subsequently, the Commission (ICZN, 1987) ruled by order of Opinion 1436 to place on the Official List of Family-Group Names in Zoology the names Harpidae Bronn, 1849, type genus *Harpa* Röding, 1798 (Gastropoda) and Harpetidae Hawle & Corda, 1847 (an emendation under the plenary powers of "Harpides"), type genus *Harpes* Goldfuss, 1839 (Trilobita). As a result of this action, the familial name Harpidae is available in its accustomed sense in the Neogastropoda and the emended names Harpaidae and Harpainae are now superfluous.

Literature Cited

Bronn, H. G. 1849. Handbuch der Geschichte der Natur, 3(3) Index Palaeontologicus. Stuttgart. 980 pp.

Goldfuss, G. A. 1839. Beiträge zur Petrefactenkunde. Nova Acta Acad. Caes. Leop. Carol. 19(1):358–359.

Hawle, I. & A. J. C. Corda. 1847. Prodrom einer Monographie der Böhmischen Trilobiten. K. Böhm. Gesell. Wiss. (Prague), (Abhandl.) 5:1–176.

Hughes, R. N. & W. K. Emerson. 1987. Anatomical and taxonomic characters of *Harpa* and *Morum* (Neogastropoda: Harpaidae). Veliger 29(4):349–358.

ICZN. 1987. Opinion 1436, Harpidae Hawle & Corda, 1847 (Trilobita) and Harpidae Bronn, 1849 (Mollusca, Gastropoda): a ruling to remove the homonymy. Bull. Zool. Nom. 44(2):137–138.

Raven, J. G. M. 1985. Homonymy in the families Harpidae Hawle & Corda, 1847 (Trilobita) and Harpidae Bronn, 1849 (Mollusca, Gastropoda). Z.N.(S.)2331. Bull. Zool. Nom. 42(1):79–80.

Röding, P. F. 1798. Museum Boltenianum, part 2. Hamburg. viii + 199 pp.

A Note on Unjustified Emendations

by

Rüdiger Bieler

Smithsonian Marine Station at Link Port,

5612 Old Dixie Highway,

Fort Pierce, Florida 34946, U.S.A.

There seems to be some misunderstanding in recent literature about the status of the "Appendix D: Recommendations on the Formation of Names" in the International Code of Zoological Nomenclature. These recommendations are appended to the rules, and are "provided as a guide to good usage in nomenclature. They do not have the force of rules" (ICZN, 1964:93; ICZN, 1985:181; see also p. 1 in either edition). They are meant to serve as guidelines for the original describer of a taxon, and, among other things, they suggest that the prefix "mac" be used instead of "Mac," "Mc," or "M," when a zoological name is formed (ICZN, 1985:197).

The following are three examples of instances in which authors use this recommendation while citing "the rules" to emend such names.

Ortiz-Corps (1983) listed *Petaloconchus erectus macgintyi* Olsson & Harbison, 1953, and stated (1983:56): "I am modifying *mcgintyi* to *macgintyi* to conform it to the rules of Zoological Nomenclature."

Clarke (1986:92) stated "ICZN Rules require that *Elliptio mcmichaeli,* as originally proposed [by Clench & Turner, 1956], should be emended to *Elliptio macmichaeli.*"

Another name change by Ortiz-Corps (1983:170) is a little more complicated. He emended the original spelling of *Atys m'andrewii* E. A. Smith, 1872, to *Atys macandrewii,* "to conform it to the International Code of Zoological Nomenclature (Article 27, p. 29; p. 109)" (Ortiz-Corps, 1983:171). The references given by Ortiz-Corps refer to the then valid second edition of the Code (ICZN, 1964), specifically to Article 27 ("no diacritic mark, apostrophe, or diaeresis is to be used . . .") and to the recommendations concerning prefixes as described above. In both the old (2nd) and new (3rd) editions of the Code, there are provisions to emend original spellings that contain diacritic marks, apostrophes, diaereses, or hyphens (ICZN, 1964: Art. 32(c)(i); ICZN, 1985:Art. 32(d)(i)). However, the text in that article reads "A name published with . . . apostrophe is to be corrected . . . by the deletion of the mark concerned and by uniting any resulting parts." Therefore, *Atys mandrewii* is the required, justified emendation of *A. m'andrewii*; Ortiz-Corps' *Atys macandrewii* is not.

Unfortunately such unjustified emendations cannot be ignored by subsequent authors, since they are available names according to the Code: ". . . the name thus emended is available with its own author and date and is a junior objective synonym of the name in its original spelling; it enters into homonymy and can be used as a replacement name" (ICZN, 1985:Art. 33b(iii)).

Thus, careless emendations can produce "instant synonyms" that have to be carried through subsequent literature. Although not intended by the authors in the abovementioned cases, these actions could have resulted in the introduction of three invalid, but available, new nominal taxa, *Petaloconchus erectus macgintyi* Ortiz-Corps, 1983, *Atys macandrewii* Ortiz-Corps, 1983, and *Elliptio macmichaeli* Clarke, 1986! I write "could have resulted," because there is a further complicating factor that warrants individual checking of each case. Although the act of emendation was stressed by each author, they were not necessarily the first to take that action. *Atys m'andrewii,* for instance, was changed to *macandrewi* (sic) at least twice before, by von Martens (1872:140) and by Odhner (1931:24) (the use of the suffix -i for -ii has no nomenclatural bearing and is to be treated as an incorrect subsequent spelling, even if the change was deliberate; ICZN, 1985: Art. 33(d)).

Such emendations are not merely *not* required by the Code—they are unjustified, cause confusion, and burden the literature with junior synonyms.

Acknowledgments

I thank Paula M. Mikkelsen, Harbor Branch Oceanographic Institution, Fort Pierce, Richard E. Petit, North Myrtle Beach, and two anonymous reviewers for helpful comments on the manuscript.

Literature Cited

Clarke, A. H. 1986. *Elliptio judithae,* new species (Bivalvia, Unionidae) from the Neuse River, North Carolina. Malacology Data Net (Ecosearch Series) 1(4):78–96.

International Commission on Zoological Nomenclature (ICZN). 1964. International Code of Zoological Nomenclature. 2nd ed. London. xix (+i) + 176 pp.

International Commission on Zoological Nomenclature

(ICZN). 1985. International Code of Zoological Nomenclature. 3rd ed. London, Berkeley, and Los Angeles. xx + 338 pp.

ODHNER, N. H. 1931. Beiträge zur Malakozoologie der Kanarischen Inseln. Lamellibranchien, Cephalopoden, Gastropoden. Arkiv för Zoologi 23A(14):1–116, pls. 1–2.

ORTIZ-CORPS, E. 1983. An annotated checklist of the Recent marine Gastropoda (Mollusca) from Puerto Rico. Memorias del Quinto Simposio de la Fauna de Puerto Rico y el Caribe. Humacao, Puerto Rico. ii + 220 pp.

VON MARTENS, E. 1872. Mollusca. Zoological Record for 1872, 9:103–174.

Note on *Leaflets in Malacology*

by
Richard E. Petit
806 St. Charles Road, North Myrtle Beach,
South Carolina 29582, U.S.A.

Leaflets in Malacology was privately published by the late S. S. Berry, with 26 numbers issued between 1946 and 1969 (see HERTZ, 1984, *The Festivus* 15(Suppl.):1–42).

Among Berry's papers have been found copies of *Leaflets* No. 13, with an accompanying note in Berry's handwriting stating that "these are the suppressed first printing but can be used as work copies & rough reprints." This "suppressed" printing is dated 7 July 1956. The printing that received distribution is dated 9 July 1956.

The 7 July number, as printed, contained numerous errors and Berry evidently, and rightfully, felt that it should be reprinted. Comparison of the page proof of the first printing shows that the printer corrected most, but not all, of the errors.

Several dozen copies of this 7 July printing exist, most with corrections made thereon by Berry. Considering the state of Berry's effects during the last few years of his life, it is possible that copies of the 7 July printing were inadvertently distributed. Since we have it in Berry's own hand that the 7 July printing was suppressed, *Leaflets* No. 13 cannot be considered to have been published, in the sense of the *International Code of Zoological Nomenclature,* on 7 July, and the actual publication date is 9 July as shown on the revised printing.

Berry's note, the page proof, and all copies of the 7 July printing that have been located are now in the Santa Barbara Museum of Natural History.

International Commission on Zoological Nomenclature Official Lists and Indexes of Names and Works in Zoology

A revised and updated edition of the *Official Lists and Indexes of Names and Works in Zoology* has now been published. For the first time all the names and works on which the International Commission on Zoological Nomenclature has ruled since it was set up in 1895 are brought together in a single volume. Entries are arranged in four sections giving in alphabetical order the family-group names, generic names, specific names and titles of works which have been placed on the Official Lists or the Official Indexes. There are about 9900 entries of which 134 are for works. In addition, there is a full systematic index and a reference list to all relevant Opinions and Directions. The volume is 366 pages, size A4, casebound.

Copies can be ordered from:

The International Trust for Zoological Nomenclature, % British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K. Price £60 or $110 or

The American Association for Zoological Nomenclature, % NHB Stop 163, National Museum of Natural History, Washington DC 20560, U.S.A. Price $110 ($100 to members of A.A.Z.N.).

California Malacozoological Society

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed 6 January 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger.* Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); or Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C.M.S., Inc., are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, and devises are deductible for Federal estate and gift tax purposes under sections 2055, 2106, and 2522 of the Code. Upon request, the Treasurer of the C.M.S., Inc., will issue suitable receipts which may be used by donors to substantiate their tax deductions.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on 8 October 1987, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 31 of *The Veliger.* For affiliate members of the Society, the subscription rate for Volume 31 will be US$28.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will be US$56.00, also now with postage to domestic addresses included. An additional US$4.00 is required for

all subscriptions sent to foreign addresses, including Canada and Mexico.

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. There is a one-time membership fee of US$2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription.

Send all business correspondence, including subscription orders, membership applications, payments for them, and changes of address to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Page Charges

Although we would like to publish papers without charge, high costs of publication require that we ask authors to defray a portion of the cost of publishing their papers in *The Veliger.* We wish, however, to avoid possible financial handicap to younger contributors, or others without financial means, and to have charges fall most heavily on those who can best afford them. Therefore, the following voluntary charges have been adopted by the Executive Board of the California Malacozoological Society: $30 per *printed* page for authors with grant or institutional support and $10 per page for authors who must pay from personal funds (2.5 manuscript pages produce about 1 printed page). In addition to page charges, authors of papers containing an extraordinary number of tables and figures should expect to be billed for these excess tables and figures at cost. It should be noted that even at the highest rate of $30 per page the Society is subsidizing well over half of the publication cost of a paper. However, authors for whom the regular page charges would present a financial handicap should so state in a letter accompanying the original manuscript. The letter will be considered an application to the Society for a grant to cover necessary publication costs.

We emphasize that these are *voluntary* page charges and that they are unrelated to acceptance or rejection of manuscripts for *The Veliger.* Acceptance is entirely on the basis of merit of the manuscript, and charges are to be paid *after* publication of the manuscript, if at all. Because these contributions are voluntary, they may be considered by authors as tax deductible donations to the Society. Such contributions are necessary, however, for the continued good financial health of the Society, and thus the continued publication of *The Veliger.*

Reprints

While it was hoped at the "*birth*" of *The Veliger* that a modest number of reprints could be supplied to authors free of charge, this has not yet become possible. Reprints are supplied to authors at cost, and requests for reprints should be addressed directly to the authors concerned. The Society does not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

Patronage Groups

Since the inception of *The Veliger* in 1958, many generous people, organizations, and institutions have given our journal substantial support in the form of monetary donations, either to *The Veliger* Endowment Fund, *The Veliger* Operating Fund, or to be used at our discretion. This help has been instrumental in maintaining the high quality of the journal, especially in view of the rapidly rising costs of production.

At a recent Executive Board Meeting, we felt we should find a way to give much-deserved recognition to those past and future donors who so evidently have our best interests at heart. At the same time, we wish to broaden the basis of financial support for *The Veliger,* and thus to serve our purpose of fostering malacological research and publication. Accordingly, it was decided to publicly honor our friends and donors. Henceforth, donors of $1000.00 or more will automatically become known as **Patrons** of *The Veliger,* donors of $500.00 or more will be known as **Sponsors** of *The Veliger,* and those giving $100.00 or more will become **Benefactors** of *The Veliger.* Lesser donations are also sincerely encouraged, and those donors will be known as **Friends** of *The Veliger.* To recognize continuing support from our benefactors, membership in a patronage category is cumulative, and donors will be listed at the highest applicable category. As a partial expression of our gratitude, the names only of donors in these different categories will be listed in a regular issue of the journal. Of course, we will honor the wishes of any donor who would like to remain anonymous. The Treasurer of the California Malacozoological Society will provide each donor of $10.00 or more with a receipt that may be used for tax purposes.

We thank all past and future donors for their truly helpful support and interest in the Society and *The Veliger.* Through that support, donors participate directly and importantly in producing a journal of high quality, one of which we all can be proud.

Notes to Prospective Authors

The increasing use of computers to prepare manuscript copy prompts the following notes. We request that the right margin of submitted papers be prepared "ragged," that is, *not* justified. Although right-justified margins on printed copy sometimes look "neater," the irregular spacing that results between words makes the reviewer's, editor's, and printer's tasks more difficult and subject to error. Similarly, the automatic hyphenation capability of many machines makes for additional editorial work and potential confusion; it is best not to hyphenate words at the end of a line. Above all, manuscripts should be printed with a

printer that yields unambiguous, high-quality copy. With some printers, especially some of the dot-matrix kinds, copy is generally difficult to read and, specifically, the letters "a, p, g, and q" are difficult to distinguish, especially when underlined as for scientific names; again, errors may result.

Other reminders are (1) that three copies of everything (figures, tables, and text) should be submitted to speed the review process, and (2) absolutely everything should be double-spaced, including tables, references, and figure legends.

Because *The Veliger* is an international journal, we occasionally receive inquiries as to whether papers in languages other than English are acceptable. Our policy is that manuscripts must be in English. In addition, authors whose first language is other than English should seek the assistance of a colleague who is fluent in English *before* submitting a manuscript.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date and not less than *six weeks* before our regular mailing dates. Send notification to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges:

change of address and re-mailing of a returned issue—$5.00.

Sale of C.M.S. Publications

All back *volumes* still in print, both paper-covered and cloth-bound, are available only through "The Shell Cabinet, 12991 Bristow Road, Nokesville, VA 22123. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Morgan Breeden at the above address.

Volumes 1 through 13, 24, 26, and 27 are out of print.

Supplements still available are: part 1 and part 2, supplement to Volume 3, and supplements to Volumes 7, 11, 14, 15, and 16; these can be purchased from "The Shell Cabinet" only. Copies of the supplement to Volume 17 ("Growth rates, depth preference and ecological succession of some sessile marine invertebrates in Monterey Harbor" by E. C. Haderlie) may be obtained by applying to Dr. E. C. Haderlie, U.S. Naval Post-Graduate School, Monterey, CA 93940.

Single copies of back issues of the *The Veliger* still in print are available *exclusively* from:

Conchylien Cabinet,
Grillparzerstrasse 22,
D-6200 Wiesbaden, BRD (West Germany).

Student Research Grant in Malacology

The Santa Barbara Shell Club has announced the availability of funds to support student research in malacology through the Sara T. DeLaney Scholarship.

The successful applicant must be a full-time student in a formal graduate degree program, and the thesis topic must be primarily focused on some aspect of eastern Pacific or west American malacology (including marine, freshwater, or terrestrial mollusks).

The following documents are required for each application: (1) A proposal, limited to three pages, that discusses the research project and details the work to be aided by this grant and its malacological significance; (2) A budget that outlines how these funds will be used; (3) A curriculum vita or resume; (4) A letter of recommendation from the applicant's thesis advisor; and (5) A list of grants and amounts that are currently being received or are anticipated to be received in the 1988–89 academic year.

A single research grant of up to $1000 is available. Funds are available for the purchase of research materials, usage fees (electron microscope and computer), and travel costs to museums or institutions having resources vital to the research topic.

Completed applications must be received no later than **1 June 1988.** Please send to:

Sara T. DeLaney Scholarship
Santa Barbara Shell Club
P.O. Box 30191
Santa Barbara, CA 93130.

For further information, contact Paul Scott (805) 682-4711.

The Veliger 30(4):427 (April 1, 1988)

THE VELIGER

BOOKS, PERIODICALS & PAMPHLETS

Two New Audio Cassettes Say It Right!

by R. Tucker Abbott. 1987. American Malacologists, P.O. Box 1192, Burlington, MA 01803. Stereo cassette, 35 min. Price: $7.90 plus $2.10 for shipping.

On *Say it right! How to pronounce the scientific names of Seashells of North America* R. Tucker Abbott pronounces the Latin, scientific names of 1250 species of mollusks from both coasts of North America. The list is from the index of the 1986 revised edition of Abbott's *Seashells of North America,* and also includes some names of authors, family names, and technical terms. The tape begins with the important note that there is no one "correct" pronunciation, only a "customary" one, and even this may vary from region to region.

If the tape encourages someone with a fear of scientific names to plunge ahead and use them, then it will have served a fine purpose. The format of a tape cassette, however, seems rather cumbersome and limited. I do not keep a cassette player handy and indeed had to listen to the tape in my car! Some assistance is provided for finding a particular name of interest by means of an index keyed to a tape counter.

Some seekers of information on customary pronunciation of scientific names will undoubtedly appreciate hearing someone actually pronounce the names in question (and Abbott's voice is a pleasant one). Others may prefer the visual, phonetic approach taken in the book *It's Easy to Say Crepidula* by J. M. Cate & S. Raskin reviewed in the July 1987 issue of *The Veliger.*

D. W. Phillips

Exploring Collectible Shells

by R. Tucker Abbott. 1987. American Malacologists, P.O. Box 1192, Burlington, MA 01803. 90-min cassette, and 64-pp paperback book. Total price for cassette and book: $12.95, postage included.

The tape is a 90-min commentary keyed, page by page, to the included book by Abbott, *Collectible Shells of the Southeastern U.S., Bahamas & Caribbean.* The book is a nicely produced, all-color guide to mollusks of Florida and the Caribbean, which includes in addition to the many plates of Recent mollusks some information on fossils and how to collect, clean, and store shells. The tape contains additional information on the habits and uses of the mollusks pictured.

D. W. Phillips

Marine Invertebrates of the Pacific Northwest

by Eugene N. Kozloff. 1987 (actually published 24 February 1988. University of Washington Press: Seattle, Wash. 520 pp. Price: $35.

This is a greatly expanded second edition of Kozloff's 1974 "Keys to the Marine Invertebrates of Puget Sound, the San Juan Archipelago, and Adjacent Regions." It is more than double in size, set in better type, printed on better paper, and has many more illustrations. It is designed as an identification manual and key to some of the more important taxonomic literature.

The Mollusca are covered on 112 pages (pp. 184–295) in four chapters with 188 illustrations, including many photographs. This is in contrast to the 55 pages and 21 line drawings of the first edition. Of course, only a relatively small proportion of the species keyed could be illustrated, even in the expanded book.

The quality of particular parts of the molluscan coverage depends on whether a specialist was found to help and whether relevant literature was located. Thus, Hochberg's treatment of the cephalopods, Marshall & Shimek's coverage of the scaphopods, and Shimek's work on the Turridae are especially good. The limpets show the advice of David Lindberg and the chitons that of the late Tony Ferreira. However, the Rissoidae/Rissoinidae show that Ponder's (1985) key paper has been missed.

The Mollusca seem relatively error free, though I spotted *Tellina "nucleoides"* instead of *T. nuculoides.*

Gene Coan

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

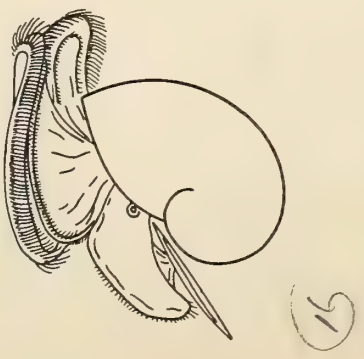
It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.



SMITHSONIAN INSTITUTION LIBRARIES