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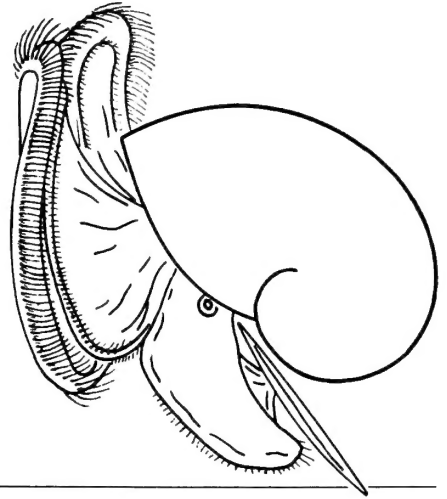
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THE VELIGER

A Quarterly published by
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R. Stohler, Founding Editor



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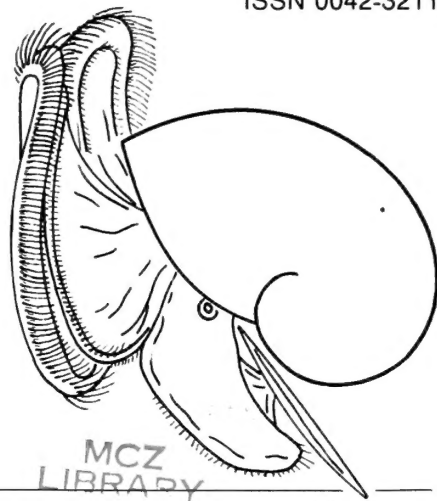
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THE VELIGER

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.

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

This issue of *The Veliger* is dedicated
to the memory and many contributions of
A. Myra Keen
(1905–1986)

A. Myra Keen (1905–1986)

IT IS MOST APPROPRIATE that we dedicate this issue of *The Veliger* to Dr. A. Myra Keen, a member of both the editorial and the executive boards of this journal for many years. This journal, now of international scope, has its roots in the fauna of the western United States and the eastern Pacific. Myra Keen's roots were similarly planted, though her own work came to have an impact throughout the malacological world.

A full-scale biography, together with a complete bibliography of her papers and books and a listing of her taxa, is slated to appear in volume 27, number 2, of *Malacologia*. We see little reason to repeat that material here, but we do want to call attention to what we believe to be her major accomplishments and attributes.

What many will remember about Dr. Keen is that she was highly skilled at making people feel appreciated. She was a master at it. To her, every person was to be treated with the greatest respect and patience. She gave individual attention to each person with whom she had contact—both in person and in her thorough, carefully phrased letters. Her valuable criticisms and suggestions often had to be searched for between the lines of understated conversation and text.

She had a strength of character and determination seldom matched. No matter what the job, from tasks of a magnitude that might have discouraged Sisyphus to routine correspondence from those who should have known better than to trouble her about trivia, her approach was the same—a serene resolve to do the best job possible with the tools at hand, and to do this day after day, month after month, until the job was done.

Perhaps longest remembered will be her major compilations, including the two editions of her book on the fauna of the tropical eastern Pacific, her checklists and keys, the catalogue of Californian Tertiary mollusks, and her treatments of various groups for the *Treatise on Invertebrate Paleontology*.

The role of synthesizer and compiler is not as popular now as it has been in the past. Professional acceptance and advancement now seem to demand specific contribu-

tions to knowledge using fashionable techniques. Yet, great compilations, such as those for which Myra Keen is deservedly famous, serve to advance science in many, sometimes unappreciated ways: (1) to make much information available to a diverse audience and to provide entree into more detailed literature; (2) to facilitate identification of material, both by those whose central interest is mollusks and by those whose chief interests lie elsewhere; (3) to pose an array of unresolved questions to catalyze investigation and to challenge potential contributors to knowledge, both professional and amateur; (4) to provide data for ecological and biogeographical analysis and comparison; and (5) to popularize scientific information, thereby helping to establish the constituency and public acceptance so essential in ensuring adequate funding and recognition for malacological institutions and researchers.

We must also recognize her major contributions to the knowledge of specific groups that set precedents for their time—the Vermetidae, Cardiidae, Veneridae, Muricidae, Juliidae, and the Typhinae. She had considerable patience and thoroughness in working out long-ignored nomenclatural problems, laying many such difficult questions to a final rest. Also significant were her several early papers on faunal analysis using statistical analysis and her series of papers on eastern Pacific type specimens in European museums.

Myra Keen touched the lives and influenced the work of so many of us in so many ways: her unwavering kindness and strength of character, her major compilations, and her contributions to our knowledge of certain groups. All of these ensure her an enduring place in the history of malacology.

Eugene Coan

Research Associate
Department of Invertebrate Zoology
California Academy of Sciences
Golden Gate Park
San Francisco, California 94118, U.S.A.

Sulfide-Oxidizing Symbiosis in Lucinaceans: Implications for Bivalve Evolution

by

R. G. B. REID AND D. G. BRAND

Department of Biology, University of Victoria, Victoria, British Columbia V8W 2Y2, Canada

Abstract. Symbiotic sulfide-oxidizing bacteria are present in the bivalve families Solemyidae, Lucinidae, Thyasiridae, Vesicomomyidae, and Mytilidae. In *Parvilucina tenuisculpta* the gills have extensive subfilamental tissues composed of storage epithelia and bacteriocytes housing bacteria and many granules of varied composition. Numerous bacteria are present in the gills of *Thyasira flexuosa*. In this species there is less cytological differentiation in the subfilamental tissue. It is proposed that a sulfide-oxidizing symbiosis was responsible for the emergence of the Lucinacea and associated with this symbiosis was a series of paedomorphic events involving gills, siphons, guts, and feeding and ventilatory behavior. The Bivalvia are particularly suitable hosts for sulfide-oxidizing bacteria due to their microphagous habits, their distribution at the interface between aerobic and sulfide-generating anaerobic environments, and their potential ability to control the supply of sulfide and oxygen required by the bacterial symbionts, by partitioning them spatially or temporally. The possible role of sulfide-oxidizing symbiosis in the early evolution of bivalves in relation to the shift from labial palp feeding to ctenidial filtration is discussed.

INTRODUCTION

THE DISCOVERY of symbiotic sulfide-oxidizing bacteria in the vestimentiferan worm *Riftia pachyptila* finally shed light on the perennial question of nutrition in the gutless Pogonophora (CAVANAUGH *et al.*, 1981; SOUTHWARD *et al.*, 1981; SOUTHWARD, 1982). This discovery led also to the identification of symbiotic bacteria in the thermal vent bivalve *Calyptogena magnifica* (CAVANAUGH, 1983), and suggested a solution to questions raised by the gutless condition of the inshore protobranch bivalve species *Solemya reidi* (REID, 1980; REID & BERNARD, 1980). Sulfide-oxidizing enzymes, and enzymes of the Calvin-Benson cycle characteristic of the symbiotic bacteria were identified in these bivalves (FELBECK *et al.*, 1981), and bacteria visualized by transmission electron microscopy were found to inhabit the gills of *Solemya reidi* (FELBECK, 1983) and *Solemya velum* (CAVANAUGH, 1983). Subsequently, similar bacteria have been tentatively identified in all members of the Lucinidae that have been investigated (FELBECK *et al.*, 1981; BERG *et al.*, 1983; BERG & ALATALO, 1984; FISHER & HAND, 1984; SCHWEIMANN & FELBECK, 1985; DANDO *et al.*, 1985). It is inferred that the bivalve controls the availability of oxygen and sulfide for the bacteria in these associations, and that the bivalve benefits from the detoxification of sulfide and the trans-

located carbohydrate and amino acid products of the bacterial metabolism.

In this report *Parvilucina tenuisculpta* (Carpenter, 1864), a bivalve belonging to the Lucinidae, which has already been shown to possess symbiotic bacterial enzymes (FELBECK *et al.*, 1981) is taken as a model for the study of the impact of the symbiosis on bivalve functional morphology. Two species of the related family Thyasiridae are also studied, and drawing upon the extensive survey of the Lucinacea conducted by ALLEN (1958) we re-interpret the evolution of this group in the context of the symbiosis with sulfide-oxidizing bacteria. Furthermore we report on a TEM survey of other bivalves inhabiting sulfide substrates and consider some of the general implications of these symbioses for bivalve evolution.

MATERIALS AND METHODS

Specimens of *Parvilucina tenuisculpta* (Carpenter, 1864) were collected with a Van Veen grab from fine silt with a strong odor of hydrogen sulfide at a depth of 40 m in Pipestem Inlet, Barkley Sound, W. Vancouver Island, British Columbia. For a discussion of the taxonomic status of the genus *Parvilucina* refer to BRITTON (1972). Other numerous mollusks from this environment included *Macoma carlottensis* (Whiteaves, 1880) and *Dentalium rectius*

(Carpenter, 1864). Specimens of the two bivalve species were transported to the University of Victoria and allowed to burrow in mud from the biotope contained in glass vessels submerged in circulated seawater. *Axinopsida serricata* (Carpenter, 1864) and *Thyasira flexuosa* (Montagu, 1803) were obtained at a depth of 30 m off the Crofton pulp mill, S.E. Vancouver Island. A preserved specimen of the E. Pacific hydrothermal vent mytilid was borrowed from V. Tunnicliffe for a general anatomical scrutiny. Specimens of *Compsomyx subdiaphana* (Carpenter, 1864), *Acila castrensis* (Hinds, 1843), *Yoldia scissurata* (Dall, 1897), *Macoma lipara* (Dall, 1916), *M. brota* (Dall, 1916), *M. calcarea* (Gmelin, 1791), and *M. elimata* (Dunnill & Coan, 1968) were obtained by dredging from silt substrates at 30 to 60 m off Moresby Island, S.W. British Columbia. *Macoma nasuta* (Conrad, 1837), *M. secta* (Conrad, 1837), and *M. inquinata* (Deshayes, 1855) were dug intertidally at Cordova Bay, S.E. Vancouver Island.

The morphology of *Parvilucina tenuisculpta* was examined by dissection and by serial sectioning. Ciliary currents in the mantle cavity were traced with suspensions of alumina (about 30 μm), 280-mesh carborundum (35–75 μm), and Sephadex G10 beads (60–120 μm).

Freshly collected specimens were removed from the shell and fixed in cold, neutral paraformaldehyde fixative (HUMASON, 1979) for 3 h at 8°C, then infiltrated and embedded in JB4 plastic at 8°C. The plastic blocks were stored dry at 4°C until sectioned. Sections 2 μm thick were cut from these blocks and subjected to incubating and staining media for the visualization of non-specific esterases and acid and alkaline phosphatases (REID, 1966). Some of the blocks were used for serial sectioning, with sections being stained with Mayer's haematoxylin and xyridene Ponceau. Selected slides were stained with alcian blue to reveal acid mucopolysaccharides, or with periodic-acid-Schiff (PAS) for general staining of polysaccharides. Diastase-treated sections provided a control for the presence of glycogen in PAS-stained sections.

Freshly dissected gills of *Parvilucina* and gills and labial palps of the other bivalves mentioned above were prepared for transmission electron microscopy (TEM) according to the following protocol based on EISENMAN & ALFERT (1982): 10 min prefixation in a medium consisting of 1 part postfix to 20 parts mainfix, followed by 12 h fixation in mainfix consisting of 4% glutaraldehyde in 0.2 M sodium cacodylate buffer (pH 7.2), and 0.35 M sucrose, followed by 1 h postfixation in postfix consisting of 1% osmium tetroxide, in 0.3 M sodium chloride, 0.2 M sodium cacodylate buffer, and 0.35 M sucrose. Dehydrated samples were embedded in epon (EMbed 812). Sections were examined in a Philips EM 300 microscope.

For scanning electron microscopic examinations (SEM) freshly dissected gills of *Parvilucina tenuisculpta* were fixed for 2 h in 3.5% glutaraldehyde in 0.1 M sodium phosphate buffer and 3.5% sucrose (pH 7.2), followed by postfixation for 1 h in 1% osmium tetroxide in 0.1 M phosphate buffer and 3.5% sucrose at 4°C. Dehydrated specimens

were critical point dried, gold coated, and examined in a JEOL JSM-35 scanning electron microscope.

For examination of granular inclusions by energy dispersive X-ray microanalysis (EDX) dissected gills were homogenized in a Polytron sonic/mechanical homogenizer and centrifuged at 10,000 rpm for 10 min and then for two 10-min periods at 5000 rpm. After each centrifugation the supernatant was discarded and pellets were resuspended in deionized water. The final resuspension was filtered through 0.2- μm polycarbonate nucleopore filters. The filters containing the granules were dried, carbon coated, and examined in the SEM mode of a JEOL JEM 1200 EX microscope, and X-ray analysis was conducted by means of a Tracor X-ray detector linked to a Tracor-Northern computer. Semiquantitative analysis of the proportions of metals in the granules were made following methods based on Kramer's model, outlined by GOLDSTEIN *et al.* (1981), and programmed by Tracor-Northern TN-5550-10 Quantitative Software for Scanning Electron Microscopes and the TN-5500 X-ray Analyzer, 1984.

For the detection of hemoglobin, aqueous extracts of whole body homogenates were centrifuged at 12,000 rpm and 4°C for 2 h. The supernatants were scanned spectrophotometrically to detect absorption peaks between 400 and 700 nm. The effect of deoxygenation by 1% sodium dithionate on the absorption profile was also observed.

RESULTS

Functional Morphology of *Parvilucina tenuisculpta*

The pallial morphology of *Parvilucina tenuisculpta* has many features in common with the other members of the Lucinidae. There is no inhalant siphon; the exhalant siphon is short and can be inverted so that its opening comes into close contact with the suprabranchial chamber; the foot, a long organ with a pointed expanded tip, can be extended many times the length of the shell; and the anterior adductor is elongated ventrally (Figure 1). The lateral extensions of the visceral mass, containing part of the reproductive organs, form distinct pouches, and the ducts and tubules of the digestive gland are placed superficially over the pouches (Figure 2). The much thickened ctenidia are the most striking feature of the pallial morphology. These consist of single demibranchs. The individual gill filaments, which have longitudinal streaks of brown and yellow-brown pigment, are held close together by multiple tissue bridges. A distinct, but shallow food groove is present at the ventral margin of each demibranch (Figure 3). For most of their length the inner, ascending lamellae are connected by a thin septum to the visceral mass. Posteriorly the dorsal margins of the gills are fused to the mantle edge, as shown in Figures 1 and 2. The descending gill filaments are fused to the opposite ascending filaments for most of their length through extension of the granular, pigmented subfilamentar tissue, effectively combining the filaments into narrow blades arranged like the teeth of a comb. Alumina particles, carborundum particles, and

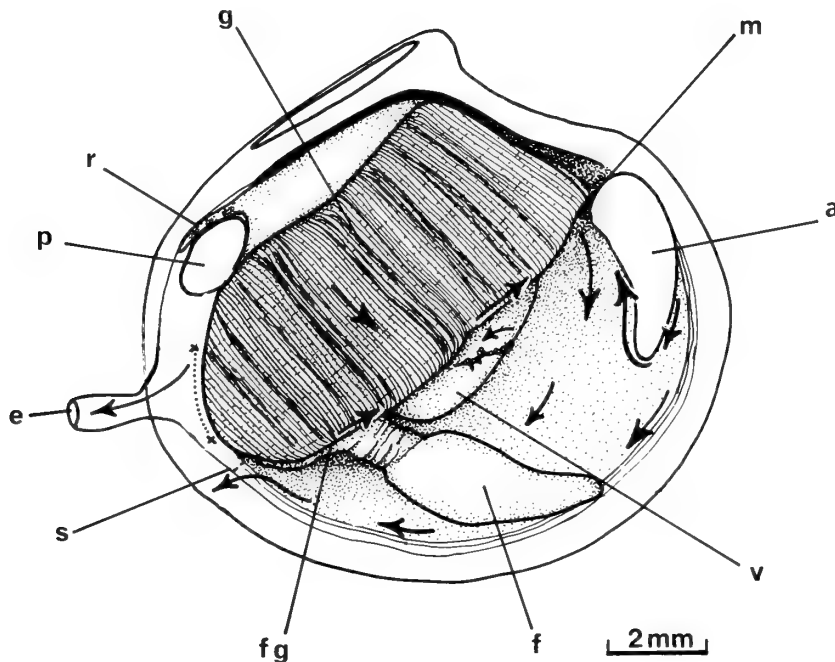


Figure 1

Right lateral view of *Parvilucina tenuisculpta*, mantle removed. Dotted line under the posterior adductor muscle indicates the region where the dorsal edges of the outer gill lamellae are fused to the mantle edge. a = anterior adductor muscle; e = exhalant siphon; f = foot; fg = food groove; g = gill; m = position of mouth; p = posterior adductor muscle; r = rectum; s = point of separation of fused mantle edges, where pseudofeces are ejected; v = visceral mass.

Sephadex particles smaller than $75 \mu\text{m}$ are swept over the surface of the gill and carried in mucus-bound strings to the mouth. The labial palps are reduced to a narrow pair of dorsal and ventral lips, together with two small papillae arranged at each end of the lips adjacent to the food groove (Figure 2). The gills communicate with the mouth by isthmuses whose cilia carry food particles from the ctenidial food grooves to the mouth. The ciliation of the lips and palp papillae appear to have a cleansing function only. Serial sections indicate a slight folding of the mantle epithelia in the region of the mouth and anterior adductor muscle but there is no distinct pallial gill, such as ALLEN (1958) describes for other lucinids. A surface ciliation of the anterior adductor muscle carries particles in the direction of the mouth but it is not clear if there is any direct contact between particles collected in this manner and the mouth. The mantle edges are separate for the anterior two-thirds of their length. Posteriorly they are fused and form an elastic ribbon that can relax to about four times its contracted width. Its musculature is complex, consisting of transverse, radial, longitudinal, and oblique fibers. As noted above, the postero-dorsal descending gill filaments are connected to this muscular organ. Although we did not observe its manner of operation, its contraction must have a bellows-like effect on the gills, thereby agi-

tating or flushing the mantle and suprabranchial water. Rejectory currents on the inner mantle surfaces carry particles of pseudofeces to the point where the mantle edges fuse (Figure 1).

The stomach of *Parvilucina tenuisculpta* is relatively small, and its internal morphology is simple, similar to that of the lucinid *Lucinoma borealis* (PURCHON, 1958). The major typhlosole is a thin ribbon of tissue, adjacent to the intestinal groove, which continues ventrally into the mid-gut, open to the style sac. Particles retrieved from the stomach included silt, small diatoms, and organic detritus in the size range of $5\text{--}40 \mu\text{m}$. There appear to be four duct openings giving rise to four diverticular ducts, each of which gives rise to up to eight digestive tubules. The ciliated epithelia of the ducts give a positive reaction for alkaline phosphatase. The tubule cells are positive for acid phosphatase and non-specific esterase. A relatively short mid-gut continues into a short hind-gut, ending in a rectum that carries fecal pellets dorsal to the posterior adductor to the exhalant siphon.

Whole-body aqueous extracts submitted to scanning spectrophotometry show absorption peaks at 500, 538, 569, and 608 nm. When the extracts are deoxygenated with sodium dithionite the absorption peaks shift to 532 and 565 nm. These absorption peaks and their deoxygenation

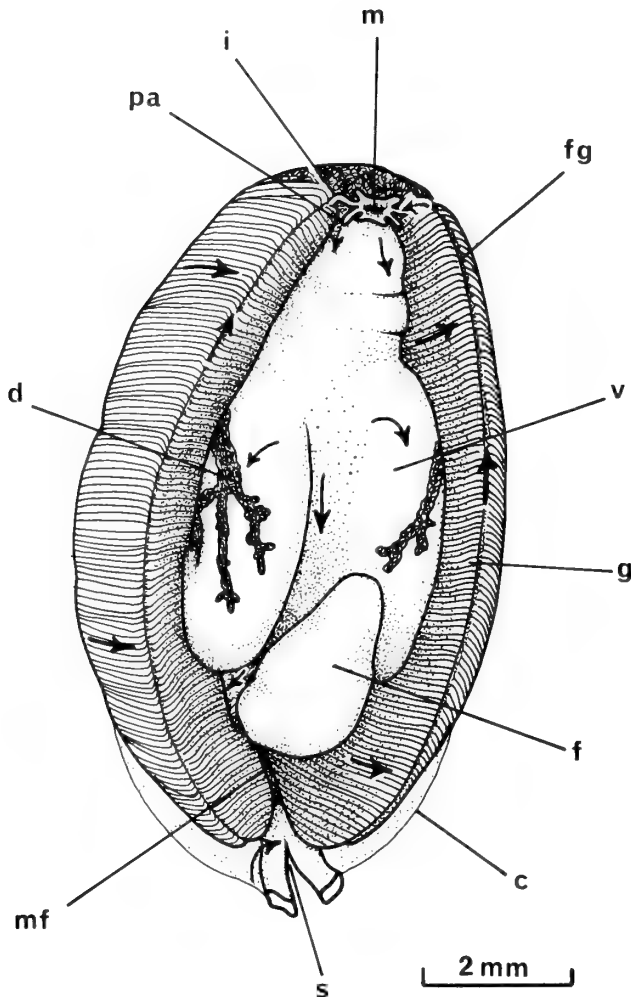


Figure 2

Anteroventral view of *Parvilucina tenuisculpta*, removed from valves, mantle removed. c = cut edge of mantle; d = digestive diverticula; f = foot; fg = food groove; g = gill; i = isthmus of ciliated tissue connecting ctenidial food groove to mouth; m = mouth; mf = region of fusion of dorsal margins of gills to mantle edge; pa = vestigial papilla of labial palp; s = point of separation of fused mantle edges, where pseudofeces are ejected; v = visceral mass.

shifts are similar to those found for the hemoglobin of the lucinid *Phacoides pectinatus* by READ (1962) and in *Solemya reidi* (McMAHON & REID, 1984; DOELLER & COLACINO, 1985).

Fine Structure and Inclusions of the Gills of *Parvilucina tenuisculpta*

Due to fusion of the subfilamental (or abfrontal filamental) tissues the demibranchs of *Parvilucina tenuisculpta* form a series of narrow lamellae that are formed of three cell types (Figure 4). The cells of the frontal region are

typical of the normal bivalve filament, being ciliated and containing numerous mitochondria (Figures 4A, 5A). Adjacent to these are large cells whose inclusions consist of a granular mucopolysaccharide that stains weakly with alcian blue and strongly with PAS. Numerous granules of glycogen are also present. This tissue will be called *storage epithelium* (Figures 4, 5, 6). The remainder of the subfilamental septum consists of bacteriocytes that contain a variety of large granules, which vary in appearance under the light microscope, and are colored various shades of yellow, orange, and brown. Alternating with the bacteriocytes are small single *intercalary cells* with extensive microvilli on their distal surfaces. This is the term used by DANDO *et al.* (1985), who report a similar arrangement in *Myrtea spinifera* (Montagu). Alternating intercalary cells are also found by us in *Solemya reidi*, but are sometimes obscured by poor fixation. As Dando *et al.* note, the microvillar surface of the intercalary cells partially extends over the bacteriocytes. These cells may divide to produce new bacteriocytes, and may also have a transport role linked to bacterial metabolism. The bacteria in the bacteriocytes are contained in distinct vacuoles, as in *Myrtea* (Figures 4D, 5A, B, C). FISHER & HAND (1984) report a similar bacterial type in vacuoles in the gill bacteriocytes of *Lucina floridana*. Some bacteria are found extracellularly in the spaces between the gill lamellae, together with free granules (Figure 5C). These may have come from the degradation of senescent bacteriocytes, or may have been actively exocytosed. Amoebocytes found between the bacteriocytes and in the ctenidial blood sinuses contain a few bacteria and granular inclusions, some of which have a distinctly membranous appearance (Figure 6A).

There are various types of granular particles in the bacteriocytes (Figures 6B, C). Granules with low sulfur, silicon, phosphorus and calcium, and relatively high chromium, iron and nickel are the most common type in *Parvilucina* (Figure 7A). The presence of the calcium and phosphorus suggest that these may be nephrolith-like bioaccumulation granules that have sequestered iron, nickel, and chromium from the water column or from the blood (TIFFANY, 1982; REID & BRAND, 1985). EDX microanalysis demonstrates that sulfur is the dominant elemental inclusion of the bacteria themselves (Figure 7B). In some granules, sulfur predominates, but significant levels of chromium, iron, and nickel are also present (Figure 7C). In contrast, the type of granule shown in Figure 7D has the elemental make-up of plagioclase feldspar, a common constituent of sand and silt in the environment. A few fine particles of this type may have been accidentally endocytosed by the gill epithelia, or may simply have adhered to the surface of the gill prior to preparation for EDX analysis. GAILL *et al.* (1984) note that sulfur in the hydrothermal vent polychaete *Alvinella pompejana* is associated with high levels of zinc and arsenic, and conclude that these metals may have a biological role in bacterial metabolism. They also report the presence of arsenic in *Calyptogena magnifica* from the same community. Zinc

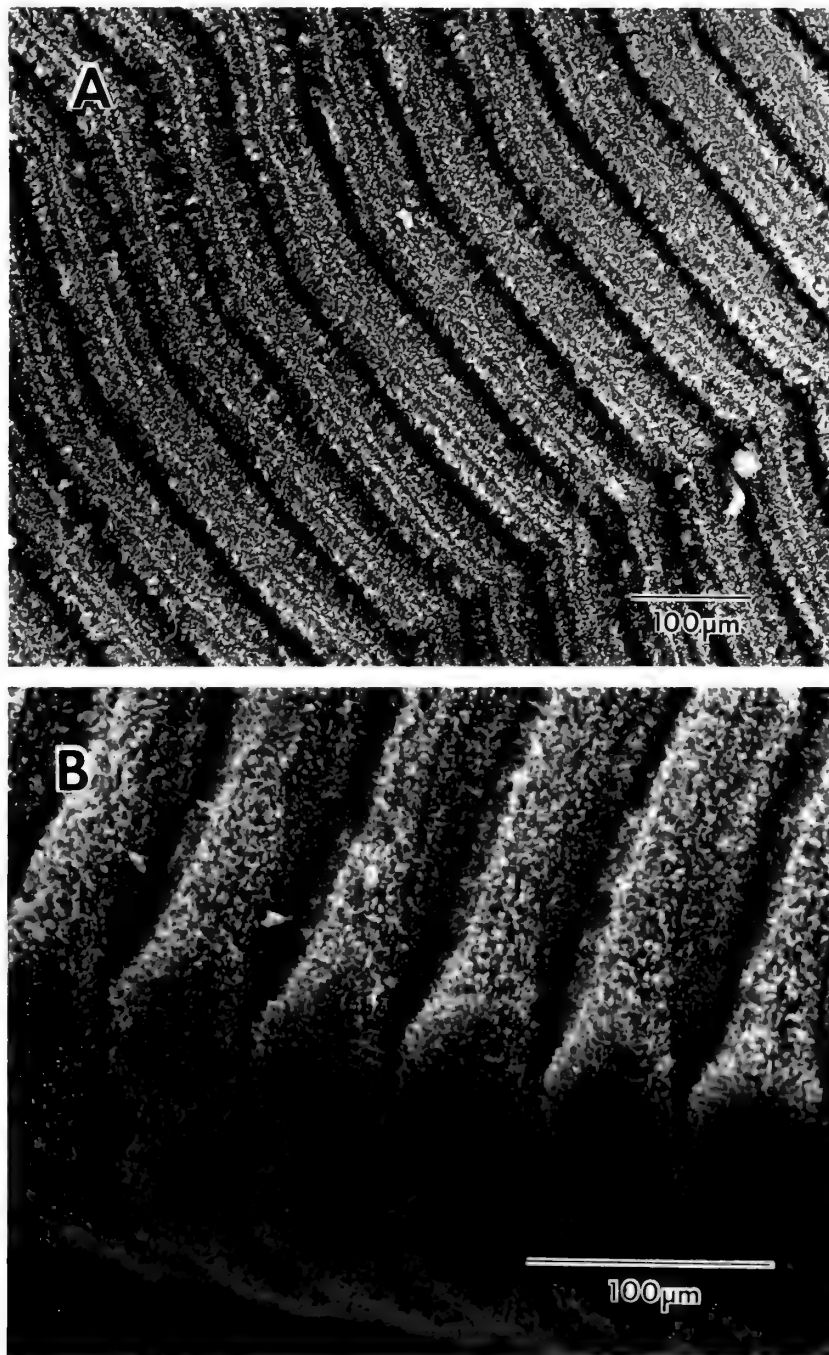


Figure 3

Scanning electron micrographs of gills of *Parvilucina tenuisculpta*. A. Lateral view of filaments. B. Ventral margin showing weak food groove.

could, they allow, be absorbed from the water column without any special biological power of concentration. Arsenic is not detected in *Parvilucina tenuisculpta*, and the zinc that is present may come directly from the water

column. Most of the sulfur present in *Parvilucina* granules is probably the end product of bacterial metabolism. However, sulfur is also present in the numerous cysteine residues of the metal-binding protein metallothionein. The

precise role of these proteins in metal deposition in bivalve granules is not yet defined. GEORGE (1983a, b) notes that, although metallothionein is involved in cadmium detoxification in *Mytilus*, the sulfur present in the accumulation granules cannot be traced to cysteine derived from the protein. Table 1 provides the data from a semi-quantitative analysis of the inorganic heavy elements from these particles together with a rough percentage of the common granule types. Owing to the significant environmental levels of iron in the sediment and in the water column it should not be assumed that the iron content of these granules is correlated with respiratory pigments or cytochromes.

The Gills of *Thyasira flexuosa* and *Axinopsida serricata*

Both of these species of the lucinacean family Thyasiridae have extensive subfilamental tissues. In *Axinopsida* these tissues are similar to the storage epithelium of *Parvilucina* (Figure 8A). There are occasional inclusions that might be bacteria, but these are scarce, and there are no specialized bacteriocytes. In *Thyasira* it appears as if the storage epithelia double as bacteriocytes. Numerous bacteria are contained in large vacuoles, or "bacteriosomes," at the distal surfaces of these cells (Figure 8B). This creates the impression that formerly epifloral gill symbionts were phagocytosed and the symbionts now conduct their affairs from within a phagosome. However, we find no extant epiflora remaining on the gill surfaces. Some of the bacteria appear to be further ingested into the storage cell proper (Figure 8C). This arrangement suggests that sul-

fide is taken in through the microvillar distal surfaces of the subfilamental epithelium, rather than from the blood.

TEM Survey of the Gills of Eleven Bivalve Species

Only one of these species showed evidence of gill bacteria. An extensive survey of *Macoma* was conducted because *M. carlottensis* is often found along with *Solemya reidi*, *Parvilucina tenuisculpta*, and *Thyasira flexuosa*. JONES & THOMPSON (1984) list the common faunal associates of *P. tenuisculpta*. A number of other *Macoma* spp., in particular *M. inquinata*, *M. lipara*, *M. brota*, and *M. calcarea*, inhabit sulfide silts and we had the unrequited hope that this study would solve a problem of niche partition pertaining to *Macoma* (REID & REID, 1969). *Compsomyax subdiaphana* is another common bivalve of sulfide silts in the northeastern Pacific. *Acila castrensis* was chosen because of its similar habitat and its central role in discussions of the evolution of habit in the bivalves. However, with all of these species we drew blanks. Only in *Yoldia scissurata* did we find some ctenidial cells containing bacterium-like inclusions somewhat similar to those of *Axinopsida serricata*. These inclusions were found in only a few cells, and not in the kinds of arrays of bacteriocytes found in *Parvilucina*, *Thyasira*, and *Solemya*. Granules in the gills of *Yoldia* did not have high sulfur levels.

DISCUSSION

The Functional Morphology of *Parvilucina tenuisculpta*

The features of the functional morphology of *Parvilucina tenuisculpta* that may be correlated with the bacterial

Figure 4 (page 9)

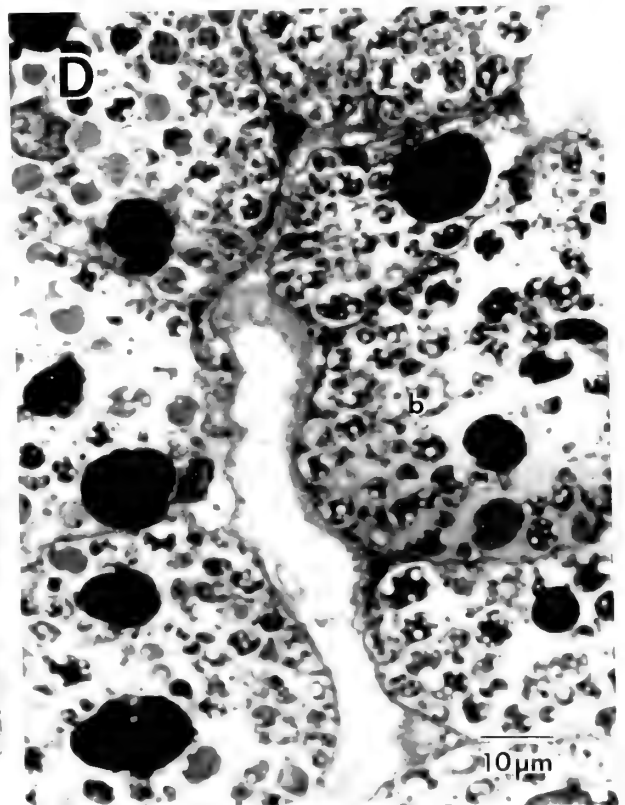
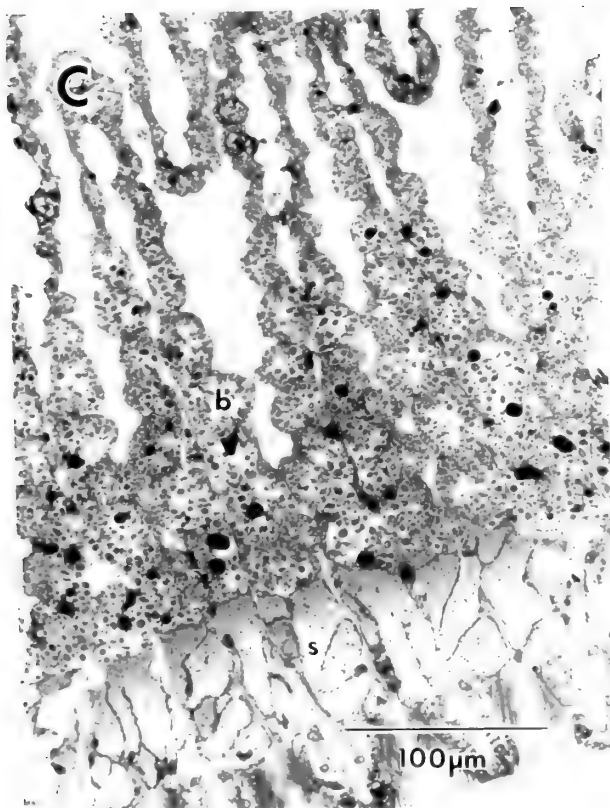
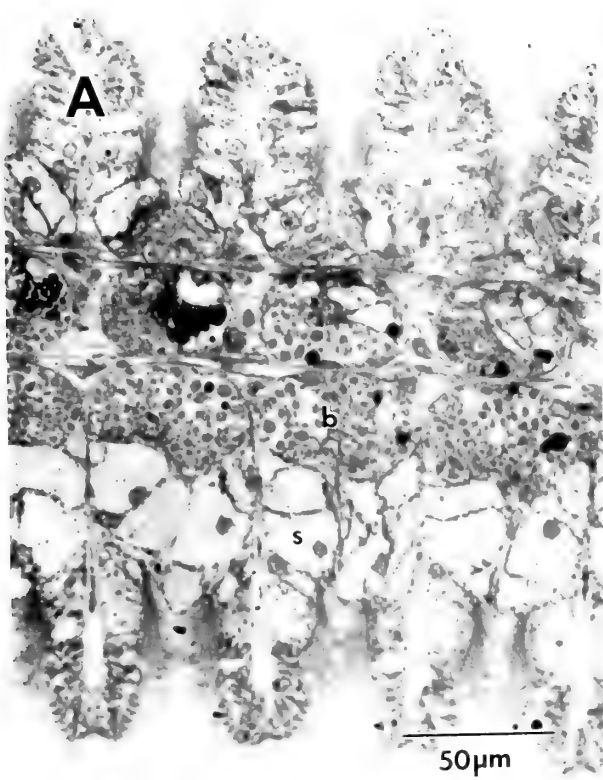
Light micrographs of thick epon sections of gill filaments of *Parvilucina tenuisculpta*. A. Section near ventral margin showing the ciliated frontal portions of filaments, the bacteriocytes (b) with large granules, and between these the storage epithelia (s). B. Section in central region of gill showing transverse fusion of the ascending and descending filaments. The subfilamental (abfrontal) tissue consists of bacteriocytes and intercalary cells. C. Section near dorsal region of gill. Gill filaments are no longer fused transversely. D. Higher magnification of bacteriocytes showing large mineral granules and bacteria.

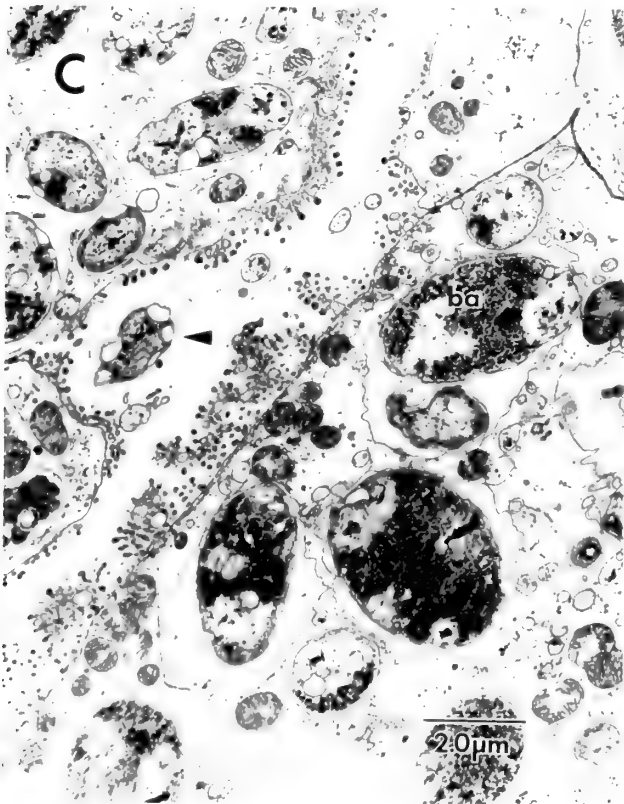
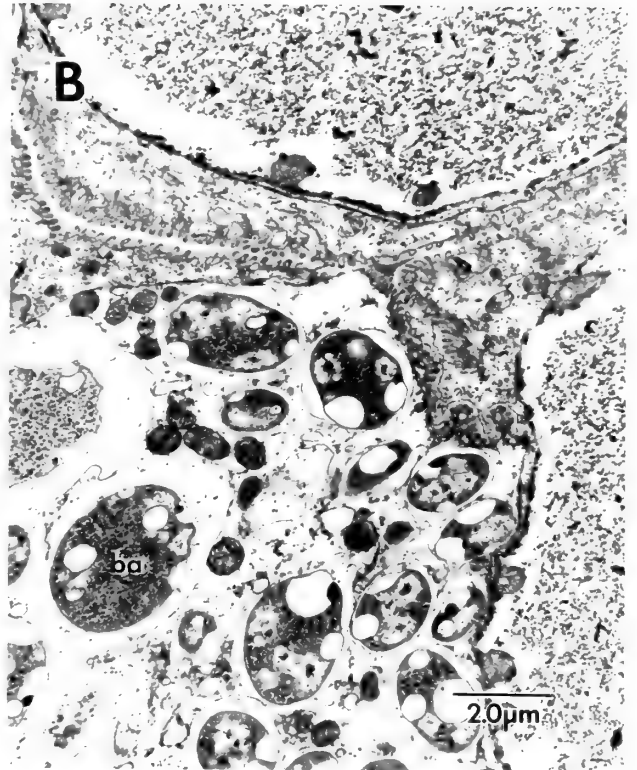
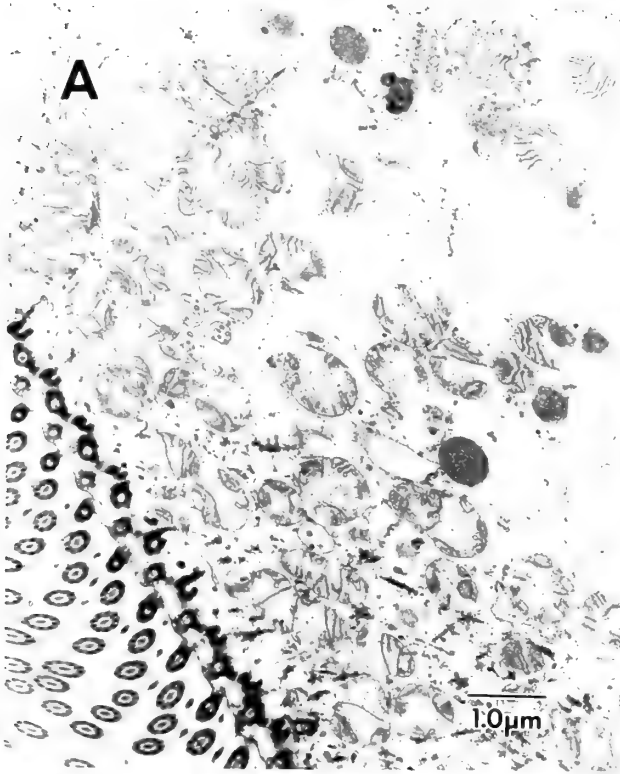
Figure 5 (page 10)

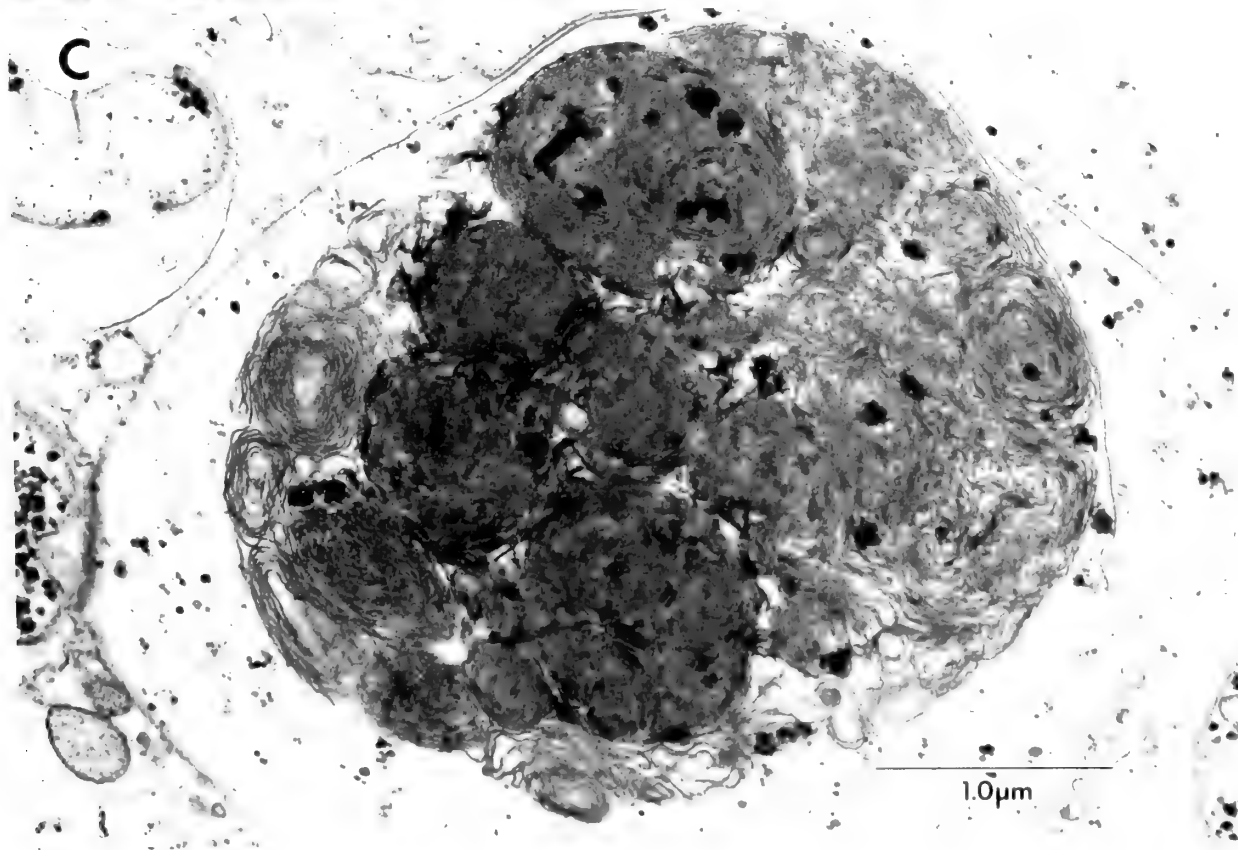
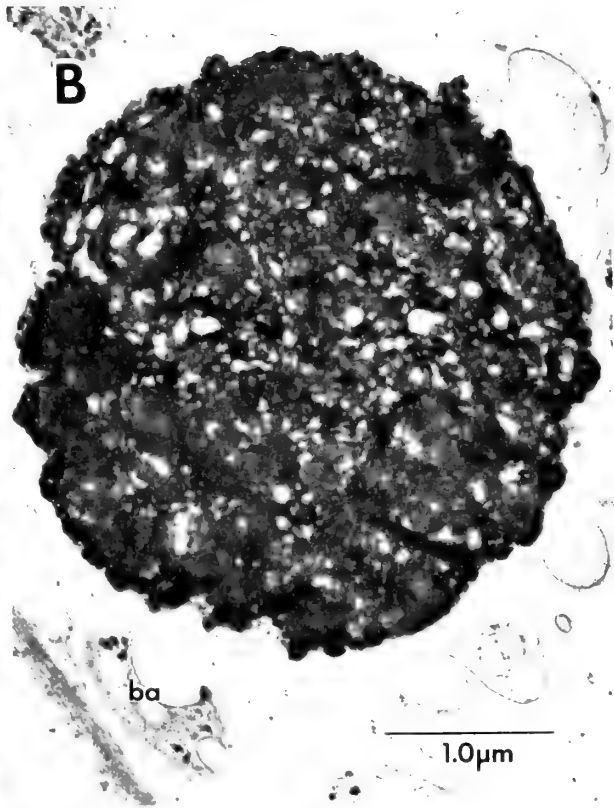
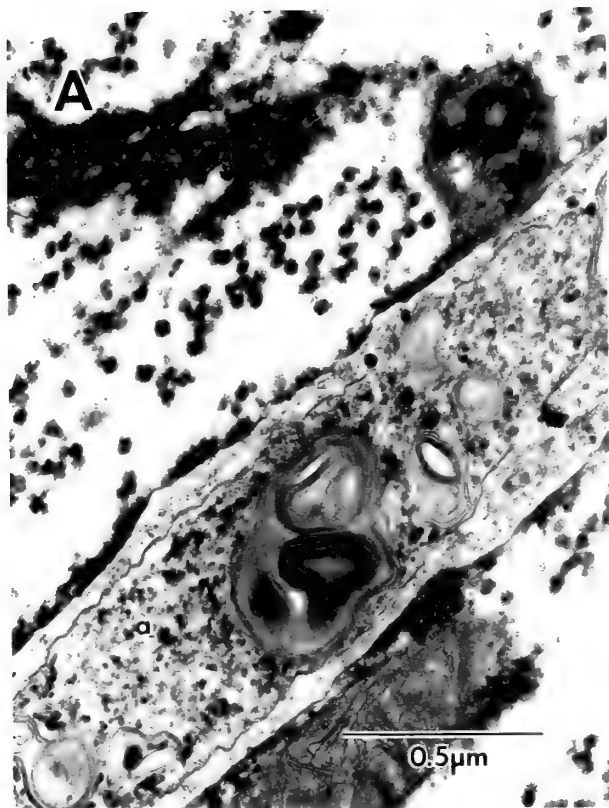
Transmission electron micrographs of gill filaments of *Parvilucina tenuisculpta*. A. Frontal epithelia with cilia and numerous mitochondria. B. Bacteriocyte with bacteria (ba). C. Bacteriocytes; note the microvillar borders and free bacterium in suprabranchial space between the cells (indicated with arrow). D. Amoebocyte between storage cell (upper left) and bacteriocyte (lower right); amoebocyte contains bacteria (ba) and has mitochondria.

Figure 6 (page 11)

Granular deposits in gill filaments of *Parvilucina tenuisculpta*. A. Amoebocyte in filamental blood sinus contains compound lamellar inclusion. B. Dense granule from bacteriocyte, may be older form of C. C. Compound lamellar granule of bacteriocyte. Note that these granules do not have the same ultrastructure as the calcium phosphate nephroliths mentioned in the text.







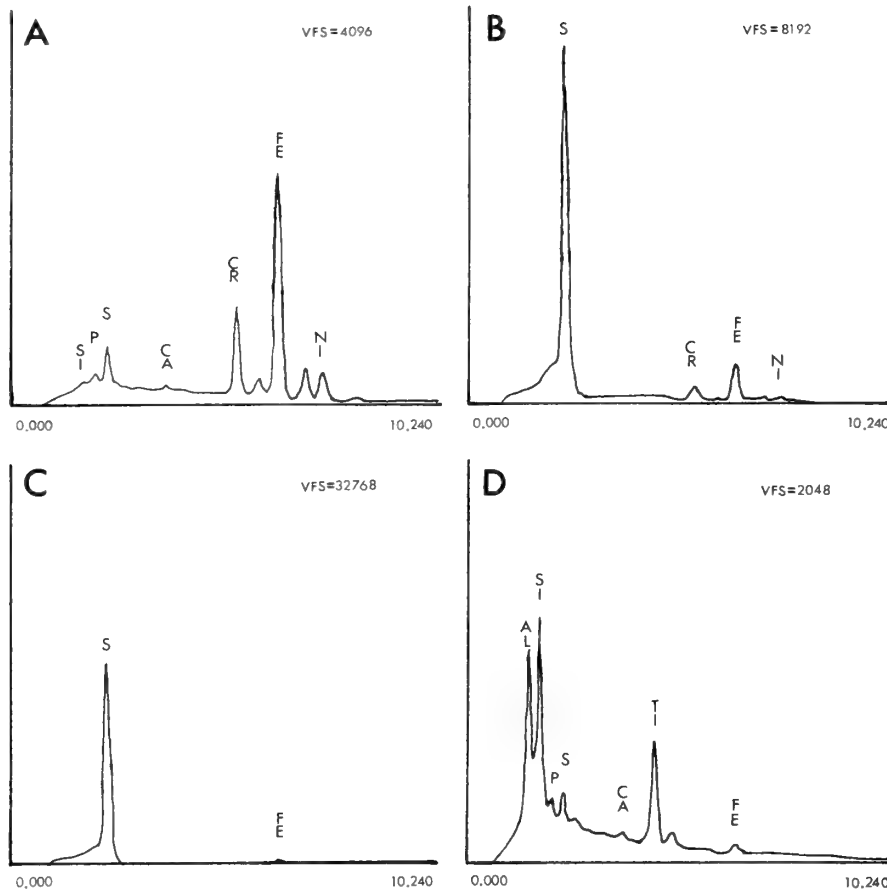


Figure 7

EDX assays of mineral granules from the gills of *Parvilucina tenuisculpta*. A. The most common type of granule characterized by high iron, chromium, and nickel. B. Granule with combined features of iron-chromium-nickel granule and bacterial sulfur granule. C. Bacterium. D. Plagioclase feldspar granule (artifact from environment). Note that the height of the peaks is not proportionate to element concentration. For semi-quantitative analysis refer to Table 1.

symbiosis include the expansion of the subfilamental tissue of the gills, the insertion and fusion of the posterodorsal margins of the gills with the muscular posterior mantle edge, the reduction of the labial palps, the hypotrophy of the gut, the capacity to construct a ventilation burrow, and the absence of an inhalant siphon. The absence of the outer demibranch is also significant, though not exclusively correlated with symbiosis. The probable presence of hemoglobin and the deposition of sulfur granules in the gills are additional correlations. Among these features only the posterior fusion of the gills with the mantle edge has not been reported for the Lucinidae. Because the gills are not themselves muscular the contraction of the mantle edge may give the gills a bellows-like action to bring solutes such as sulfide from the immediate external environment. Conceivably this arrangement could cause a tidal flushing of the suprabranchial chamber via the exhalant siphon, thus bringing sulfide into immediate con-

tact with bacteriocytes, while limiting exposure of the ciliated frontal cells. In all probability the lack of other instances of this arrangement in the Lucinacea is not due to its uniqueness in *Parvilucina tenuisculpta*, but rather that it has been overlooked elsewhere. From this point the discussion will generalize about the Lucinidae.

Uptake of Sulfide and Oxygen

The Lucinidae often show one character that is not developed in *Parvilucina tenuisculpta*, the mantle gills. In many lucinids these are composed of vascularized diagonal folds, which ALLEN (1958) interprets as supplementary oxygen-absorbing organs. This could be a major point of oxygen uptake or, in some cases, sulfide absorption. Hemoglobin was first discovered in the Lucinidae by READ (1962) and is probably present in *Lucina floridana* (FISHER & HAND, 1984) as well as in *Parvilucina tenuisculpta*. The bivalve requires oxygen and the bacterial symbiont re-

Table 1
Percent weight of heavy elements of ctenidial granules of *Parvilucina*.

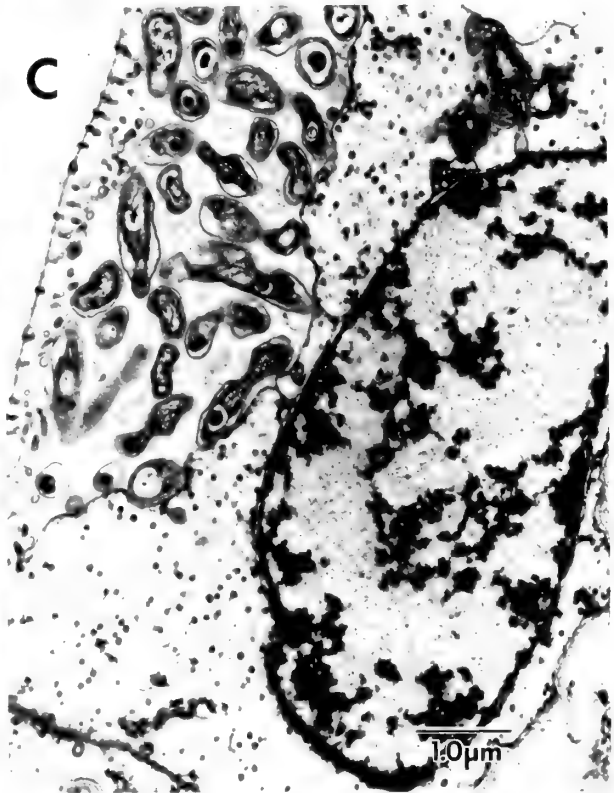
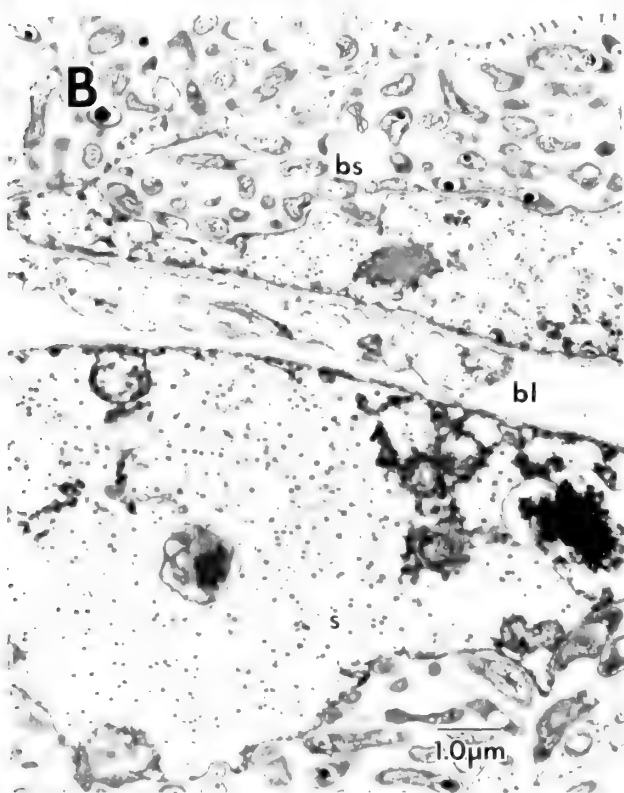
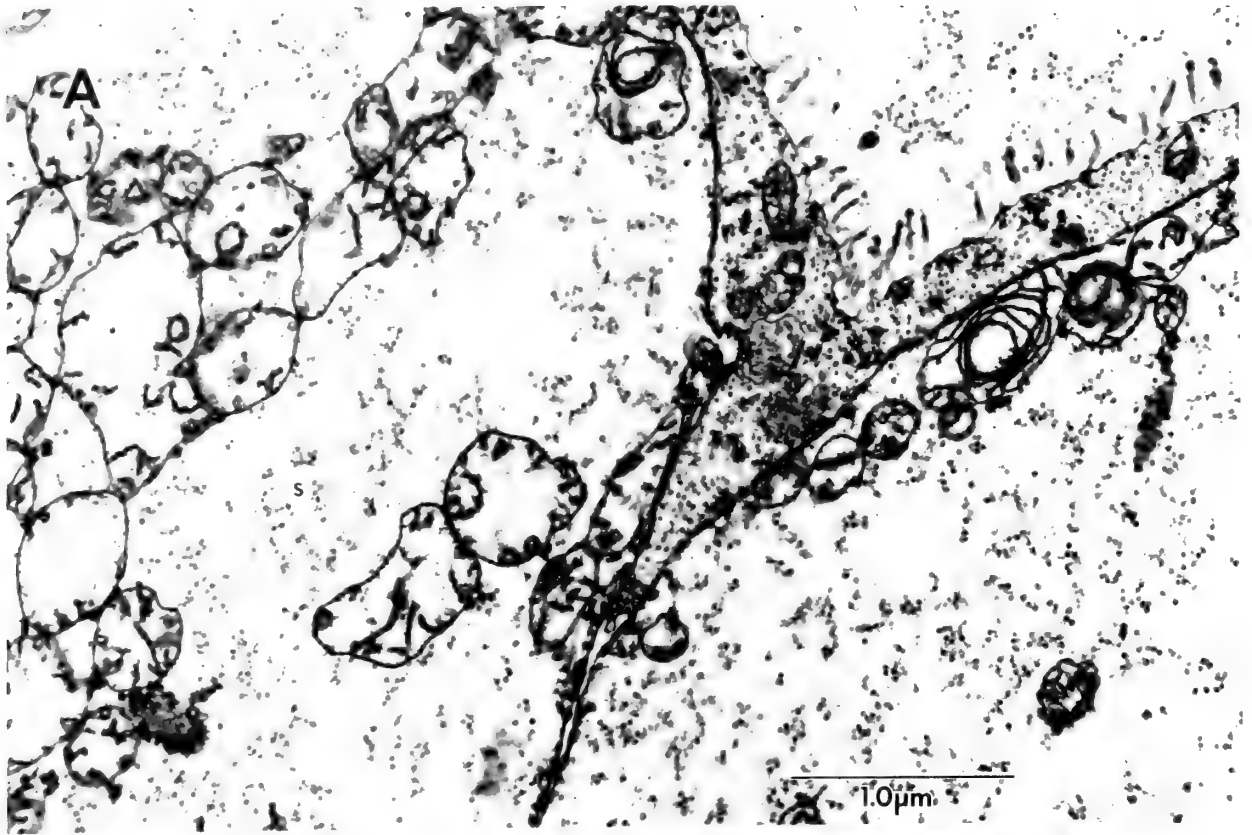
Al	Si	P	S	Ca	Ti	Cr	Fe	Ni	% of 25 granules examined
0.00	0.83	2.29	2.21	0.00	0.00	15.01	64.82	14.91	28
±0.00	±0.41	±1.61	±0.96	±0.00	±0.00	±1.82	±1.52	±1.41	
0.00	1.46	11.32	60.75	1.34	0.00	1.33	19.85	4.27	32
±0.00	±1.02	±4.16	±6.60	±2.17	±0.00	±1.82	±5.86	±0.56	
0.00	1.68	5.47	86.00	5.05	0.00	0.46	2.33	0.69	24
±0.00	±0.92	±1.56	±8.24	±9.97	±0.00	±0.65	±2.67	±0.88	
21.67	32.64	8.85	9.69	0.00	23.40	0.00	3.38	0.37	8
±0.47	±0.88	±1.02	±0.79	±0.00	±1.03	±0.00	±0.52	±0.08	
0.00	0.34	0.94	3.30	92.39	0.00	0.32	2.67	0.30	8
±0.00	±0.47	±0.13	±0.59	±3.59	±0.00	±0.45	±3.38	±0.12	

quires both oxygen and sulfide. Because the two molecules rapidly inter-react, a spatial or temporal separation is required. Spatial separation could be achieved by separate routes of ingress to the bacteriocytes, one route being direct diffusion from the mantle cavity and the other from the blood and hemoglobin. As already suggested, sulfide could be brought directly to the bacteriocytes in the suprabranchial chamber via the exhalant siphon. The juxtaposition of bacteriosomes and storage epithelia in *Thyasira* suggest a similar route for sulfide absorption rather than from the blood. Temporal partition of the oxygen and sulfide supply could be achieved, as proposed for *Solemya reidi*, by changes in ventilatory behavior (McMAHON & REID, 1984). *Solemya reidi* can cease ventilation but still remain open for the absorption of sulfide accumulated in the burrow. After the gill bacteriocytes have been loaded with sulfide, the restoration of ventilation would supply the required oxygen. DOELLER (1984) pointed out that *Solemya velum* could achieve the same ends by moving in its burrow between the aerobic and anaerobic zones. DOELLER & COLACINO (1985) have indicated a mechanism in *Solemya velum* and *S. reidi* that integrates the spatial and temporal alternatives for the separation of oxygen and sulfide. In these species hemoglobin, which has a moderate to high oxygen affinity, binds sulfide reversibly, and thus can act as a store providing sulfide while the organism is in an aerobic environment, and providing oxygen when in an anaerobic environment. McMahan (personal communication) has found that in a respiration chamber where sulfide is not available and environmental oxygen has all been absorbed, *S. reidi* releases oxygen back into the environment. Presumably, under natural conditions in an anoxic environment sulfide would be present and the oxygen from the hemoglobin would be used for bacterial metabolism. The Lucinidae do not have the option of ascending and descending in the burrow between the aerobic and anaerobic zones. However, one common feature of the Solemyidae and Lucinacea is the absence of a tubular inhalant siphon that

would physically impede sulfide absorption, both when extended and contracted. One interesting ecological twist is the photosynthetic oxygen acquired by *Lucina floridana* from the roots of eelgrass (FISHER & HAND, 1984). DANDO *et al.* (1985) have discovered another ecological element pertaining to sulfide-oxidizing symbioses. In a community with the pogonophoran *Siboglinum fiordicum* Webb, which is known to have sulfide-oxidizing symbionts (SOUTHWARD *et al.*, 1981), three bivalves were found that possessed enzymes in the ctenidia characteristic of the symbiosis: *Lucinoma borealis* Linné, *Myrtea spinifera* (Montagu), and *Thyasira flexuosa* (Montagu). Strikingly, free sulfide in the sandy silt of the environment is lower than 0.5 μM , in contrast with levels of 160 μM to 25 mM reported for Galápagos Rift and *Solemya* environments (FELBECK, 1981, 1983). Sediment-bound sulfide is, however, relatively high, indicating that the organisms are able to draw upon it. Without this source of sulfide there would be insufficient energy to account for known levels of basal metabolism, growth, and reproduction. DANDO *et al.* (1985) further suggest that pseudofeces enhance sulfide production, and that thiosulfate derived from iron-bound sedimentary sulfide in the vicinity of the inhalant tube is absorbed for use by the symbiotic bacteria. We would propose the intriguing possibility that bound sulfide is released from ingested particles due to the low pH and anoxic state of the gut. This would then be a third point of possible sulfide absorption in addition to the suprabranchial chamber and pallial gills. We also observe that at our Crofton site *Parvilucina* is limited to sediments with high free sulfide, as determined by the semi-quantitative olfactory test proposed by DANDO *et al.* (1985). *Thyasira flexuosa*, which is present there in small numbers, becomes more numerous in contiguous sandy silts with lower free sulfide.

Paedomorphic Characteristics

The loss of the outer demibranchs in the Lucinidae, and the fusion of the subfilamental tissues that house the symbionts, points up a physical requirement of the bi-



valve-bacterial association. In a filter-feeding bivalve the chief criterion for particle collection and selection is a large ciliated surface area, and relative freedom of flow between the infrabranchial and suprabranchial chambers. This requirement is served by the double demibranchs found in most lamellibranchiate bivalves. This large surface area provides for far more respiratory gaseous exchange than these animals would ever require; therefore, the double demibranch gill is primarily a feeding organ. But for symbiotic gill bacteria the primary requirement is an adequate volume of host tissue, albeit arranged in cellular monolayers, to allow access to dissolved sulfide and oxygen both in the blood and mantle water. The lucinid lamellar gill structure is slightly convergent with that of the Solemyidae (Figure 9), but represents a compromise between total commitment to symbiosis and the requirement of a filtering and food-collecting gill for conventional alimentation. STASEK (1963) has observed that the failure to develop a second demibranch is paedomorphic. The hypotrophy of the gut may be a similar manifestation, presenting no dietary embarrassment because of the symbiotic nutritional supplement. However, gut reduction can occur as an independent process, as in *Solemya reidi* and in four other gutless solemyid species discovered by KUZNETSOV & SHILEIKO (1984). Paedomorphosis could also clear up the problem of how the stomach form should be classified. PURCHON (1956, 1957, 1958, 1960) delineates five stomach types and places the lucinid *Lucinoma borealis* and *Thyasira flexuosa*, in the type-IV category. However, ALLEN (1958) clearly shows that in three species of *Diplodonta* (Lucinacea: Ungulinidae) the stomachs belong to Purchon's type V, having the distinctive major typhlosole with two extensions entering a pair of duct caeca. Allen then argues convincingly that the smaller and less complex stomachs of the Thyasiridae and Lucinidae are simplifications of the type-V form found in the Ungulinidae. PURCHON (1978) admits that a number of bivalve stomachs consigned to the rather loose type-IV assemblage may indeed be paedomorphic simplifications of other gastric types. Allen suggests further that gut regression in the Thyasiridae and Lucinidae represents an adaptive trend toward a more macrophagous habit, correlated with their relatively poor environments, a trend similar to that taken by the carnivorous Septibranchia. Although this has a *faute de mieux* plausibility we find nothing in the histochemistry and cytology of the digestive tract to support it, and the food particles found in the *Parvilucina* rarely exceed 40 μm , while the gills reject most

particles longer than 75 μm . The proven existence of a nutritive symbiosis in the Lucinidae and the existence of gill bacteria in some Thyasiridae suggest that the simplification of the gut reduction or loss of the outer demibranchs, and gill filament modifications are correlates of symbiosis. *Axinopsida serricata* proves this rule, but we interpret this minute, ubiquitous species as one in which symbiosis has regressed, and r-selected qualities have been emphasized.

Transmission of Symbionts

The method of transmission of the symbiotic bacteria from one generation to the next in *Parvilucina* is not known. In *Solemya reidi* there appears to be an intimate vertical transmission from parent to offspring, with recognizable bacteria developing in the larval test tissues, from which they are released into the mantle cavity (GUSTAFSON, 1985). At this stage of development the larva has unconnected oesophageal, gastric, and rectal rudiments. An oral ciliary feeding organ draws into the oesophagus bacteria and infected fragments of the test tissue, which autolyzes during metamorphosis. When the gut itself degenerates at metamorphosis its population of bacteria is released into the hemocoel, whence they are presumed to be passed to the developing ctenidia. GUSTAFSON (1985) assumes this transmission to be holobiotic, that is, the eggs of *S. reidi* are already infected. In *Parvilucina* the form and size of the recognizable symbiotic bacteria are different from those of *Solemya*. Moreover they are contained in distinct vacuoles, and also are found free in the suprabranchial chamber. ALLEN (1958) notes that the ctenidial pigmented granules in the Thyasiridae are found free between the gill filaments and he describes this as an excretory process. Bacteria may also be released in the same way, becoming available to uninfected intercalary cells in the subfilamental tissue. We do not find uninfected adults, nor any obvious variations in the level of infection. Intimate symbioses tend to produce symbionts that are immune to the defense mechanisms of the hosts, and whose metabolic capabilities have been adjusted to those of the host, through a history of regression of labile enzymes, whose loss could be compensated by the host. Therefore, a transmission mechanism that ensures infection of the young bivalves is almost essential and, although there may be many free-living species of sulfide-oxidizing bacteria, it is unlikely that the transmission mechanism involves a random post-metamorphic infection by such free-living bacteria.

Figure 8

Transmission electron micrographs of the gills of *Axinopsida serricata* and *Thyasira flexuosa*. A. Subfilamental tissue of *Axinopsida*, composed of storage epithelia (s) with mitochondria. B. Portion of gill filament of *Thyasira* showing central blood sinus (bl) and subfilamental storage cell (s) with distal "bacteriosomes" (bs), vacuoles containing bacteria. C. Storage epithelium (s) with bacteriosome.

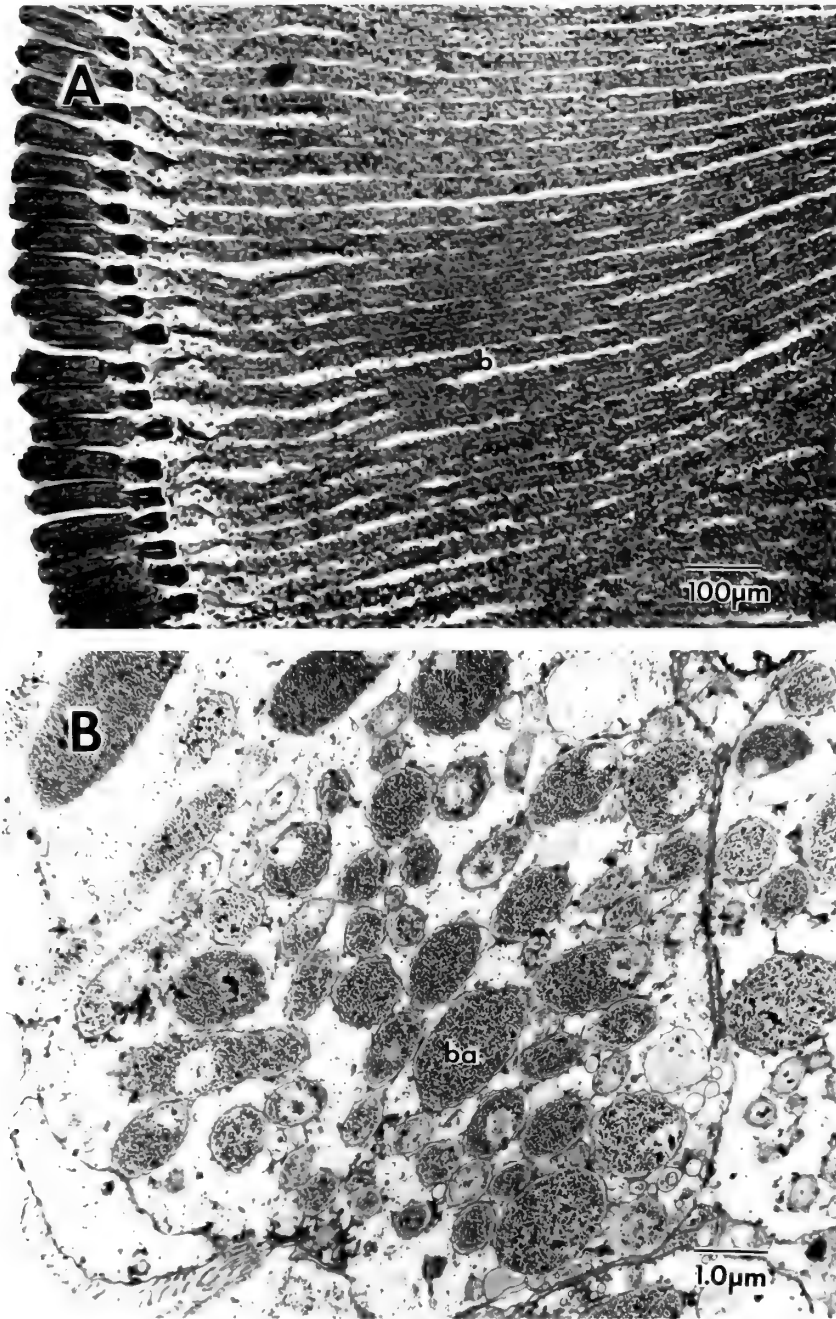


Figure 9

Sections of the gill of *Solemya reidi*. A. Light micrograph of gill filaments; ciliated frontal margins are at left; to right of the chitinous supporting rods the larger portion of the gill consists of bacteriocytes (b). This is the functional analogue of the subfilamental tissues of the Lucinidae and Thyasiridae. B. *Solemya* bacteriocyte. Note the larger bacteria (ba) than those found in *Parvilucina* and *Thyasira*.

The Evolution of the Lucinacea

Firstly we accept the scheme suggested by ALLEN (1958) for the extant forms with the qualification that the evolutionary trends in form and habit have been toward the refinement of symbiosis rather than toward macrophagy. The Ungulinidae represent the primitive form, possessing the most typical eulamellibranch gills and a typical digestive tract morphology, with no gastric simplification, nor expansion of the subfilamental tissue. The Thyasiridae have somewhat expanded the subfilamental tissue, reduced the outer demibranchs, and simplified the gut, and the Lucinidae represent the greatest commitment to symbiosis. The most significant question is where and when was the symbiosis first established? On the face of it, and taking a parsimonious view, the symbiosis should have occurred in an unguulinoid species, with a type-V stomach and double demibranchs, providing a line that then diverged to found the Thyasiridae and the Lucinidae; alternatively, a less likely diphyletic evolution came from two independently symbiotic ancestral species. But this leaves out a fundamental, albeit paraphyletic, character of the Lucinacea, the absence of the inhalant siphon. For a suspension-feeding bivalve inhabiting anoxic silt this would seem to be a reckless omission, reducing the efficiency of filtration and the selectivity of ingestion, increasing the risk of clogging the filtering organs with indigestible matter, and inviting immolation by sulfide. On the other hand, if the bivalve already had the beginnings of a symbiosis with sulfide-oxidizers, even a loose association with bacteria in the mantle cavity and on the gill surfaces, there would be every advantage to the loss of the inhalant siphon, provided that the foot were able to make an adequate ventilation tube for acquiring the oxygen necessary for bacteria and bivalve alike. Adding these ideas to the evolution of the Lucinacea the ancestral form may already have had the symbiosis, which provided most of the evolutionary drive for the group, with the exception of the modern Ungulinidae; the Ungulinidae would have to be seen as a line that abandoned the symbiosis, which might not have shifted from an ectosymbiotic to an endosymbiotic relationship, before the morphological modifications seen in the other two families had occurred (Figure 10A). One hypothesis would suggest a shallow-burrowing, short-siphoned suspension-feeder as the ancestor, possessing a loose symbiosis that provided the incentive to burrow deeper into anoxic sulfide-generating layers, to lose the inhalant siphon by paedomorphosis, and to develop the foot as an organ for constructing the burrow that would double as a ventilation and feeding route.

The lucinoids are an ancient Palaeozoic group, traceable to the late Early Ordovician, if *Babinka* is a natural relative of the other lucinoids as MCALESTER (1965) has argued (Figure 10B). POJETA (1978) who supports this contention, provides a brief review of the *pros* and *cons*. The radiation of the Lucinacea was a later event, occur-

ring in the late Mesozoic (MCALESTER, 1966). The problem with the stratigraphic evidence, based on shell-form, is that it runs counter to the evolutionary sequence that we are hypothesizing on the basis of functional morphology, and which agrees in general outline with the assessment made by ALLEN (1958). MCALESTER (1966) shows the Lucinidae arising in the Silurian, and the Thyasiridae and Ungulinidae in the Cretaceous (Figure 10B). However, the only shell features that are suggestive of habit are the absence of siphonal muscle scars and the presence of extensive anterior adductor scars, this feature being regarded by Allen as of nutritive significance, because the adductor surface provides a supplementary collecting surface. Coincidentally one of the oldest known bivalve mollusks, *Fordilla troyensis*, found in the upper Lower Cambrian, has similarly extensive adductors (POJETA, 1978). These characters are found in all Lucinacea, so the stratigraphic evidence does not necessarily contradict our hypothesis of habit evolution: the early Lucinidae probably had a morphology like that of the modern Ungulinidae. McAlester's most radical contention is that the lucinoids represent an independent line of bivalve evolution, with the Babinkidae arising from an Early Cambrian monoplacophoran ancestor (MCALESTER, 1966). However, the possession of typical eulamellibranch gills and a type-V stomach by the Ungulinidae undermines both the latter hypothesis and the argument that the functional morphology of the Ungulinidae is the most recent type to appear in the Lucinacea.

Occurrence of Sulfide-Oxidizing Symbiosis in Bivalves

That a symbiosis could provide sufficient momentum for a major evolutionary departure is an example of emergent evolution, a phenomenon discussed elsewhere in the larger context of animal evolution by REID (1985). Malacologists already familiar with the allometric shifts and modifications in the Tridacnidae, whose evolution was spurred by symbiosis with photosynthetic dinoflagellates, will not be surprised at the evolutionary impact of such associations. But with a few minor exceptions the algal-bivalve symbiosis is unique to the Tridacnidae. Has the bacterial-bivalve symbiosis been of more general evolutionary significance? We will commence with the negative evidence.

Although the Tellinacea were generally regarded as specialist deposit-feeders inhabiting coarse substrates (YONGE, 1949), there are many exceptions to this rule (POHLO, 1969). REID & REID (1969) demonstrated three feeding categories in the tellinid genus *Macoma*: coarse sand deposit-feeders, fine silt deposit-feeders, and suspension-feeders. Several species inhabit silts with various sulfide levels. *Macoma carlottensis* is frequently found in the company of *Solemya reidi*, *Parvilucina tenuisculpta*, and *Thyasira flexuosa*, and we double-checked this species from

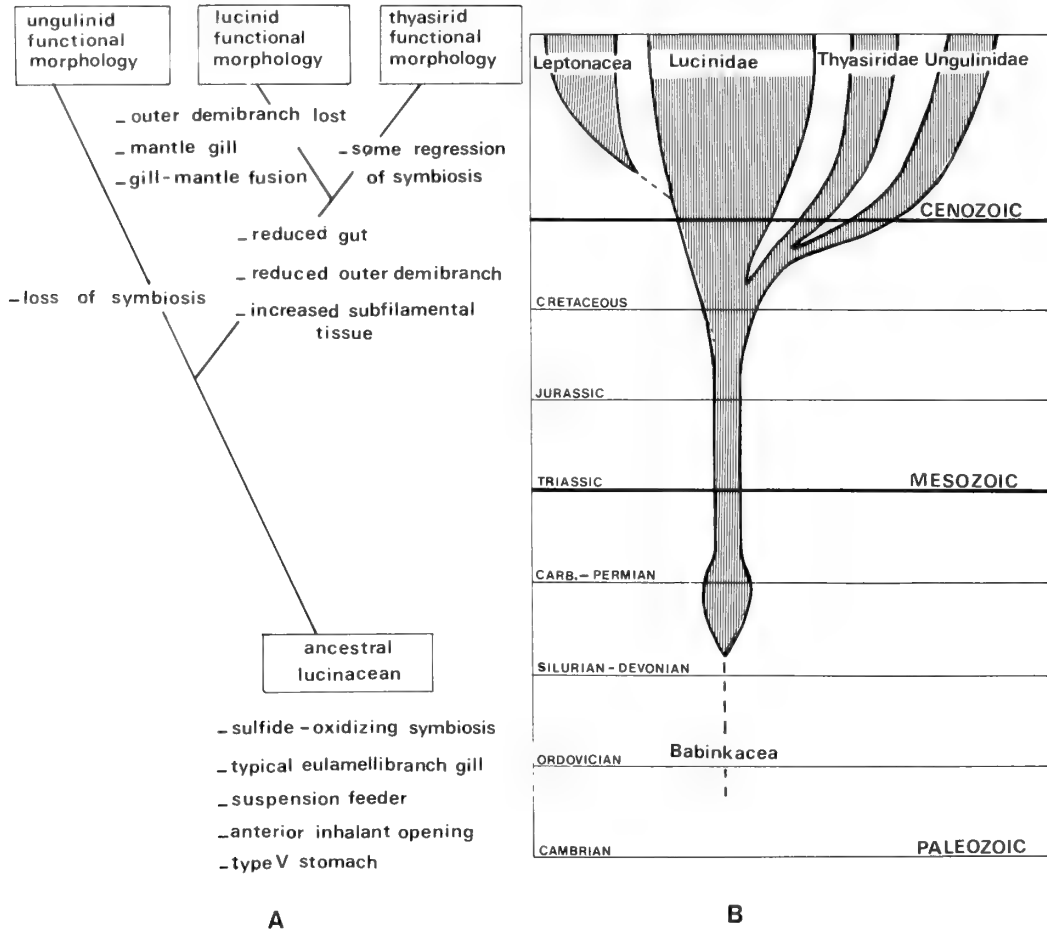


Figure 10

Evolution of the Lucinacea. A. Scheme proposed for the evolution of the Lucinacea. B. Diversification of the Lucinacea (after MCALESTER, 1966).

our Pipestem Inlet and Crofton sites to confirm that it lacks symbiotic bacteria, like all the other members of the genus that we have examined. *Macoma nasuta* was included in the enzymological survey by FELBECK *et al.* (1983) and found negative. Other common inhabitants of anoxic benthic muds, such as the cockle *Fulvia hungerfordi* (REID & SHIN, 1985) and the venerid *Compsomyx subdiaphana*, also lack the ctenidial bacteria. This symbiosis is neither casual nor random. Its original establishment seems to have depended on access to numerous potential symbionts, together with a regular supply of oxygen and sulfide. In burrowing, benthic bivalves the inhalant siphon would likely impede sulfide uptake from the burrow. On the other hand, an anterior inhalant current, or simply the pedal aperture, provides a potential route for sulfide absorption if the normal tendency to "clam-up" in the presence of this molecule is inhibited.

In *Calyptogena* (Vesicomysidae) the siphons are short and the pedal aperture large (Figure 11). BERNARD (1974),

BOSS & TURNER (1980), and MORTON (1985) note the presence in *Calyptogena* spp. of expanded subfilamental gill tissue, suggesting that the genus arose from a symbiotic ancestor. BOSS & TURNER (1980) did not find food grooves in *Calyptogena magnifica* and consider this a correlate of the symbiotic habit. MORTON (1985) identifies a small food groove at the margin of the inner demibranch of *C. magnifica* and argues that this feature, together with a gut and digestive diverticula of "normal" proportions, indicates that the digestion of free-living bacteria is an important part of this bivalve's alimentation, and that its dependence on symbiotic bacteria has perhaps been exaggerated. Nevertheless, FIALA-MEDIONI (1984) has identified numerous gill bacteria in this species. ARP *et al.* (1984) have shown that the vascularized foot of *C. magnifica* is protruded down between the lumps of debris of the hydrothermal vent regions to reach interstitial water with a high sulfide content. At the same time it can take in oxygen through the inhalant siphon. In the vent mytilid

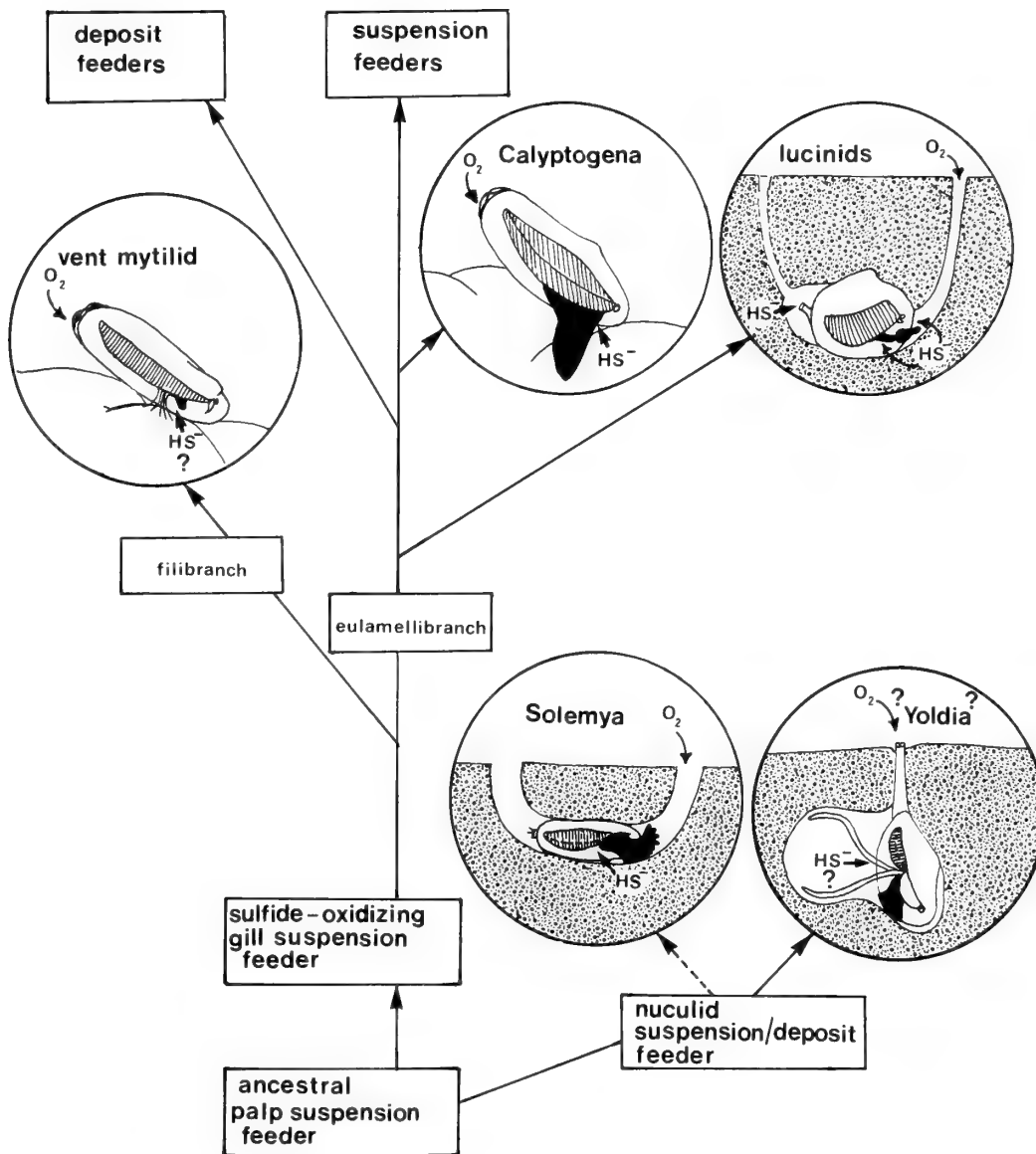


Figure 11

Distribution of sulfide-oxidizing symbiosis in relation to bivalve evolution. Gills are indicated with vertical hatching, feet in solid black; palps are indicated to the anterior (right) of the gills. The sketch of the lucinid is based on ALLEN (1958); that of *Calymene* is based on ARP *et al.* (1984) and MORTON (1985). The *Yoldia* drawing is after BENDER & DAVIS (1984). The inclusion of *Yoldia* in this scheme is debatable, because it has not been established that the few bacteria in the gills are sulfide-oxidizing.

Bathymodiolus thermophilus (Kenk & Wilson, 1985) there may be a similar route of sulfide acquisition. LE PENNEC & HILY (1984) report that the gills of this organism have a bacterial epiflora as well as intracellular symbionts. The gill filaments are broad and fused ventrally to form septa, and distinct food grooves are present. KENK & WILSON (1985) note that the gut is simplified. We observe, as do KENK & WILSON (1985), that the mantle edges of this

species are fused between the pedal aperture and the inhalant siphons. This may be correlated with the partitioning of sulfide and oxygen. It is obvious that in a crowded community where the primary producers are sulfide-oxidizing bacteria, and where one or more of the metazoa have entered mutualistic symbioses, there is great potential for this type of association to become established in other members of the community, through interphyletic

transmission of symbionts. Interestingly, HICKMAN (1984) identifies a distinct *Thyasira-Lucinoma-Solemya* community from Cenozoic deep-water deposits. This could also be characterized as a sulfide-oxidizing community, similar to what we find at the present time.

The Significance of the Anterior Inhalant Current

In the Lucinacea, the anterior inhalant opening and absence of the inhalant siphon are more likely paedomorphic than primitive. Members of another bivalve assemblage, the Leptonacea, which MCALESTER (1966) presents as a possible offshoot of the Lucinacea (Figure 10B), also lack the inhalant siphon and have an anterior inhalant opening; in some a short, anterior inhalant siphon is present. Members of the Leptonacea, a group of debatable lineage, comprising small, ephemeral bivalves on the whole, are generally regarded as paedomorphs subject to r-selection. This condition would also be receptive to sulfide-oxidizing bacteria, and once a symbiosis were established an increase in size and prolongation of the lifespan could follow. Although one species of the leptonacean genus *Kellia* is known to lack the usual symbiotic enzymes (FELBECK *et al.*, 1981), members of this group from high sulfide silts deserve further examination.

In other bivalves the juvenile habit involves an anterior feeding current created by the pedal ciliation. Indeed, OCKELMANN & MUUS (1978) point out that there are no known exceptions, observing that this is a necessary means of separating inhalant from exhalant flow in minute bivalves. Details of this ciliation are available for *Macoma balthica* (CADDY, 1969), *Mytilus edulis* (BAYNE, 1971), and *Abra alba* (AABEL, 1983). In *Panope abrupta* juveniles, pedal ciliation and muscular activity direct a stream of food particles through the pedal aperture on to the labial palp surfaces (KING, 1985, and personal communication). In mature *Mysella bidentata* the inhalant current has been described by OCKELMANN & MUUS (1978) and pedal detritus-feeding in this species is discussed by O'FOIGHIL (1981). McMahon (personal communication) has discovered that adult *Corbicula fluminea* are pedal detritus-feeders. AABEL (1983) observes that juvenile *Abra alba* ingest deposit material anterior to the foot, and that they continue to feed in anoxic deposits. If this is a common habit in juvenile Tellinacea it is all the more surprising that the most opportunistic genus *Macoma* has not taken up with sulfide-oxidizing symbionts, especially *Macoma carlottensis*, which is so frequently found in the company of *Solemya reidi*, *Parvilucina tenuisculpta*, and *Thyasira flexuosa*. We conclude that the specialized feeding behavior and functional morphology of this and other species is an obstacle to the sulfide uptake necessary for symbiosis, despite the potential susceptibility of the juveniles.

In the Protobranchia, which include the Solemyidae, the anterior inhalant opening and the absence of an inhalant siphon are regarded as a primitive condition. LILJEDAHL (1984) has proposed the Silurian protobranch *Ja-*

neia silurica as an intermediate between nuculoids and solemyoids, possessing smaller gills than modern symbiotic *Solemya* species. Somewhere along this evolutionary line the symbiotic association was formed, allowing the enlargement of the aspidobranchiate gills, regression of the labial palps and gut, and modifications in burrowing and ventilation behavior, features that the Lucinacea have partially paralleled. Indeed, gill enlargement and palp reduction are evolutionary processes that have been followed in all bivalves, and the question that we wish to pose here is whether or not sulfide-oxidizing symbiosis might have had a much more central role in bivalve evolution than has hitherto been suspected. To begin to answer this it is first necessary to consider the more general question of the habit of the most primitive protobranch bivalves.

Feeding Habits of the Nuculidae

The detritus-feeding habit of the recent Nuculidae, together with their shell dentition, are taken to represent the founding condition of the Bivalvia by YONGE (1939). However, STASEK (1965) argues from a study of *Acila castrensis* that the nuculids were primitively suspension-feeders, their gills being functional food-collecting organs, and that the detritus-collecting palp proboscides are a secondary development of the terminal posterior ciliated ridges of the food-sorting palp lamellae. On the basis of previously unpublished observations of *Nucula sulcata* by the senior author we agree with Stasek. Specimens of *N. sulcata* whose palp proboscides had been surgically removed in the manner employed by STASEK (1961), and which had been mounted in a suspension of *Aquadag*, effectively filtered and ingested graphite particles. The palp lamellae are the primary feeding organs; their complex, ciliated inner surfaces collect and sort suspended particles from the anterior inhalant current (Figure 12). The gills, being small, are less significant collecting organs. The detritus-collecting palp proboscides are, as Stasek suggests, an evolutionary after-thought. As we have already pointed out, feeding from an anterior inhalant current is a universal characteristic of post-larval bivalves and, in the cases noted above, the relatively large labial palps are the primary collecting and sorting organs, prior to the growth of the gills and their establishment as the most important filtration site. An anterior inhalant stream might be regarded as a necessary consequence of small size, and the primary role of the labial palps interpreted as a necessary juvenile specialization. But it must be remembered that these are also the primitive arrangements and are in all likelihood a case of ontogeny repeating phylogeny. We would argue that the primitive protobranchs received a mixture of suspended and deposit particles that were collected and sorted by the palps and that the Nuculidae became specialized detritus-feeders with the development of the palp proboscides. We find no bacteria in the gills or palps of the nuculid *Acila castrensis* and assume that this is representative of the nuculid condition.

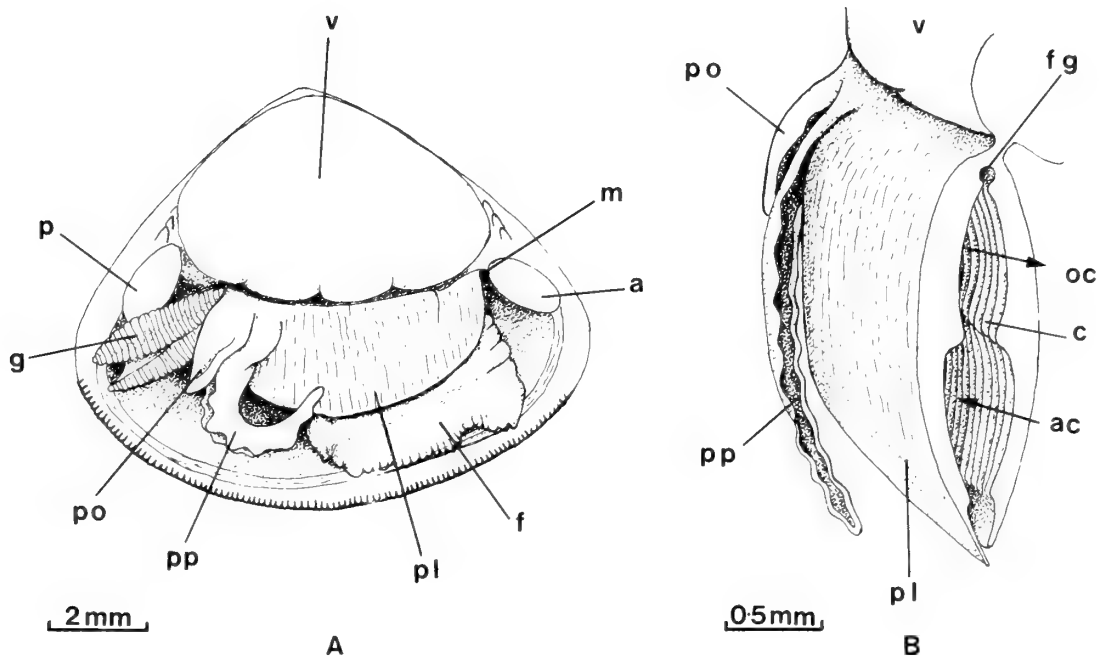


Figure 12

The feeding apparatus of *Nucula sulcata*. A. Right lateral view of animal with mantle removed. B. Solid section of the labial palp complex looking toward the posterior. The aboral current (ac) contributes to the general anterior inhalant current. The oral current (oc) is an interrupted flow due to the appression of the high ridges of the dorsal regions of the interior of the palp lamellae. a = anterior adductor muscle; ac = aboral current; c = ciliated ridge of the palp lamellar interior; f = foot; fg = food groove; g = gill; m = mouth; oc = oral current; p = posterior adductor muscle; pl = palp lamella; pp = palp proboscis; po = palp pouch; v = visceral mass. Details of the sorting ciliation of the palps are similar to those of *Acila castrensis* (STASEK, 1961).

The Protobranchia and Early Bivalve Evolution

The nuculanid Protobranchia, and *Yoldia* in particular, have continued in the trend established by the nuculids, but with more effective ctenidial food collecting (STASEK, 1965). Stasek has also elaborated an interesting ctenidial function noted by DREW (1899) and YONGE (1939). The gills can act as a muscular pump, drawing water into the infrabranchial chamber, and also, via the exhalant siphon, into the suprabranchial chamber. Moreover, although the Nuculanidae have an inhalant siphon, one species at least, *Yoldia limatula*, can create a subsurface chamber with the proboscides, as BENDER & DAVIS (1984) have demonstrated (Figure 11). All of these features suggest the possibility of a sulfide-oxidizing symbiosis in this genus. However, although we have identified bacterium-like bodies in some cells of the ctenidia of *Yoldia scissurata*, we do not know if these are capable of sulfide-oxidation, and even if this proves to be the case, the symbiosis has either regressed or failed to progress to the point where there are many well-defined bacteriocytes capable of making a significant contribution to the nutrition of the species.

Generalizing on the subject of early lamellibranchiate bivalve evolution PURCHON (1978) writes, "The emer-

gence of this filter-feeding model was a mega-evolutionary change: The stuff of which subclasses are made!" As to what this new model emerged from, there is no positive evidence for the traditional view that the founding habit was infaunal detritus-feeding. We prefer the suggestion of a palp suspension-feeder, quite possibly an epifaunal bivalve on a hard surface as inferred by STASEK (1972, and personal communication): significantly most other bivalved and quasi-bivalved invertebrates, Ostracoda and some Branchiopoda (Crustacea) and Brachiopoda, are epifaunal or planktonic suspension-feeders. Exceptions are the Juliidae, bivalved gastropods that are specialized suctional browsers on macroalgae. The functional correlates of the bivalve form are protection of the enlarged, vulnerable food-collecting organs, and energetic efficiency in generating feeding currents. Invertebrate detritus-feeders are more commonly wormlike burrowers.

If the bivalves arose monophyletically from an aspidobranchiate, suspension-feeding ancestor whose primary food-collecting organs were the labial palps, how did the switch of primary feeding function to the gills occur? A sudden allometric shift might have been responsible. A sulfide-oxidizing symbiosis might also have triggered ctenidial expansion, as in the Solemyidae, with the new po-

tential for more efficient suspension-feeding being realized before the hypotrophy of the gut became irreversible. The vascularization of the gills would make them a likely repository for blood-borne symbionts. Possibly these initially provided an exogenous epigenetic growth stimulus for the gills, which was finally genetically assimilated. The sieving mechanism of the ctenidial filter, if large enough, would certainly be more effective than the palp surfaces, providing the new model extolled by Purchon.

CONCLUSIONS

The Bivalvia are not necessarily the only class of Mollusca that have experimented with sulfide-oxidizing symbiosis. The scaphopod *Dentalium rectius* is commonly found in association with *Parvilucina tenuisculpta* and *Thyasira flexuosa*, and like other scaphopods has the potential for a regulated influx of sulfide and oxygen. Moreover, concentrations of "symbiotic" bacteria have been found in the polar region of scaphopod eggs (GEILENKIRCHEN *et al.*, 1971; DUFRESNE-DUBE *et al.*, 1983). Bacterial colonization of the gills of a new species of archaeogastropod limpet from the Juan de Fuca hydrothermal vents has been noted by DE BURGH & SINGLA (1984). Their study indicates two possible routes of entry for an incipient symbiont: the gill epithelia endocytose and digest the bacteria, and also the hypotrophic gut contains similar bacteria. De Burgh and Singla admit the possibility that if some bacteria were resistant to digestion by the host a mutualistic symbiosis could result, although they are disinclined to conclude that the subject of their study is on the road to endosymbiosis. Nevertheless, this route to a symbiotic destination seems to have been taken by *Solemya reidi*. WILKINSON (1984) has argued that, because according to immunological analysis the bacterial symbionts in sponges are closely related, symbiosis must have been a unique Precambrian event. This does not preclude transspecific infection within the phylum, nor even interphyletic transmission, as may be the case in the dinoflagellate symbionts of reef corals and giant clams (FITZ & TRENCH, 1981) and in the hydrothermal vent communities (STAHL *et al.*, 1984). The latter authors also find that the symbionts of the intertidal *Solemya velum*, though morphologically distinct, are related to the hydrothermal vent community symbionts in terms of ribosomal RNA sequence similarities.

In conclusion, one, or a small number of free-living species of sulfide-oxidizing bacteria, seems to have had the potential for endosymbiosis with sedentary marine invertebrates living at the interface between an aerobic environment and a sulfide-generating anoxic environment. Once established, the potential for interphyletic transmission was realized. Amongst the bivalves the primitive anterior inhalant feeding current, or its paedomorphic retention, together with the absence of an inhalant siphon, seem to have enhanced susceptibility to the symbiosis. Paedomorphic gill and gut structures were other corre-

lates, along with the development of subfilamental tissue to accommodate bacteria and the ability to partition the supply of oxygen and sulfide either physically or temporally. As far as the bacteria are concerned the bivalve is a dependable interface between the anaerobic and aerobic environments, the obligatory sources of their metabolic needs, releasing them from vacillations and other vicissitudes of the free-living condition. These symbioses have provided the major evolutionary drive for the emergence of the Lucinacea and the Solemyidae, and they may have participated in other areas of molluscan evolution.

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Roles of the Home Scar of *Collisella scabra* (Gould)

by

CAROLINE KUNZ

Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, California 94923, U.S.A., and
Department of Entomology, ETH Zürich, Clausiusstr. 21, 8092 Zürich, Switzerland

AND

VALERIE M. CONNOR

Department of Zoology, University of California, Davis, California 95616, U.S.A.,
and Bodega Marine Laboratory

Abstract. Most individuals of the prosobranch limpet species *Collisella scabra* (Gould, 1846) form a permanent home depression or home scar from which they forage. Laboratory experiments indicate that while on a scar, limpets are significantly less vulnerable to predation by *Pycnopodia helianthoides* (Asteroidea), *Pachygrapsus crassipes* (Crustacea), *Clinocottus* spp. (Pisces), *Octopus dofleini* (Cephalopoda), and *Freemania litoricola* (Turbellaria). A home scar effectively reduces predation by *Cancer antennarius* (Crustacea) only when limpets without home scars are more abundant than limpets on home scars. A home scar does not significantly reduce predation by *Pisaster ochraceus* (Asteroidea). Field work suggests that other roles of the home scar include a reduction in desiccation-induced mortality, as well as improved survival following sand burial. Limpets on home scars adhere to the rock more tightly than limpets off home scars.

INTRODUCTION

MANY SPECIES of prosobranch and pulmonate limpets consistently return to the same site after their foraging activities (reviewed by UNDERWOOD, 1979, and BRANCH, 1981). Homing limpet species frequently form distinct substrate depressions called home scars. Usually a limpet will fit precisely into these depressions. LINDBERG & DWYER (1983) have shown that the home depression consists of two structural levels, an outer level that conforms to the shell margin and a central deeper depression that corresponds to the limpet's foot dimensions. It is important to distinguish homing behavior (site specificity) from scar formation because each can have several distinct roles, none of which are mutually exclusive. GARRITY & LEVINGS (1983) and LINDBERG & DWYER (1983) have reviewed the major hypotheses concerning the role of a home scar. A home scar can provide protection from biotic factors such as predation (BRANCH, 1975; VERMEIJ, 1978; COOK, 1980; WELLS, 1980; GARRITY & LEVINGS, 1983) and agonistic encounters from competitors (WRIGHT, 1977). A home scar also can provide protection from abiotic factors such as desiccation stress (FRETTER & GRAHAM, 1962; McALISTER & FISHER, 1968; DAVIES, 1969; HA-

VEN, 1971; WOLCOTT, 1973; BRANCH, 1975; COOK, 1976; VERDERBER *et al.*, 1983; GARRITY, 1984), dislodgement by wave impact, and injury or dislodgement by sand scour (WOLCOTT, 1973).

These potential adaptive functions of home scars have been invoked widely, but there is little direct experimental evidence to support them (see BRANCH, 1981). In this paper we present evidence that the home scar of the prosobranch limpet *Collisella scabra* reduces predation rates for several predators. We also provide new evidence suggesting that the home scar reduces mortality induced by abiotic factors.

Collisella scabra (Gould, 1846) is found in the upper intertidal and splash zones on rocky shores of North America from the tip of Baja California to Cape Arago, Oregon (LINDBERG, 1981). This limpet has been well studied (reviewed by ABBOTT & HADERLIE, 1980), and its ability to home and form home scars is well documented (HEWATT, 1940; VILLEE & GROODY, 1940; BRANT, 1950; JESSEE, 1968; LINDBERG & DWYER, 1983). The natural predators of limpets include several species of small mammals, birds, fish, seastars, crabs, mollusks, and flatworms (reviewed by WELLS, 1980, and BRANCH, 1981).

Table 1

Predators used in laboratory feeding experiments, including numbers and sizes used. Sizes of limpets offered to each predator are also indicated.

Species	Number of predators	Size of predators	Limpet size (mm)
<i>Pisaster ochraceus</i>	4	11 cm, arm length 8 cm, arm circumference	15–20
<i>Pycnopodia helianthoides</i>	1	20 cm, diameter	15–20
<i>Pachygrapsus crassipes</i>	4	3 cm, carapace width 2.5 cm, chelae length	15–20
<i>Cancer antennarius</i>	4	9 cm, carapace width 3.5 cm, chelae length	12–23
<i>Freemania litoricola</i>	5	2 cm, length	<10
<i>Clinocottus</i> spp.	6	8 cm, standard length	10–15
<i>Octopus dofleini</i>	1	15 cm, arm length	10–15

Specifically, this study focused on the following predators of *Collisella scabra*: *Pisaster ochraceus* Brandt, 1835 (Asteroidea), *Pycnopodia helianthoides* Brandt, 1835 (Asteroidea), *Pachygrapsus crassipes* Randall, 1839 (Crustacea), *Cancer antennarius* Stimpson, 1856 (Crustacea), *Freemania litoricola* (Heath & McGregor, 1912) (Turbellaria), *Octopus dofleini* Wülker, 1910 (Cephalopoda), *Clinocottus recalvus* Girard, 1857 (Pisces), and *Clinocottus analis* (Girard) (Pisces).

MATERIALS AND METHODS

Laboratory Predation Experiments

Collisella scabra and predators were collected during spring 1983 from rocky sites located on, or adjacent to, the Bodega Marine Laboratory Reserve (Sonoma Co., California). Rocks containing *C. scabra* on home scars were brought directly into the laboratory. Limpets that were to be offered without home scars to predators were gently pried off field rocks with a small spatula. These limpets were allowed to attach to rocks, but lacked home scars. Animals were maintained in aquaria coupled to a flow-through seawater system. Predators were starved for 48 h prior to the start of an experiment, and experiments were conducted within 3 days of animal collection.

For each experiment three to six rocks were situated on the bottom of a flow-through aquarium. On the rocks were 10 pairs of *Collisella scabra*; for each limpet with a home scar there was one limpet without a home scar. To eliminate handling bias, each limpet on a home scar was removed with a spatula (in the same way as limpets with-

out home scars) and then returned to its home scar. *Collisella scabra* individuals, with and without scars, were distinguished from each other by small lines or dots of paint applied to the top of each shell. Specific predators were introduced into each aquarium, and the experiments were run for 3 days. To keep the number of *C. scabra* constant, aquaria were checked every 12 h for consumed limpets; consumed limpets were replaced. Limpets with home scars were replaced by adding rocks with the appropriate number of limpets on home scars. The procedure was changed for the experiment involving *Freemania*. The lower feeding activity of these flatworms necessitated longer trials; this experiment ran for 23 days and 5 pairs of limpets were used in each trial.

The number of predators and predator size varied for each experiment (Table 1). Preliminary studies and literature sources were used to determine the range of limpet sizes offered to each predator (Table 1).

Behavioral Observations

Collisella scabra with home scars may be consumed while on scars or when off (e.g., while foraging). The laboratory predation experiments did not discriminate between these alternatives. In order to obtain a better understanding of the predation process, seastar and crab predators were observed directly during the feeding experiments. Because crabs feed primarily at night, they were observed by using a red light. All other observations took place during the day. An additional set of observations was made on *Cancer* crabs that were offered 20 limpets without home scars (instead of 10) and 10 limpets with home scars.

Field Experiments

A field study was conducted to assess the differential survival of *Collisella scabra* individuals with and without home scars. Two experimental plots were established on exposed, rocky surfaces. In a 2 × 1.5-m plot, 101 *C. scabra* were removed, marked, and replaced on their home scars. An equal number of *C. scabra* were removed from another location, marked, and positioned next to the limpets located on home scars. In order to control for emigration, a second plot, 2 × 1 m, was outlined with Tanglefoot® to prevent limpet movement out of the plot. In this plot, 53 limpets with scars and 53 limpets without scars were handled in the same way as limpets in the first plot. After 8 days, the number of remaining *C. scabra* individuals with and without home scars was determined. This experiment was repeated 2 wk later at the same sites with 103 pairs of limpets in the first plot and 45 pairs of limpets in the plot outlined with Tanglefoot. During the first experiment, low tides occurred at midday during a week of unusually hot and sunny weather. The second experiment was run during a more typical week of early morning tides and cool, cloudy weather. Exposure and intertidal height (+1.6 m above MLLW) of the two sites were

Table 2
Numbers of *Collisella scabra* consumed during predation experiments.

Predator	Total	With-		G	P
		out scar	With scar		
<i>Pisaster ochraceus</i>	73	42	31	1.67	>0.10
<i>Pycnopodia helianthoides</i>	66	47	19	12.26	<0.001
<i>Pachygrapsus crassipes</i>	29	21	8	6.04	<0.025
<i>Cancer antennarius</i>	60	36	24	2.41	>0.5
<i>Freemanian litoricola</i>	10	8	2	3.86	<0.05
<i>Clinocottus</i> spp.	21	18	3	11.88	<0.001
<i>Octopus doffeini</i>	4	4	0	4.92	<0.05

comparable except the site without Tanglefoot contained horizontal and vertical surfaces; the site with Tanglefoot consisted of only horizontal surfaces.

RESULTS

Laboratory Predation Experiments

The importance of a home scar in reducing predation depended on the predator species. Based on a G-test (William's correction when $n < 10$) (Table 2), *Pycnopodia*, *Pachygrapsus*, *Freemanian*, *Octopus*, and *Clinocottus* consumed significantly more *Collisella scabra* without a home scar than *C. scabra* with a home scar. The results for *Cancer* and *Pisaster* were not statistically significant, but more predation on *C. scabra* without home scars did occur.

Behavioral Observations

Pycnopodia. *Pycnopodia* covered an entire rock while it was feeding, so ingestion could not be observed directly.

The *Pycnopodia* moved over each of 6 rocks, stopping for 5 to 10 min on each. After 45 min all but one of the limpets without a home scar were eaten, but no limpets on scars were eaten (Table 3). After 1.5 h the seastar became active again, but it passed over rocks on which there were limpets on home scars. At one point, however, the seastar moved onto a section of a rock where 2 of 3 limpets possessing home scars were not in their scars. When the seastar left the rock after 10 min, both limpets that had been off of their home scars had been consumed. The seastar continued to move over the rocks within the aquarium and did not feed on any *Collisella scabra* individuals located on home scars, but consumed the last limpet that was without a home scar.

Pisaster. After the tube feet of a *Pisaster* encountered a limpet, the seastar would move in the limpet's direction and cover it for about 10 min. *Pisaster* did not seem to distinguish between limpets on or off of home scars; numbers of limpets consumed and handling time were not substantially different for limpets on or off home scars (Table 3).

Pachygrapsus. Frequently, *Pachygrapsus* would touch limpets with its legs or chelipeds. On several occasions a crab would sit for up to 5 min in front of a limpet without touching it. Other times, a crab quickly would touch a limpet with a claw. Crabs attacked limpets by grasping a limpet shell with a cheliped. If the limpet was removed, it was held with one cheliped while the limpet flesh was removed with the other. The crabs frequently switched the limpet from one claw to the other.

Pachygrapsus was never observed removing a *Collisella scabra* from a home scar, but frequently tried to do so. Usually a crab would try for 1 or 2 sec, but attempts occasionally lasted up to 60 sec. For limpets not on home scars, crabs never required more than 5 to 10 sec to remove the limpet from the substrate (Table 3).

Table 3

Summary of predator behavioral observations. Predators were offered 10 limpets with home scars and 10 limpets without home scars, except for the second *Cancer* observation period. Twenty limpets without home scars were used in that second trial.

Predator	Observation period	Number limpets consumed			Handling time (min)	
		With scars		No scar	On scar	Off scar
		On	Off			
<i>Pisaster ochraceus</i>	1400-1730 hours (210 min)	4	1	7	10-15	10-15
<i>Pycnopodia helianthoides</i>	1400-1730 hours (210 min)	0	2	10	5-10*	5-10
<i>Pachygrapsus crassipes</i>	0000-0600 hours (360 min)	0	2	3	0.08-1*	0.08-0.17
<i>Cancer antennarius</i>	0000-0600 hours (360 min)	4	4	10	0.5-10	0.05-0.08
		2	2	15	up to 0.5	0.05-0.08

* Unsuccessful attempts.

Table 4

Numbers of *Collisella scabra* missing from field plots after eight days.

Number of missing limpets	Experimental plot (no Tanglefoot)		Control plot (Tanglefoot)	
	Sunny/hot period n = 101	Cloudy/cool period n = 103	Sunny/hot period n = 53	Cloudy/cool period n = 45
With home scars	12 (14%)	3 (3%)	8 (15%)	2 (4%)
Without home scars	46 (45%)	26 (25%)	45 (85%)	15 (33%)

Cancer. These crabs appeared to search actively for limpets. Crabs repeatedly spread their chelipeds, and took a step forward while bringing their chelipeds close together anteriorly. After a *Cancer* encountered a limpet with its chelae, the crab would try to remove it by squeezing the limpet between a chela and pulling it off the rocks. The crabs used both claws for feeding. The shell was crushed and the flesh pulled out using the maxillipeds. One dominant *Cancer* individual consumed 75% of the limpets ingested. Two of the four crabs ate no limpets.

Limpets with and without home scars were consumed by *Cancer*, but the handling time was longer for limpets in scars (up to 10 min compared with about 0.08 to 0.17 min). Crabs always were successful in removing limpets without home scars, but would frequently be unsuccessful if a limpet was on a scar (Table 3). Crabs seemed to remember the location of limpets and would return to try again if another limpet was not quickly encountered. During the second observation period, the crabs were placed in an aquarium containing 10 limpets within scars and 20 (instead of 10) limpets without scars. During this period, the time spent attacking limpets on scars decreased after crabs encountered several limpets without scars. Subsequent attacks on limpets on scars were rare.

Field Experiments

A survey of the experimental plots after 8 days indicated that more limpets without home scars were missing from the plots than limpets with home scars. For both the sunny, hot period and the cloudy, cool period, greater numbers of scar-denied limpets were missing from both the Tanglefoot plots ($\chi^2 = 24.4$, $P < 0.05$; $\chi^2 = 8.5$, $P < 0.05$) and the non-Tanglefoot plots ($\chi^2 = 18.8$, $P < 0.05$; $\chi^2 = 16.7$, $P < 0.05$). The relative loss of limpets with and without home scars was higher in the Tanglefoot plots for each trial. Mortality was greater for limpets both with and without home scars during the sunny, hot period when compared to mortality during the cloudy, cooler period (Table 4).

DISCUSSION

Behavioral observations and the results of the laboratory experiments indicate that the effectiveness of a home scar in the reduction of predation depends on the predatory species. Possession of a home scar effectively reduced predation by the seastar *Pycnopodia*. Behavioral observations suggest that limpets with home scars were consumed only when they were off their scars foraging. In nature *Collisella scabra* lives higher in the intertidal zone than *Pycnopodia*, and their distributions rarely overlap. WELLS (1980) has shown that *C. scabra* forages only while awash; during high tide limpets remain on their home scars. The possession of a home scar (coupled with the above mentioned activity pattern) appears to be an effective predation avoidance mechanism.

Pachygrapsus is another predator that cannot prey as effectively on limpets on home scars. CHAPIN (1968) suggests that one method by which a *Pachygrapsus* attacks a limpet is by prying the limpet off a rock using a cheliped. However, Chapin notes that this method is effective only if the limpet does not have its shell clamped to the substrate; the crab must be able to get underneath the shell edge. A home scar eliminates this mode of attack. Behavioral observations suggest that *Pachygrapsus* also removes limpets by pinching the top of the shell and pulling. This was never successful when a limpet was on a home scar, but took only 5 to 10 sec when limpets were not on scars.

In contrast to *Pachygrapsus*, *Cancer antennarius* are able to prey upon *Collisella scabra* on home scars. The specimens of *Cancer* used in this study were larger and presumably stronger than those of *Pachygrapsus*. *Cancer* was never observed prying limpets off the rocks; instead it grasps limpet shells with a cheliped and pulls. Behavioral observations indicate that limpets without home scars are removed from rocks much more quickly than limpets with home scars (0.05–0.08 min versus 0.5–10 min). The number of attempts and the amount of time crabs spent attacking limpets on scars decreased when the proportion of limpets without home scars was increased. In nature one might expect a home scar to reduce predation rates on *C. scabra* because other gastropod species without home scars (or escape responses) presumably would represent a food resource with a shorter handling time.

Freemania may be a significant predator on *Collisella scabra*. *Freemania* and *C. scabra* do overlap in their intertidal distributions, although *C. scabra* is characteristically found higher than *Freemania* (PHILLIPS & CHIARAPPA, 1980). PHILLIPS & CHIARAPPA (1980) suggest that the snug fit of *C. scabra* in its home scar may reduce the probability that a limpet would be detected by a foraging flatworm, and if detected, successfully engulfed. In this study fewer limpets with home scars were consumed by *Freemania*.

WELLS (1980) showed that the home scar of *Collisella scabra* reduces the rate of predation by *Octopus bimaculatus*

(Verrill) and *Octopus bimaculoides* (Pickford & McConnaughey) in the laboratory. Wells reports that twice as much time was required for *Octopus* spp. to consume all of the limpets with home scars as was required to consume limpets without scars. The results of the present study provide further evidence that a home scar reduces predation by *Octopus* spp.

The home scar also effectively reduces predation by the sculpins *Clinocottus recalvus* and *Clinocottus analis*. The ability of a home scar to reduce fish predation was demonstrated experimentally for the pulmonate limpet *Siphonaria gigas* by GARRITY & LEVINGS (1983). Their experiments and observations on a pulmonate limpet agree with those of this study on a prosobranch limpet. Fish commonly forage for limpets in the intertidal zone, and limpets off their scars are quite vulnerable. Both *S. gigas* and *Collisella scabra* further reduce predation by remaining on their home scars during the most active fish feeding period (GARRITY & LEVINGS, 1983; WELLS, 1980).

In contrast to the other predators used in this study, *Pisaster* does not appear to distinguish between limpets on or off home scars. FEDER (1963) found that *Collisella scabra* is the most abundant limpet in the diet of *Pisaster*, even though the overlap of distributions of the seastar and *C. scabra* is minimal. GARRITY & LEVINGS (1983) report that home scars afford no protection for *Siphonaria gigas* from the seastar *Heliaster microbrachius*, but state this seastar is extremely uncommon.

The field experiments clearly indicate the survival value of a home scar for *Collisella scabra*. Limpets on home scars consistently exhibited higher survival than limpets without scars. One probable reason for enhanced survival is that home scars help reduce desiccation-related mortality. In both plots, mortality rates were higher during the hot and sunny experimental period than during the cool and cloudy experimental period. WOLCOTT (1973) reported that when individuals of *C. scabra* were placed on smooth surfaces, limpets with smooth shell margins had significantly lower desiccation rates than limpets with rough margins. This situation is analogous to limpets with and without home scars. Several studies have found that a home scar helps emerged limpets reduce water loss, and thus reduce desiccation-related mortality. This has been demonstrated for prosobranch (GARRITY, 1984) and pulmonate limpets (MCALISTER & FISHER, 1968; VERDERBER *et al.*, 1983). However, GARRITY (1984) found that although possession of a home scar resulted in a significant reduction in water loss for both *Siphonaria maura* and *Siphonaria gigas*, there was no significant difference in mortality between limpets on and off scars.

VERDERBER *et al.* (1983) present laboratory and field data that suggest that if *Siphonaria alternata* individuals are denied home scars they desiccate, causing a loss of muscular control, and become increasingly vulnerable to both predators and waves. Thus, *Siphonaria* may suffer mortality directly and indirectly due to desiccation effects.

This possibly was the situation in the current study. Visual examination of scar-less limpets during the sunny period revealed that almost all were desiccated and limpets were easy to pry manually off the substrate.

A priori, one would expect more scar-less limpets to have disappeared from the field plot without Tanglefoot because limpets could emigrate and benthic predators immigrate. However, in this study limpet disappearance was higher in the plot with Tanglefoot. Perhaps this is because the site outlined with Tanglefoot did not contain vertical surfaces while the Tanglefoot-free plot contained both horizontal and vertical surfaces. Limpets on vertical surfaces would be less vulnerable to predation by birds (Lindberg, personal communication; FRANK, 1982) and possibly desiccation stress (HAVEN, 1971). Unfortunately, limpet disappearance as a function of surface orientation was not noted in this study.

Another home-scar function was suggested in the spring of 1980, when one of us (V. Connor) had a study site that suddenly was covered with 2–3 m of sand. Before the sand appearance, the site contained large populations of *Collisella scabra* and another limpet *Collisella digitalis* (Rathke, 1833). After two months, sand levels were low enough to recensus the populations. Nearly all of the *C. scabra* (80%) had survived, but most of the *C. digitalis* (80%) had disappeared. As both species can survive starvation for this amount of time, one possible explanation for this observation is that the limpets with home scars can better resist the deleterious effects of sand burial than can limpets without home scars, such as *C. digitalis*.

An additional role of the home scar of *Collisella scabra* not examined in this study has been suggested by WRIGHT (1977). A home scar allows individual *C. scabra* to inhabit areas near the larger agonistic limpet *Lottia gigantea* Sowerby, 1834. The home scar prevents *C. scabra* from being pushed off the substrate by the aggressive *Lottia*.

The results of this and other studies indicate that it is more difficult to dislodge a limpet while it is on a home scar. This is in part due to the absence of a space between the shell margin and the substrate, but may also be due to an increase in the tenacity exhibited by limpets on home scars. Connor (in preparation) found that the shear force required to dislodge a stationary *Collisella scabra* from a home scar always exceeded 5.0 kg cm², while only 2–3.5 kg cm² were required to remove scar-denied limpets. Similar values were reported by Wright (in BRANCH, 1981: 348). This increase in tenacity exhibited by limpets on home scars may be an additional reason why a home scar provides protection from predators. It also may play a role in preventing dislodgement by wave forces, but under normal conditions this is probably not as significant. Other limpet species co-occur with *C. scabra* and typically exhibit tenacity values similar to scar-denied *C. scabra* (Connor, unpublished data).

The formation of home scars is cited most often as a mechanism to minimize desiccation and associated effects.

However, it also frequently is inferred that the primary role is not to prevent desiccation, but rather to prevent dislodgement (WOLCOTT, 1973). This idea is supported by the fact that subtidal species and intertidal species inhabiting tide pools also form home scars, even though there is little threat of desiccation (LINDBERG & DWYER, 1983). BRANCH (1975) suggests that home scars serve different functions in different species, including both predation and desiccation resistance. This is supported for both prosobranchs and pulmonates by the studies presenting direct evidence for home scar function. WELLS (1980), studying *Collisella scabra*, and GARRITY & LEVINGS (1983), studying *Siphonaria gigas*, propose that home scars serve to reduce predation. VERDERBERGER *et al.* (1983), studying *Siphonaria alternata*, and GARRITY (1984), studying *Scurria stipulata*, suggest that home scars serve to reduce desiccation. However, there is no reason for assuming the exclusivity or primacy of any one function or that home scars serve the same roles in both prosobranch and pulmonate limpets. In this study, the home scar of *C. scabra* simultaneously affords protection against many factors. The multiple roles of a home scar occur simultaneously because the mechanisms by which scars afford protection appear to be the same. Higher tenacity while in the home scar increases the force necessary to dislodge a limpet by any force, including predators, competitors, or wave shock. The close fit of the shell margin to the substrate reduces rates of water loss and the effectiveness of predators that need to get under the shell, as well as protecting vulnerable tissue from injury by moving sand particles and predators.

We suggest that the home scar has no single role in *Collisella scabra*, but rather serves to protect this limpet from a variety of factors that an individual limpet may encounter during its lifetime.

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Observations on the Mechanism of Detecting Mucous Trail Polarity in the Snail *Littorina irrorata*

by

D. STIRLING AND P. V. HAMILTON¹

Department of Biology, University of West Florida, Pensacola, Florida 32514, U.S.A.

Abstract. Marsh periwinkles, *Littorina irrorata*, can detect the polarity of conspecific mucous trails for at least 60 min after they are deposited. Experiments indicate that trail polarity detection does not involve discriminating a longitudinal concentration macro-gradient of a volatile chemical substance using the paired cephalic tentacles. If only one cue provides trail polarity information, then a bilateral trail asymmetry, a topography-based physical map, and a reflected light pattern are probably not involved either. The possibility that trail polarity information is obtained from directional microstructures in gastropod mucous trails is discussed.

INTRODUCTION

CRAWLING GASTROPOD MOLLUSKS typically deposit a mucous trail on the substratum, and this trail may subsequently be detected by a predator or conspecific. Many early studies of conspecific trail following by gastropods were surveyed by COOK & COOK (1975), COOK (1977), and HAMILTON (1977a). More recent studies have documented conspecific trail following in *Ilyanassa obsoleta* (TROTT & DIMOCK, 1978), *Achatina fulica* (CHASE *et al.*, 1978), *Onchidium verruculatum* (MCFARLANE, 1980), *Mariella dussumieri* (USHADEVI & KRISHNAMOORTHY, 1980), *Nerita textilis* (CHELAZZI *et al.*, 1985), and other *Littorina* species (GILLY & SWENSON, 1978; RAFTERY, 1983).

Many of these gastropods exhibit a preference for following their own or a conspecific's mucous trail in a specific direction. In *Biomphalaria*, *Ilyanassa*, *Littorina*, and *Physa*, the trail is followed preferentially in the same direction in which the trail-depositing snail was traveling; we refer to this response as following the trail "with polarity." In *Onchidium*, *Nerita*, and *Siphonaria*, the trail is followed preferentially in the opposite direction, or "against polarity." In either case, directional trail following probably involves a two-stage response: recognition of the presence of a conspecific mucous trail, followed by determi-

nation of trail polarity. Each stage could involve different stimuli and sensory mechanisms.

Contact with a mucous trail by cephalic or anterior tentacles appears necessary for detecting the presence of a trail in *Littorina planaxis* (PETERS, 1964) and some other gastropods. The tentacles are required to detect the polarity of a trail in *L. irrorata* (Robbins & Hamilton, in preparation). The exact mechanism involved in trail polarity detection has not been determined for any gastropod, although the following mechanisms have been suggested:

Concentration macro-gradient mechanism—involves sampling a longitudinal concentration gradient of some volatile chemical substance in the trail, at the points where the two anterior tentacles contact the trail (usually 6 to 10 mm apart). This mechanism requires use of the two tentacles, and it assumes that the snail's approach path is approximately perpendicular to the trail when contact is made.

Concentration micro-gradient mechanism—involves sampling a similar longitudinal concentration gradient, but along a distance equivalent to the width of one tentacle tip (usually less than 1 mm). According to this mechanism, only one tentacle would be required to detect trail polarity. Using both tentacles would merely furnish duplicative information.

Physical map mechanism—involves detecting some physical feature of the trail across an area in the plane

¹ Author to whom all correspondence should be addressed.

of the trail. The feature could be a repetitive pattern of topography (ridges and troughs in the surface of the mucus) or of viscosity (thin and thick mucus). Only one tentacle would be required for this mechanism, but the tentacle would have to contact a large enough area of the trail to discern the physical pattern. This mechanism was suggested by the mucous trails of *Littorina* and some other gastropods, which show repetitive patterns when stained (see Figure 2).

Bilateral asymmetry mechanism—involves the two sides of the trail having different chemical or physical properties (e.g., substance A in left side and substance B in right side), and the existence of some simple decision rule for determining trail polarity (e.g., turn left if A is detected first when a trail is contacted, but turn right if B is detected first). This mechanism would require only one tentacle. This mechanism was suggested by the fact that the foot of *Littorina*, and other gastropods that locomote by ditaxic pedal waves, exhibits bilateral organization in structure and neuromotor control.

Reflected light mechanism—involves determining trail polarity visually, by optical effects of mucus on light reflected from the trail. This mechanism was suggested by the fact that some gastropods can orient relative to light patterns reflected from the substratum (CHARLES, 1961).

Directional microstructure mechanism—involves detecting microstructures in the trail which are morphologically or chemically polarized. This mechanism would require only one tentacle.

GILLY & SWENSON (1978) hypothesized that a concentration macro-gradient mechanism is involved in trail following by *Littorina sitkana* and *L. littorea*. RAFTERY (1983) concluded that a concentration macro-gradient mechanism was likely for *Littorina* and that, if a structure-based mechanism was involved, the structural units providing polarity information must be smaller than 35 μm .

We have studied trail following in *Littorina irrorata* Say, a common inhabitant of marshes along the northern Gulf of Mexico. Snails rest on plant stems during high tide, but once the tide recedes they usually descend to the sand-mud substratum, where they crawl about and feed. When encountering conspecific mucous trails on the substratum, snails often follow these trails with polarity (HALL, 1973; HAMILTON, 1977b). RUSSELL (1980) found that those *L. irrorata* following mucous trails in laboratory arenas followed them with polarity 92.2% of the time ($n = 421$).

Our primary objective was to determine whether *Littorina irrorata* uses a concentration macro-gradient mechanism to detect the polarity of conspecific mucous trails. Experiments were conducted using a Y-maze enclosed within a controlled-stimulus environment. In addition, several other hypothesized mechanisms of polarity detection were examined, the effect of trail age on the ability to detect trail polarity was evaluated, and some general features of trail following behavior and mucous trail organization were described.

GENERAL METHODS

Adult *Littorina irrorata* (shell length >15 mm; shell width >11 mm) were collected from marshes bordering on Santa Rosa Sound, Escambia County, Florida. Snails were housed in plastic containers under simulated natural lighting conditions, and were used within 3 days after collection. General observations were made in shallow pans. All observations and experiments were conducted with the snails in air, the medium in which they are normally active.

Polarity detection tests were conducted in a Y-maze constructed of white plexiglas (Figure 1). A 3-cm length of mucous trail, specially modified in most experiments, was positioned near the junction and oriented perpendicular to the approach path of a test snail. The 4-cm wide path cut in the plastic base was restricted to a 2-cm wide path by overhanging strips of plastic bonded to the base (Figure 1B). This design forced snails approaching the junction to follow a fairly straight path while preventing them from climbing up the side of the maze. Three pieces of flat-black paper (9 cm high) were attached vertically at the ends of the maze opposite from the approach path of a test snail. One piece of paper (9 cm wide) was oriented perpendicular to the approach path of a test snail; the other two pieces (4 cm wide) were positioned at the ends of the left and right forks of the maze. The black pieces of paper ensured that test snails oriented first toward the maze junction, and then along one of the two forks. (The visual responses of *Littorina irrorata* are described by HAMILTON & WINTER [1982].)

Two identical mazes were constructed and used, and subsequent data analysis showed no significant differences between mazes. To eliminate any effect of possible left or right turning preferences on the data, tests were organized so that the same choice required left turns and right turns to be made equally often.

Straight lengths of mucous trail for testing were obtained using a 5-mm thick wooden base in which was cut a straight, 12-cm long channel designed with overhangs similar to those of the Y-maze. A piece of black paper (12 \times 9 cm) was attached vertically at one end of the channel in order to better orient the trail-depositing snail. The mucous trails were deposited on either glass plates or disposable clear plastic strips (0.1 mm thick) positioned beneath the channel.

During polarity detection tests, the Y-maze was placed inside a special arena having homogeneous white walls and a diffuse overhead light source. Light intensity on the arena floor was 2800 lux for all experiments, except for Experiment 7, which was run in darkness. A mirror beneath the arena floor permitted observation of a snail's progress during a test. For further details of arena structure see HAMILTON & WINTER (1982).

Certain response criteria were used in all experiments. Any snail not moving within 3 min after placement in the Y-maze, or taking longer than 10 min to enter one arm of the maze after initial movement, was discarded and

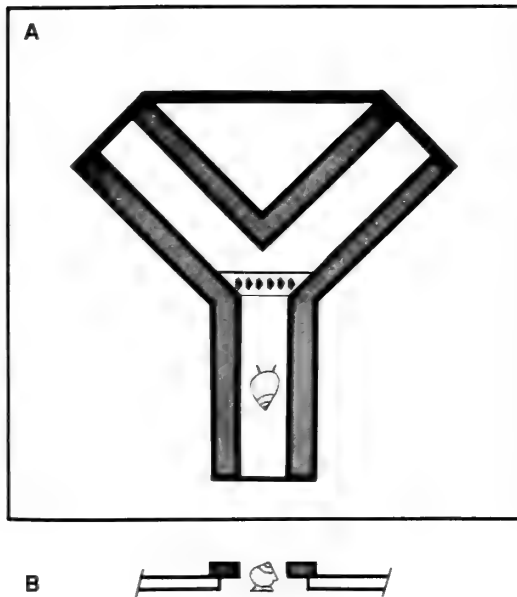


Figure 1

A. Top view of Y-maze used to study trail polarity detection. Three black paper targets (thickest lines) were 9 cm high. The maze was placed on the surface bearing the test mucous trail (stippled) so that the trail was positioned at the end of the approach path. The trail is drawn wider than normal. The arrows indicate the direction in which the trail-depositing snail was traveling. A mucous trail's width is normally about 50% of the depositing snail's shell width. A test snail is shown halfway along the approach path. B. Cross-sectional view of test snail on approach path showing overhangs (shaded). All tests with the maze were conducted in a special arena.

never used again. Also, we ignored the response of any snail not traveling up the center of the approach arm of the maze. Each snail's actual path was determined by direct observation from beneath during a test, and by examination of the test snail's mucous trail by misting (HAMILTON, 1977a) after the test. These precautions, and the narrow width of the approach arm of the maze, ensured that each cephalic tentacle of a test snail sampled a different section of those mucous trails that had been cut transversely and manipulated; this was especially important in Experiments 3 and 4. A snail had to move at least 2 cm into either fork of the maze to have made a choice. The choice of fork was assumed to have been influenced by trail polarity cues, even if the test snail did not follow the trail along its full available length, as was often the case. Each snail was tested only once.

RESULTS

General Observations

Figure 2 shows a *Littorina irrorata* mucous trail deposited on a white enamel surface and subsequently stained with 1% methylene blue for 2 min. The difference in stain

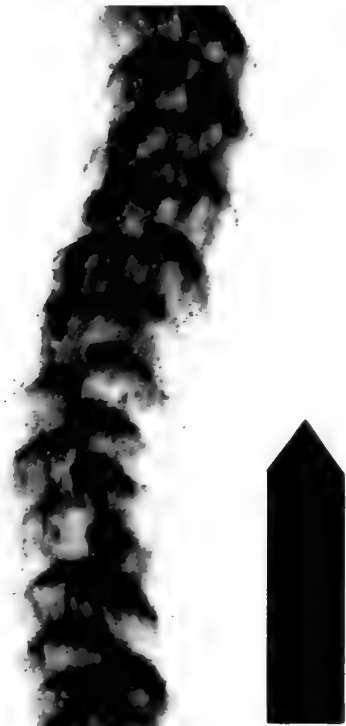


Figure 2

Stained mucous trail of *Littorina irrorata* showing chevron-shaped pattern of zones of high stain uptake. The 1-cm long arrow indicates the direction in which the trail-depositing snail was traveling.

pattern between left and right halves of the trail reflects the ditaxic pedal waves characteristic of littorinid locomotion. Chevron-shaped zones of high stain uptake are located at regular intervals; these zones appear to be produced by the front edge of each half of the foot as each half proceeds forward incrementally. Observations with the light microscope revealed a complex arrangement of microfibrils within the trail. Fibers have been reported in the mucous trails of *Ariolimax* (DENNY & GOSLINE, 1980), *Helix* (SIMKISS & WILBUR, 1977), and *Ilyanassa* (BRETZ & DIMOCK, 1983).

When a *Littorina irrorata* is crawling over a surface, the tip of each cephalic tentacle is brought into contact with the surface about once every 3 s. In an adult, contact points on the surface are spaced about 8 mm apart. As a tentacle tip is lifted, it is often dragged toward the snail a short distance (less than 1 mm) before "popping free" from its adhesive bond with the surface. Many snails begin turning with polarity only a few seconds after the tentacles make their first contact with the edge of a trail

Experiment 1: Polarity Detection

This experiment was conducted to determine the normal frequency of trail polarity detection in the test apparatus. Test mucous trails were deposited on glass plates

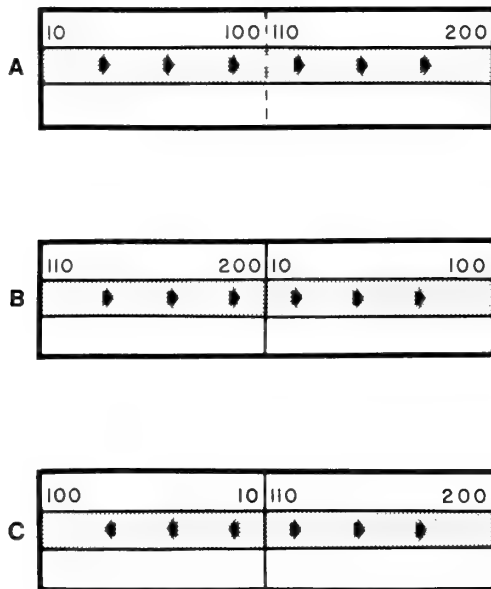


Figure 3

A. Length of mucous trail on long plastic strip. Numbers indicate approximate times (in s) when different sections of the trail were deposited. Dashed line shows where plastic and trail were cut after trail deposition. B. Manipulation of trail for Experiment 3. Assumed concentration gradient was made artificially high at the center, but the actual trail polarity was unchanged. C. Manipulation of trail for Experiment 4. Assumed concentration gradient was made artificially high at the center, while other potential cues were rendered directionally ambiguous. Arrows as in Figure 1.

Of 40 snails tested, 34 (85%) turned with polarity and 6 turned against polarity ($\chi^2 = 19.6$, $P < 0.001$). We conclude that *Littorina irrorata* shows a significant tendency to follow mucous trails with polarity in the experimental apparatus.

Experiment 2: Time Study

A 5- to 10-min interval normally occurred between deposition of a test mucous trail and actual testing of that trail. This experiment was designed to ensure that the polarity information provided by the trail did not change significantly over even longer periods. Test mucous trails were deposited on plastic strips which were then air dried for either 30 or 60 min before testing. Of 20 snails tested for each time interval, 18 snails turned with polarity and 2 turned against polarity ($\chi^2 = 12.8$, $P < 0.001$, for each time interval). The data show that *Littorina irrorata* mucous trails retain polarity information after at least 60 min of air exposure.

Experiment 3: Concentration Macro-gradient Mechanism—I

We tested the concentration macro-gradient hypothesis in two experiments. The first experiment was designed to

determine whether snails could detect correct trail polarity when the assumed concentration macro-gradient was artificially reversed at the point on the test trail where a test snail first made contact with it. Each test mucous trail was deposited on a plastic strip. For illustration purposes here, approximate time values are assigned to four points on the trail. The oldest end of the trail was designated $T = 10$ s, and the most recently deposited end was designated $T = 200$ s (see Figure 3A). The plastic strip was then cut transversely between the $T = 100$ and $T = 110$ s points on the trail, thus producing two sections of mucous trail on plastic. The positions of both sections of mucous trail were then switched, thereby connecting the $T = 10$ s part of the trail to the $T = 200$ s part of the trail. The actual direction in which the mucous trail was deposited thus remained the same for each section (see Figure 3B). The manipulated trail was then positioned in the Y-maze so that the test snail first contacted the trail at the junction of the two sections, and hence had the opportunity to sample both sections of trail. As mentioned above, pre- and post-test observations ensured that test snails actually sampled both sections of trail.

If a test snail turned toward the most recently deposited part of the trail ($T = 200$ s), it would turn against polarity; alternately, if a test snail turned toward the oldest part of the trail ($T = 10$ s), it would turn with polarity. Of 20 snails tested, 18 turned with polarity and 2 turned against polarity ($\chi^2 = 12.8$, $P < 0.001$). Thus, these data suggest that trail polarity detection does not depend primarily on a concentration macro-gradient mechanism.

Experiment 4: Concentration Macro-gradient Mechanism—II

This experiment was designed to determine whether snails could detect an assumed concentration macro-gradient when other potential cues about trail polarity were rendered directionally ambiguous. Test mucous trails were deposited on plastic and cut into two sections, as in the previous experiment. However, for this experiment, the oldest section of trail (time values from $T = 10$ to $T = 100$ s) was rotated 180° (see Figure 3C).

In this situation, if a concentration macro-gradient could be detected, most snails would be expected to turn right; alternatively, if a concentration macro-gradient could not be detected, an equal number of snails would be expected to turn left as right. Of 20 snails tested, 11 turned left and 9 turned right ($\chi^2 = 0.01$, $P > 0.25$). Thus, these data suggest that a concentration macro-gradient of a volatile chemical substance is not involved in trail polarity detection by *Littorina irrorata*.

Experiment 5: Physical Map Mechanism—Topography

As mentioned above, when a *Littorina* mucous trail is stained with methylene blue, chevron-shaped zones appear where more stain is taken up than by immediately surrounding areas (Figure 2). We considered the possi-

bility that the darkly stained zones might contain a deeper layer of mucus than in surrounding areas, and that the entire trail might have a regular pattern of topographic relief in the form of alternating ridges and troughs. This experiment was designed to learn if snails could still detect trail polarity after the trail was compressed so as to reduce or eliminate any assumed topographic relief.

Test mucous trails were deposited on glass plates. Each trail was compressed by applying finger pressure evenly against a plastic strip placed over the trail. A few mucous trails treated in this fashion still revealed a faint chevron pattern when stained, but most did not. Each glass plate bearing a compressed trail was tested in the Y-maze in the arena. Of 20 snails tested with compressed trails, 19 turned with polarity and 1 turned against polarity ($\chi^2 = 16.2$, $P < 0.0005$). These data suggest that a physical map in the form of a topographic relief pattern is not required for trail polarity detection.

Experiment 6: Bilateral Asymmetry Mechanism

The plastic strips used for compressing mucous trails (Experiment 5) hardly ever revealed the chevron pattern when stained, but imprints of the mucous trails were clearly visible on them. The left and right edges of these trail imprints coincided with the right and left edges of the original trails. This experiment was designed to learn if trail polarity detection requires a bilateral trail asymmetry coupled with a simple decision rule.

The plastic strips produced in Experiment 5 were placed at the junction of the Y-maze in the arena. If the trail edges were physically or chemically different, and a simple decision rule were involved, then snails tested with the trail imprints should have turned against polarity. Of 20 snails tested with these trail imprints, 18 turned with polarity and 2 turned against polarity ($\chi^2 = 12.8$, $P < 0.005$). Thus, this result suggests that a bilateral trail asymmetry, coupled with a simple decision rule, is not required for trail polarity detection. Retention of a stainable chevron pattern is apparently not critical either.

Experiment 7: Reflected Light Mechanism

As *Littorina irrorata* can see quite well (HAMILTON & WINTER, 1982; HAMILTON *et al.*, 1983), this experiment was conducted to test the possibility that reflected light patterns might reveal trail macrostructure, and hence trail polarity. Test mucous trails were deposited on glass plates. The arena lights were off during this experiment. The measured light intensity on the arena floor was less than 1 lux, which is below the threshold intensity required for *L. irrorata* to orient significantly toward a 5°-wide vertical black bar (HAMILTON & WINTER, 1982). Test snails were reluctant to run the Y-maze in such darkness, so two changes in protocol were effected to stimulate their movement. First, the arena slope was adjusted so that the approach path ran 5° upslope toward the junction. *Littorina irrorata* can detect slopes this small (Hamilton, unpublished data). Second, each *L. irrorata* was permitted to

wipe its cephalic tentacles on the mucus of a *Melongenella corona* for 30 s before release in the maze. *Littorina irrorata* orient upslope at almost twice their normal speed after contact with a *Melongenella*, their natural gastropod predator (Hamilton, unpublished data).

Of the 20 snails that ran the maze, 17 turned with polarity and 3 turned against polarity ($\chi^2 = 9.6$, $P < 0.005$). These data indicate that *Littorina irrorata* can detect trail polarity using other than visual cues.

DISCUSSION

A *Littorina irrorata* contacting a conspecific mucous trail with its cephalic tentacles usually turns with polarity almost immediately, and proceeds along the trail. The most commonly proposed hypothesis for the mechanism enabling this rapid determination of trail polarity has been a concentration macro-gradient involving some volatile chemical substance.

Three pieces of evidence argue against a concentration macro-gradient mechanism being involved in polarity detection in *Littorina irrorata*. First, although polarity information appears to last less than 30 min in the trails of some gastropods, this information lasts for at least 60 min (the longest time that we tested) in *L. irrorata* (Experiment 2); furthermore, Russell (unpublished data) found that *L. irrorata* showed a significant ability to detect polarity in trails dried in air for 24 to 36 h before testing. (A trail's presence could be detected for more than 72 h.) If a single volatile chemical substance were involved, such long-lasting trail polarity information would require a slow evaporation rate and, in turn, an incredibly low difference discrimination threshold for the snail's chemosensory system. A chemical macro-gradient involving several substances, each with a different evaporation rate, might be more easily detected over a long period. Second, snails tested with a manipulated trail ignored an artificially high (and assumed) concentration gradient in favor of some other cue or cues (Experiment 3). GILLY & SWENSON (1978) obtained the same result in a similar experiment (their "point of paradox test") with *L. littorea*. And third, snails showed no directional preference when encountering a manipulated trail having an artificially high (and assumed) concentration gradient, but being directionally ambiguous otherwise (Experiment 4).

Our experiments indicated that several other mechanisms were not required for polarity detection to occur. A physical map depending on topographic cues (Experiment 5) and retention of a stainable chevron pattern (Experiment 6) are probably not required for trail polarity detection. These findings were expected because simple observation reveals that snails often begin turning with polarity after the cephalic tentacle tips make a single contact with the edge of a trail. After contacting the substratum, a tentacle tip is dragged a distance of less than 1 mm before "popping free" from the substratum, and the entire trail is 5 to 7 mm wide in adults; sampling 1/3 of a trail's width is probably insufficient to determine its gross physical features (*e.g.*, chevron curvature). Also, tests with trail

imprints showed that polarity detection does not require bilateral asymmetry cues. Finally, snails tested in light levels below the threshold for detecting a large high-contrast target still followed trails with polarity (Experiment 7). Therefore, trail polarity detection apparently does not require reflected light cues.

These experiments suggest that detection of a concentration macro-gradient of a volatile chemical substance is not *involved* in trail polarity detection, and that detection of a bilateral trail asymmetry, a reflected light pattern, or a gross topographic pattern are not *required* for trail polarity detection. The distinction in terminology and conclusion is important. Interpretation of data from animal orientation experiments must be made with recognition that many species possess redundant sensory systems and orientational strategies, arranged in a hierarchy of dependence (ABLE, 1980). For example, just because snails can still detect trail polarity in darkness, one should not conclude that trail polarity cannot be detected from reflected light patterns under lighted conditions; snails may possess several methods of detecting trail polarity, and even depend *primarily* on reflected light patterns during the day, but they may simply use an alternative method when tested in darkness. Failure to recognize this point is probably responsible for many of the ambiguous conclusions obtained in some studies of homing mechanisms in mollusks.

We could not determine if a viscosity-based physical map mechanism is involved in trail polarity detection. However, we consider it unlikely that a repetitive viscosity pattern is necessary for trail polarity detection because, again, snails often begin turning with polarity after only a single contact with just the trail edge. The concentration micro-gradient hypothesis was not examined either. However, the concentration difference in a gradient would be greater over a distance of 8 mm (the distance between the points where the tentacle tips contact the substratum) than over a distance of 1 mm (the width of a tentacle tip). So, because *Littorina irrorata* seem unable to use a concentration macro-gradient to detect trail polarity, it seems unlikely that the more difficult micro-gradient mechanism would be involved.

If one is willing to risk assuming that redundant trail polarity cues are not involved here, and that a viscosity-based physical map and a concentration micro-gradient are not involved, then one is left with the directional microstructure mechanism. In the mucous trails (and pedal glands) of *Helix*, a terrestrial pulmonate, SIMKISS & WILBUR (1977:fig. 12) found many 4.5- μ m long rodlets. The rodlets were all frayed at one end and pointed at the other end, and were all oriented with their unfrayed end pointing in the direction in which the trail-depositing snail had been traveling. How such small structures become arranged in such an orderly fashion is unknown. We have found no reports that *Helix* follows mucous trails. *Ilyanassa* does detect trail polarity; BRETZ & DIMOCK (1983) reported seeing occasional frayed or split filaments in the trail and, after treating trails in various ways, they con-

cluded that the structural integrity of the mucous trail is important for trail following.

We have found no equally detailed studies of mucous trail microstructure for other gastropods, so it is not known whether other species possess similar polarized structures in their trails. COLE *et al.* (1977) described what is apparently a morphologically unique bacterium from various tissues in an aquatic snail; in its cephalotrichous form, this bacterium looks very similar to the frayed rodlets described for *Helix*. It is interesting that both the frayed rodlets in *Helix* trails, and the cephalotrichous bacteria, fit easily within RAFTERY's (1983) 35- μ m size criterion for the possibility that the trail polarity cue in *Littorina* might be structural, rather than chemical. Information on trail microstructure and pedal gland morphology for species from different taxonomic groups and ecological settings would be useful for comparison.

Whatever mechanism for trail polarity detection is eventually shown to be involved in trail following by *Littorina irrorata*, there is no reason to believe that the same mechanism is involved in other gastropods. Mucus is chemically and structurally complex (GRENON & WALKER, 1980; BOUSFIELD *et al.*, 1981), and there are probably several ways of including polarity information in it. *Littorina irrorata* is behaviorally terrestrial, and its trail retains polarity information for a much longer period than the trail of some other gastropods. Species active when submerged in water may use a very different mechanism than *L. irrorata*.

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Size-Selective Predation in a Sea Anemone, Nudibranch, and Fish Food Chain

by

LARRY G. HARRIS

Zoology Department, University of New Hampshire, Durham, New Hampshire 03824, U.S.A.

Abstract. A series of field and laboratory observations and experiments was used to determine whether size-selective predation by the aeolid nudibranch *Aeolidia papillosa* on its principal prey in the Gulf of Maine, the anemone *Metridium senile*, was a mechanism capable of producing the patterns of anemone population structure observed in subtidal habitats. Similar techniques were also used to test the hypothesis that size-selective predation by the wrasse *Tautoglabrus adspersus* on *A. papillosa* could account for the inverse relationship between aggregations of fish and the reduced presence of *A. papillosa* in association with *M. senile*. Field and laboratory studies showed that *A. papillosa* has a disproportionately negative impact on the smaller size classes of *M. senile*. An important factor in this preference was the size-related effectiveness of acontia extrusion as a defense by *M. senile* against *A. papillosa*. The results indicated that *M. senile* was a preferred prey for all life stages of *A. papillosa*, but that relative sizes of predator and prey were important factors. Field tests demonstrated that *T. adspersus* would eat *A. papillosa*, and the nudibranch is uncommon in habitats containing schools of the wrasse. Laboratory experiments showed that predation was size-selective, though investigative attacks were made on all size classes of nudibranchs offered. The results verify that size-selective predation by wrasses would explain the delayed appearance and reduced presence of *A. papillosa* with concentrations of *M. senile* in those habitats as compared to nearby areas without wrasses. Size-selective predation on the sea anemones would in turn provide a mechanism for the difference in sea anemone population structure, from scattered, large and solitary individuals to aggregated, small and clonal individuals, between areas with high and low nudibranch populations, respectively. It is proposed that indiscriminate investigative attacks by visual predators on the young stages of specialized grazing predators such as nudibranchs could be a significant factor influencing the co-evolution of predator-prey associations with sessile invertebrates, particularly in the tropics.

INTRODUCTION

PREDATION on nudibranch mollusks has been suggested but seldom documented, particularly for fish (see TODD, 1981). A similar lack of information is available on how nudibranchs impact prey populations, other than the studies by TODD (see review, 1981), and in these cases the emphasis is on the nudibranch predation. EDMUNDS (1966, 1974) and HARRIS (1973) have suggested that fish predation must be an important selective force, and TODD (1981) reported that wrasses readily consumed small nudibranchs and sacoglossans exposed when coral heads were overturned in the Red Sea. Similarly, several workers (EDMUNDS, 1966; HARRIS, 1973, 1976; SCHICK *et al.*, 1979) have hypothesized that the sea anemone-eating nudibranch *Aeolidia papillosa* (Linnaeus) may affect the pop-

ulation structure of its prey, but no effort has been made to document such an effect.

In the southern Gulf of Maine, the sea anemone *Metridium senile* is the only common species on hard substrates in the shallow subtidal (low water to -25 m). The principal predator is *Aeolidia papillosa* (CLARK, 1975). There is also one epibenthic picking fish, the wrasse *Tautoglabrus adspersus* (Walbaum, 1792). *Metridium senile* occurs in two conspicuous population structures: (1) scattered solitary individuals or small groups of moderate (> 40 mm column diameter) to large size individuals (SCHICK *et al.*, 1979) or (2) clones or aggregates of many individuals dominated by small (<20 mm column diameter) sea anemones (HOFFMANN, 1976). Populations of *A. papillosa* tend to occur more commonly with the dispersed

phase of *M. senile* than with the clonal form. *Tautogolabrus adspersus* is a conspicuous member of habitats containing clones of *M. senile*. Preliminary observations suggested that *T. adspersus* would eat *A. papillosa* and that the nudibranch had an effect on anemone population structure. The purpose of this report is to describe the results of observations and experiments investigating the effect of prey size on predation by the respective predators in this three-level predator-prey system.

MATERIALS AND METHODS

The majority of studies described here was conducted in subtidal locations in the Gulf of Maine in an area encompassing southern Maine and New Hampshire. Animals used in laboratory studies were maintained at 12°C in closed, recirculating seawater systems, housed in the Zoology Department at the University of New Hampshire.

Metridium senile

Sea anemone populations were sampled either with 0.1-m² quadrats placed randomly over sections of dense aggregations or by counting and measuring every sea anemone within a predetermined region when only scattered individuals were present. Sea anemones were measured to the nearest 5 mm in column diameter. More accurate measurement of *Metridium senile* is almost impossible due to the variability in pedal disc attachment configuration.

Information on asexual reproduction and survival was obtained by placing specimens of *Metridium senile* on granite blocks in Gosport Harbor, Isles of Shoals, at a depth of 10 m and monitoring them on a monthly basis from June 1977 to present. Wire cages (1.25-cm mesh) were used to exclude larger predators, particularly winter flounder, crabs, and lobsters. Individuals of *Aeolidia papillosa* were removed from the blocks as soon as they were observed.

Sea anemones for most laboratory experiments were collected from the undersides of floats at a boat marina in Beverly, Massachusetts. In this habitat there were extensive populations of *Metridium senile*, dominated by small individuals due to both asexual (pedal laceration) and sexual reproduction.

Nudibranchs for experiments were collected from aggregations of *Metridium senile*. Each individual was measured to the nearest mm for small (≤ 15 mm) individuals and 5 mm for animals greater than 15 mm. Nudibranchs were maintained in glass or plastic containers in which the water was changed daily. Pedal lacerates of *M. senile* were used as food.

Nudibranch Predation

To test for the influence of *Aeolidia papillosa* on *Metridium senile* population structure, groups of sea anemones were set up in four separate dishpans. The sea anemones ranged in number from 80 to 110 individuals and in each

container the size range in column diameter was 2 to 75 mm. Once the sea anemones were attached, counted, and measured, five to ten *A. papillosa* were introduced into each container. The nudibranchs were allowed to feed for six weeks while the sea anemones were counted and measured on a weekly basis. A large sample of *M. senile* free in the same sea table served as the control. There was no mortality of sea anemones in the control tank during the experiment; *M. senile* of all sizes normally survive for months in the closed seawater system used.

The effect of prey size on *Aeolidia papillosa* survival and growth was tested by culturing small (3 to 12 mm) nudibranchs with either small (≤ 10 mm) or large (≥ 30 mm) sea anemones. Fifty nudibranchs in two tests (10 and 15 individuals per treatment, respectively) were cultured for one month in 40-cm glass stacking dishes. Water was changed every other day and small sea anemones were replaced as food when needed. Survival and growth rate were monitored.

Fish Predation

To test for possible wrasse predation on *Aeolidia papillosa*, nudibranchs were offered to individuals of *Tautogolabrus adspersus* in the field. To stimulate feeding behavior in two of the four tests, pieces of mussel (*Mytilus edulis*) were added to the area where the nudibranchs were placed. In one test, 26 nudibranchs were set out around sea anemones where no fish were in residence. A second set of 31 *A. papillosa* was taken to a small cave containing numerous *Metridium senile* and wrasses. The nudibranchs were placed on a rock among several anemones and set at the mouth of the cave. No bait was added and the fish were observed until all nudibranchs were consumed. The control nudibranchs were then collected. The fish behavior and any attacks were observed and recorded.

Once it was demonstrated that the wrasses did eat *Aeolidia papillosa*, a laboratory experiment was conducted to test for size-selective predation by wrasses on *A. papillosa*. Young *Tautogolabrus adspersus* (70 to 100 mm in length) were maintained in a shallow sea table. The fish were fed pieces of mussel tissue daily on a flat piece of slate to condition them to one specific feeding site. The experiment consisted of setting 10 small (1.5 to 15 mm) *A. papillosa* in a petri dish (6 cm in diameter) along with pieces of mussel tissue and placing it into the sea table on the slate. Ten replicates of this experiment were carried out. The behavior of the fish, number of attacks, and sizes of any nudibranchs consumed were recorded.

RESULTS AND OBSERVATIONS

Anemone Populations

Metridium senile is essentially the only sea anemone in the southern Gulf of Maine from the low tide mark to 25

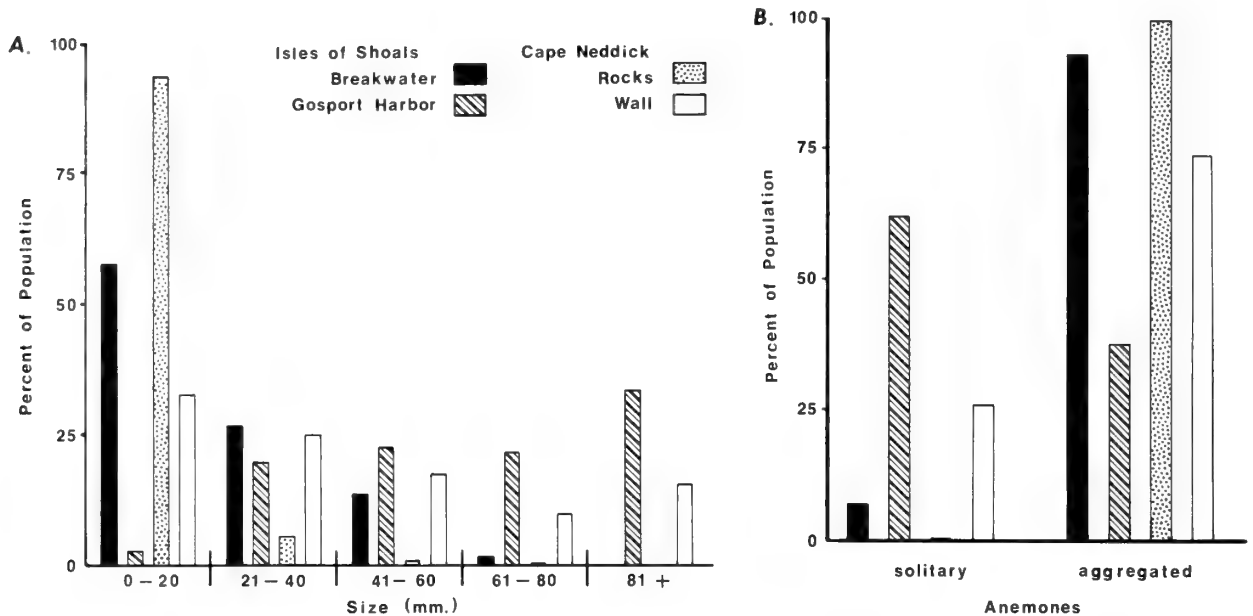


Figure 1

A comparison of the population structure of *Metridium senile* from two adjacent habitats at two locations in the Gulf of Maine. Sea anemone aggregations at the north Breakwater, Isles of Shoals, New Hampshire, and the rocks at Cape Neddick, Maine, occur in large numbers and were sampled using 0.1-m² quadrats. The populations of Gosport Harbor, Isles of Shoals, and the wall at Cape Neddick consist of scattered anemones on rock outcroppings with densities of less than 1/m², and sampling was done by measuring every anemone within a predetermined area. The two populations at each site are within 100 m of each other. Section A gives the population structure in percentage in each size class. Section B gives the population structure in terms of solitary individuals *versus* sea anemones aggregated into groups of two or more.

m in depth. Individuals may reach a column diameter of 30 cm, but few animals are greater than 10 cm in most habitats. The population structure varies considerably with the habitat (HOFFMANN, 1976; SCHICK *et al.*, 1979). Figure 1 illustrates the two major patterns of *M. senile* population structure in the Gulf of Maine. The sea anemone population structures at the sites given in Figure 1 have remained stable for the 16 years I have been working in these habitats, and the same patterns have been observed in numerous other locations from Eastport, Maine, to Boston, Massachusetts. Large aggregations of *M. senile* occur in many fouling communities, on large subtidal, vertical, or undercut rock faces and breakwaters, and on large boulders at depths greater than 20 m. These aggregations typically contain a high percentage (>50%) of small sea anemones less than 20 mm in column diameter—the products of asexual and sexual reproduction.

Scattered on hard substrates in almost any habitat are populations of *Metridium senile* occurring in small clumps of less than 10 individuals and primarily as solitary individuals. A majority of the sea anemones in the dispersed populations is larger in size (≥ 50 mm).

Asexual reproduction occurs throughout the year, but it reaches a peak in early summer, beginning shortly after the barnacle *Balanus balanoides* (L.) completes its plank-

tonic phase. The stomach contents of *Metridium senile* are dominated by *B. balanoides* cyprids at this time. Sexual reproduction as indicated by the release of planulae, and the appearance of small sea anemones occurs in June and early July (unpublished observations). Therefore, by late summer, small sea anemones (≤ 10 mm) are common in all habitats.

In mid-July, small (<5 mm) *Aeolidia papillosa* begin to appear in large numbers wherever *Metridium senile* is found and this pattern continues into November (HARRIS, 1973). These small nudibranchs remain in close proximity (<5 cm) to sea anemones. As is illustrated in Figure 2, higher numbers of nudibranchs are associated with the scattered sea anemones. Also, the early appearance of large *A. papillosa* in association with the dispersed sea anemones suggests higher survival of nudibranchs settling in these habitats; as is seen in Figure 2B, there was a large population of nudibranchs already established on the wall at Cape Neddick, before any were found among the sea anemones at the rock site. *Aeolidia papillosa* tends to be cryptic in coloration and nocturnal in activity, but it seldom moves far from sea anemones, so it is easy to observe on large rock surfaces where *M. senile* is most common in subtidal habitats.

The nudibranchs that occur with aggregated *Metridium*

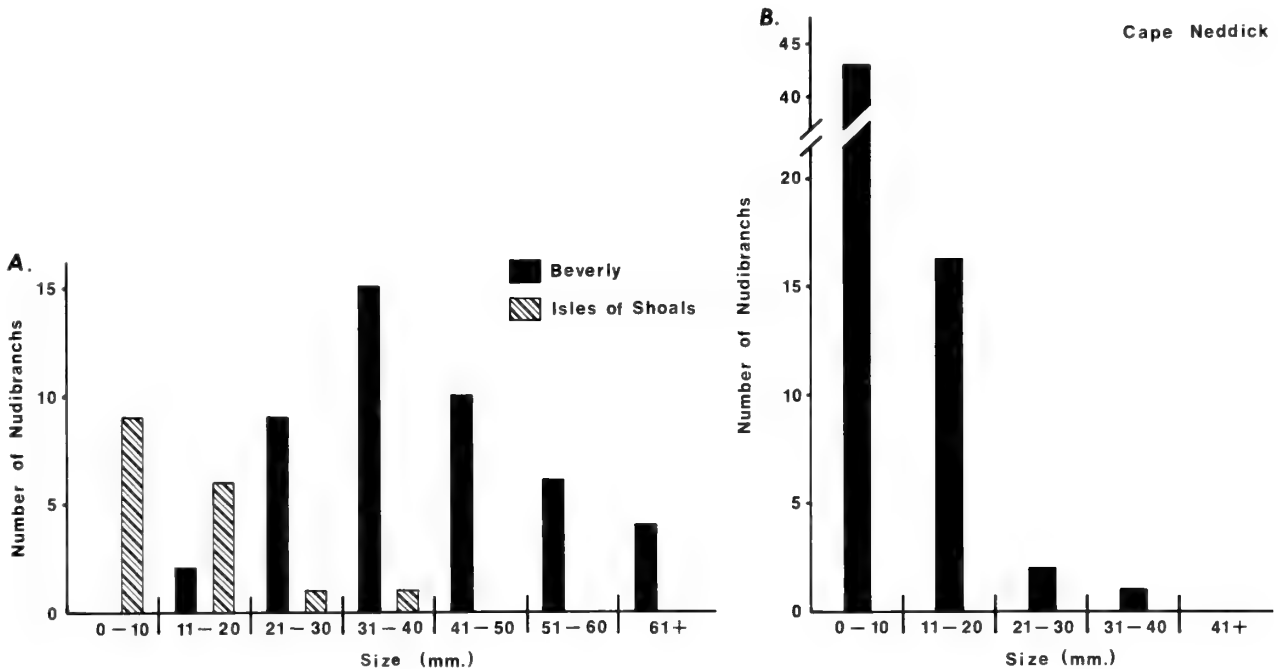


Figure 2

A comparison of numbers and size distributions of *Aeolidia papillosa* collected from sites where anemones were dispersed or primarily aggregated into clones. A. The nudibranchs from under and around small rocks below floats in Beverly, Massachusetts, took 5 min to collect; there were also numerous egg masses present. The *A. papillosa* collected on the breakwater at the Isles of Shoals during the same week in March 1978, required 45 min of intensive searching and no egg masses were seen (chi square, $P < 0.01$). B. Approximately 30 min were spent hunting for nudibranchs at each site as part of a single SCUBA dive at Cape Neddick, Maine (October 1978). No nudibranchs were found at the rocks site (see Figure 1A) where wrasses are common, but *A. papillosa* were common around sea anemones at the wall site.

senile tend to be fewer in number and to appear later in the fall. This suggests either differential survival or differential settlement depending on the habitat. One of the most conspicuous differences between the habitats where scattered versus aggregated *M. senile* are found is the presence of the wrasse *Tautoglabrus adspersus*. *Tautoglabrus adspersus* tends to aggregate in habitats where there is cover in the form of crevices and caves. It is on the vertical and undercut walls of these refuges that *M. senile* occurs in aggregated populations. The delayed appearance of *Aeolidia papillosa* in these areas correlates with the fall disappearance of *T. adspersus* as it migrates to deeper water or hibernates (GREEN & FARWELL, 1972). Nudibranchs were also found with sea anemones on the caged granite blocks (Table 1) well before any were observed with *M. senile* on nearby rocks containing resident populations of wrasses.

Aeolidia papillosa remains common through the winter. Reproduction begins in the southern Gulf of Maine in February and peaks in May, though it is still possible to find a few large reproducing animals into July. There is much variation in this cycle, but the general pattern has

been consistent from the fall of 1969 to the summer of 1985.

In scattered sea anemone populations, survival of small sea anemones produced each summer is low and coincides with the presence of numerous *Aeolidia papillosa* in these habitats through the late summer and fall. The results of caging experiments given in Table 1 illustrate the pattern of asexual reproduction by *Metridium senile*, followed by the disappearance of young sea anemones associated with the appearance of nudibranchs. These observations suggest that *A. papillosa* is having a disproportionate impact on the young sea anemones (HARRIS, 1976). This hypothesis was tested in a laboratory experiment (Figure 3). The differential predation by *A. papillosa* on sea anemones of smaller column diameter is clearly documented. There was no mortality of sea anemones in either the experimental or the control populations from factors other than feeding by nudibranchs, which was readily observed. No sea anemones under 15 mm remained in any of the experimental containers. The patterns documented in Figure 3 and Table 1 have been consistently observed when maintaining *A. papillosa* in the laboratory. Over a period

Table 1

Summary of field data illustrating the impact of *Aeolidia papillosa* predation on *Metridium senile* population structure. Sea anemones (30–80-mm column diameter) were placed on granite blocks on a sand substrate in Gosport Harbor, Isles of Shoals, in June 1977, and then monitored monthly. The blocks were caged to exclude large predators. Nudibranchs were removed when encountered. The data for sea anemones on four blocks are given for two summers (1978 and 1979).

Ms = adult *M. senile*; pl = pedal lacerates <10 mm; Ap = *A. papillosa*.

Block no.	Dates and numbers of individuals								
	June 1978	August 1978		September 1978		March 1979	July 1979		September 1979
5	5 Ms	4 Ms	4 pl	4 Ms	0 pl	4 Ms	4 Ms	30 pl	0 Ms
				1 Ap	(25 mm)				
6	1 Ms	1 Ms	14 pl	1 Ms	0 pl	1 Ms	1 Ms	0 pl	0 Ms
				1 Ap	(25 mm)				
7	5 Ms	5 Ms	31 pl	5 Ms	0 pl	5 Ms	5 Ms	51 pl	1 Ms
		1 Ap	(6 mm)	5 Ap	(7, 15, 14, 5, 10 mm)		1 Ap	(2 mm)	6 Ap
									(8, 12, 22, 20, 20, 20 mm)
8	4 Ms	4 Ms	0 pl	4 Ms		3 Ms	3 Ms	11 pl	2 Ms
		1 Ap	(40 mm)						2 Ap
									(30, 12 mm)
Totals	15 Ms	14 Ms		14 Ms		13 Ms	13 Ms		3 Ms
	0 pl	49 pl		0 pl		0 pl	92 pl		0 pl
	0 Ap	2 Ap		7 Ap		0 Ap	1 Ap		8 Ap

of time, all sea anemones will be consumed except for a few large individuals. These larger sea anemones will be attacked and suffer some tissue loss, but they are able to survive repeated attacks and often to repel the nudibranch.

The reason for the preference of *Aeolidia papillosa* for small sea anemones is obvious. *Metridium senile* releases nematocyst-laden acontia (string-like extensions of the mesenterial filaments) through small pores (cinclides) in the column. If these acontia become tangled in the cerata of the nudibranch, the massive discharge of nematocysts can kill the nudibranch. This defensive mechanism appears to be (1) size-related and (2) more effective in the quiet conditions in the laboratory than in the much more complex environment of the field. The results in each of the two culturing experiments were not quite significant, although the combined results are certainly suggestive of the advantages of attacking small *Metridium*: 19 out of 25 survivors and a 4.5% increase in length per day for nudibranchs eating small sea anemones, and 9 out of 25 survivors and a mean growth rate of 2.42% increase in length per day for those fed large sea anemones. Not only was survival and growth rate higher for the animals fed small sea anemones, but only those nudibranchs forced to eat larger sea anemones suffered tissue damage or mortality from acontia—7 animals out of 25. It is quite common for small nudibranchs to stop eating and slowly starve to death when offered only larger *M. senile*. The same pattern of poor growth and survival of small *A. papillosa* cultured with large *M. senile* has been observed in studies conducted at Hopkins Marine Station in Pacific Grove, California, using animals collected in Monterey Bay (un-

published observations). Freshly killed *A. papillosa* wrapped in acontia have also been found in the field.

Fish predation on *Aeolidia papillosa* was verified first in the field by offering nudibranchs to wrasses in three habitats with positive results in each case. The observations indicated that size was an important component of this predation. The first set of tests illustrates this point. Two *A. papillosa* 20 mm in length were collected from the wall, Cape Neddick (Figures 1, 2), and taken to the rock site where numerous *Tautoglabrus adspersus* were aggregated. One nudibranch was tossed into the water column. A 15-cm long fish took it into its mouth and spat it out. A second wrasse, 25 cm in length, engulfed the nudibranch, spat it out, engulfed and spat it out again, and then swallowed it. The second *A. papillosa* was also eaten by this same wrasse after rejecting it three times. In fact, it was only eaten when a second fish came up to investigate. The test was repeated using a specimen of the aeolid *Coryphella verrucosa* (Sars) also 20 mm in length. Several fish looked closely at it and the wrasse that had eaten the *A. papillosa* tasted it once and would not go near it again. *Coryphella verrucosa* has bright red cerata with contrasting white markings, whereas *A. papillosa* is mottled brown and pale white. *Coryphella verrucosa* is conspicuously active during the day, whereas *A. papillosa* tends to be nocturnal and cryptically positioned during the day, although still visible to divers and fish on open surfaces. Wrasses offered *C. verrucosa* in the laboratory consistently rejected them. In both of the other field tests individuals of *A. papillosa* were eaten and it was always by the largest wrasses present.

One field experiment was also conducted to further de-

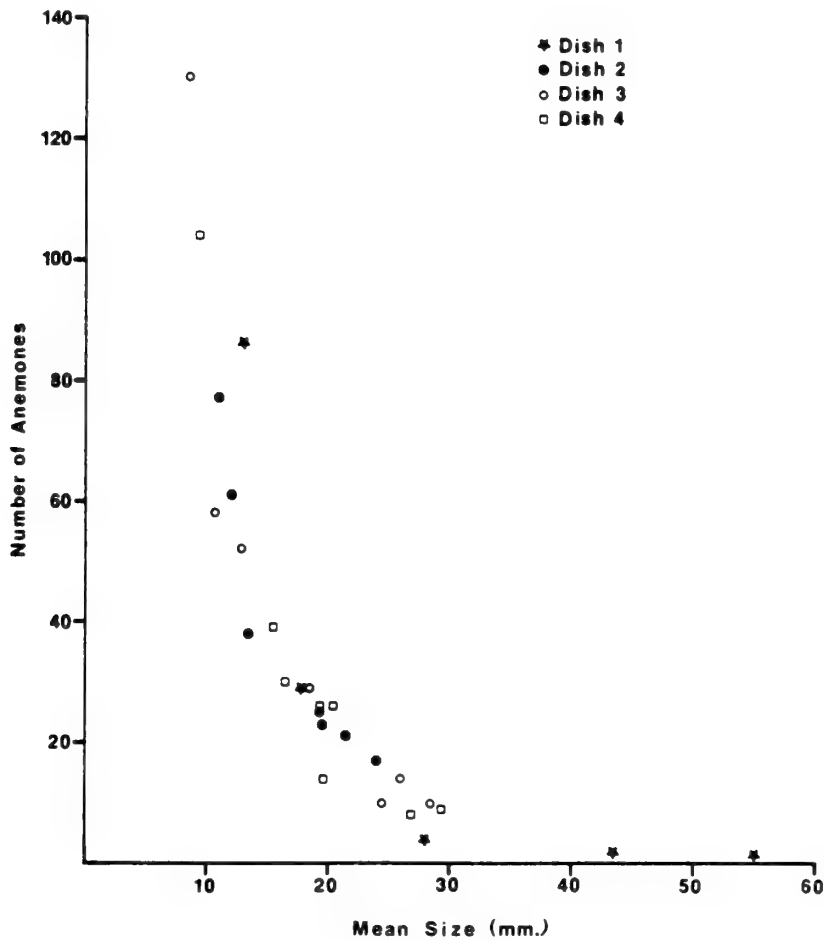


Figure 3

Summary of four feeding experiments in which individuals of *Aeolidia papillosa* were placed in containers with individuals of *Metridium senile* ranging in column diameter from 2 to 75 mm. The nudibranchs were allowed to feed for 6 wk and changes in the number and mean column diameter of all sea anemones were recorded. There was no mortality among the 300+ sea anemones serving as a control held in the same sea table with the experimental treatments. (Spearman-rank correlation coefficient <0.05 for dish one and <0.1 for dishes 2-4.)

termine whether *Tautoglabrus adspersus* predation could explain the lack of *Aeolidia papillosa* among *Metridium senile* where wrasses are common. The 26 nudibranchs placed among sea anemones on the wall at Cape Neddick (see Figure 1A) remained in place for about 3 h, and all individuals were retrieved. Thirty-one *A. papillosa* (1.5 to 2.5 cm in length) were taken to a cave at the rock site at Cape Neddick (Figure 1A) where more than 15 *T. adspersus* (15 to more than 30 cm in length) were in residence. A rock from the cave was retrieved and the nudibranchs were placed on the rock among several individuals of *M. senile*. There was a surge and 15 nudibranchs were lost in the transfer to the rock. The rock with the remaining 16 *A. papillosa* was placed just inside the cave mouth. No bait was used.

After about 3 min, individual fish began to swim up to the rock and investigate the surface, as they were doing to other rock surfaces in the vicinity of the cave. A number of fish bit at objects on the rock. Eleven nudibranchs were seen being engulfed and all 16 *Aeolidia papillosa* were removed in 17 min. None of the observed fish remained at the rock to attack several nudibranchs consecutively, but each fish tended to spend a short time at the rock and then move on. Several fish did return to the rock more than once during the period of observation. Fish often mouthed the nudibranchs before swallowing them, but in only two cases were nudibranchs spit out and then engulfed a second time. None of the fish rejected an engulfed *A. papillosa*.

Large (>30 cm body length) winter flounder forage on

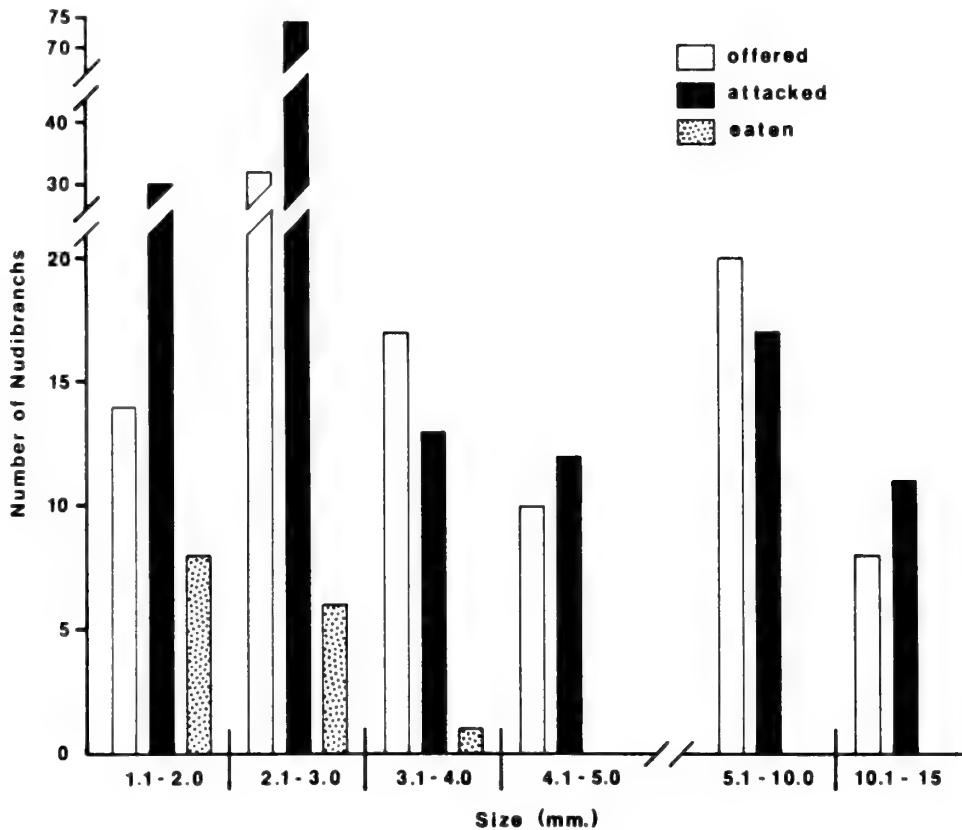


Figure 4

Summary of feeding experiments in which 10 replicates of *Aeolidia papillosa*, along with small pieces of mussel tissue, were offered to a group of *Tautoglabrus adspersus* to test for size-selective predation. The total number of nudibranchs used, number of attacks, and number eaten are presented by mm size class. A nudibranch was often attacked more than once by one or more fish before it was rejected or eaten. All three categories were statistically different, $P < 0.01$, using the Kolmogorov-Smirnov test for goodness of fit.

rocky substrates and eat a variety of sessile algae and invertebrates including *Metridium senile*. On one occasion two large (about 50 mm) *Aeolidia papillosa* were found in a flounder stomach that also contained numerous anemones. Starved lobsters and spider crabs will eat *A. papillosa* after removing the cerata. However, the process is a slow one and the crustaceans will readily drop the nudibranchs if offered other food. *Aeolidia papillosa* is able to regenerate lost cerata and it is common to find large nudibranchs in the field regenerating cerata. Neither *Cancer borealis* (Stimpson), *Cancer irroratus* (Say), nor any asteroid species has been observed to eat *A. papillosa*.

The laboratory experiment testing fish predation on *Aeolidia papillosa* is summarized in Figure 4. The results clearly show that fish did selectively consume the smallest nudibranchs present, although they made investigative attacks on all sizes. Often a nudibranch that was eaten would be engulfed and rejected several times by more than one fish before it was swallowed; this was particularly true for the 2.1-3.0-mm size class. Many of the fish made

exaggerated ventilating movements after mouthing a nudibranch as if the lining of the mouth were irritated. *Aeolidia papillosa* releases both nematocysts and secretions from epidermal glands in the cerata when disturbed. Future experiments are planned to determine whether nematocysts are affecting the lining of the fish's mouth.

The fish used in the laboratory experiments became wary of attacking nudibranchs after the sixth trial. In the first six trials there was a mean of 22 investigative attacks per trial and only 7.5 attacks per trial for the last four. The fish became much more selective in picking pieces of mussel tissue and avoiding nudibranchs, which they visually investigated. The behavior of the fish suggested that they were learning from the larger nudibranchs in the dish and then avoiding the smaller individuals; no nudibranchs were consumed in the last two trials.

The results from one additional trial are suggestive of the mechanism involved in the avoidance, but the lack of small nudibranchs precluded further experiments at the time. To test the hypothesis that the wrasses were learning

from the larger nudibranchs, the following sequence was tested in a 30-min period:

- one 2-mm *Aeolidia papillosa* was introduced along with food—it was eaten; a second 2-mm nudibranch was added without food—it was attacked and eaten;
- the normal complement of 10 nudibranchs of various sizes (2–12 mm) plus food was added—there were nine investigative attacks, but no nudibranchs were eaten;
- one 2-mm nudibranch plus food was introduced—the fish looked at it and ate the food, but would not touch the nudibranch.

DISCUSSION

This report concerns predation as a mechanism regulating nudibranch and sea anemone populations in the Gulf of Maine. Although the evidence described suggests that predation may be responsible for the observed population patterns, there are certainly other abiotic and biotic factors that influence the population structure and distribution of the species in question. Factors such as currents, food availability, competition, and disturbances other than predation almost certainly play a role in determining the population patterns of sea anemones and their nudibranch predators. HARRIS & IRONS (1982) suggested that population and community patterns are the result of a suite of factors that interact synergistically to produce the observed results. Therefore, the emphasis on predation here assumes that this factor is only one of several that interact to determine population patterns.

The observations and experiments described herein show that the wrasse *Tautoglabrus adspersus* does prey on the nudibranch *Aeolidia papillosa*, and laboratory experiments suggest that this predation is most intense on smaller nudibranchs. There is also evidence from both the field and laboratory that *A. papillosa* is a size-selective predator on its principal prey, the sea anemone *Metridium senile*. Clonal aggregations of sea anemones are typically found in habitats also containing schools of wrasses; in these conditions the appearance of nudibranchs is delayed and their numbers lower than in adjacent habitats where fish are scarce and sea anemones are large and scattered.

Metridium senile is an effective space competitor in fouling communities capable of outcompeting most other sessile invertebrates (HARRIS & IRONS, 1982) and dominating large areas of primary space (HOFFMANN, 1976; PURCELL, 1977). SCHICK *et al.* (1979) and I (HARRIS, 1973, 1976) have suggested that predation by *Aeolidia papillosa* can alter the population structure of *M. senile* by consuming small individuals.

The results of observations (Table 1) and experiments (Figure 3) verify that this hypothesis is at least one mechanism capable of producing the patterns observed. R. T. Paine (personal communication) found that clones of *Metridium senile* protected by cages suffered size-selective mortality relating to the presence of *Aeolidia papillosa*, re-

sulting in the disappearance of all smaller sea anemones. I recorded a similar direct relationship between *M. senile* mean size and *A. papillosa* density in comparing sea anemone populations on the pilings of the Commercial Wharf in Monterey Bay and on rock piles below the pilings, where *A. papillosa* commonly hide (1973, 1976, unpublished observations).

The defensive response of *Metridium senile* has been described previously (HARRIS, 1973; EDMUNDS *et al.*, 1976). The effectiveness of acontia extrusion is suggested by growth experiments, but even here it is relative size that is important. Numerous observations over the last 16 yr indicate that acontia extrusion is most effective as a defense under laboratory conditions where there is no water movement or structure to interfere with the acontia. I have often observed *Aeolidia papillosa* attacking large *M. senile* in the field with acontia drifting back and forth in the surge or hung up on nearby sea urchin spines, algae, or hydroids. This increased effectiveness in the laboratory is almost the exact opposite of the situation described for the west coast sea anemone *Anthopleura elegantissima* (Brandt), in which the sea anemone is almost totally defenseless against *A. papillosa* under laboratory conditions (HARRIS & HOWE, 1979).

The selection for small *Metridium senile* by *Aeolidia papillosa* has another implication relative to prey preference by this nudibranch. WATERS (1973), HARRIS (1973), and EDMUNDS *et al.* (1975) have reported from laboratory studies that *M. senile* was one of the least preferred prey of *A. papillosa*. However, in the field, *A. papillosa* is typically found associated with *M. senile*, even where more preferred prey are available. This led to the hypothesis that settling veligers of *A. papillosa* had a different preference hierarchy than the adults (HARRIS & HOWE, 1979). The previous studies had all used large *M. senile* which, as demonstrated here, are most effective in repelling attacks in the laboratory. HARRIS & DUFFY (1980) found that *A. papillosa* fed small *M. senile* and *Anthopleura elegantissima* showed no preference for either species in olfactometer tests, but switched to a strong selection for *A. elegantissima* when offered only large *M. senile* in combination with *A. elegantissima*. The results reported here suggest that *M. senile* is a preferred prey of *A. papillosa* throughout their overlapping ranges in the Atlantic and Pacific oceans, but that size is an important influencing factor.

Differential mortality on the young stages of many groups of plants and animals is a well documented phenomenon (DEEVEY, 1947; MECK, 1966; THORSON, 1966; JANZEN, 1970; CONNELL, 1970; DAYTON, 1971; SUTHERLAND, 1974; PAINE, 1976; RUSS, 1980). Conversely, large size as a defensive mechanism is also well known (MECK, 1966; CONNELL, 1970; JANZEN, 1970; DAYTON, 1971; PAINE, 1974, 1976). SEBENS (1979) has suggested that the trend to larger sizes in the lower intertidal in the anemone *Anthopleura elegantissima* is due to energetic considerations—the longer submersion time allows greater feeding

time and therefore greater size. A complementary explanation for the large size of lower intertidal, as well as subtidal, sea anemones is defense from predators (HARRIS & HOWE, 1979). This appears to be an important selective force for *Metridium senile* in the Gulf of Maine. *Aeolidia papillosa* is also a major sea anemone predator on the Pacific Coast of North America, but it is not as conspicuous as the seastar *Dermasterias imbricata* (Grube) which also eats sea anemones (MAUZEY *et al.*, 1968). *Dermasterias imbricata* grows to a much larger size than *Aeolidia papillosa* and kills anemones by covering them in folds of its cardiac stomach. Field and laboratory observations indicate that *D. imbricata* is size-limited in its ability to attack anemones (Harris, unpublished observations) and this starfish may exert a greater selective force on the size and habitat selection of subtidal sea anemones on the West Coast of North America than *A. papillosa*.

Fish predation on the young stages of fouling community organisms has been shown by SUTHERLAND (1974), DAY (1977), and RUSS (1980). The results of this predation were to alter community structure. MONTGOMERY *et al.* (1980) have documented size-selective grazing on brown algal species that are avoided as adults by surgeon fishes in the Gulf of California. EDMUNDS (1966) concluded that fish predation must be an important selective factor in the development of aeolid nudibranch defensive mechanisms. I (HARRIS, 1973) proposed that investigative attacks by fish on the young stages of two coral-eating nudibranchs of the genus *Phestilla* (Bergh) was an important selective force and source of mortality for these species. Both *Phestilla* species are similar to *Aeolidia papillosa* in that they are cryptic, nocturnal, and aggregate. The results of this study (Figure 4) represent the first documentation of size-selective predation by fish on nudibranchs. The behavior observed during these experiments, as well as previous studies (HARRIS, 1973; TODD, 1981), strongly suggests that the mechanism involved is a combination of image recognition coupled with a concentration level of defensive secretions and (or) nematocysts. *Tautogolabrus adspersus* is an epibenthic predator that visually selects small prey items, sessile and motile, from the substrate (CHAO, 1973; SHUMWAY & STICKNEY, 1975; HARRIS & IRONS, 1982). This wrasse plays a role in the Gulf of Maine similar to that of the great diversity of more specialized epibenthic pickers so conspicuous in the tropics (BAKUS, 1964, 1966; RANDALL, 1967; RANDALL & BROCK, 1960; RANDALL & HARTMAN, 1968; SALE, 1980; CHOAT, 1982). It appears that individuals of *T. adspersus* do not recognize as distasteful small specimens of *A. papillosa*, which are cryptically colored and inactive during the day. This suggests that below some relative size the nudibranchs are neither distinctive enough nor distasteful enough for avoidance learning to take place (WICKLER, 1968; EDMUNDS, 1974). Larger specimens of *A. papillosa* do appear to achieve a size at which *T. adspersus* learns to avoid them. If the observations suggesting *T. adspersus* learns to recognize small *A. papillosa* as distasteful from

encounters with larger individuals are valid, then the strong tendency for *A. papillosa* to aggregate would have a defensive advantage as well as the obvious one for successful reproduction.

The size at which wrasses avoid *Aeolidia papillosa* is relative. Although 10-cm long wrasses did not eat any nudibranchs greater than 3.5 mm, a 25-cm wrasse ate two 20-mm *Aeolidia papillosa*. *Tautogolabrus adspersus* seldom reaches much more than 35 cm in length, but *A. papillosa* grows to over 80 mm and does appear to have a refuge in size, at least from wrasse predation. Also, *A. papillosa* is cryptic and uncommon in most habitats, so it is unlikely that *T. adspersus* would encounter enough individuals to develop the obvious avoidance response shown to the common and brightly colored (red and white) *Coryphella* spp.

Tautogolabrus adspersus and numerous tropical species tested refused to eat large nudibranchs (HARRIS, 1973; EDMUNDS, 1974), which have an impressive array of defensive secretions and in some cases nematocysts (EDMUNDS, 1966, 1974). However, fish that feed by selecting items from epibenthic surfaces make many investigative attacks, rejecting the distasteful or inedible objects. It is not necessary for visual pickers to actively seek out the young stages of nudibranchs to have a negative impact on their distribution—indiscriminate investigative attacks should have the same adverse influence on the young stages of a species. It is therefore proposed that this mechanism of indiscriminate investigative attacks on the young stages of specialized grazers (*i.e.*, opisthobranchs) on sessile organisms may be a significant selective factor influencing the co-evolution of specialized predator-prey associations. The result of such selection would be to relegate most associations to cryptic habitats, which is where most tropical opisthobranchs are found. Conversely, sessile forms adapted to occupy open surfaces would be relatively free of specialized grazers, but must then emphasize competitive mechanisms and strategies to avoid generalized grazers (see WELLS *et al.*, 1964).

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Preservation Artifacts and Their Effects on the Study of Euthecosomatous Pteropod Mollusks

by

RONALD W. GILMER

Department of Biology, Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543, U.S.A.

Abstract. Inaccurate anatomical observations based on preserved specimens of euthecosomatous pteropod mollusks are shown to result from artifacts of preservation. All "aberrant" forms previously described in the literature (including the "minute" and "skinny" stages) can be induced in the laboratory by the addition of preservatives to normal living animals. That these aberrant forms have never been observed in nature further supports the contention that they are preservation artifacts.

INTRODUCTION

PROPER PRESERVATION of delicate zooplanktonic organisms is a troublesome and sophisticated art. The effects of preservation on anatomical structures are often hard to interpret, particularly if living specimens have not been studied, and while one preservation method may work well for a particular species, it can have quite different effects on closely related species (GOHAR, 1937; RUNHAM *et al.*, 1965; UNESCO, 1976). Through necessity, oceanic zooplankton samples are often collected and preserved months or years before they are analyzed and, therefore, knowledge of preservation artifacts is particularly important. The routine use of formaldehyde, added without prior relaxation of specimens, is not satisfactory for preserving many of the more delicate zooplanktonic species (UNESCO, 1976).

A number of disproportionately small "minute" and "aberrant" individuals have been reported in adult-sized shells of preserved members of the family Cavoliniidae (BONNEVIE, 1913; TESCH, 1946; SPOEL, 1962, 1967, 1979, and references cited therein; PAFORT-VAN IERSEL, 1982; PAFORT-VAN IERSEL & SPOEL, 1979; LEYEN & SPOEL, 1982). Rather than regarding these so-called minute forms as fixation artifacts, the works cited above have regarded them as natural stages in the life cycles of cavoliniids. In attempting to explain how these very small individuals could secrete such large shells, SPOEL (1967) suggested that they whirl around inside their disproportionately large shell, adding new shell layers until the fully formed adult shell is completed. SPOEL (1967) further discounts the possibility that the mantle accounts for shell secretion (WILBUR & SALEUDDIN, 1983) by pointing out that the mantle can-

not possibly reach to the upper margins of the shell. These assertions are contrary to the results of other workers who have examined shell development in thecosomes (BÉ *et al.*, 1972). More recently, SPOEL (1973, 1979) and PAFORT-VAN IERSEL (1982), in an attempt to explain the "aberrant" morphological forms found in preserved specimens of *Clio pyramidata* Linnaeus (Figure 1b), have suggested that some pteropods reproduce asexually by a scyphozoan-like strobilization process.

There are no reported observations of living aberrant forms and I know of no studies that have seriously examined whether any of these "aberrations" in morphology are based on preservation artifacts. The data presented here give evidence that the proposed "minute" and "aberrant" developmental stages and the process of "asexual strobilization" in cavoliniid pteropods are based entirely on preservation artifacts.

MATERIALS AND METHODS

Various relaxants and fixatives were used in the preservation of live euthecosome pteropods. Animals were either collected by hand using glass jars while SCUBA diving or taken alive from net samples. How formaldehyde affects the contraction of live animals was observed using specimens of *Clio pyramidata* (Figures 1a, b, 2). Animals were preserved directly in 5% formaldehyde without prior relaxing and then examined. They were then dried to constant weight at 80°C for 48 h and used for dry weight and dimensional comparisons. The entire animal and shell were cooled and stored in a desiccator over silica gel and then weighed on a Mettler micro-gram A balance. The soft parts were then removed by crushing the shell and

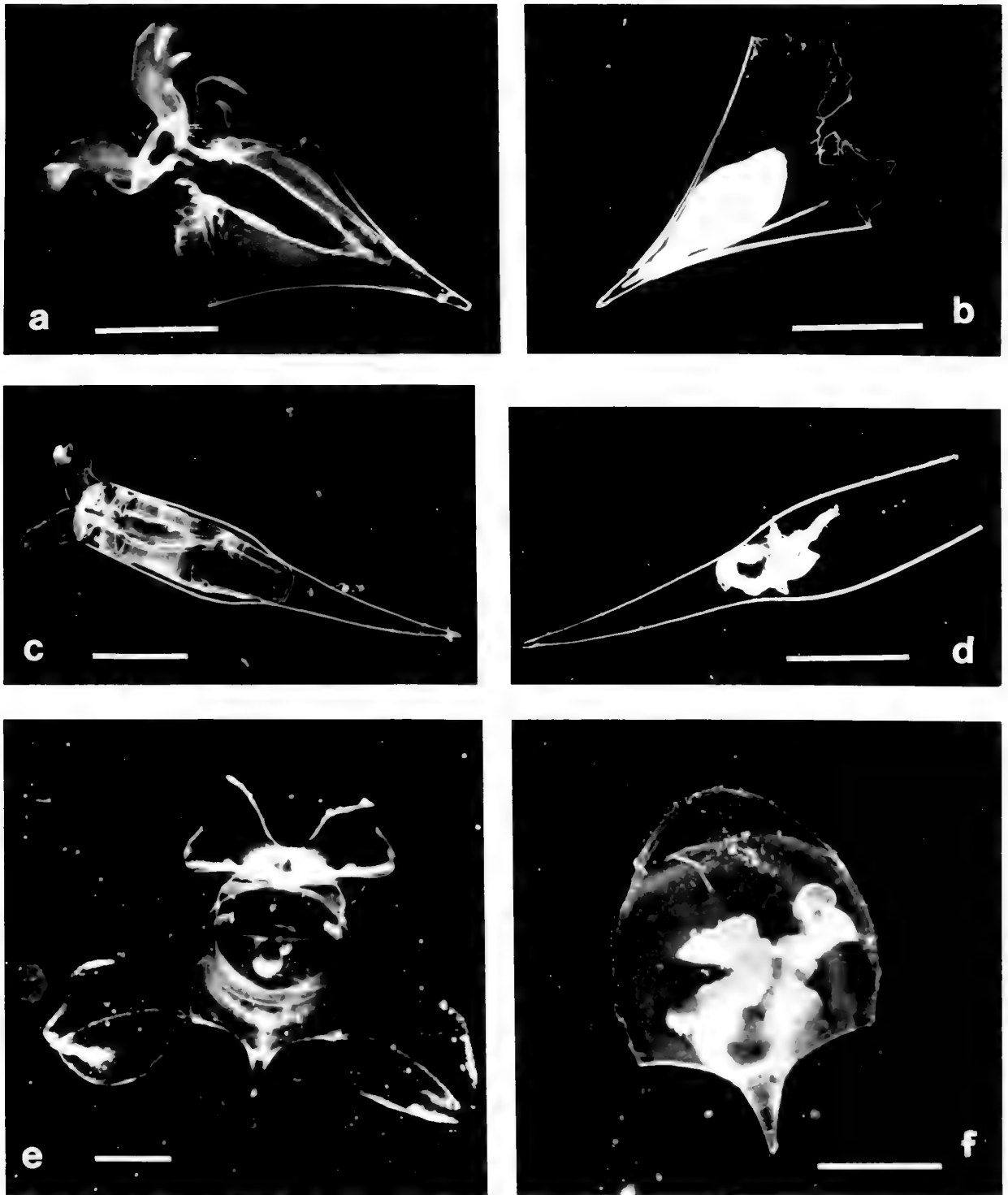


Figure 1

Effects of adding 5% buffered formaldehyde to living adult specimens of theosome pteropods. a, live *C. pyramidalis*. b, the same animal as "a" after preservation, compare with PALORI-VAN DERSE (1982 pl. D). c, live *C. columnella*. d, the same animal as "c" after preservation. e, live *Carolinia tridentata*. f, the same animal as "e" after preservation. Scale bar for all figures is 0.5 cm.

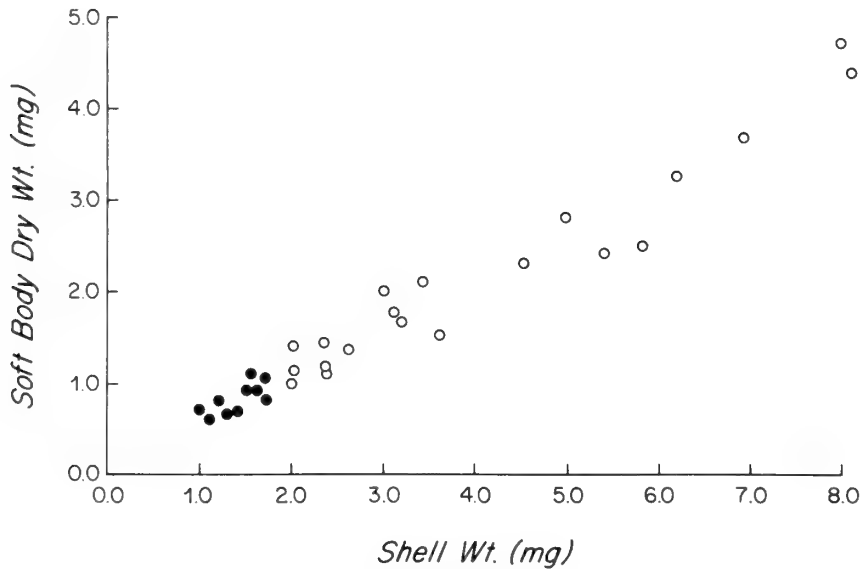


Figure 2

Shell weight to soft-part body weight (dry) for similar dimensions (length, width) of adult-sized specimens of *Clio pyramidata* collected in the western North Atlantic. Shell-wall thickness increases with age and accounts for the differences in shell weight. Solid circles represent preserved specimens showing severe contraction, *i.e.*, the animal occupies less than $\frac{1}{3}$ of shell space; open circles are preserved specimens showing little contraction.

weighed separately. Shell dimensions for each specimen of *C. pyramidata* were measured as described by PAFORT-VAN IERSEL (1982). Ability to narcotize animals was examined using small amounts of MS-222 (ethyl m-aminobenzoate), ethanol, urethane or menthol crystals, magnesium chloride (osmotic), and by cooling and then preserving animals in 5% buffered formaldehyde.

RESULTS

Most live euthecosome pteropods examined retract violently into their shells when subjected to most common preservatives. They also retract in response to many relaxants if these are added too rapidly. Figure 1a shows a live specimen of a young adult *Clio pyramidata*, while Figure 1b is the same individual after addition of 5% formalin buffered with Borax with no previous narcotization. In Figure 2, all specimens were collected and observed in the living state and were seen to be normally active with their wings well extended. They all had shells of equivalent dimensions in both length (13 ± 0.5 mm) and width (8 ± 0.3 mm) ($n = 30$). Ten specimens that I preserved became so contracted that the wings and mantle were indistinguishable (Figure 1b). In Figure 2, these 10 contracted specimens composed the entire lower end of the graph, accounting for all of the specimens with adult shells between 0.95 and 1.7 mg dry weight. Shells of animals used in Figure 2 varied between 0.95 and 8.00 mg in dry weight, but all had identical length-width dimensions. Specimens preserved in formaldehyde for 6 months or less showed

no differences in soft-part-to-shell-weight ratios when compared to animals that were only frozen before drying with no preservative added.

In Figure 1c the living specimen of *Cuvierina columnella* (Rang) measured 13 mm in body length when fully extended. In 5% buffered formaldehyde, the soft parts of this animal contracted into a formless mass 3.5 mm in length (Figure 1d) at the bottom of the shell. A second specimen that had similar proportions when alive and was fixed in a similar manner retracted into a "skinny attenuate" animal measuring 8 mm in length inside the shell. Both of these resulting body forms are depicted by SPOEL (1967) as supposed living stages of this animal's life cycle. I have similar observations on resulting diminutive body forms in preserved specimens for *Cavolinia tridentata* (Niebuhr) (Figures 1e, f), *C. longirostris* (deBlainville), *C. uncinata* (Rang), *C. gibbosa* (d'Orbigny), *Diacria trispinosa* (deBlainville), *D. quadridentata* (deBlainville), *Creseis virgula* (Rang), *Styliola subula* (Quoy and Gaimard), and *Hyalocylis striata* (Rang), all of which are proposed as having diminutive "aberrant" stages (SPOEL, 1967). I was also able to produce "aberrant" specimens like those in Figures 1b, d, and f by adding 10% ethyl alcohol, Bouin's solution, or 2% glutaraldehyde (unbuffered) to unrelaxed specimens.

Results using relaxants varied depending on species, the specimen's age, its condition after collection, and its time in the relaxant. No relaxant I tried prevented severe contraction during fixation in all species. Most species of

Cavolinia and *Creseis*, as well as *Clio pyramidata*, and *Cuvierina columnella* were best relaxed for fixation in a weak solution of MS-222 added a few drops at a time and then left on the specimen in the dark for at least 2 h. Sodium pentobarbital crystals added in small amounts also prevented severe contraction of *Cavolinia* spp. during fixation but required at least 8 h on the specimen to work. Cooling animals below 5°C is also effective against contraction in all cavoliniids but usually kills them. Ethyl alcohol, menthol or urethane crystals, and magnesium chloride required at least 12 h to show effects and only narcotized animals so that they could be manipulated in the uncontracted state prior to fixation.

DISCUSSION

Juvenile and adult euthecosomes use a large mucous web to entrap food for transport to the mouth (GILMER & HARBISON, in press). This feeding method involves the full extension of the mantle and wings. Thus, in living animals, the wings are always fully developed and capable of great extension beyond the shell regardless of the animal's developmental stage. In most species of cavoliniids, the mantle is only seen at its fullest extension on undisturbed animals observed in the field by SCUBA divers. It is unlikely that these tissues are ever normally contracted or that they regress for a supposed metamorphic or strobilization change. Furthermore, thecosome pteropods have little storage tissue (BAALSRUD, 1950; SPOEL, 1967), and food particles are present in the guts of all "aberrant" forms (SPOEL, 1962, 1967). Because there is no evidence based on observations of living animals that the feeding mechanism changes during the course of a pteropod's development, Spoel's observations can only be explained as fixation artifacts. This is not a problem unique to the shelled forms. The severe contraction of the foot, wings, body, and buccal apparatus is recognized as a major problem in the taxonomy of gymnosomatous pteropods as well (MORTON, 1954; LALLI, 1970).

It is evident that animals for which the soft parts are to be used for histology or other descriptive purposes must be examined alive to assess their proportional sizes in relation to the shell size. The extensive mantle tissue seen on living animals became indistinct on all of the preserved specimens of Figure 1 (b, d, f). Other characters such as color or degree of transparency have little meaning in the preserved state without prior knowledge of living animals. Euthecosomes often become opaque and amorphous within minutes of fixation, although the shell may remain transparent for several months in well-buffered fixative.

Several other factors must be considered when working with preserved thecosomes. As is evident from Figure 2, the highly contracted young adult animals occupy shells of the same dimension as older less contractile animals, but differ in the degree of shell weight. This is due to an unusual shell-wall microstructure (BÉ *et al.*, 1972) in which new shell material is added to the inner walls over time

with very little shell growth at the aperture. Shells of cavoliniids attain the basic form of their maximum dimensions rapidly, and then gradually thicken (BÉ *et al.*, 1972; GILMER, 1974). Therefore, measurements of shell-wall thickness or shell weight will give a better indication of the relative ages of individuals than comparisons of shell dimensions. I have only found diminutive contracted forms when preserving those with the thinnest shells. The heavier and correspondingly older animals do not contract as violently. Variation in the degree that thin-walled specimens contract to form "minute" stages appears to be related to the concentration of the preservative that initially contacts them (*i.e.*, whether or not they lie in the direct path of the fixative when it is added to the sample).

Factors other than preservation artifacts may also contribute to the formation of diminutive soft parts inside adult shells. By means of SCUBA observations, I have seen that thecosomes are the prey of a number of animals, such as gymnosomatous pteropods, hyperiid amphipods, medusae, siphonophores, and ctenophores, that are all capable of removing or digesting all or part of the thecosome body without damaging the shell. Thecosomes are also parasitized by nematodes, pennellid copepods, and probably other amphipods and micro-organisms. These relationships are not well understood but could produce degenerated animals in undamaged shells.

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Population Genetics of *Crepidula onyx*: Variation in a Californian Slipper Snail Recently Established in China

by

DAVID S. WOODRUFF, LORI L. McMEEKIN, MARGARET MULVEY,¹
AND M. PATRICIA CARPENTER

Department of Biology, University of California at San Diego, La Jolla, California 92093, U.S.A.

Abstract. *Crepidula onyx* Sowerby, a common slipper snail on the coast of southern California, was first reported in Hong Kong Harbor in 1979. The genetic variation in and between three Californian populations and one Hong Kong population was determined using starch-gel electrophoresis. Seventeen enzyme systems were examined, yielding data on 23 presumptive loci in each individual studied. Sixteen loci were polymorphic in *C. onyx*. The percentage of polymorphic loci (P) ranged from 56.5 to 69.6%; mean heterozygosity (H_0) by direct count ranged from 0.14 to 0.18. Heterozygote deficiencies were found in all populations. For comparative purposes we also investigated the genetic variability in one population of *C. adunca* from central California.

An average genetic distance (Nei's unbiased D) between Hong Kong and California was 0.053. In contrast, the intersample D for the three Californian samples was 0.023. As the trans-Pacific D value was inflated by the inclusion of 10 alleles undetected in China we interpret the data as showing that the *Crepidula* introduced into Hong Kong are clearly derived from autochthonous Californian populations. The presence of six alleles found in Hong Kong and San Diego, but not at Balboa Island, suggest that the Chinese colonists were derived originally from the San Diego area rather than Los Angeles. Testing this hypothesis would require additional samples from the Los Angeles area and from Japan where *C. onyx* (not *C. fornicata*) became established in the 1960's.

INTRODUCTION

COLONIZING SPECIES afford us opportunities to study some of the major problems of theoretical ecology and evolutionary biology. Successful colonists reveal a great deal about population regulation, ecobehavioral aspects of habitat selection, interspecific interactions, and other coevolutionary phenomena (BAKER & STEBBINS, 1965; FUTUYMA & SLATKIN, 1983; PARSONS, 1983). Speciation may occasionally follow from genetic changes associated with the founder event and models of speciation by genetic revolution, founder-flush, and genetic transience may be tested by observation of the colonization process (CARSON & TEMPLETON, 1984). Discussions of the proper taxonomic treatment of colonists and other disjunct populations per-

meate the systematic literature and the relevancy of the colonization process to the phyletic gradualism-punctuated equilibrium debate is increasingly clear. Yet, despite their considerable importance, we still lack a general theory of colonization that permits predictive statements about the success, failure, and biological impact of founding populations on the communities into which they are introduced. This conclusion was reached more than 20 years ago by ELTON (1958) and WILSON (1965) and is dramatically underscored by our experience with insects (REMINGTON, 1968; PRICE, 1980) and plants (BROWN & MARSHALL, 1981; CLEGG & BROWN, 1983). The same is true for mollusks; existing theory was inadequate to predict recent events involving the giant African land snail *Achatina fulica* (MEAD, 1961, 1979) and the Asiatic clam *Corbicula fluminea* (BRITTON, 1985) to name just two examples. Furthermore, as mollusks are an extraordinarily diverse group from a genetic viewpoint (SELANDER & OCHMAN, 1983) additional studies of a wide range of col-

¹ Present address: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801.

onists and noncolonists are needed before we can expect useful generalizations to emerge. For this reason we have been studying genetic aspects of various molluscan colonists including *Biomphalaria straminea* (WOODRUFF *et al.*, 1985a, b), *Cerion* spp. (WOODRUFF & GOULD, 1981, submitted), and *Achatina fulica* (Woodruff, in preparation). In the present paper we report on the population genetics of a Californian slipper snail that recently became established in China.

Crepidula onyx Sowerby is a common slipper snail on the coast of southern California. It ranges from southern California in the north to Chile in the south according to ABBOTT & HADERLIE (1980). However, earlier records of its southern range extent are suspect as the taxonomy of the central American *Crepidula* needs revision. Also, reports of *C. onyx* found north of California may be in error (Elaine Hoagland, personal communication, 1985). Within its range it is found on rocks, *Tegula* and mussel shells, pilings, and debris in the low intertidal and subtidal zones. Its life history was studied by COE (1942a) who found that this protandric hermaphrodite lived from 2 to 3 years in southern California. Following a two-week or longer pelagic larval stage the juveniles settle and grow quickly, attaining a shell length of 6–60 mm in one year. Snails with a shell length of 6 to 10 mm were functional males. Females were between 10 and 60 mm in length. Males were often found on the shells of females and, although COE (1942b) reports finding stacks of up to 17 snails, we have observed no more than three snails together. We can find no record of *C. onyx* occurring outside its natural range until, in 1968, it was noted (as *C. fornicata*) in Tokyo Bay, Honshu, Japan, by HABA & MAZE (1970). All references to *C. fornicata* in the Pacific are most likely misidentifications of *C. onyx* (Brian Morton, personal communication, 1985). *Crepidula onyx* subsequently spread south along the coast of Honshu and to the southern islands of Shikoku and Kyushu. In 1979 it was found on Hong Kong island by Dr. M. W. Yipp. Two years later a survey showed it was widespread in Hong Kong Harbor (Victoria Harbor) (HUANG *et al.*, 1983). Numerous earlier malacological surveys provide no evidence that it reached Hong Kong more than a few years before its discovery in 1979. We speculate that *C. onyx* arrived in this busy port in the mid-1970's either directly from California or, more likely, by way of Japan.

To investigate genetic aspects of the Chinese colonists we employed electrophoretic techniques to study allozymic variation (FERGUSON, 1980). Previous studies of allozyme variation in molluscan colonists have been very successful in elucidating the roles of demography, breeding system, and genetic drift in shaping the daughter populations (see Discussion). We were able to build on the contributions of HOAGLAND (1984) who established the basic patterns of genetic variability in *Crepidula*. She used starch-gel electrophoresis to resolve 24 loci in 7 species: *C. onyx* from California, *C. fornicata* from New England, *C. protea* from

Brazil, and two pairs of sibling species presently referred to *C. plana* and *C. convexa* from the Atlantic coast of North America. From data published in the Appendix to her paper one can calculate the proportion of loci that are polymorphic in *C. onyx* to be $P = 0.435$. This relatively high value suggested that the species was variable enough to warrant this attempt to trace the colonization process geographically and monitor its genetic consequences in the derived populations. Further, HOAGLAND's (1984) demonstration that the various species she studied were very well differentiated from one another (Nei's $D \geq 0.39$) gave us reason to believe that we would be able to confirm the identity of the Chinese snails genetically. For comparative purposes we examined the population genetic variability in a second species of *Crepidula* from California; this is the first report on the genetics of *C. adunca* Sowerby.

MATERIALS AND METHODS

Specimens of *Crepidula onyx* were collected from three intertidal sites along the southern California coast in 1983 and from one site in Hong Kong:

1. The SAN DIEGO BAY site is a rocky bank adjacent to the Municipal Fishing Pier on Shelter Island. It is the southernmost collection site. *Crepidula onyx* was found on the surface of the rocks.
2. The MISSION BAY site is a rocky edge of a muddy channel located under the Ingraham Street traffic bridge, approximately 8 km north of the San Diego Bay site. Some *C. onyx* were found on mussels on the bridge pilings, although most were found on the surfaces of flat rocks.
3. The BALBOA ISLAND site (at Newport Beach, approximately 132 km north of San Diego) is a sandy beach with small boat piers, on the ocean side of the island, at the end of Jade Street. *Crepidula onyx* was found on mussels, on pilings, and on miscellaneous debris.
4. Dr. May Yipp provided us with a sample of *C. onyx* from North Point on the south shore of HONG KONG HARBOR (site F on fig. 1B of HUANG *et al.*, 1983).

Crepidula adunca was collected from a single intertidal site on the central California coast, at the southernmost end of Monterey Bay, also in 1983:

5. The ASILOMAR (central California) site is a rocky beach facing open ocean. *Crepidula adunca* was found on *Tegula* shells among tide pools.

Individuals were collected at each site during low tide using laboratory spatulas. Each collection consisted of approximately 40 individuals. All individuals were removed from the shells, sexed, and stored in centrifuge tubes at -70°C until electrophoresed. Voucher specimens are deposited with the California Academy of Sciences and Academy of Natural Sciences, Philadelphia.

Before electrophoresis, individual *Crepidula* were thawed, then homogenized in 0.1–0.2 mL of a grinding solution (0.01 M Tris, 0.001 M EDTA, 0.05 mM NADP; pH 7.0). The homogenate was centrifuged at 10,000 g for

Table 1
Presumptive loci and electrophoretic conditions for *Crepidula onyx*.

Isozyme	No. alleles	Buffer	Voltage	Run time (hours)
Acid phosphatase (<i>Acp</i>)	1	TC 6.0	110 V	4.0
Alkaline phosphatase (<i>Alkp</i>)	3	TBE 9.0	250 V	4.0
Aspartate amino transferase (<i>Aat</i>)	3	TBE 9.0	250 V	4.0
Esterase-1 (<i>Es-1</i>)	3	TBE 9/8	210 V	2.5
Esterase-2 (<i>Es-2</i>)	3	TBE 9/8	210 V	2.5
Esterase-3 (<i>Es-3</i>)	1	TBE 9/8	210 V	2.5
Glucose-6-phosphate dehydrogenase (<i>G6pdh</i>)	4	Poulik	200 V	4.5
Glucose phosphate isomerase (<i>Gpi</i>)	3	TC 6.0	110 V	4.0
Hexokinase (<i>Hk</i>)	1	TBE 8.0	260 V	4.0
Isocitrate dehydrogenase (<i>Idh</i>)	1	TBE 8.0	260 V	4.0
Lactate dehydrogenase (<i>Ldh</i>)	3	TBE 9/8	210 V	2.5
Malate dehydrogenase-1 (<i>Mdh-1</i>)	2	TC 6.0	110 V	4.0
Malate dehydrogenase-2 (<i>Mdh-2</i>)	5	TC 6.0	110 V	4.0
Malic enzyme (<i>Me</i>)	1	TBE 9.0	250 V	4.0
Peptidase-1 (<i>Pep-1</i>) (leucylglycylglycine)	4	TBE 8.0	260 V	4.0
Peptidase-2 (<i>Pep-2</i>) (L-leucyl-L-alanine)	4	TBE 8.0	260 V	4.0
Peptidase-3 (<i>Pep-3</i>) (L-leucyl-L-alanine)	3	TBE 8.0	260 V	4.0
Phosphoglucomutase-1 (<i>Pgm-1</i>)	3	TC 6.0	110 V	4.0
Phosphoglucomutase-1 (<i>Pgm-1</i>)	3	TBE 9/8	210 V	2.5
Phosphoglucomutase-2 (<i>Pgm-2</i>)	5	TBE 9/8	210 V	2.5
6-Phosphogluconate dehydrogenase (<i>Pgd</i>)	3	TBE 8.0	260 V	4.0
Sorbitol dehydrogenase (<i>Sordh</i>)	3	TBE 9.0	250 V	4.0
Superoxide dismutase (<i>Sod</i>)	1	TBE 8.0	260 V	4.0
Xanthine oxidase (<i>Xdh</i>)	1	Poulik	200 V	4.5

2 min and then absorbed onto filter paper wicks which were inserted into 12.5% (w/v) horizontal starch gels (25 g ElectroStarch Lot #392, 25 g Sigma starch/400 ml buffer).

Electrophoresis was carried out at constant voltage for approximately 4 h or until a bromophenol blue dye marker had migrated 10 cm from the origin. Electrophoretic conditions for the 17 enzymes are described in Table 1. Gels were stained at 37°C following the methods of SHAW & PRASAD (1970), SELANDER *et al.* (1971), HARRIS & HOPKINSON (1976), and HOAGLAND (1984). Esterases were stained using α -naphthyl-acetate as the substrate; peptidases used leucylglycylglycine or L-leucyl-L-alanine as substrate.

Isozymes were numbered in order of decreasing anodal mobility in multilocus systems. Relative mobilities of electromorphs at each locus were calculated using the most common allele at San Diego Bay as a standard. Typically several populations were run on each gel to facilitate comparison of alleles across populations.

The proportion of polymorphic loci (P) was based on direct count. Average heterozygosity per individual was based on direct count and Castle-Hardy-Weinberg expectations. For each polymorphic locus a χ^2 statistic was used to test the fit of the observed data to the random mating expectations of the Castle-Hardy-Weinberg model. Expected frequencies were calculated using LEVENE's (1949)

correction for small samples. Exact significance probabilities were also calculated (analogous to Fisher's exact test for 2×2 contingency tables).

The genetic structure among the populations was analyzed using WRIGHT's (1978) F-statistics. The F_{is} value is the inbreeding coefficient of an individual relative to its sample. The F_{st} value is a measure of interdemographic variation among samples relative to the total, and the F_{it} value provides a correlation between gametes combined within an individual relative to the total sample. A hierarchical analysis of population differentiation based on the F-statistics was performed using the partitioned variance equation: $H_T = H_L + D_{LA} + D_{AC} + D_{CT}$ (where T = total, L = locality, A = area, and C = country) and then setting $H_T = 1$ and partitioning each value. Unbiased estimates of genetic distance were calculated by the methods of NEI (1978) and ROGERS (1972). The distance measures for the five populations were clustered using UPGMA algorithms. Finally, Roger's distances were used to construct a Wagner tree. All these statistical analyses were carried out using the BIOSYS-1 program (SWOFFORD & SELANDER, 1981).

RESULTS

The 17 enzyme systems examined yielded data on 23 genes in each individual studied. Seven gene loci were monomorphic (*i.e.*, invariant) in all specimens of *Crepidula onyx*

Table 2

Allele frequencies for *Crepidula onyx* and *C. adunca*.

Locus	<i>Crepidula onyx</i>				<i>C. adunca</i>
	San Diego	Mission Bay	Balboa Island	Hong Kong	Asilo-mar
<i>Acp</i>					
(n)	40	21	46	66	28
5.0	0.000	0.000	0.000	0.000	1.000
1.0	1.000	1.000	1.000	1.000	0.000
<i>Alkp</i>					
(n)	45	41	46	66	28
1.10	0.011	0.012	0.000	0.000	0.000
1.00	0.922	0.793	1.000	0.970	1.000
0.85	0.067	0.195	0.000	0.030	0.000
<i>Aat</i>					
(n)	43	40	38	53	27
1.25	0.000	0.000	0.000	0.000	0.574
1.20	0.000	0.000	0.000	0.000	0.426
1.13	0.163	0.050	0.013	0.170	0.000
1.00	0.558	0.600	0.697	0.642	0.000
0.81	0.279	0.350	0.289	0.189	0.000
<i>Es-1</i>					
(n)	45	40	45	65	26
1.10	0.044	0.125	0.033	0.000	0.231
1.05	0.400	0.538	0.744	0.777	0.019
1.00	0.556	0.338	0.222	0.223	0.346
0.94	0.000	0.000	0.000	0.000	0.404
<i>Es-2</i>					
(n)	44	41	46	66	27
1.00	0.818	0.573	0.837	0.242	0.926
0.95	0.182	0.415	0.163	0.652	0.074
0.91	0.000	0.012	0.000	0.106	0.000
<i>Es-3</i>					
(n)	46	43	46	66	28
1.00	1.000	1.000	1.000	1.000	0.000
0.89	0.000	0.000	0.000	0.000	1.000
<i>G6pdh</i>					
(n)	44	37	40	42	13
1.06	0.193	0.324	0.313	0.262	0.000
1.03	0.000	0.054	0.000	0.000	0.000
1.00	0.807	0.622	0.663	0.738	0.000
0.92	0.000	0.000	0.000	0.000	1.000
0.90	0.000	0.000	0.025	0.000	0.000
<i>Gpi</i>					
(n)	38	22	46	55	14
1.3	0.066	0.000	0.065	0.209	0.000
1.0	0.934	1.000	0.935	0.673	0.000
0.89	0.000	0.000	0.000	0.118	0.000
0.68	0.000	0.000	0.000	0.000	1.000
<i>Hk</i>					
(n)	44	40	36	65	28
1.00	1.000	1.000	1.000	1.000	1.000
<i>Idh</i>					
(n)	44	39	46	53	27
1.50	0.000	0.000	0.000	0.000	1.000
1.00	1.000	1.000	1.000	1.000	0.000

Table 2

Continued.

Locus	<i>Crepidula onyx</i>				<i>C. adunca</i>
	San Diego	Mission Bay	Balboa Island	Hong Kong	Asilo-mar
<i>Ldh</i>					
(n)	46	43	46	66	28
1.10	0.000	0.000	0.000	0.000	1.000
1.05	0.207	0.093	0.000	0.197	0.000
1.00	0.793	0.814	1.000	0.576	0.000
0.98	0.000	0.093	0.000	0.227	0.000
<i>Mdh-1</i>					
(n)	46	40	46	66	28
1.15	0.098	0.025	0.022	0.015	0.000
1.00	0.902	0.975	0.978	0.985	0.000
0.77	0.000	0.000	0.000	0.000	1.000
<i>Mdh-2</i>					
(n)	44	40	42	36	28
2.4	0.034	0.000	0.060	0.014	0.000
2.0	0.386	0.438	0.286	0.528	0.000
1.5	0.045	0.087	0.131	0.167	0.000
1.0	0.523	0.438	0.381	0.250	0.000
0.5	0.011	0.038	0.143	0.042	0.000
0.4	0.000	0.000	0.000	0.000	1.000
<i>Me</i>					
(n)	46	42	46	62	27
1.30	0.000	0.000	0.000	0.000	1.000
1.00	1.000	1.000	1.000	1.000	0.000
<i>Pep-1</i>					
(n)	46	40	44	60	28
1.12	0.054	0.063	0.170	0.192	0.268
1.04	0.348	0.338	0.375	0.417	0.304
1.00	0.489	0.412	0.307	0.267	0.071
0.84	0.109	0.188	0.148	0.125	0.357
<i>Pep-2</i>					
(n)	40	38	46	52	28
1.00	0.675	0.329	0.717	0.654	0.964
0.95	0.150	0.118	0.000	0.000	0.036
0.92	0.175	0.553	0.239	0.346	0.000
0.76	0.000	0.000	0.043	0.000	0.000
<i>Pep-3</i>					
(n)	45	34	46	31	28
1.35	0.000	0.000	0.000	0.000	0.054
1.25	0.000	0.000	0.000	0.000	0.946
1.00	0.489	0.309	0.609	0.919	0.000
0.95	0.100	0.324	0.000	0.000	0.000
0.90	0.411	0.368	0.391	0.081	0.000
<i>Pgm-1</i>					
(n)	37	27	42	61	
1.08	0.392	0.167	0.131	0.205	
1.00	0.419	0.593	0.429	0.270	
0.91	0.189	0.241	0.440	0.525	
<i>Pgm-2</i>					
(n)	24	20	46	33	28
1.15	0.021	0.150	0.000	0.000	0.000
1.10	0.000	0.050	0.000	0.000	0.000

Table 2
Continued.

Locus	<i>Crepidula onyx</i>				<i>C. adunca</i>
	San Diego	Mission Bay	Balboa Island	Hong Kong	Asilomar
1.00	0.917	0.775	0.880	0.970	0.000
0.91	0.042	0.025	0.076	0.000	0.000
0.90	0.021	0.000	0.043	0.030	0.000
0.79	0.000	0.000	0.000	0.000	0.518
0.70	0.000	0.000	0.000	0.000	0.482
<i>Pgd</i>					
(n)	44	37	46	47	14
1.17	0.034	0.000	0.000	0.043	0.000
1.00	0.966	0.986	1.000	0.915	1.000
0.75	0.000	0.014	0.000	0.043	0.000
<i>Sordh</i>					
(n)	44	42	43	54	28
1.88	0.205	0.036	0.221	0.343	0.036
1.25	0.341	0.321	0.070	0.435	0.000
2.00	0.455	0.643	0.709	0.222	0.964
<i>Sod</i>					
(n)	42	37	42	26	
1.00	1.000	1.000	1.000	1.000	
<i>Xdh</i>					
(n)	46	43	45	59	28
1.00	1.000	1.000	1.000	1.000	1.000
Percentage of loci polymorphic (<i>P</i>)	69.6	65.2	56.5	69.6	34.8
Mean heterozygosity (<i>H</i>)	0.156	0.176	0.169	0.141	0.052

examined: *Acp*, *Es-3*, *Hk*, *Idh*, *Me*, *Sod*, and *Xdh*. Sixteen loci were polymorphic: one locus had two alleles (*Mdh-1*), 10 loci had three alleles (*Alkp*, *Aat*, *Es-1*, *Es-2*, *Gpi*, *Ldh*, *Pep-3*, *Pgm-1*, *Pgd*, *Sordh*), three loci had four alleles (*G6pdh*, *Pep-1*, *Pep-2*), and two loci had five alleles (*Mdh-2*, *Pgm-2*). In *C. adunca*, no data were obtained for *Pgm-1* and *Sod*. Of the remaining loci, six had two alleles (*Aat*, *Es-2*, *Pep-2*, *Pep-3*, *Pgm-2*, *Sordh*), two had three alleles (*Es-1*, *Pep-1*), and the remainder were monomorphic. The relative mobilities of these allozymes are shown in Table 2. The allele frequencies for all loci in *C. onyx* and *C. adunca* are also shown in Table 2 along with values for *P* (percentage of polymorphic loci) and *H* (mean heterozygosity).

In *Crepidula onyx* it can be seen that *P* has a range of 56.5 to 69.6%; *C. adunca* has a lower value of 34.8%. Mean heterozygosity by direct count ranges from 0.14 to 0.18 in *C. onyx*, and again *C. adunca* has a lower value (0.05). These values consistently underestimate intrapopulation *H* as the populations of adult snails sampled all show consistent heterozygote deficiencies (see below). Mean heterozygosities according to panmictic expectations were 0.24–0.30 in *C. onyx* and 0.12 in *C. adunca*.

The data were examined for evidence of panmixia, and heterozygote deficiencies were found in all populations (Table 3). There are 16 loci in the four populations of *Crepidula onyx* at which observed allele frequencies can be compared with those expected on the basis of panmixia. Simple χ^2 tests on the raw genotypic data showed that out of 60 tests, fully 40 failed at the 0.05 level. However, because of inadequacies of the χ^2 test, we chose to calculate exact significance probabilities (Table 4). In San Diego Bay, it can be seen that significance tests for 11 out of 16 loci fail using this procedure. For comparison, in Mission Bay 7 out of 15, at Balboa Island 6 out of 13, and in Hong Kong Harbor 9 out of 16 loci all show significant heterozygote deficiencies. *Crepidula adunca* (the outgroup) shows the same pattern. Looking at Table 4 by specific locus, it can be seen that *Es-1*, *G6pdh*, *Ldh*, and *Pgm-1* are out of equilibrium in all populations and *Es-2* is out at all populations except Asilomar. Only *Mdh-1* and *Pep-1gg-1* are segregating according to panmictic expectations in all populations; *Mdh-2* is in equilibrium at all populations except Hong Kong.

Values for Wright's *F*-statistics are presented in Table 5. The mean F_{is} value was 0.415 and is significantly different from zero; F_{st} was 0.079 and the F_{it} value was 0.461.

A matrix of genetic similarity and distance coefficients is shown in Table 6. The UPGMA phenogram resulting from Nei's genetic identity is shown in Figure 1; its cophenetic correlation coefficient was 0.999. A similar phenogram resulted from Rogers' distance with San Diego Bay, Balboa Island, Mission Bay, and Hong Kong each having distances of approximately 0.12 and Asilomar having a distance of 0.58. The correlation was 0.998. The Rogers distance values were used to prepare the Wagner tree shown in Figure 2.

DISCUSSION

We are confident that the dark-shelled Chinese snails we have studied are correctly identified as *Crepidula onyx*. Identifications based on morphology (CHRISTIAENS, 1980; HUANG *et al.*, 1983; Hoagland, personal communication, 1983) are herein confirmed genetically. The only other calyptraeoid snail known from the Hong Kong area is *Crepidula (Siphopatella) walshi* (Reeve) and the two species differ in gross appearance and habit (CHRISTIAENS, 1980). *Crepidula walshi* is white-shelled and commensal on the inner surface of gastropod shells occupied by pagurid hermit crabs (YIPP, 1980).

Autochthonous populations of *Crepidula onyx* from southern California are genetically variable. Our study of variation at 23 loci in 135 animals representing 3 populations gave an estimate of the mean proportion of polymorphic loci (*P*) of 0.637. If we add to these data, the estimate of *P* = 0.565 for 58 animals from Balboa Island published by HOAGLAND (1984; identical to our estimate) then we obtain a value for *C. onyx* of *P* = 0.619. Com-

Table 3
Coefficients for heterozygote deficiency or excess in all polymorphic loci.

Locus	San Diego			Mission Bay			Balboa Island			Hong Kong			Asilomar		
	Obs. hets	Exp. hets	<i>D</i>	Obs. hets	Exp. hets	<i>D</i>	Obs. hets	Exp. hets	<i>D</i>	Obs. hets	Exp. hets	<i>D</i>	Obs. hets	Exp. hets	<i>D</i>
<i>Alkp</i>	3	6.6	-0.55	11	13.8	-0.21	—	—	—	4	3.9	0.02	—	—	—
<i>Aat</i>	13	25.4	-0.49	10	20.9	-0.52	11	16.5	-0.34	19	28.0	-0.32	5	13.5	-0.63
<i>Es-1</i>	6	24.1	-0.75	13	23.6	-0.45	4	18.0	-0.78	5	22.7	-0.78	5	17.6	-0.72
<i>Es-2</i>	6	13.2	-0.55	11	20.7	-0.47	3	12.7	-0.76	6	33.6	-0.82	4	3.8	0.06
<i>G6pdh</i>	9	13.9	-0.35	4	19.0	-0.79	11	18.7	-0.41	2	16.4	-0.88	—	—	—
<i>Gpi</i>	5	4.7	0.06	—	—	—	4	5.7	-0.30	12	27.2	-0.56	—	—	—
<i>Ldh</i>	5	15.2	-0.67	4	13.9	-0.71	—	—	—	6	38.4	-0.84	—	—	—
<i>Mdh-1</i>	7	8.2	-0.15	2	2.0	0.01	2	2.0	0.01	2	2.0	0.01	—	—	—
<i>Mdh-2</i>	23	25.6	-0.10	23	24.6	-0.07	27	31.1	-0.13	16	23.0	-0.30	—	—	—
<i>Pep-1</i>	27	29.1	-0.07	25	27.4	-0.09	30	31.8	-0.06	28	42.5	-0.34	13	20.1	-0.35
<i>Pep-2</i>	4	19.9	-0.80	15	22.0	-0.32	12	19.8	-0.40	22	23.8	-0.07	0	2.0	-1.00
<i>Pep-3</i>	14	26.5	-0.47	12	22.9	-0.48	22	22.2	-0.01	5	4.7	0.07	1	2.9	-0.65
<i>Pgm-1</i>	10	23.8	-0.58	4	15.5	-0.74	20	25.7	-0.22	20	37.5	-0.47	—	—	—
<i>Pgm-2</i>	4	3.9	0.04	3	7.7	-0.61	11	10.1	0.09	2	2.0	0.02	5	14.2	-0.65
<i>Pgd</i>	1	2.9	-0.66	1	1.0	0.00	—	—	—	0	7.6	-1.00	—	—	—
<i>Sordh</i>	16	28.3	-0.43	17	20.5	-0.17	11	19.3	-0.43	21	35.1	-0.40	0	2.0	-1.00

parable data are available for seven other species of *Crepidula* (HOAGLAND, 1984). Over all eight species, studied at 21–24 loci, estimates of *P* range from 0.348 in *C. adunca* (this study) to 0.875 in *C. fornicata*. The grand mean *P* = 0.468 (SD = 0.287).

The Californian samples of adult *Crepidula onyx* we studied have a mean heterozygosity by direct count (*H*) of 0.167. This value is, however, not simply comparable to the mean value of *H* = 0.148 for 46 other molluscs published by NEVO *et al.* (1984) as we have detected a consistent pattern of heterozygote deficiency in *C. onyx*. As our value underestimates *H*, *C. onyx* falls into the "above-average" class for levels of individual genetic variability in molluscs. Turning now to the allochthonous (and probably adventive) Chinese snails we estimate *P* = 0.696 and *H* = 0.141 (Table 2). These values are very similar to those found in the Californian samples. Again, *H* is an underestimate of individual variability.

The rich genetic endowment of *Crepidula onyx* held the promise that we might be able to reconstruct the colonization process by careful comparison of the Californian and Chinese snails. Multilocus comparisons of the samples from the two areas do, in fact, confirm the genetic relatedness of the populations now over 11,000 km apart. Estimates of overall genetic differentiation based on formulae developed by NEI (1978) give an average genetic distance (*D*) between Hong Kong and California of 0.053 (range 0.049–0.058). In contrast, the intersample *D* for the three Californian samples is 0.023 (0.021–0.027). In mammals, fish, reptiles, and amphibians interspecific variation is such that congeneric populations of outcrossing species typically have *D* values of 0.10 or more (AVISE & AQUADRO, 1982). The average genetic distance between

local populations for a wide range of plants, invertebrates, and vertebrates ranges between 0.013–0.058 (AYALA, 1983). As the trans-Pacific *D* value is inflated by the inclusion of 10 Californian alleles that apparently did not become established in China, we interpret the data as showing that the Asian snails are clearly derived from, and poorly differentiated from, their American ancestors. Thus, despite its recent range expansion, *C. onyx* is not more differentiated than other species of *Crepidula* where intraspecific differences are in the range: 0.003–0.016 (*C. fornicata*), 0.008–0.076 (*C. cf. convexa*), 0.037–0.057 (*C. convexa*), 0.052–0.097 (*C. plana*), and 0.045 (*C. cf. plana*) (HOAGLAND, 1984).

San Diego (samples from San Diego Harbor and nearby Mission Bay) and Balboa Island at Newport Beach, about 30 km from the port of Los Angeles, are representative of the two major commercial and naval ports within the range of *Crepidula onyx*. Accordingly, we applied a variety of clustering techniques to the multilocus data in an attempt to establish whether the Chinese population was more closely related to San Diego or Balboa Island, California populations. A phenogram, based on the UPGMA method using Nei's *D* (Figure 1) and a Wagner tree based on Rogers' *S* (Figure 2) showed that the Chinese population was equidistant from the three Californian populations sampled, or (insignificantly) closer to Balboa Island than San Diego. These analyses are, however, misleading as they do not allow for the known historical relationship between the Asian and American snails. A closer analysis of the original data (Table 2) suggests a different conclusion—one that points to San Diego as the likely source of the colonists. We detected 58 alleles segregating in Californian *C. onyx* and 48 of these were found

Table 4

Exact significance probabilities of agreement with Hardy-Weinberg expectations.

Locus	San Diego	Mission Bay	Balboa Island	Hong Kong	Asilomar
<i>Alkp</i>	0.013	0.330	—	1.000	—
<i>Aat</i>	0.001	0.000	0.059	0.072	0.001
<i>Es-1</i>	0.000	0.005	0.000	0.000	0.000
<i>Es-2</i>	0.002	0.004	0.000	0.000	1.000
<i>G6pdh</i>	0.035	0.000	0.029	0.000	—
<i>Gpi</i>	1.000	—	0.159	0.000	—
<i>Ldh</i>	0.000	0.000	—	0.000	—
<i>Mdh-1</i>	0.351	1.000	1.000	1.000	—
<i>Mdh-2</i>	0.237	1.000	0.207	0.008	—
<i>Pep-1</i>	0.081	1.000	0.332	0.064	0.240
<i>Pep-2</i>	0.000	0.114	0.024	0.759	0.018
<i>Pep-3</i>	0.016	0.077	1.000	1.000	0.055
<i>Pgm-1</i>	0.000	0.000	0.026	0.002	—
<i>Pgm-2</i>	1.000	0.023	1.000	1.000	0.001
<i>Pgd</i>	0.034	1.000	—	0.000	—
<i>Sordh</i>	0.003	0.314	0.021	0.002	0.018

in Hong Kong. Ten Californian alleles were not seen in the 26–66 Chinese animals studied. These alleles varied in frequency in California between 0.012 and 0.324 ($\bar{X} = 0.101$); it seems most probable that they were lost by chance during the colonization process. Of the 48 Californian alleles segregating in Hong Kong six were found in San Diego and not at Balboa Island: *Alkp*^{0.85}, *Es-2*^{0.91}, *Ldh*^{1.05}, *Ldh*^{0.98}, *Pgd*^{1.17} and *Pgd*^{0.75}. Combining the Mission Bay and San Diego Harbor data, these six alleles had an estimated average frequency of 0.07 (range 0.01–0.21) in California and 0.11 (0.04–0.23) in China. As these six San Diego markers were not found at Balboa Island their presence in Hong Kong strongly suggests that the Chinese colonists were derived originally from San Diego Harbor rather than Los Angeles. Although our sampling of *C. onyx* is inadequate to prove this assertion, it is a reasonable hypothesis on the basis of existing data.

The phenograms based on the allozyme data obscure this pattern because they do not allow for the known derivation of the Chinese population from America. The UPGMA methods overemphasize similarities in allele frequencies and, in this respect, Hong Kong is rather like the Balboa Island sample, *e.g.*, *Pep-2*^{0.95}, *Pep-3*^{0.95}, and *Es-1*^{1.05}. The method ignores the fact that we would expect a sequential loss of rarer alleles during the population bottleneck(s) associated with the colonization process. The observation that six alleles associated only with San Diego and none associated exclusively with Balboa Island are now established in Hong Kong suggests that one can reach more definitive conclusions than those based on standard analytical procedures.

It should not surprise us that it is difficult to trace the origin of the Hong Kong stock back to America. *Crepidula onyx* is very variable and a hierarchical analysis of F-sta-

Table 5

Summary of F-statistics for *Crepidula onyx*.

Locus	F _{is}	F _{it}	F _{st}
<i>Aat</i>	0.415	0.427	0.020
<i>Acp</i>	1.000	1.000	0.084
<i>Alkp</i>	0.264	0.323	0.081
<i>Es-1</i>	0.663	0.693	0.087
<i>Es-2</i>	0.644	0.716	0.201
<i>Es-3</i>	1.000	1.000	0.018
<i>G6pdh</i>	0.619	0.626	0.020
<i>Gpi</i>	0.406	0.475	0.171
<i>Ldh</i>	0.761	0.788	0.111
<i>Mdh-1</i>	0.073	0.100	0.029
<i>Mdh-2</i>	0.141	0.170	0.034
<i>Me</i>	-0.025	-0.012	0.012
<i>Pep-1</i>	0.132	0.149	0.019
<i>Pep-2</i>	0.393	0.449	0.092
<i>Pep-3</i>	0.303	0.411	0.154
<i>Pgd</i>	0.802	0.808	0.027
<i>Pgm-1</i>	0.493	0.527	0.065
<i>Pgm-2</i>	0.236	0.274	0.049
<i>Sod</i>	0.725	0.733	0.027
<i>Sordh</i>	0.359	0.428	0.107
Mean	0.415	0.461	0.079

tistics reveals that fully 93% of the detected variation resides in any single sample. Less than 6% of the known genetic variation in the species is partitioned between populations. Even if we had multiple samples from Los Angeles and elsewhere it is unlikely that we could ever prove that the Chinese snails arose from one single region of the original species range. In fact, we already know that our sampling in California was unequal to this task as we discovered *Gpi*^{0.89} at a frequency of 0.118 in Hong Kong and have yet to find this allele in America. (The alternative hypothesis, that this allele arose by post-colonization mutation is unlikely in view of the fact that snails have been in Hong Kong for only about 10 generations.)

One of the problems with deciphering the history of Hong Kong *Crepidula onyx* arises from the fact that we do not know whether the colonists came from California

Table 6

Matrix of genetic similarity and distance coefficients for *Crepidula onyx* and *C. adunca*. Below diagonal: ROGERS' (1972) genetic distance. Above diagonal: NEI's (1978) unbiased genetic identity.

Population	<i>C. onyx</i>			<i>C. adunca</i>	
	1	2	3	4	5
1 San Diego Bay	*****	0.978	0.980	0.948	0.413
2 Ingraham Bridge	0.102	*****	0.973	0.944	0.401
3 Balboa Island	0.093	0.109	*****	0.952	0.421
4 Hong Kong	0.139	0.151	0.122	*****	0.615
5 Asilomar	0.572	0.585	0.563	0.361	*****

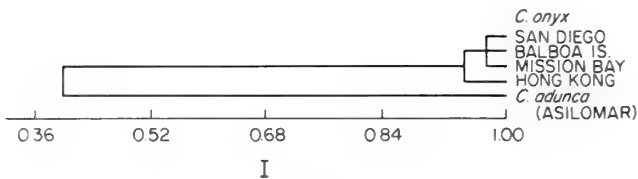


Figure 1

Genetic relationships revealed by UPGMA cluster analysis based on NEI's (1978) genetic identity.

directly or indirectly by way of Japan. A survey of genetic variability among Japanese *C. onyx* may clarify this issue.

A second problem arises because *Crepidula onyx* is so polymorphic that single samples may not adequately represent its geographic and temporal variability. A comparison of our results (Table 2) for *C. onyx* from Balboa Island with those published by HOAGLAND (1984) reveals identical or insignificantly different allele frequencies at five of the 11 loci studied in both laboratories, but significant differences at the remaining six loci. The latter are probably not due to technical differences in our procedures but, rather, reflect the considerable geographic and temporal variability we have recently discovered by monitoring selected populations of this species over a 2-yr period (MCMEEKIN, 1985; MCMEEKIN & WOODRUFF, in preparation).

We can be a little more confident in our reconstruction of the colonization event. It is most probable that the founding population was not very small and that once established it grew rapidly. The high levels of individual heterozygosity (H) and the high overall value for P in the Hong Kong sample indicate no major bottleneck occurred. Such a scenario would account for the preservation of most of the ancestral variability (NEI *et al.*, 1975) and is the most frequently observed result of molluscan colonization (SELANDER & OCHMAN, 1983). As there are up to five alleles segregating per locus in Hong Kong there could be no fewer than three founders; there were probably at least 10 times that many. Once settled in Hong Kong there is no doubt that the population could grow very rapidly. *Crepidula onyx* is a protandrous hermaphrodite that can begin egg laying within two months of settling and can produce 5000–20,000 larvae during its 2–3-yr life (COE, 1942a). Ten or more generations of such growth in Hong Kong, coupled with dispersal during the 2-wk planktonic larval stage, would account for the present abundance and distribution of the species in this part of China. It is unnecessary, at this time, to postulate that multiple introductions have occurred, although it is quite likely that they have.

We find no obvious evidence for any major change in the population structure of the Hong Kong colonists. The mean number of alleles per locus (2.2) is not different from that seen in California (2.1–2.3). As noted above, the proportion of polymorphic loci (0.696 in Hong Kong

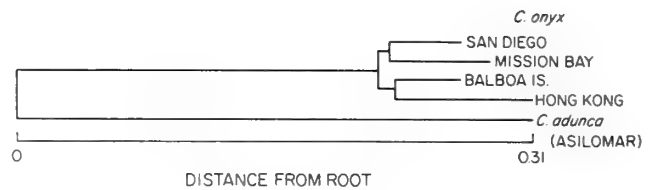


Figure 2

Cluster relationships of samples revealed by an outgroup rooted Wagner tree based on Rogers' genetic distance.

vs. 0.619 in California) and the mean heterozygosity (0.167 *vs.* 0.141) are also very similar. A decrease in genetic variability has not occurred and we find no evidence for a genetic revolution of the type envisaged by MAYR (1954) associated with this founder event. Whether the Chinese populations will diverge from their ancestors according to the founder-flush or genetic transience models (CARSON & TEMPLETON, 1984; BARTON & CHARLESWORTH, 1984) is more difficult to rule out given our present knowledge of the *Crepidula* genome. It does, however, seem most unlikely as future gene flow from America would retard local differentiation. Nevertheless, it would be interesting to examine the reweighting of fitness components due to the changes in allele frequencies associated with the founder event. If such genetic drift-induced shifts involve major loci with many pleiotropic effects, then the stage is set for transience to occur.

Crepidula onyx resembles a number of colonizing species of plants and animals in having a richly variable genome that appears resistant to significant change by founder effect. BAKER (1965) suggested such species have a general purpose genotype that is resistant to repatterning. These "weedy" species are alleged to have complex balanced systems of heterosis that can survive bottlenecks intact and may even underlie the colonizing habit. Although we feel it is too early to state that such colonizing species have genetic properties that distinguish them from "speciose" species, it seems most likely that *C. onyx* fits the above pattern. We foresee no nomenclatural problems arising from the success of the Asian colonists; they seem likely to remain genetically very similar to their allopatric ancestors.

The most striking thing about the population structure of the Chinese *Crepidula onyx* is, of course, the striking heterozygote deficiencies at 11 of the 16 polymorphic loci. One might seize on this observation as evidence for dramatic genetic restructuring of the colonizing population. This, however, cannot be the explanation, as the same phenomenon occurs in the three Californian samples.

Over two dozen studies of genetic variability in marine mollusks have shown heterozygote frequencies lower than expected under panmixia (discussed by ZOUROS & FOLTZ, 1984). SINGH & GREEN (1984) propose four possible explanations for this phenomenon: inbreeding, presence of null alleles, Wahlund effect, and selection. In addition,

the explanations of scoring bias (AYALA *et al.*, 1973) and sex-linked loci (ZOUROS *et al.*, 1980) have been offered to account for this deficiency of heterozygotes.

The present paper was not aimed at resolving this issue; however, it can be shown that three of the above hypotheses are unlikely to account for the heterozygote deficiency in this study. First, inbreeding as an explanation is not compatible with the species' biology. *Crepidula* have a dispersed larval stage for at least two weeks, making it improbable for gametes from closely related individuals to combine in high frequencies. Because *Crepidula onyx* are sequential hermaphrodites, and are usually not sexually functional during the transition stage from male to female (COE, 1942a), self-fertilization is not a factor. Second, null alleles are unlikely to cause the heterozygote deficiency, as co-dominant null alleles would be recognizable as "blank" spots on the gel and would not be expected at such high frequency. No evidence for this has been seen in this study. Third, the Wahlund effect does not explain the deficiency, as this is not a local problem; relatively low heterozygote frequencies are found in all of the populations. We are at present conducting a study of *C. onyx* in Mission Bay, San Diego, which will, among other questions, assess the relative role of natural selection, age effects, sex-linked loci, and scoring bias in explaining the observed heterozygote deficiencies.

The same phenomenon of heterozygote deficiency was also noted in our sample of *Crepidula adunca* (a species with brooded larvae) from central California and it may be a general feature of slipper snails. In other respects *C. adunca* seems quite different from *C. onyx*. Genetically it is less variable: $A = 1.5$ vs. 2.3 where A is the number of alleles per locus, $P = 0.348$ vs. 0.619 and $H = 0.052$ (SE = 0.023) vs. 0.167; it is in fact less variable than any of the six Atlantic species studied by HOAGLAND (1984). Although additional samples are needed to confirm this result the two Californian species seem to have very different population genetic structures. *Crepidula adunca* and the California samples of *C. onyx* are also well differentiated from one another: NEI's (1978) $D = 0.888$ (range 0.884–0.913) ($I = 0.401$ –0.421) and ROGERS' (1972) $D = 0.563$ –0.585. These distances are a little greater than those found between the six Atlantic species which had Nei's D of 0.31–0.87, with most comparisons falling in the range of 0.65–0.80 (HOAGLAND, 1984). Although our studies are not completely comparable it is interesting to note that HOAGLAND (1984) also estimated the genetic distance between *C. onyx* and the six Atlantic taxa: *C. fornicata*, 0.70–0.71; *C. convexa* and its unnamed sibling, 0.79–0.84; *C. plana* and its unnamed sibling, 0.76–0.82; and Brazilian *C. protea*, 0.72. Clearly, the geographic proximity of *C. onyx* and *C. adunca* belies their genetic unrelatedness and our observation that the two species differ markedly in genetic variability should not surprise us.

As a genetically variable and successful colonist *Crepidula onyx* is reminiscent of *C. fornicata*, which has spread from the Atlantic coast of North America to Europe

(HOAGLAND, 1985). *Crepidula fornicata* is the most variable *Crepidula* yet described (HOAGLAND, 1984, 1985). As it forms long breeding chains of stacked individuals it is regarded as a fouling organism in some areas. ORTON (1912) surmised how this habit contributes to their success in oyster beds by not only increasing the chance of copulation but also by enhancing feeding and respiratory efficiency. *Crepidula onyx* also forms stacks and, although it is not presently a nuisance in California harbors and oyster beds, its habits in exotic locales deserve some attention. Its ecological impact in the warmer waters of Hong Kong might be expected to be greater than that along the coast of Japan. One thing is certain; with 10,000 ships entering Hong Kong waters each year the species will undoubtedly spread to other areas.

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The Laboratory Culture of Two Aplysiids, *Aplysia brasiliana* Rang, 1828, and *Bursatella leachii plei* (Rang, 1828) (Gastropoda: Opisthobranchia) in Artificial Seawater

by

JOHN A. PAIGE¹

Department of Zoology, University of Florida, Gainesville, Florida 32611, U.S.A.

Abstract. Techniques for the laboratory culture of the sea hares *Aplysia brasiliana* Rang, 1828, and *Bursatella leachii plei* (Rang, 1828) in artificial seawater are described. The simplified methods allowed high yields (70–80% of the starting density) to metamorphic competency. The larvae of both species grew an average of 10 μm per day and were successfully metamorphosed in artificial seawater on appropriate substrata—red algae for *A. brasiliana* and blue-green algae for *B. l. plei*. These methods provide a basis for investigations into the chemical requirements of larval development in a defined medium.

INTRODUCTION

SEA HARES (Opisthobranchia: Anaspidea) have been the focal point for an extensive amount of biomedical research during the past two decades. They have played an important role in our understanding of the cellular and molecular aspects of nervous function and the control of behavior (KANDEL, 1976, 1979). With the introduction of laboratory techniques for the culture of sea hares (KRIEGSTEIN *et al.*, 1974; STRENGTH & BLANKENSHIP, 1978; SWITZER-DUNLAP & HADFIELD, 1977, 1981), research interest in these forms has expanded to include the development of neural systems and behavior (JACOB, 1984; KANDEL *et al.*, 1980; KRIEGSTEIN, 1977a; SCHACHER *et al.*, 1979a, b).

The major bottleneck in the culture of aplysiids is the planktonic larval phase, which often requires 30–35 days to complete. Previous methods have utilized natural seawater as the culture medium. At inland laboratories, where access to natural seawater is limited, and at coastal labo-

ratories, where natural seawater quality is variable or unfit for culture, research on the development of these forms is difficult. The use of a defined medium would provide standardized environmental conditions throughout the life cycle and provide a basis for research into the chemical requirements for optimum development and physiological function. This paper is a report on the successful culture of two aplysiid species in artificial seawater.

MATERIALS AND METHODS

Maintenance of Breeders and Eggs

Mature adults of *Aplysia brasiliana* Rang, 1828, and *Bursatella leachii plei* (Rang, 1828) were collected from shallow-water habitats around Florida. These breeders were maintained in laboratory aquaria in Instant Ocean Sea Salts (ASW) at 32–35 ppt and 20–24°C. Daily they were fed freshly collected or laboratory cultured algae. Both species normally spawned large masses of eggs within a few days after capture and attached the egg strands to the aquarium walls or vegetation. The eggs were isolated from the adults by means of a perforated partition and were left where deposited to ensure that the environ-

¹ Present address: Howard Hughes Medical Institute, Environmental Systems Laboratory, Woods Hole, MA 02543, U.S.A.

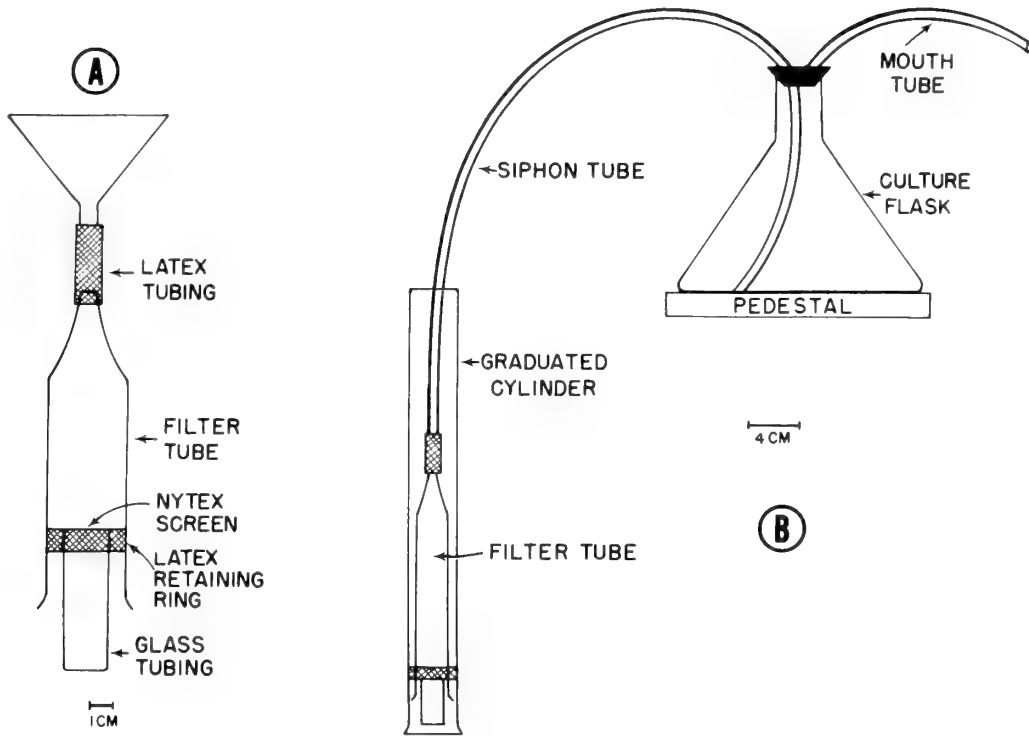


Figure 1
Apparatus for larval transfer. A. Filter unit. B. Larval culture and filter assembly.

mental conditions for embryonic development remained stable. Occasionally, eggs were removed and placed in a one-gallon jar in approximately 3.0 L of prefiltered ASW. These cultures were gently aerated and sealed with cellophane to prevent evaporation. Both techniques worked well.

Just prior to hatching (8-9 days after deposition), as evidenced by the brown coloration of the egg mass, small sections (1-2 cm) were cut from the center of the mass and placed in a bowl filled with prefiltered ASW, where they remained until hatching.

Larval Culture

Larval culture was carried out in a 3-L, low-form Erlenmeyer flask. This vessel had several advantages. The low, wide base allowed ample light penetration to enhance the growth of single-celled algae used as the larval food source. In addition, this flask had a narrow opening which minimized the area of surface where larvae could become trapped, a common problem in opisthobranch culture (FRANZ, 1975). The culture medium (ASW) was mixed to the desired salinity (33-35 ppt) in glass-distilled water. After the salts had dissolved, the solution was aerated for three days to ensure pH stability at 8.2-8.4. Prior to use in the larval cultures, the seawater was prefiltered to re-

move precipitates. No apparent benefit was derived from using one or a combination of the antibiotics Penicillin G, Streptomycin Sulfate, or Rifampicin, so no antibiotics were used.

After hatching, larvae were added to a flask to a final density of one larva per 10 mL of seawater. They were fed the single-celled alga *Isochrysis galbana* Parke, which was added directly from stock cultures grown in Guillard's "f/2" medium (GUILLARD, 1975) in ASW. The final concentration in the larval cultures was 10^4 algal cells per mL. The flask was filled to the top with ASW and sealed with Parafilm so as to eliminate completely air bubbles. These cultures were incubated at $24 \pm 1^\circ\text{C}$ under continuous illumination from one fluorescent light. Cultures could be maintained without transfer for up to 12 days. Routinely, they were transferred every 5-7 days using the siphoning apparatus shown in Figure 1.

The filter tube (Figure 1A) was constructed from glass tubing (22 mm I.D.). One end was pulled out to a narrow neck (5 mm I.D.) and the opposite end was flared to facilitate the insertion of the filter. The filter was made of glass tubing (18 mm O.D.) to which a small piece of nylon screen was attached by means of latex tubing (12 mm I.D., 18 mm O.D.). The filter was pushed up into the filter tube, producing a tight seal between the latex ring and the filter tube, to prevent larvae from passing

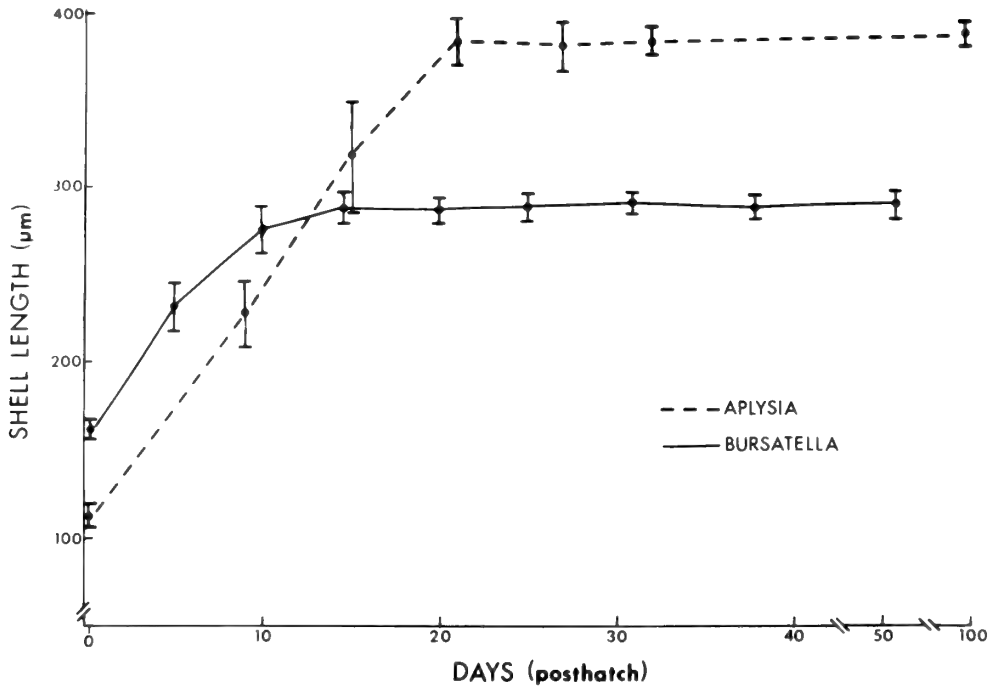


Figure 2

Larval growth of *Aplysia brasiliiana* and *Bursatella leachii plei* in artificial culture. Each point represents the average shell size (maximum dimension) of 50 individuals. The bar is ± 1 standard deviation.

through. Several of these units were made with screens of various mesh sizes (90–220 μm) to retain different sizes of larvae.

To transfer the larvae, the filter unit with the funnel attached (Figure 1A) was placed in a graduated cylinder that had been filled with prefiltered ASW. The larval culture vessel was opened and a small amount of seawater was poured into the funnel. A siphon tube was attached as shown in Figure 1B. By sucking on the mouth tube, air and water were pulled from the filter tube into the flask. Once all the air had been removed from the tubing, suction was stopped and an automatic siphon started that drained the flask, retaining the larvae on the screen. Water in the graduated cylinder was allowed to overflow into a gallon jar. This water was prefiltered and reused for the same culture, thus minimizing the need for excessive amounts of ASW. Routinely, culture water was reused 2 or 3 times and then discarded; however, recycled water could be used up to 70 days in culture before any detrimental effects were noted. After the flask was emptied, the funnel was reattached and all tubing and glassware were rinsed with fresh ASW to remove trapped larvae. The latex tubing was clamped and the funnel removed. The larvae could be dispensed directly into a new culture, or a bowl for observation, by inverting the filter unit and releasing the clamp. The screen was flushed with ASW

to wash off remaining larvae. The larvae of both species were transferred and cultured in this manner until they showed signs of competency to metamorphose. Competency of larval *Aplysia brasiliiana* was determined by the appearance of pigmented lateral spots and a mantle line according to KRIEGSTEIN (1977b). Because no lateral spots or mantle line appear in larval *Bursatella leachii plei*, competency was determined by the initiation of crawl-search behavior.

Larval Settlement and Postlarval Culture

Competent larvae were exposed to an appropriate settlement substrate using the techniques of SWITZER-DUNLAP & HADFIELD (1977). Ten to twenty larvae were placed in a small bowl in 100 mL of prefiltered ASW and were fed *Isochrysis galbana* at 10^4 cells per mL. Small pieces of substrate—red algae for *Aplysia brasiliiana* and blue-green algae for *Bursatella leachii plei* (PAIGE, 1981)—were added. Cetyl alcohol was lightly sprinkled over the surface to prevent larval entrapment (HURST, 1967). The bowls were covered and incubated under continuous illumination at 22–24°C.

After settlement, the postlarvae were isolated in small bowls and fed the alga that had induced metamorphosis. Juveniles were maintained in this manner until they were large enough to be placed in aquaria.

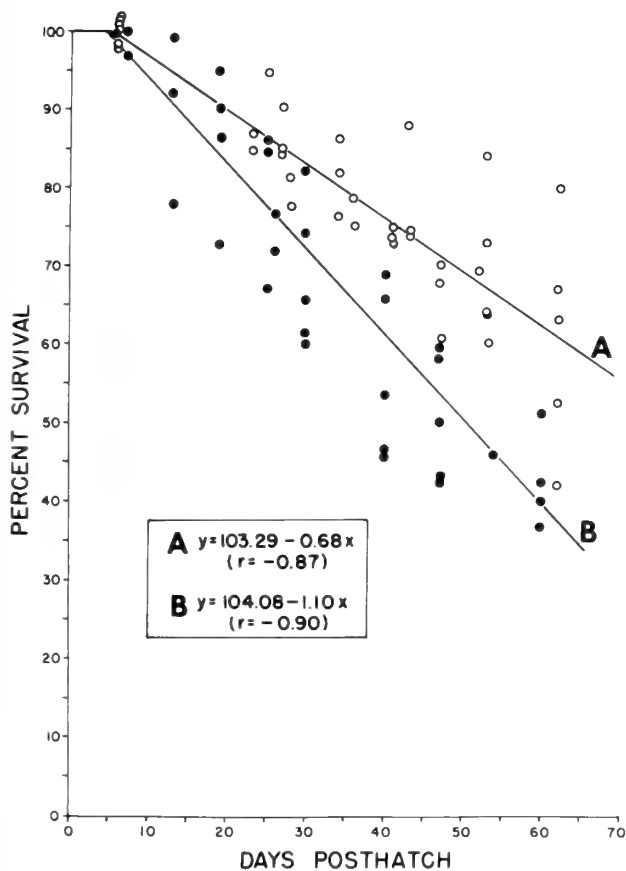


Figure 3

Percent survival of *Aplysia brasiliana* larvae in artificial seawater culture. Regression line A represents survivorship data (open circles) for six cultures of second generation larvae (n = 1846). Regression line B represents survivorship data (closed circles) for five cultures of first generation larvae (n = 1516).

RESULTS

The egg masses of *Aplysia brasiliana* and *Bursatella leachii plei* were characteristic of aplysiid spawn. The eggs were deposited in transparent capsules, embedded in a long, tangled gelatinous cord. Each capsule contained from 1 to 30 eggs, depending on the size of the adult depositing the mass. The color of the egg mass varied, but was normally yellow to light green for both species. The color changed to dark brown near the end of embryonic development, which required 8-9 days to complete. Development and hatching in ASW was complete and no detrimental effects of the medium or disease were observed.

The shell size at hatching was species specific. The larvae of *Aplysia brasiliana* hatched at a maximum shell diameter of $111 \pm 7 \mu\text{m}$, whereas newly hatched *Bursatella leachii plei* larvae were $160 \pm 4 \mu\text{m}$. Larval growth in ASW (Figure 2) was approximately linear and aver-

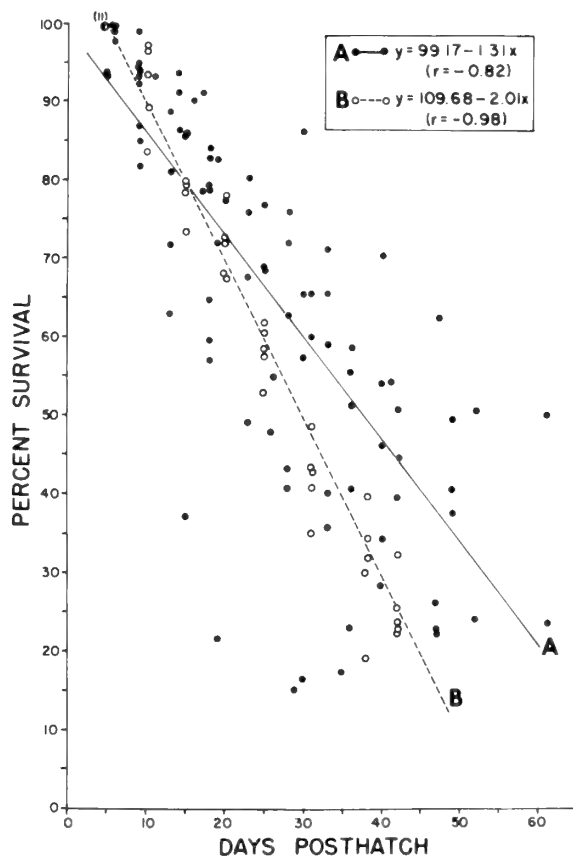


Figure 4

Percent survival of *Bursatella leachii plei* in artificial seawater culture. Regression line A represents survivorship data (closed circles) for thirteen cultures of larvae (n = 3988). Regression line B represents survivorship data (open circles) for five cultures of larvae (n = 1471).

aged $10 \mu\text{m}$ per day for both species. The growth of *Aplysia brasiliana* veligers stopped in 21 days posthatch at a maximum shell size of $382 \pm 14 \mu\text{m}$. *Bursatella l. plei* larvae stopped growing in 15 days at a shell size of $286 \pm 9 \mu\text{m}$. At this time in development, the larvae of both species were not competent to metamorphose, even if exposed to the substrate on which they would eventually settle. *Aplysia brasiliana* larvae required 34 days to reach metamorphic competence; *B. l. plei* larvae required only 19 days.

Survivorship in the larval cultures was determined at each culture transfer. It was computed as the number of larvae surviving weighted against the number of larvae placed in the culture at hatching. Consequently, the mortality included both the number of larvae found dead and the number that were physically lost during the transfer process. Regression lines were fitted to the data and regression coefficients computed. For each set of data, an

analysis of covariance was performed to determine whether cultures of different egg masses differed significantly within the same species.

The survival of two different series of cultures of *Aplysia californica* is shown in Figure 3. Line A represents a second generation of larvae ($n = 1846$) raised through metamorphosis in the laboratory. Line B represents larvae ($n = 1516$) produced by a wild adult collected at Cedar Key, Florida. These data were significantly different ($\alpha = 0.01$). In each case, a high proportion of larvae (55–80%) survived to competency from days 34 to 44 and, of those exposed to substrates, 80–90% metamorphosed in ASW.

The survivorship curves for *Bursatella leachii plei* larvae (Figure 4) represent data from three different egg masses raised in 18 separate cultures ($n = 5459$). No significant differences ($\alpha = 0.01$) could be detected between two of the culture sets, so these data were lumped and are shown as regression line A. The third set (line B) was significantly different ($\alpha = 0.01$) from the other two. A large portion of the initial larval population (50–73%) did survive to competency on days 19 to 29. Of these competent larvae, 70–80% could be induced to metamorphose on appropriate substrates.

Two generations of each species were raised to maturity in the laboratory, using the above techniques. Growth rates of the juveniles varied greatly depending on the size of the individual and availability of macroalgal food. Both species attained sexual maturity within 2 to 3 months after metamorphosis.

DISCUSSION

These techniques for raising aplysiid larvae using artificial seawater produced percent yields as good as or better than techniques previously developed using natural seawater. This success was due, at least in part, to the constancy of the larval environmental conditions and to a reduction in the amount of handling necessary to maintain the cultures. Where daily transfers have been necessary in previously reported procedures (KRIEGSTEIN *et al.*, 1974; SWITZER-DUNLAP & HADFIELD, 1977), artificial seawater cultures could be left standing for 5 to 12 days without increases in mortality. The filter apparatus used here allowed rapid transfer of the larvae to new cultures and minimized the stresses of handling and exposure to air. The use of Parafilm as a seal for the culture vessels completely eliminated the problem of larval entrapment at the surface (FRANZ, 1975) and was easier to use than cetyl alcohol (SWITZER-DUNLAP & HADFIELD, 1977).

The techniques described here were designed for, and can be performed at, any inland laboratory. The restrictions of natural seawater have been eliminated. Although juveniles in this study and others (SWITZER-DUNLAP & HADFIELD, 1981) have been raised to maturity in small aquaria in artificial seawater, at the present time we are tied to coastal supplies of adult food and the larval settlement substrates. STRENGTH & BLANKENSHIP (1978) have

had success raising juveniles and adults of *Aplysia brasiliana* on commercially available dried seaweed. CAPO *et al.* (1979) have reported the successful culture in the laboratory of the red alga *Agardhiella subulata* (C. Agardh) Kraft & Wynne (1979) that supports the metamorphosis and postlarval development of *Aplysia californica* Cooper, 1863. More work is needed on the isolation and characterization of the metamorphic inducer(s) to realize the potential of inland culture.

The use of a defined medium for the culture of aplysiids now affords researchers the opportunity to investigate the chemical requirements of larval development and the effects of changing environments on adult neurophysiology and behavior.

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Shell Microstructure and Observations on
Internal Banding Patterns in the Bivalves
Yoldia thraciaeformis Storer, 1838, and
Nuculana pernula Müller, 1779 (Nuculanidae),
from a Deep-Sea Environment¹

by

K. D. GILKINSON,² J. A. HUTCHINGS, P. E. OSHEL, AND R. L. HAEDRICH

Department of Biology and Newfoundland Institute for Cold Ocean Science,
Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

Abstract. Shell microstructure and internal banding patterns are described for deep-sea (895-1490 m) populations of *Yoldia thraciaeformis* and *Nuculana pernula* (Bivalvia: Nuculanidae) from the north-west Atlantic Ocean off Newfoundland. Both species possess homogeneous, aragonitic shell microstructure. The shell of *N. pernula* is comprised of two distinct shell layers whereas that of *Y. thraciaeformis* has one layer. Internal bands (growth increments) are prominent within the shells of both species. Shell microstructure is similar within and between band regions. Internal bands may be deposited annually in response to discrete seasonal or annual pulses of surface production to the deep sea.

INTRODUCTION

SHELL MICROSTRUCTURE and mineralogy in bivalves have been the focus of many paleoecological and biological examinations which have been useful in understanding phylogenetic relationships among bivalves and documenting periodic growth increments (banding patterns) within the shells of these mollusks (see LUTZ & RHOADS, 1980, for a review).

TAYLOR *et al.* (1969) examined the shell structure and mineralogy in 12 species within the Nuculanacea and found all shells to be entirely composed of aragonite. Furthermore, a homogeneous shell microstructure is characteristic among all species except *Yoldia eightsii*, which has a prismatic microstructure underlying the pallial myostracum. The existence of either one or two shell layers varies within and between genera. For example, *Y. lima-*

tula and *Nuculana crassa* each possess two shell layers whereas the shells of *Y. eightsii*, *Y. myalis*, and *N. oblongoides* are comprised of a single layer (TAYLOR *et al.*, 1969). Shells of the nuculanaceans *Y. thraciaeformis* and *N. pernula* are here documented for the first time in terms of their mineralogy, microstructure, and shell layers.

Growth increments in bivalves are understood to be records of growth (LUTZ & RHOADS, 1980). The underlying cause of growth increment formation in bivalves has been variously attributed to both environmental and physiological processes (JONES, 1981). Examples from the literature dealing with shallow-water bivalves reveal changes in shell growth rate at a time when growth bands are deposited (MACDONALD & THOMAS, 1980; PETERSON *et al.*, 1983; SHAUL & GOODWIN, 1982; DEITH, 1985). In some cases associated changes in crystal size between band and interband shell material have been recorded (DEITH, 1985; LUTZ, 1976). The majority of growth increment studies on bivalves have been undertaken on populations inhabiting shallow-water habitats (<60 m) which are subjected to dramatic seasonal and annual environmental fluctuations. Previous shell studies of deep-sea bivalves (>500 m) have included growth rate investigations based

¹ Newfoundland Institute for Cold Ocean Science Contribution No. 108.

² Address to which reprint requests should be sent: Newfoundland Institute for Cold Ocean Science, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada.

upon radioisotope analysis (TUREKIAN *et al.*, 1975, 1979). Internal banding patterns were documented in the deep-sea clam *Tindaria callistiformis* collected from depths of 3800 m, although shell microstructure was not reported (TUREKIAN *et al.*, 1975). In a study of molluscan micro-growth patterns, RHOADS & PANNELLA (1970) recorded indistinct banding patterns in specimens of several deep-sea (933–4970 m) bivalve species, including the proto-branch *Nucula cancellata*.

Shell microstructure and internal banding patterns were examined from specimens of *Yoldia thraciaeformis* and *Nuculana pernula* collected from a deep-sea environment (895–1490 m) off Newfoundland. In a previous growth and population structure study of these populations, HUTCHINGS & HAEDRICH (1984) postulated that internal growth increments (bands) present in the shells of these species were of the first-order type (annual), as defined by BARKER (1964).

Bands were analyzed in detail through scanning electron microscopy in order to document any variation in shell microstructure concomitant with band formation. The suspected annual periodicity of band deposition in these bivalves is discussed in terms of the physical conditions that exist in this deep-sea environment and their implications to influences upon biological cycles.

The basic terminology is that of CARTER (1980). Hereafter, shell architecture refers to the orientation of the largest units of shell microstructure with respect to shell form. Shell microstructure refers to the arrangement of the various basic structural units (*e.g.*, granules).

MATERIALS AND METHODS

Deep-water specimens of *Yoldia thraciaeformis* and *Nuculana pernula* were collected during cruises of the M/V *Gadus Atlantica* in Carson Canyon, on the southeastern edge of the Grand Banks in the northwest Atlantic (Table 1; see HUTCHINGS & HAEDRICH, 1984, for collection procedure). Material was fixed in 10% formalin at the time of collection and later transferred to 80% ethanol. The *Y. thraciaeformis* analyzed were 35–45 mm and the *N. pernula* were 20–25 mm in shell length.

Light Microscopy

Shell valves of *Yoldia thraciaeformis* were fractured radially (passing through the umbo) for viewing of internal banding. Vertical sections were photographed ($\times 16$ power) using a 16-mm Zeiss Luminar lens with bellows, a Leica R3MOT back, and fiber optic illumination.

Scanning Electron Microscopy (SEM)

Shells were washed in absolute ethanol, air-dried, and vertically fractured along a radial plane. The fragments were further broken into smaller pieces to fit on SEM stubs. Specimens were also fractured at an angle tangential to the shell surface to produce a horizontal fracture

surface. Shell fragments were mounted on aluminum SEM stubs with silver conducting paint, sputter coated with gold, and then examined in a Hitachi S-570 SEM or a Cambridge MK2A Stereoscan.

Shell Internal Band Microstructure

Two vertical notches (*i.e.*, normal to the outer shell surface) were made in shell sections of *Yoldia thraciaeformis* to frame a segment of a band region for comparison by light microscopy and scanning electron microscopy. The notched piece of shell was mounted on an SEM stub and shell microstructure was compared within and between bands.

Shell Mineralogical Determinations

Periostracum was scraped from shells of both species in preparation for grinding. Through SEM analysis it was apparent that there was a single shell layer in *Yoldia thraciaeformis*, whereas there were two distinct shell layers in *Nuculana pernula*. The two shell layers of *N. pernula* were analyzed separately. This was accomplished by removing shell material from both inner and outer shell surfaces with a scalpel.

Shell material from single specimens was ground to a fine powder with mortar and pestle. Smear-slide preparations were made by making a slurry of powdered carbonate in a drop of methanol, and spreading this slurry in a thin layer on a glass slide for mounting in an X-ray diffraction instrument. Analyses were conducted using a Philips Co. X-ray diffraction unit and recorder, and a goniometer.

RESULTS

Shell Architecture, Microstructure, and Mineralogy

Yoldia thraciaeformis shells were 1–2 mm thick. The periostracum was relatively thick although absent from the eroded umbonal regions. *Nuculana pernula* possessed a thin and fragile shell (about 0.5 mm thick) with a thin periostracum which also was eroded at the umbones.

Nuculana pernula possessed two distinct shell layers, which were separated by the pallial myostracum (Figure 1a). Both layers had a homogeneous microstructure. In these vertical shell sections there was a distinct difference in the density of structural units (granules) between the two shell layers. The inner shell layer consisted of compactly arranged shell material (Figure 1b) in which it was difficult to identify individual structural units. Structural units in the outer shell layer (Figures 1c, d) consisted of irregularly arranged spherical granules, with a high degree of porosity. Granules (smallest discrete units) were 0.8 μm in diameter.

Figure 2 shows inner and outer shell layers in a plane horizontal to the outer shell surface. Granules were coalesced into a sheet-like arrangement in the inner shell layer (Figures 2a, b). They appeared to be "cemented"

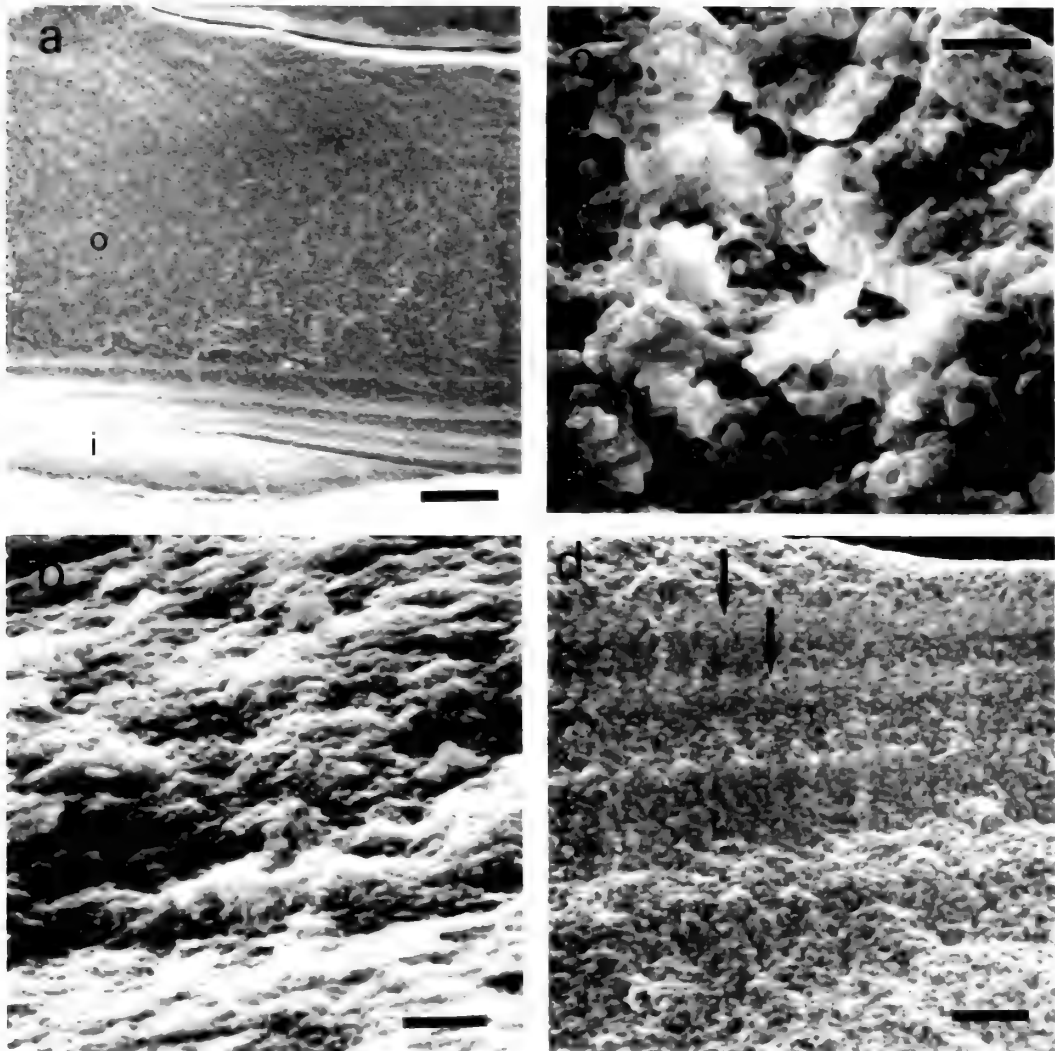


Figure 1

Radial, vertical shell sections of *Nuculana pernula*. a. Inner (i) and outer (o) shell layers (scale bar = 100 μm). b. Inner shell layer (scale bar = 2 μm). c. Outer shell layer (scale bar = 2 μm). d. Outer shell layer. Arrows point to internal bands (scale bar = 50 μm).

together by an amorphous deposit of calcium carbonate. Outer shell layer microstructure consisted of irregularly arranged granules 0.2–0.4 μm in greatest dimension (Figures 2c, d). Thus, granule sizes in the horizontal plane were roughly half of those in the vertical plane.

Yoldia thraciaeformis possessed a single, homogeneous shell layer. In radial, vertical section (Figures 3a, b, c) this consisted of densely packed, irregularly arranged granules. Shell microstructure in the horizontal plane (Figures 3d, e) was very similar to that seen in the vertical plane.

In summary, no pattern was evident in either species in the arrangement of granules within shell layers. There

was an apparent difference in density of granules between the two shell layers in *Nuculana pernula*. Shell calcium carbonate in both species was in the form of aragonite.

Internal Shell Banding Patterns

Internal banding patterns were readily apparent at low magnification ($\times 16$) in vertical shell sections of both species. The bands in *Yoldia thraciaeformis* were visible without magnification. Growth bands in *Y. thraciaeformis* were studied at the microscopic and microstructural levels (Figures 4a, b). Bands extended throughout the shell, running parallel to the inner shell surface, gradually becom-

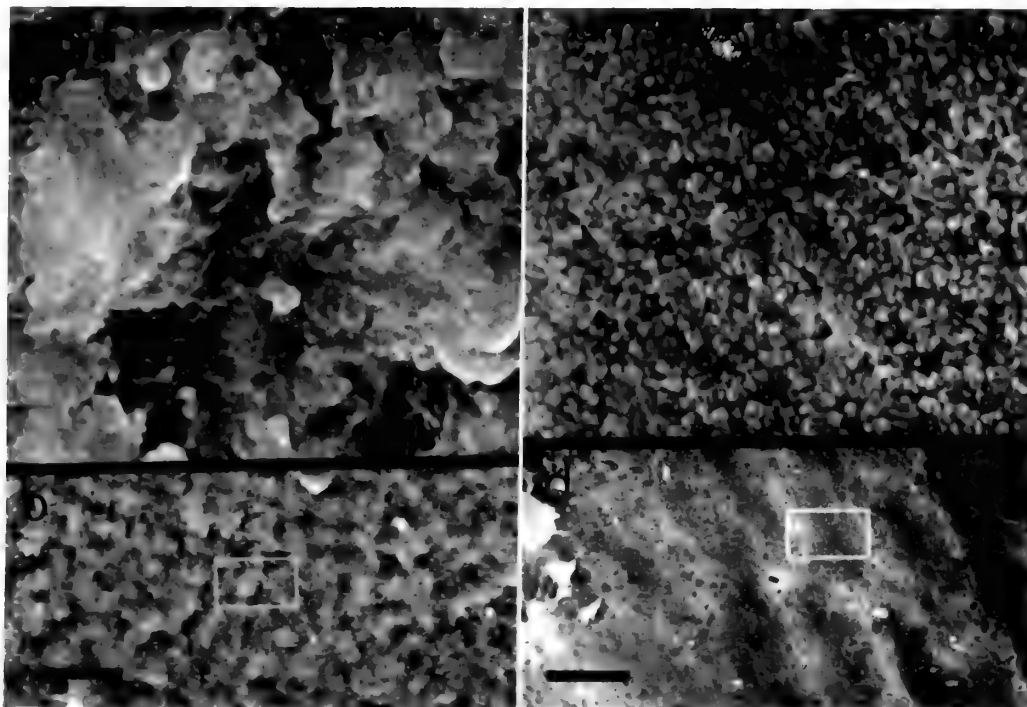


Figure 2

Horizontal plane views of *Nuculana pernula* shell. a. Inner shell layer magnification of inset region in "b" (scale bar = 1 μm in "a" and 10 μm in "b"). c. Outer shell layer magnification of inset regions in "d" (scale bar = 1 μm in "c" and 10 μm in "d").

ing deflected toward the outer shell surface (Figure 4a). In reflected light, individual bands (0.08–0.10 mm in width) appeared dark in contrast to the surrounding lighter colored interband shell surface. In transmitted light, the reverse was true. Shell microstructure appeared similar inside and outside a band as viewed at a band-interband border region (Figure 3a). Band spacing was not regular and interband distances were widest toward the umbo, becoming progressively narrower toward the ventral shell margin. Nevertheless, bands were markedly periodic and there were no unusually large gaps without bands.

The band delimited by the two notch marks in Figure 4a is shown as viewed under SEM and appears as a light "streak" in the center of Figure 4b. Figures 3a, b, and c show various magnifications of this band region. Grooves appearing in band regions appear to indicate lines of fracture.

Banding in *Nuculana pernula* was confined largely to the inner shell layer. The exception occurred at the inner shell-outer shell boundary where banding extended briefly into the the outer shell layer (Figures 1a, d). Bands were non-reflected and were oriented parallel to the shell surface. Bands were uniformly closely spaced and, in this thinner-shelled species, were narrower (about 13 μm) than in *Yoldia thraciaeformis*.

DISCUSSION

Both *Nuculana pernula* and *Yoldia thraciaeformis* possess homogeneous shell microstructures and aragonite mineralogy in conformity with other nuculanacean species studied to date.

Nuculana pernula possesses two distinct shell layers whereas *Yoldia thraciaeformis* develops only a single shell layer. Given the current state of knowledge of the calcification process in mollusks, it is difficult to speculate upon reasons for this variation in shell layer systems within and among genera in the Nuculanacea. However, this variation cannot be attributed simply to thin-shelled *vs.* thick-shelled bivalve life history strategies as both thin-shelled and thick-shelled species within the Nuculanacea can possess either one or two shell layers (TAYLOR *et al.*, 1969).

Both *Nuculana pernula* and *Yoldia thraciaeformis* possess internal banding patterns throughout their shells but on different scales. In the thin-shelled *N. pernula*, bands were thin (13 μm) and were largely confined to the inner shell layer. This banding pattern may be similar to that reported for other thin-shelled nuculanacean species by TAYLOR *et al.* (1969). Banding patterns within *Y. thraciaeformis* shells are similar to descriptions of the thick-shelled *N. crassa* and *N. oblongoides* by TAYLOR *et al.* (1969). These authors remark upon the similarity to first-

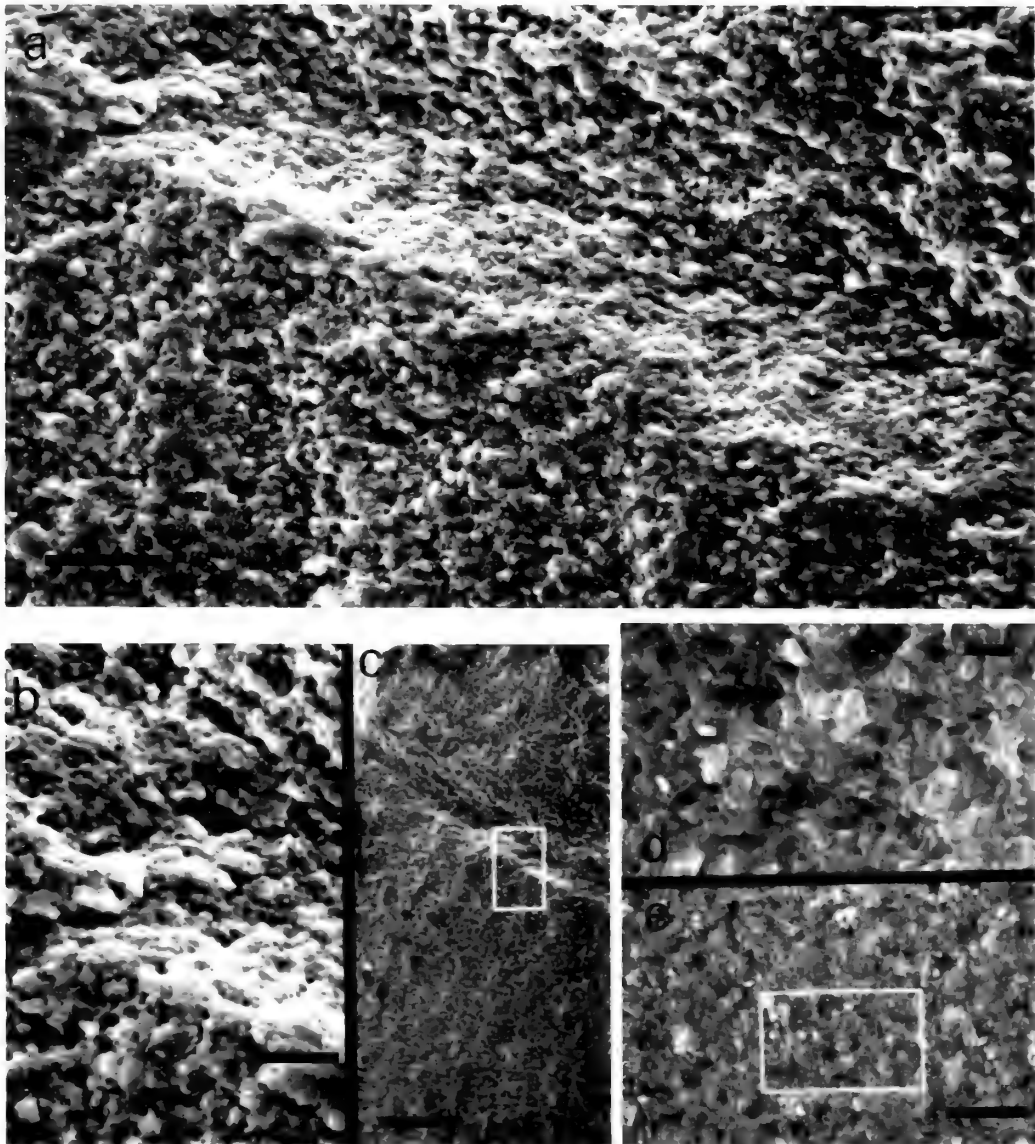


Figure 3

Radial, vertical shell sections of *Yoldia thraciaeformis*. a. Internal band region running diagonally across photograph from top left to bottom right (scale bar = 20 μm). b. Magnification of a region of an internal band identified by the inset in "c" (scale bar = 20 μm). c. Internal band region (scale bar = 100 μm). Horizontal plane views of *Y. thraciaeformis* shell. d. Magnification of inset region in "e" (scale bar = 1 μm in "d" and 10 μm in "e").

order banding patterns seen in *Arctica islandica*, an observation corroborated in the present study. The existence of fracture zones along growth bands in *Y. thraciaeformis* would seem to indicate a difference in density or structural strength between band and interband shell material even though differences in microstructure were not observed.

The fact that deep-water bivalves such as *Yoldia thraciaeformis* have internal banding patterns is not in itself surprising considering the variety of biological and envi-

ronmental factors that may be responsible for growth increment formation in bivalves (see LUTZ & RHOADS, 1980, for a review). What is interesting is the remarkable definition or clarity of banding patterns seen in *Y. thraciaeformis* considering the fact that RHOADS & PANELLA (1970) observed indistinct banding patterns in the deep-sea bivalves they examined. They observed banding patterns that consisted of uniformly spaced growth increments lacking sharply defined boundaries, which were recogniz-

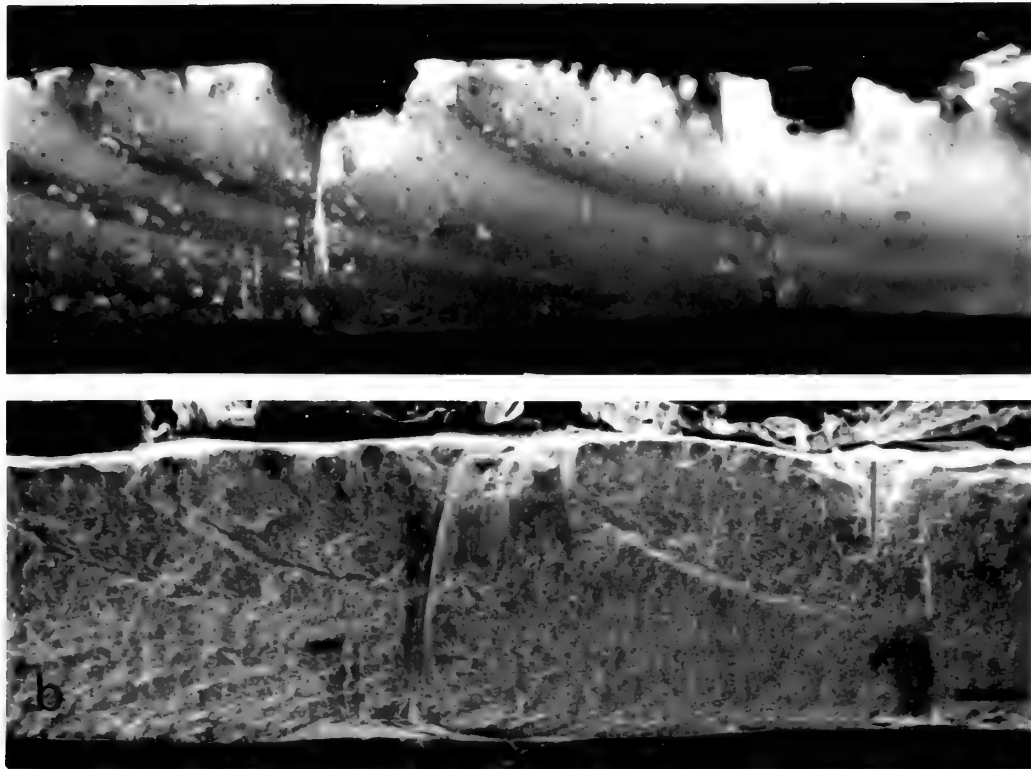


Figure 4

Radial, vertical shell sections of *Yoldia thraciaeformis* showing internal bands. Outer shell surface towards top of page. a. Photomicrograph showing an internal band bordered by two notch marks. b. Same section as viewed through SEM. Scale bar = 250 μm in both photographs.

able only through color variation. CLARK (1974) stated that the degree of exposure to environmental extremes can correlate well with growth line prominence. If we modify this to read that the magnitude of the causative biological or environmental variable can correlate with growth line prominence, then we see that whatever these factors are they can have as strong an influence in bivalves at 1000 m as in nearshore or intertidal bivalves.

Important to all environments, including the deep sea, is an understanding of environmental and biological processes in order to interpret growth increments. Unfortunately, seasonal data within Carson Canyon, at depths of 1000 m, are lacking. Measurements that have been taken at these depths elsewhere on the slope of the Newfoundland Grand Banks reveal temperatures in the 3–4°C range (CLARKE *et al.*, 1980). Limited seasonal data from the study region at depths of 500 m show almost constant temperature (3.5°C) and salinity (34.7 ppt) (Table 2). It is probable that there is little or no annual variation in temperature and salinity at slope depths of 1000–1500 m either; instead, minor variations (<1°C) occurring on a higher frequency basis (*e.g.*, 10-day period) probably exist (Clarke, personal communication). ELLETT & MARTIN

Table 1

Collection sites of *Nuculana pernula* and *Yoldia thraciaeformis* in Carson Canyon.

Date	Latitude	Longitude	Trawl depth (m)	Number of <i>Y. thraciaeformis</i>	
3 June 1980	45°23'N	48°31'W	0895–0905	4	0
4 June 1980	45°18'N	48°35'W	1420–1500	32	85
4 June 1980	45°20'N	48°36'W	1020–1200	23	35
5 June 1980	45°18'N	48°33'W	1220–1280	101	20
8 June 1980	45°24'N	48°35'W	1000–1050	18	9
16 May 1981	45°33'N	48°10'W	1290–1320	1	0
16 May 1981	45°36'N	47°56'W	1460–1490	4	0
Total				183	149

Table 2

Mean monthly temperature and salinity at 500 m over the Newfoundland continental slope (polygonal area delimited by 45°50'N, 47°56'W; 45°00'N, 48°56'W; 45°20'N, 48°56'W). Compiled data from stations (n) occupied over the period 1932 to 1983.¹

		J	F	M	A	M	J	J	A	S	O	N	D	Overall
Temperature (°C)	\bar{X}	nd	nd	3.55	3.58	3.61	3.23	nd	3.33	nd	nd	nd	3.58	3.52
	SD			—	0.59	0.33	0.15		—				—	0.42
	n			1	9	8	4		1				1	24
Salinity (ppt)	\bar{X}	nd	nd	34.74	34.79	34.67	34.74	nd	34.75	nd	nd	nd	34.46	34.72
	SD			—	0.06	0.26	0.04		—				—	0.17
	n			1	9	8	3		1				1	23

nd = no data available.

1 = data courtesy of Marine Environmental Data Service, Department of Fisheries and Oceans, Ottawa, Canada.

(1973) recorded little or no variation in temperature and salinity throughout the year at depths of 2900 m in the Rockall Trough. However, at similar depths at this location, LIGHTFOOT *et al.* (1979) observed seasonal reproductive cycles in two deep-sea bivalve and brittlestar species. LIGHTFOOT *et al.* (1979) suggested that the timing of reproductive cycles in deep-sea bivalves and other deep-sea invertebrates indicated adaptive coupling to seasonal pulses in surface production. They cite evidence indicating that particulate organic material sinks to the deep sea rapidly enough that seasonal pulses in surface production are not completely damped out by differential sinking rates (BISHOP *et al.*, 1978; MCCAVE, 1975; TURNER, 1977; VIEBE *et al.*, 1976; see also DICKSON *et al.*, 1982).

The distinctiveness of growth bands in the shells of *Yoldia thraciaeformis* and *Nuculana pernula* indicate that these deep-sea bivalves are strongly affected by an annual event throughout the lifetime of the organisms. Internal growth bands in these bivalves may represent reproductive cycle "markers" within the shell. Correlations have been made between timing of growth band formation and the reproductive cycle in shallow-water bivalves (JONES, 1980; PETERSON *et al.*, 1983); however, in these cases there is the compounding problem of significant annual water temperature changes, a factor absent from the deep-sea environment. Alternatively, growth bands in *Y. thraciaeformis* and *N. pernula* may represent shell-mediated changes in growth rate resulting from fluctuations in food supplied from surface waters.

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Early Development of *Crassostrea iredalei* (Faustino, 1932) (Bivalvia: Ostreidae), with Notes on the Structure of the Larval Hinge¹

by

LEO MICHAEL M. VER

Aquaculture Department, Southeast Asian Fisheries Development Center, Iloilo, Philippines

Abstract. Larvae of the oyster *Crassostrea iredalei* were reared in the laboratory from eggs through settlement. The oysters were induced to spawn by increasing the temperature by 5–10°C and sometimes by adding stripped oyster sperm to the spawning dishes. Eggs averaged 48 μm in diameter.

The straight-hinge veligers appeared 22 to 26 h after fertilization. The larval shell length increased from 64 to 84 μm in the straight-hinge stage, from 85 to 275 μm in the umbo stage, and from 210 to 275 μm in the pediveliger stage. Eye-spotted pediveligers were observed mostly at lengths greater than 225 μm . The hinge line did not increase much with larval growth. Although length was initially greater than height, the increase in height was much faster due to the development of the umbo. Height was greater than length in more advanced larvae. Valve growth was asymmetrical and unequal, with the left valve generally larger. Settlement and metamorphosis occurred 20 days from fertilization at lengths of 270 μm and greater, when the oyster larvae were reared at 26.5 to 30°C and salinities of 30 to 32 ppt.

The larval hinge structure consisted of minute dentition on the central portion of the provinculum and large rectangular teeth on both ends. These teeth became obscured in advanced larvae due to the skewed development of the umbo.

Data derived from the laboratory culture of larvae of *Crassostrea iredalei* may be used in spatfall forecasts for the collection of larvae from the wild and as baseline information for the hatchery culture of oyster larvae.

INTRODUCTION

Crassostrea iredalei (Faustino, 1932) is a large, non-incubatory oyster common in most estuarine and plankton-rich marine waters of the Philippines (CARREON, 1969). It is a fast-growing species and is the most economically important mollusk in the country.

The biology and ecology of *Crassostrea iredalei*, as well as its farming aspect, have been well studied (VILLALUZ, 1938; BLANCO *et al.*, 1951; BLANCO & MONTALBAN, 1955; ESCRITOR, 1962; CARREON, 1973) and the work of CARREON (1969) has clarified its position in the family Ostreidae. However, the larval biology of *C. iredalei* has hitherto been unreported, leaving a gap in the knowledge of its life history.

The recruitment period of new populations of oysters

for cultivation may be forecasted by monitoring (1) the start and duration of the spatfall period, (2) the intensity of the spatfall, and (3) the occurrence and abundance of oyster larvae in the plankton (see QUAYLE, 1969:65). Techniques for a scientific and effective spatfall forecast for oysters in the Philippines have not yet been well established. Thus, local oystermen make spatfall predictions based only on previous experience and traditional practices. This probably is a primary reason for the slow development of the Philippine oyster farming industry.

This study describes the development of laboratory-reared larvae of *Crassostrea iredalei* through metamorphosis. The results should enable positive identification of the larvae in the plankton and the determination of its stages of development. Data derived from this study should help in establishing a good spatfall forecasting program, which is an essential aspect of the culture and farming of this valuable Philippine food resource.

¹ SEAFDEC Aquaculture Department Contribution No. 158.

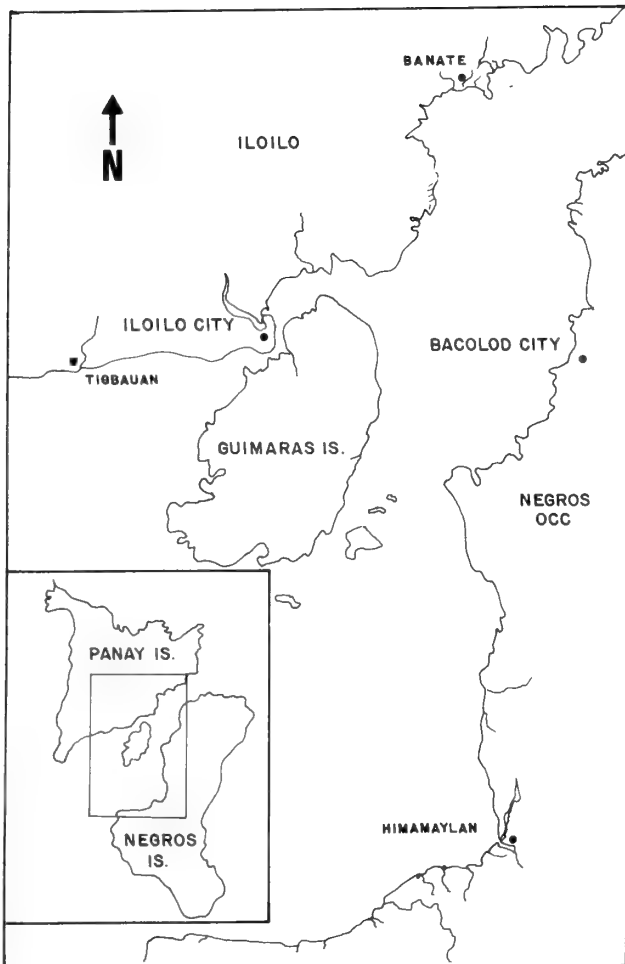


Figure 1

Map of Negros and Panay Islands. Collection areas for broodstock of the oyster *Crassostrea iredalei* (Banate, Iloilo, and Himamaylan, Negros Occidental) and the SEAFDEC Tigbauan Research Station.

MATERIALS AND METHODS

Sexually mature adult oysters, *Crassostrea iredalei* (50–80 mm long), were collected from SEAFDEC experimental farms in Himamaylan, Negros Occidental, and Banate, Iloilo. They were then transported to the SEAFDEC Tigbauan Research Station, Tigbauan, Iloilo (Figure 1). Oysters from the Himamaylan area were gathered from growing cultches suspended from floating rafts while those from the Banate site were gathered from farms that use the lattice method of oyster culture. In the lattice method of culture, the growing ropes for oysters were hung horizontally, radiating from a central point about 0.5–1 m from the bottom.

The newly gathered oysters were immediately cleaned of dirt and fouling organisms and, when possible, sepa-

Table 1

Summary of embryonic development periods of *Crassostrea iredalei* (temperature, 27–28°C; salinity, 32 ppt). Stages as described by BAYNE (1965).

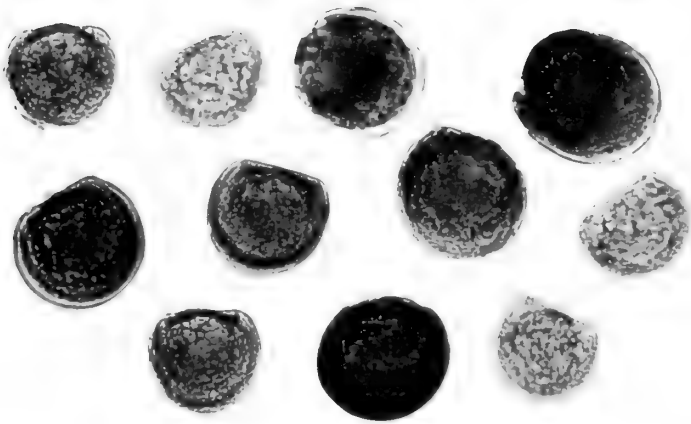
Stage	Description	Time
0	fertilization	0
1	first division	45–50 min
2	ciliated blastula	5.5 h
3	early trochophores	8 h
4	veliger	15 h
5	transitional stage	18–20 h
6	straight-hinge stage	22–26 h

rated from each other. The oysters were “cold-conditioned” in tanks by maintaining the seawater temperature at 21 to 23°C with the use of a thermostatically controlled immersion water cooler for at least three days before they were induced to spawn. The oysters were fed mixed plankton prepared by the SEAFDEC Phycology Laboratory.

Cold-conditioned oysters were induced to spawn by quickly increasing the temperature by 5 to 10°C and sometimes by adding stripped oyster sperm to the spawning dishes. After a latency period of 2 to 6 h, some males emitted gametes which often stimulated the oysters to spawn en masse. The fertilized eggs were collected and washed of excess sperm with freshly filtered seawater.

The basic techniques used in rearing the oyster larvae were as described by LOOSANOFF & DAVIS (1963), CHANLEY (1975), and CULLINEY *et al.* (1975). Larval cultures were kept under shelter but at ambient temperature and salinity (26.5–30°C and 30–32 ppt, respectively). Fiberglass and polyethylene pails (100-L capacity) and glass beakers (1–5-L capacity) were used as culture vessels. Aeration was provided only when the larvae were reared in the large culture tanks. The fertilized eggs were initially stocked in the culture vessels at a density of 30 eggs/ml of culture water and were left undisturbed for the first 24 h. After this period and every second day thereafter, the culture water was changed and larval food was added. The larval food used was *Isochrysis galbana*, which has been shown to be one of the best foods for bivalve larvae (DAVIS & GUILLARD, 1958). Food was provided at a density of 3×10^4 cells/ml of culture water in the first week of rearing, 5×10^4 cells/ml in the second week, and 8×10^4 cells/ml in the third week.

During each water change, healthy larvae swimming in the water column were collected by siphoning the culture water through a series of nylon sieves. The mesh sizes of the sieves were determined by the range of sizes of the larvae in the culture. Because debris and the dead and moribund larvae mostly settled at the bottom of the culture vessels, the last 5-cm layer of water was not siphoned off. However, to rescue any healthy larvae that might be mixed



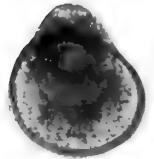
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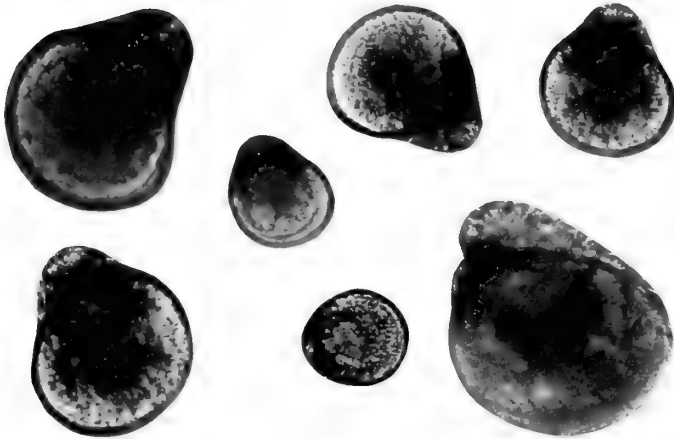
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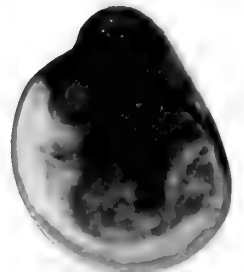
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248 x 302

Table 2

Main features of the larval development of *Crassostrea iredalei* (temperature, 26.5–30°C; salinity, 30–32 ppt).

Stage	Age	Mean size (μm)	Range (μm)	SE (μm)	n	Remarks
Straight-hinge veliger	22 h–4 days	L = 74	64–84	0.528	110	D-shaped; shell asymmetrical but equivalent
		H = 67	56–80	0.708	110	
		D = 48	41–61	0.948	41	
		Hinge-line length = 50				
Umbonate veliger	5–22 days	L = 85–275			419	rounded umbo at lengths 85–90 μm ; knob-like umbo at lengths 91–150 μm ; skewed umbo at lengths greater than 150 μm
		H = 81–305			422	
		D = 62–220			178	
Pediveliger	16–22 days	L = 210–275			18	alternately creeping and swimming vigorously
		H = 240–305			15	
		D = 171–220			6	
Eye-spotted pediveliger	18–22 days	L > 217				larvae nearing metamorphosis; eye-spot diameter, range 8–15 μm
Spat	20 days	H > 242				larvae attached on cultches
		L > 274				
		H > 328				

with the dead and moribund larvae, the “bottoms” were cultured in a separate vessel (CULLINEY *et al.*, 1975). Once the larvae reached the pediveliger stage, cultches made from adult oyster, scallop, and window-pane oyster shells were hung in the water or placed at the bottom of the culture vessels. Some larvae were transferred to petri dishes or finger bowls to facilitate observation of their settlement.

Larval samples were collected at each water change, fixed in “sucrose-formalin preservative” (CULLINEY *et al.*, 1975), and measured, photomicrographed, and studied for their shell characters. All dimensions of the larvae were measured using a calibrated filar micrometer. The descriptive terminologies used were as defined and illustrated by CHANLEY & ANDREWS (1971).

To facilitate observation of the hinge structure, the valves of the preserved larvae were separated by immersing the larvae in a solution of 10% sodium hypochlorite for a few minutes and repeatedly washing them with distilled water (REES, 1950) after which they were mounted on a depression slide.

RESULTS AND DISCUSSION

Induced Spawning

The conditioning technique for *Crassostrea iredalei* employed in this study was done to prepare the breeding

stock for induced spawning and not necessarily to stimulate gametogenesis, as was practiced by Loosanoff and colleagues (LOOSANOFF & DAVIS, 1963). The cold water (21–23°C) actually prevented spontaneous spawning by the oysters after being transported in the dry state from the collection areas. Most of the mature oysters with ripe gonads readily spawned in the laboratory after they were stimulated thermally or with the addition of sperm.

The addition of stripped sperm into the spawning dishes almost always elicited a positive spawning response, beginning mostly with the males and then the females. The relative ease in which spawning was induced may also indicate the actual gametogenic stage of the gonads since reproduction in *C. iredalei* is continuous (SEAF-DEC, unpublished data). This sensitivity to stimulation augurs well for oyster propagation in that it facilitates the mass spawning of the population.

Oysters were fed a daily ration of mixed phytoplankton in order to minimize deleterious effects on the produced larvae should the breeding stocks be starved. HELM *et al.* (1973) have shown experimentally that in *Ostrea edulis*, larval vigor is definitely enhanced when the breeding stock is not nutritionally stressed.

Embryonic Development

Unfertilized eggs of *Crassostrea iredalei* were pear-shaped and white in color. The eggs soon became spherical upon

Figure 2

Composite photomicrographs of *Crassostrea iredalei* larvae. Length \times height measurements are given in μm under each individual larva at right. Larvae are arranged with the anterior end at the right. A. Straight-hinge and early umbonate larvae, 1–5 days old. B. Group of umbonate larvae, 5–20 days old. C. Eye-spotted pediveligers, 20 days old. Note newly settled larva showing distinct dissoconch growth in bottom left photograph.

Table 3

Comparison of the major features of *Crassostrea iredalei*, *C. gigas*, and *C. virginica*.

Stage or distinctive feature	<i>C. iredalei</i>	<i>C. gigas</i> ¹	<i>C. virginica</i> ²
Straight-hinge veliger	64–84 μm	70–90 μm	68–90 μm
Conspicuous umbo			
Rounded	91–95 μm	90 μm	80–100 μm
Knobby	100–110 μm	125 μm	85–105 μm
Skewed	150 μm	150–200 μm	125 μm
Length equals height	85–90 μm	—	90–100 μm
Attached spat	>274 μm	300 μm	310–350 μm

¹ Data from LOOSANOFF *et al.* (1966) and CHANLEY & DINAMANI (1980).

² Data from LOOSANOFF *et al.* (1966) and CHANLEY & ANDREWS (1971).

fertilization and ranged in diameter from 47 to 50 μm (average, 48 μm). No measurements were made of the spermatozoa.

The periods of embryonic development up to the straight-hinge stage are presented in Table 1, with embryonic stages as described by BAYNE (1965). The approximate time of occurrence for each stage is given in the number of minutes and hours from fertilization, with fertilization time being time zero.

The formation of the first polar lobe, 45 min after fertilization marked the start of cleavage. Blastulation was observed in embryos older than 2 h and the ciliated blastula stage was reached in 5–6 h. At this stage the embryos started to roll and rotate. Early trochophores were observed 8 h after fertilization and were fully developed after an additional 7–8 h. The trochophores later developed into straight-hinge veligers in 22–26 h from fertilization.

Larval Dimensions and Shapes

The main features of larval development are summarized in Table 2. The changes in the shape and size of the larvae from the straight-hinge veliger to the newly metamorphosed spat are illustrated in Figure 2.

The smallest straight-hinge veliger observed was 64 μm long and 57 μm high, although one-day-old veligers averaged 69 \times 60 μm . The hinge-line length averaged 50 μm . The larvae were in the straight-hinge stage until the length equaled the height.

The height grew faster than the length, which in turn grew faster than the depth. Initially, the height was 5–10 μm less than the length, but these became equal when the larvae were 85–90 μm long. Eventually, the height exceeded the length by as much as 30 μm in older larvae.

The depth was 10–15 μm less than the length in the straight-hinge larvae and 90–100 μm less in the pediveliger stage.

The straight-hinge larvae were typically D-shaped, asymmetrical, and equivalved. The anterior margin of the shell was more pointed than the posterior margin. The shoulders dropped sharply in the anterior portion but more gradually in the posterior portion. The ventral margin of the shell was well rounded toward the posterior portion.

The larvae at length 85–90 μm appeared to be circular when lying on one valve due to the development of a slightly rounded umbo. The umbo of the veligers at this point developed very rapidly. In larvae 91–96 μm long, the umbos were already well rounded or slightly knoblike. The umbos became well developed knobs on the dorsal portion in larvae 100–110 μm long and eventually became skewed when the larvae were 150 μm long. The skewed umbo was characterized by CHANLEY & ANDREWS (1971) to be a variation of the “knobby” type and is found only in the genus *Crassostrea*. This larval shell characteristic of the *Crassostrea* bears much significance in the identification of the larvae of the various oyster species in the plankton.

The valves of the shell grew asymmetrically due to the highly unequal growth of the umbo, with the left valve much higher than the right by as much as 25 μm in the late stages. The hinge line did not lengthen much with additional growth of the larvae and could be discerned only until larvae were 95–100 μm long. As the umbo developed, the hinge line became more obscured.

In the pediveliger stage, the anterior portion of the shell was longer, more pointed, and was much lower than the posterior portion. The drop of the anterior margin from the shoulder was gradual and long, whereas that of the posterior margin was short, abrupt, and curved. The larvae were now alternately creeping and swimming vigorously.

The relationships of the larval dimensions and the derived regression lines are shown on the scatter diagrams in Figure 3. Each regression line describes two distinct linear relationships between the larval dimensions, with a breakpoint occurring at about the time of the rapid development of the umbo. The results here show much similarity to the growth of *Crassostrea virginica* and *C. gigas* as reported by LOOSANOFF *et al.* (1966) (see Table 3). The growth data for all three species indicate the same distinct linear relationships of the larval dimensions with a break point appearing at lengths between 115 and 125 μm .

It has been reported that *Crassostrea gigas* was imported from Japan in 1963 and experimentally farmed in southern Philippines (D. K. Villaluz, personal communication). Thus, some difficulty may arise in the identification and isolation of *C. iredalei* and *C. gigas* larvae should both these species occur together in the plankton, as experienced by LOOSANOFF *et al.* (1966) when *C. virginica* and *C. gigas* occurred together. It is also possible that these

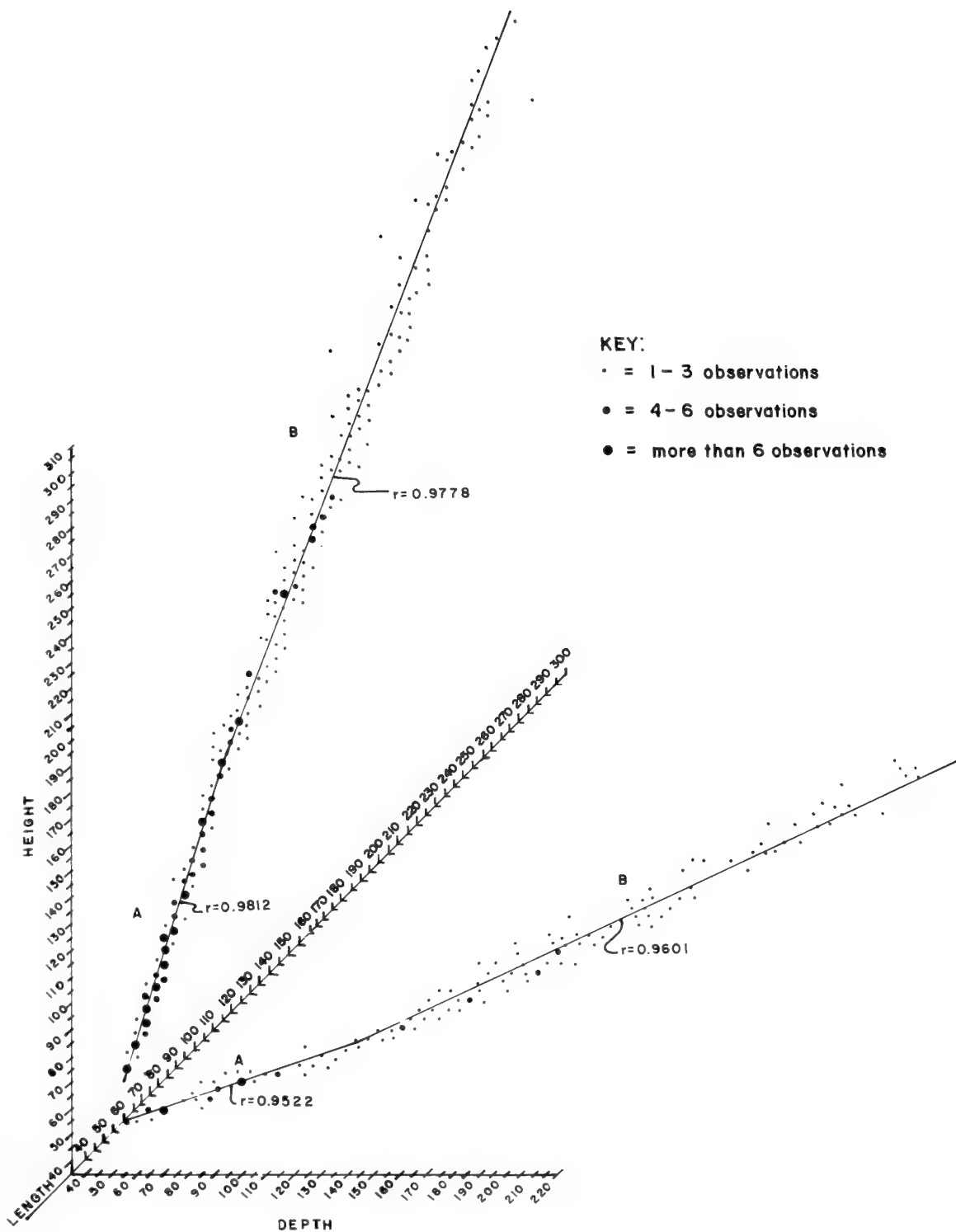


Figure 3

Dimensions of larval *Crassostrea iredalei*. Dots represent observed length-height or length-depth measurements. Height and depth coordinates run parallel to length axis. Regression lines show length vs. height and length vs. depth relationships. Regression equations are, for length-height: (A) $H = 1.5726 \times L - 49.1153$, $r = 0.9812$, (B) $H = 1.1319 \times L + 1.4758$, $r = 0.9778$; and for length-depth: (A) $L = 0.7352 \times D + 38.6897$, $r = 0.9522$, (B) $L = 1.3039 \times D - 17.0189$, $r = 0.9601$. The three-dimensional graph is adapted from CHANLEY & VAN ENGLE (1969).

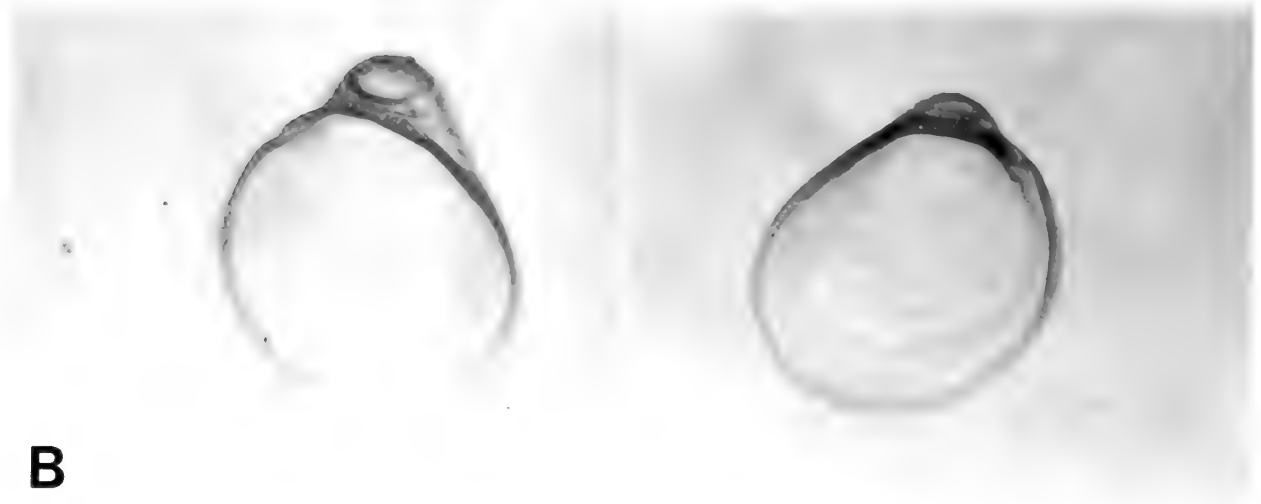


Figure 4

Larval hinge structure of *Crassostrea iredalei*. A. Dorsal view of straight-hinge larva, $89 \times 83 \mu\text{m}$, showing provinculum and hinge structure. B. Inside view of hinge structure of umbonate larval shell. Left valve (left) is $215 \times 249 \mu\text{m}$, with the anterior portion on the right. Right valve (right), $214 \times 236 \mu\text{m}$, anterior portion on the left.

two species have hybridized. Further studies on the biology of larvae caught from the wild, especially from the area of the southern Philippines, must be done.

Larval Hinge Structure

In straight-hinge larvae of *Crassostrea iredalei*, the hinge structure consisted of two to three large rectangular teeth on both ends of the provinculum and minute dentition on the central portion (Figure 4a). The left and right valves have very similar hinge structures, with the teeth perpendicular to the hinge line.

Due to the pronounced asymmetrical growth of the um-

bos of the left and right valves in umbonate larvae, the hinge structure of both valves changed progressively as the larvae matured. The slight coiling and skew of the umbo in the later stages had corresponding effects on the hinge structure.

The anterior portion of the larvae became longer, with the margin sloping more toward the ventral portion. As a result, the anterior group of hinge teeth angled inward and the posterior group of hinge teeth became obscured; in more advanced larvae, the most posterior tooth was much reduced. Likewise, the posterior margin of the valves became wider due to the coiling of the umbo (Figure 3b).

In late pediveligers, the posterior teeth of the left valve

were much reduced. The hinge line consequently slanted more toward the anterior, and the modified posterior margin became much wider.

The morphology of the larval shell, especially the hinge structure, was illustrated by DINAMANI (1976) as an important character in the systematic differentiation of the family Ostreidae at the subgeneric level. He extended the descriptions for the ostreid genera *Saccostrea* and *Crassostrea* provided by STENZEL (1971) to include distinctive features of the prodissoconchs. According to DINAMANI (1976), the prodissoconchs of the genus *Saccostrea* have "orthogyrate umbones and symmetrical teeth" whereas in the genus *Crassostrea* the prodissoconchs have "inequilateral growth, with posterior teeth modified and with the umbones tending to be opisthogyrate."

The prodissoconchs of *Crassostrea iredalei* definitely display the distinctive characters of the genus *Crassostrea*, and represent an intermediate position between *C. virginica* and *C. angulata-C. gigas* as can be gleaned from the illustrations of DINAMANI (1976).

The data derived from the laboratory culture of *Crassostrea iredalei* larvae may be used as baseline information for the mass cultivation of this bivalve in a hatchery grow-out system. However, a more important application of this study would be the use of the description of the larvae and knowledge of its biology for monitoring the start and duration of the spatfall period, its intensity, and the abundance of larvae in the plankton. These activities are necessary for the collection of oyster seeds from the wild for purposes of cultivation.

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Notes on Reproduction of a Tropical Pulmonate Limpet, *Siphonaria gigas* (Sowerby)

by

SALLY C. LEVINGS¹ AND STEPHEN D. GARRITY²

Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama

Abstract. *Siphonaria gigas* (Sowerby, 1825) is one of the most abundant mollusks on exposed rocky shores of the Pacific coast of Panama. Egg rings are laid on the rock throughout most of the year, although fewer are laid during the dry season (approximately January to March). Egg rings are deposited with a marked lunar periodicity; significantly more are found during neap than spring tides. Unless placed in a microhabitat protected from fishes, egg rings are quickly eaten. The overall pattern of reproduction is similar to that reported for other tropical members of the genus.

INTRODUCTION

ALTHOUGH the seasonal pattern and cues for spawning have been described for many temperate limpets and limpetlike pulmonates, information on the reproductive biology of tropical species is sparse (review in BRANCH, 1981). We have had the opportunity to gather information on the reproductive biology of the tropical pulmonate limpet *Siphonaria gigas* (Sowerby, 1825) during several years of study on the Pacific coast of Panama. *Siphonaria gigas* is one of the most abundant mid-intertidal zone species in Panama (LEVINGS & GARRITY, 1984).

Siphonaria gigas ranges from Ecuador to Baja California (KEEN, 1971). It occurs on exposed rocky shores (KEEN, 1971; LEVINGS & GARRITY, 1984) and can reach a shell length of 70–80 mm, making it the largest bodied member of its genus (HUBENDICK, 1945). Like other Siphonariidae, *S. gigas* is a simultaneous hermaphrodite. Individual animals exchange spermatophores before cementing gelatinous egg rings to the rock. Eggs mature after about 7 days and veligers are released into the plankton; settlement occurs after 5–7 days (R. Emler, personal communication). Here, we summarize our observations on the reproductive biology of *S. gigas* and compare it to that of other pulmonate limpets.

METHODS

Most observations were made on the inner Panama Bay islands of Taboguilla, Urava, Culebra, Flamenco, and Farallon between 1977 and 1985. Comparative data were taken throughout the Pearl Archipelago, in the Gulf of Chiriqui, and along the Darien coast. The intertidal community of this region has been described elsewhere (GARRITY & LEVINGS, 1981; LUBCHENCO *et al.*, 1984).

Seasonal and lunar patterns of reproductive behavior were determined by noting the presence or absence of egg rings or mating behavior in the field. Although this was done incidental to other work, records exist for all months of the year, except August, over an 8-yr period.

To determine the minimum size of reproductive maturity and to explore spatial relationships between pairs engaging in spermatophore transfer, the shell lengths and home scar locations of mating pairs were recorded. To estimate egg output, we counted the number of eggs in 10 randomly chosen 1 × 1 × 5-mm excised segments from each of seven freshly laid egg rings (rings collected 17 May 1978, Culebra). We measured the total length of an egg ring, then combined these data with the counts of eggs per 5-mm segment to estimate roughly the number of eggs in an "average-sized" egg ring. The inner and outer diameter, the number of whorls, and the distance from the nearest adult were measured on egg rings sampled from two bouts of deposition on Culebra in April and May 1978. To determine whether more than one egg ring could be laid during a single spawning period, we counted all egg rings and limpets of adult size on an isolated rock outcrop after a large bout of egg ring deposition.

¹ Present address: Department of Zoology, University of Rhode Island, Kingston, RI 02881, U.S.A.

² Present address: Department of Zoology, University of Massachusetts, Amherst, MA 01003, U.S.A.

To estimate the degree of predation on egg rings, egg rings were measured, the number of whorls recorded, and the percentage of the egg ring destroyed was estimated visually. When portions of an egg ring are eaten, the base is still visible and total size can be estimated (see Figure 1). These data were compared for egg rings located in microhabitats exposed to fishes (*e.g.*, horizontal, sloping and vertical surfaces) and those protected from fishes (*e.g.*, in crevices or depressions). Incidental notes were made on damage to eggs at other sites and on species that damaged egg rings.

To determine whether damage to egg rings was due to predators other than fishes, rates of damage for egg rings under cages ($n = 4$, $50 \times 50 \times 5$ -cm cages, 1-cm mesh), roofs ($n = 4$, 50×50 -cm roofs, 1-cm mesh, two sides open), and in open quadrats ($n = 8$, 50×50 -cm quadrats) were compared (Taboguilla Island, November 1977). Egg rings under cages were protected from mollusks, fishes, and crabs greater than 1 cm in the narrowest dimension; those under roofs were exposed to mollusks, crabs, and to fishes that could feed under roofs 5 cm off the substrate. Open quadrats were exposed to mollusks, fishes, and crabs.

RESULTS

Either spermatophore transfer or egg ring deposition was observed in all months except February in at least one year (August not sampled, Table 1). Egg rings were found on fewer than 33% of the observation days during the dry season (conservatively defined as January to March, $n = 32$ records). In contrast, we found eggs in more than half the observation days during all other months ($n = 81$). The bouts of egg deposition in the early wet season (April and May) in inner Panama Bay produced the largest numbers of egg rings observed in that area (>1 egg ring/adult limpet). Large numbers of egg rings were occasionally observed at other sites (*e.g.*, Uva, 5 December 1981, approximately 0.7 egg ring/adult).

Along a stretch of shore, subpopulations were often in different stages of the reproductive cycle. Egg rings might be found in only one of a number of nearby sites. For example, from 9 to 11 November 1977, eggs were found on two sections of shore on Taboguilla, but were not present on two other areas surveyed. However, on 24 October 1982, we sampled 14 islands throughout the Perlas Archipelago. Egg rings were being deposited on 12 of 14 islands. Thus, some level of synchronization is possible. We were more than twice as likely to find egg rings during neap tides (second and fourth quarter of the moon) than spring tides (G test, $P < 0.001$).

Spermatophore transfer occurred less than two weeks before egg ring deposition. Transfer occurred on falling tides, when the limpets were still being washed. In 59 of 86 cases on 29 May 1979 (Taboguilla), individuals mated with animals unambiguously identified as their nearest neighbors; often the scars of nearest neighbors are so close

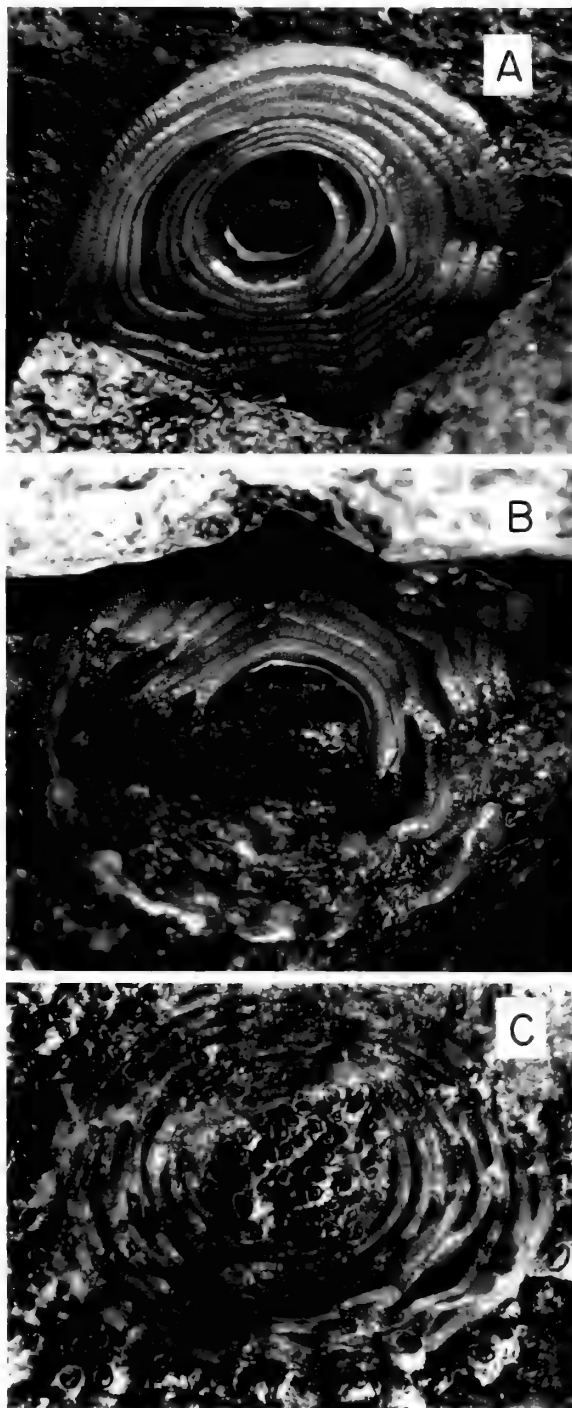


Figure 1

A. Fresh egg ring of *Siphonaria gigas*. B. Egg ring partially destroyed. Only the part of the egg ring inside the crevice remains. C. Egg ring on a homogeneous surface. Only the basal portion of the ring remains and bitemarks are visible. All rings approximately 70 mm in diameter. Culebra Island, May 1978.

Table 1

Egg ring deposition records, 1977–1985,
for *Siphonaria gigas*.

Month	No. records	Proportion with eggs present
January	17	0.59
February	2	0
March	13	0.08
April	7	0.71
May	10	0.50
June	11	0.27
July	9	0.78
August	no data	—
September	4	0.75
October	19	0.84
November	5	0.60
December	16	0.57

together that the limpets' shell edges are in contact. We never observed more than 20% of the adult population transferring spermatophores during a tidal cycle. Sizes of mating individuals were positively correlated ($r^2 = 0.31$, $P < 0.001$, $n = 156$ pairs, mean size = 43.2 mm, range 29–63, data from 23 May 1978 and 29 May 1979 on Taboguilla). This appeared to be due to the relatively narrow range of adult sizes and a weak tendency for nearest neighbors to be similar in size. No individual smaller than 29 mm in shell length was observed in reproductive behavior. In an undisturbed population, this size represents an individual approximately two years old (Levings & Garrity, unpublished data).

Egg rings consisted of a jellylike ribbon (approximately 5 mm high \times 1 mm wide) laid out on the rock in a continuous ellipsoidal spiral (Figure 1). While laying, limpets stayed in one spot and rotated slowly while extruding the ribbon of eggs; egg rings thus have an empty ellipse in the center where the limpet's foot rested. A ring was deposited over a single low tide and might be laid either during the day or at night. Although individual *Siphonaria gigas* are greater than 15 cm from a conspecific only 0–14% of the time in nine population samples (Levings & Garrity, submitted), egg rings were on average 16.8 ± 1.2 cm (mean \pm 1 SE) from the nearest adult. Limpets moved away from their home scars to deposit egg rings and most were placed in crevices or on vertical walls.

The average number of whorls in a ring was 8.2 ± 0.2 (mean \pm 1 SE, range 2–12 whorls, $n = 148$ egg rings, 30 April and 17 May 1978, Culebra). The maximum outside diameter of an egg ring ranged from 31 to 85 mm; when uncoiled, the ribbon of eggs was up to 100 cm long. Rings were about 20% longer than wide (mean length = 49.6 ± 0.8 mm, mean width = 41.9 ± 0.7 mm, outer dimensions). The inner ellipse was similar in shape (mean length = 19.5 ± 0.5 mm, mean width = 16.7 ± 0.4 mm, mean

Table 2

Amount of damage to *Siphonaria gigas* egg rings
exposed to different types of consumers.*

	Number of rings		
	Undis- turbed†	Dam- aged†	Total
Site 1			
In cages ($n = 2$)	11	0	11
Under roofs ($n = 2$)	5	0	5
In marked plots ($n = 4$)	6	14	20
Site 2			
In cages ($n = 2$)	4	1	5
Under roofs ($n = 2$)	11	0	11
In marked plots ($n = 4$)	5	17	22
Total			
Under cages or roofs ($n = 8$)	31	1	31
In open plots ($n = 8$)	11	31	42

* Data are the number of damaged *vs.* undamaged egg rings laid in cages, under roofs, or in open quadrats. Sites were sections of the shoreline of Taboguilla Island approximately 300 m apart. Sample date 9 November 1977. See text for further explanation.

† Egg rings were counted as damaged if they were disturbed in any way. In practice, damaged rings in the open quadrats were usually almost completely destroyed.

area = 2.7 ± 0.1 cm²). Each egg had a separate membrane and contained one veliger. Lengths of egg ring $1 \times 1 \times 5$ mm contained an average of 78 eggs (range 54–115 eggs; each value is the average of 10 counts from each of 7 rings). Combining these measurements, an average-sized egg ring contained more than 75,000 eggs.

During one spawning period, a single limpet could lay more than one egg ring. On 17 May 1978, 130 limpets greater than 20 mm in shell length laid 161 egg rings on an isolated rock outcrop on Culebra; no egg rings were present on 16 May. Similarly high numbers were observed occasionally at other sites. At sites we often visited, several bouts of oviposition were observed during the year; thus, individuals can lay more than one egg ring during one spawning period and there are multiple spawning periods during the year.

Egg rings not located in protected microhabitats were heavily damaged (median percent damage, exposed microhabitats = 55%, range 20–95%, $n = 22$, protected microhabitats = 0%, range 0–75%, $n = 70$, Culebra, 17 May 1978). One of 32 egg rings under cages or roofs was damaged, while 31 of 42 of those located in open quadrats were almost completely destroyed (Table 2). If an egg ring was partially in a crevice, only the fraction on open substrate was damaged (Figure 1). Most damage was probably due to fishes because crevices were accessible to crabs and mollusks. Damage occurred during high tide, bite-marks were found on most damaged rings (*e.g.*, Figure 1),

and there was usually a small amount of the base of the ring remaining. Egg rings located entirely in the open were essentially destroyed within two days of deposition.

Egg rings are rarely eaten by the predaceous gastropod *Purpura columellaris* ($n = 10$ observations in 1039 prey records, 6711 snails examined) and may be dislodged or bulldozed by *Chiton stokesi* (mean percent damaged = 20.6, range 5–33, $n = 5$ rings measured). *Pachygrapsus conver-sus*, an abundant and active crab (LUBCHENCO *et al.*, 1984), was observed probing rings on several occasions and may have eaten some eggs. Its effects, and those of mollusks, are likely to be of minor importance relative to the effects of fishes.

DISCUSSION

Reproduction in other *Siphonaria* has mostly been examined for temperate seas (see CREESE, 1980a; BRANCH, 1981, for review). Eggs tend to be deposited in spring and summer; lunar cycles are strongly marked. In *Siphonaria japonica* (Japan), *Siphonaria atra* (Palao), and *Siphonaria siphonaria* (Palao), eggs are laid during the second and fourth quarters of the moon (HIRANO, 1980; HIRANO & INABA, 1980; Abe, 1939, cited in ABE, 1940). We found this same pattern in *Siphonaria gigas*. The tropical species of *Siphonaria* also have extended breeding seasons (*Siphonaria pectinata*, *Siphonaria alternata* [ZISCHKE, 1974], *Siphonaria hispida* [MARCUS & MARCUS, 1966]). The basic breeding biology of *S. gigas* is similar to that of its conspecifics.

Most *Siphonaria gigas* probably deposit more than one egg ring during a spawning season, and may do so during a single period of spawning. However, with the data at hand, we cannot estimate fecundity either per spawning bout or per season for individual limpets; as in many species, egg ring size and number probably increase with limpet size (BRANCH, 1981). In general, *Siphonaria* appears to produce more eggs than co-occurring acmaeid limpets (CREESE, 1980a, b).

Egg rings in Panama are under strong predation pressure, as are gastropods on exposed surfaces (BERTNESS *et al.*, 1981; GARRITY & LEVINGS, 1983). If egg rings are not deposited in microhabitats where fishes cannot feed, they are quickly consumed. Other types of predators eat egg rings occasionally, but do not appear to have substantial effects. We have not been able to locate reports of fish predation on the egg rings of other Siphonariidae, so we do not know how widespread this phenomenon is.

We have suggested that egg rings are deposited in protected microhabitats to avoid destruction by predaceous fishes (Table 2). Alternatively, placement could be due to avoidance of heat stress and (or) desiccation. CREESE (1980a) transplanted egg rings of *Siphonaria denticulata* to both low and high tidal heights on the shore both in and out of tidepools. He showed that two-thirds of the rings placed in exposed microhabitats failed to hatch, while eggs in the other three microhabitats almost all hatched. He

attributed losses to desiccation. Egg rings on exposed surfaces in Panama are rapidly consumed; they might also succumb to physical stress (GARRITY, 1984) if predators were not present. *Siphonaria gigas* ranges from Baja California to Ecuador; the activities of fishes must vary over this geographical range. In areas where fishes do not eat egg rings, physical stress could still affect rings laid in open microhabitats and might have been the driving force behind the evolution of placement in protected microhabitat.

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Anatomy of the Foregut of *Morum* Röding, 1798 (Gastropoda: Tonnacea) and the Taxonomic Misplacement of the Genus

by

ROGER N. HUGHES

School of Animal Biology, University College of North Wales, Bangor, Gwynedd, LL57 2UW, U.K.

Abstract. Dissections and serial sections reveal that *Morum* differs anatomically from cassids in the following ways. There is a pair of large, acinar salivary glands that are mingled into a compact mass, but no proboscis glands. The salivary ducts do not run through the nerve ring, but become embedded in the oesophageal wall anterior to it. The proboscis sheath is capable of complete introversion and the oesophagus is attached to it, so being thrown into a Z-bend when the proboscis retracts. There are no jaws. The buccal mass and radula are microscopic. The radula has one tricuspid tooth (rachidian) per row. The mid-oesophageal epithelium is extensively folded longitudinally, not forming the distinct, transversely pleated oesophageal gland of cassids. The position of the salivary ducts anterior to the nerve ring, the lack of jaws, the reduced radula, and the arrangement of the introverted proboscis are features typical of neogastropods rather than mesogastropods. The large propodial shield, long siphon, ability to autotomize the hind-foot, microscopic radula with single tricuspid tooth per row, wide mid-oesophagus with longitudinal pleats, absence of accessory salivary, and Leiblein's and anal glands indicate that *Morum* belongs to the Harpidae.

INTRODUCTION

Morum is placed in the tonnacean family Cassidae (ABBOTT, 1968; EMERSON, 1981), yet several characteristics set this genus apart from the other cassids. The shell (Figure 1A) has some marked dissimilarities: "The anterior end of the aperture looks as though it had been broken, because it lacks the turned-back edge of most related forms. The young shell has even been mistaken for a cone by unsuspecting collectors" (KEEN & MCLEAN, 1971). These authors described the shell of *Morum vele-roae* Emerson, 1968, as "looking like a cross between a stromb and a harp shell . . ." The egg capsules, rather than being simple tubular or flask-shaped structures as in other cassids (ABBOTT, 1968; D'ASARO, 1969; BANDEL, 1976; HUGHES, 1985), are knobby, discoidal, and stacked in a row on a basal membrane, resembling certain *Conus* capsules (WORK, 1969; BANDEL, 1976). The active animal has a propodial shield, a long siphon, long cephalic tentacles, and rapid movement quite unlike other cassids (present observations). Moreover, whereas other cassids are specialized consumers of echinoids (HUGHES & HUGHES, 1981; DU SHANE, 1982; HUGHES, 1985), *Mo-*

rum oniscus (Linnaeus, 1767), the only species to be experimentally observed alive, refused all types of echinoderms offered to it (WORK, 1969; present observations) and no conclusive evidence of its diet is available.

The present paper describes the anatomy of the foregut of *Morum tuberosum* (Reeve, 1842), confirming not only the gross dissimilarity of *Morum* from other cassid genera, but also that it belongs to the Neogastropoda.

MATERIALS AND METHODS

Morum oniscus was sought by intensive scrutiny of the reef flat near the Smithsonian Tropical Research Institute's (STRI) Caribbean laboratory at Galeta Point, Republic of Panama. Despite over a week of continued effort, only one specimen was found, although several sets of egg capsules were seen. The specimen, collected at night beneath a slab of reef rock overlying coarse sand, was observed for 2 wk in the aquarium of the Pacific laboratory of STRI on Naos Island, Republic of Panama. Coelenterates, polychaetes, mollusks, crustaceans, and fish, both alive, freshly killed and decomposing, were offered as food, but none was eaten. The specimen was fixed and dissected.

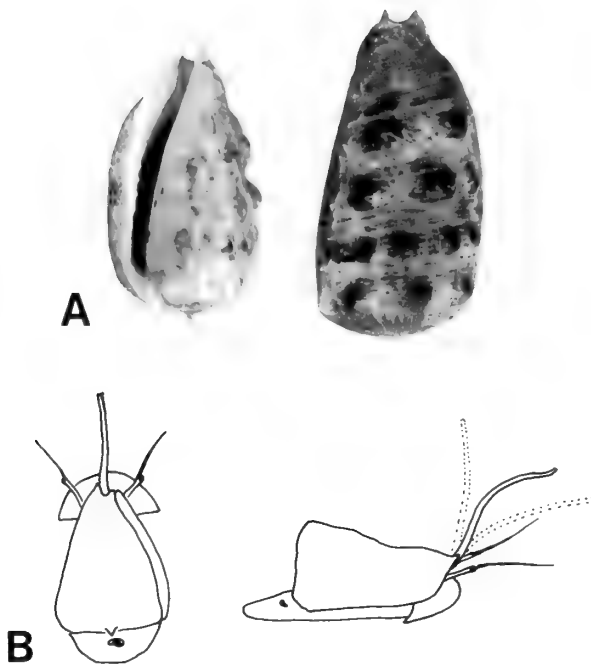


Figure 1

A. *Morum tuberculosum*. Shell length, 34 and 28 mm. B. *Morum oniscus*, showing appearance of the propodial shield, siphon, and cephalic tentacles when the snail is moving over the substratum. Shell length, 15 mm.

Searches for the Pacific species *Morum tuberculosum* on all types of shore within 10 km of the Naos laboratory were unproductive. Six intact, fixed specimens, 10–32 mm in shell length, were kindly sent at a later date by Royce E. Hubert, who had collected them under rocks and in areas of muddy sand at low tide at night on 28 February 1983. One specimen is lodged with the British Museum of Natural History, registration No. 1985118. The smallest specimen was serially sectioned at a thickness of 8 μm per section and stained with Mallory triple stain. The rest were dissected under a low-power binocular microscope. The radula was prepared by macerating the tip of the proboscis in hot, 10% sodium-hydroxide solution until almost dry (2 h) and transferring the proboscis to a drop of water on a microscope slide attached to an EM stub, whereupon the tissue dissolved leaving the microscopic radula intact. Sodium hydroxide was removed by rinsing with freshwater using a micro-pipette. A small hair from the back of the hand was dipped in cellotape glue (obtained by immersing the adhesive tape in trichloroethylene) and used to secure the radula to the coverslip. After coating with gold, but without prior sonication, the radula was examined using a scanning electron microscope. Attempts to locate the radula by clearing the proboscis in cedarwood oil or in lactophenol and lignin pink failed

because the radula is too small to be seen *in situ* under the low power of a dissecting microscope.

RESULTS

Morum oniscus

The *Morum oniscus* burrowed rapidly into the sand when illuminated by torchlight on the reef flat. In the aquarium it remained buried beneath the sand during daylight, the siphon communicating with the surface. On some nights the specimen emerged to glide over the substratum, turning erratically along its path. The impression given was of a more agile snail than the typical cassid. The propodium formed a pronounced semicircular shield; the siphon was held at various angles, extending far beyond the siphonal canal, and the cephalic tentacles were also greatly extended (Figure 1B). The animal quickly burrowed in response to any kind of disturbance and would not feed, even when undisturbed for a week. Anatomical features of the *M. oniscus* were similar to those of *M. tuberculosum* described below.

Morum tuberculosum

The siphon opens onto the tip of a large, bipectinate osphradium (Figure 2A). The gill is also large and the hypobranchial gland is well developed, producing copious amounts of mucus but no colored secretion.

On removing the dorsal wall of the cephalic hemocoel, the introverted proboscis sheath lies to the right and the solid, white salivary glandular mass to the left, occupying most of the available space (Figures 2A, 3A). The proboscis sheath is attached to the body wall by numerous short, fine muscle strands near the rhynchostome and by a series of large, straplike retractor muscles further along its length (Figure 3B). The fully retracted proboscis lies, sometimes bent into folds, within the completely introverted proboscis sheath (Figure 4B).

The anterior oesophagus emerges from the base of the introverted proboscis sheath and runs back on itself to the midway position, closely attached to the proboscis sheath by a short mesentery (Figure 4A). Here the anterior oesophagus bends posteriorly and, along with the aorta, passes as a narrow tube through the massively concentrated nerve ring (Figure 5). On emerging posteriorly from the nerve ring, the oesophagus dilates to form a wide, internally pleated mid-oesophagus that runs to the left, passing beneath the posterior salivary gland (Figure 5). The mid-oesophagus continues, without clear differentiation, into the narrower posterior oesophagus, running to the left until it merges with the simple stomach (Figures 2B, C), which lies on the opposite side of the animal, level with the nerve ring.

The salivary glands form a dense, irregularly shaped mass in which the two glands are indistinguishable. The shape and relative size of the glandular mass varies among

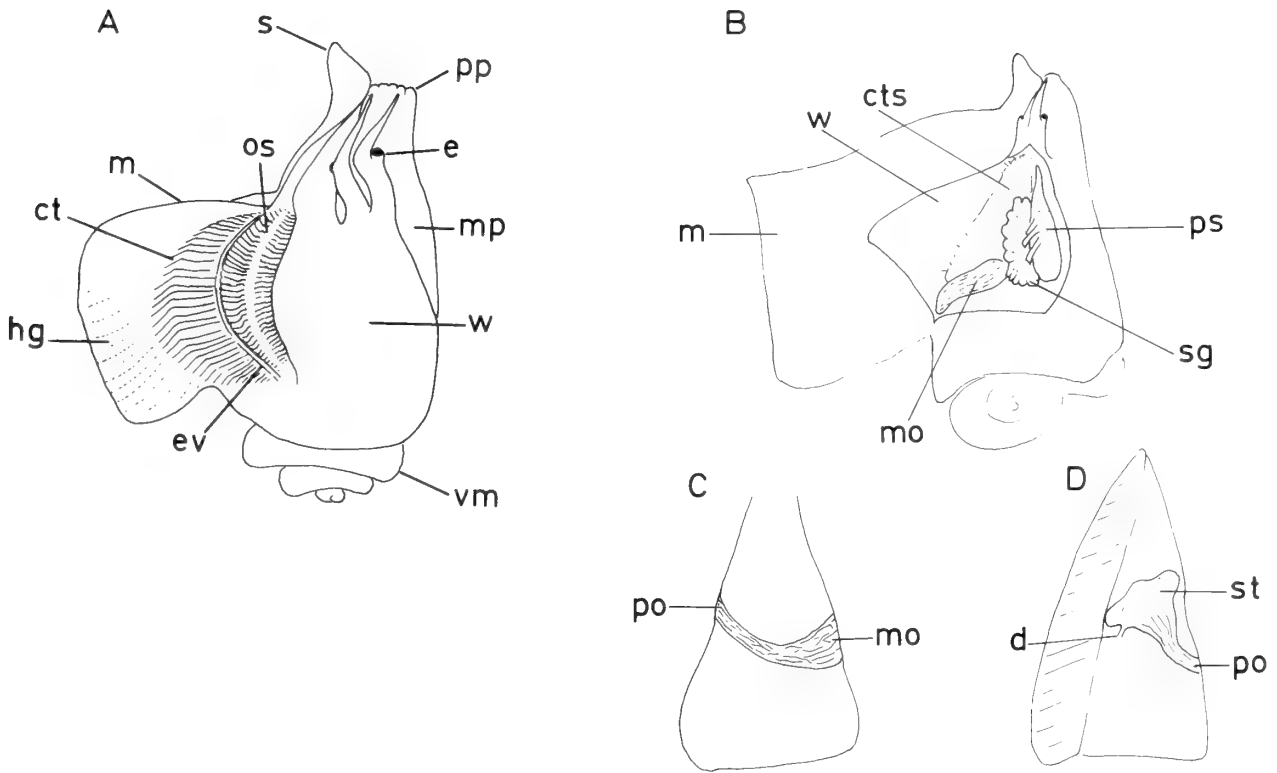


Figure 2

Morum tuberculosum, body about 20 mm long. A. The mantle is peeled to the left, showing the arrangement of the pallial organs. B. The dorsal wall of the cephalic hemocoel has been peeled to the left, revealing the natural positions of the retracted proboscis, mid-oesophagus, and salivary glands. C. The mid-oesophagus traced to the left where it merges with the posterior oesophagus. D. The posterior oesophagus traced further to the left where it joins the stomach. The hatched region shows where the foot has been cut away. ct = ctenidium; cts = connective tissue; d = digestive gland duct; e = eye; ev = efferent branchial vessel; hg = hypobranchial gland; m = mantle; mo = mid-oesophagus; mp = mesopodium; os = osphradium; po = posterior oesophagus; pp = propodium; ps = proboscis sheath; s = siphon; sg = salivary gland; st = stomach; vm = visceral mass; w = wall of cephalic hemocoel.

animals (Figures 2B, 3A, B), but is always large. Especially in specimens with smaller salivary glands, the unoccupied space on the left side of the cephalic hemocoel is filled with a gray, semi-translucent, spongy material that has no ducts and appears to be a form of connective tissue. It is closely applied to the body walls and is traversed by several large nerves and by numerous fine muscle strands.

One salivary duct serves the posterior region of the glandular mass and the other empties from the anterior region (Figure 8E). The salivary ducts become embedded lateroventrally in the anterior oesophagus where it bends away from the proboscis sheath and, therefore, they do not pass through the nerve ring (Figure 5). There is no accessory salivary gland.

The buccal mass (Figure 7) lies at the tip of the proboscis. It is supported by a pair of minute odontophoral cartilages that unite anteriorly to form a grooved boss over

which the radula runs in the normal way (Figures 7B, C). The radula itself is microscopic, about 25 μm wide in a large specimen, consisting of a single column of tricuspid teeth (Figure 6).

There is a pronounced median dorsal fold projecting down from the roof of the buccal cavity and it continues in a less pronounced form along the anterior oesophagus (Figure 8E) to the level of the nerve ring, whereupon it disappears. Behind the level where the odontophore projects into the buccal cavity, a median ventral fold projects upwards, abutting the dorsal fold and so dividing the oesophageal lumen into two lateral cavities (Figures 7B, C). Like the dorsal fold, the ventral fold disappears just before the oesophagus enters the nerve ring.

The salivary ducts open onto lateral papillae immediately in front of the buccal mass (Figures 7A, B). Throughout their length, the salivary ducts are equipped

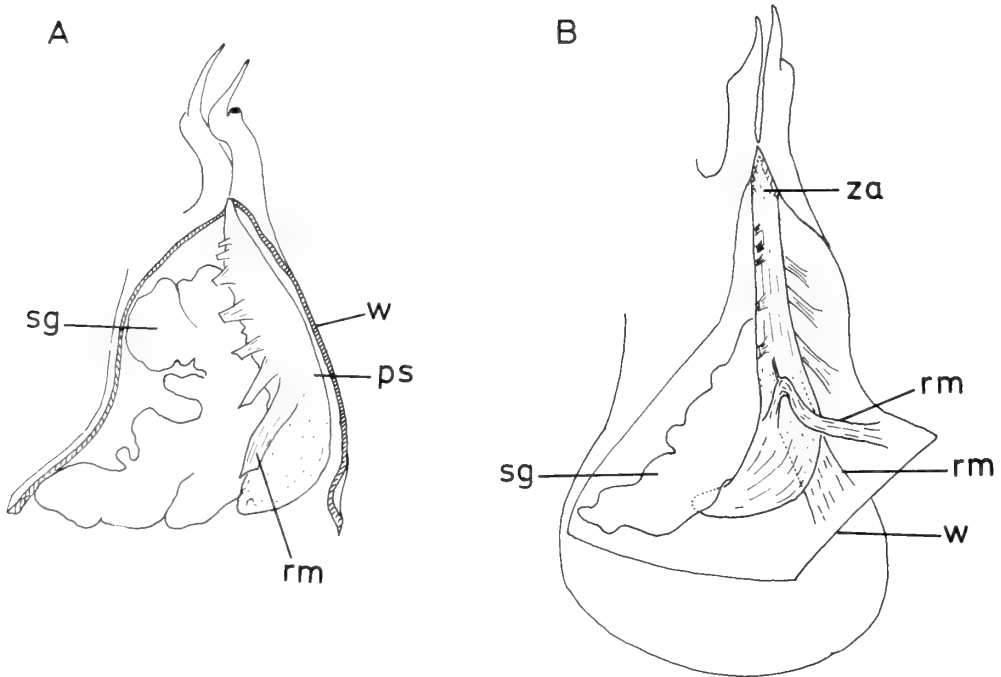


Figure 3

Morum tuberculosum. A. Details of the retracted proboscis and salivary glands. The latter are more extensive and shaped differently from the specimens in Figures 2B, 3B. B. Retracted proboscis, showing insertions of the retractor muscles on the wall of the cephalic hemocoel. ps = proboscis sheath; rm = retractor muscle; sg = salivary gland; w = wall of cephalic hemocoel; za = zone of attachment of proboscis sheath to body wall.

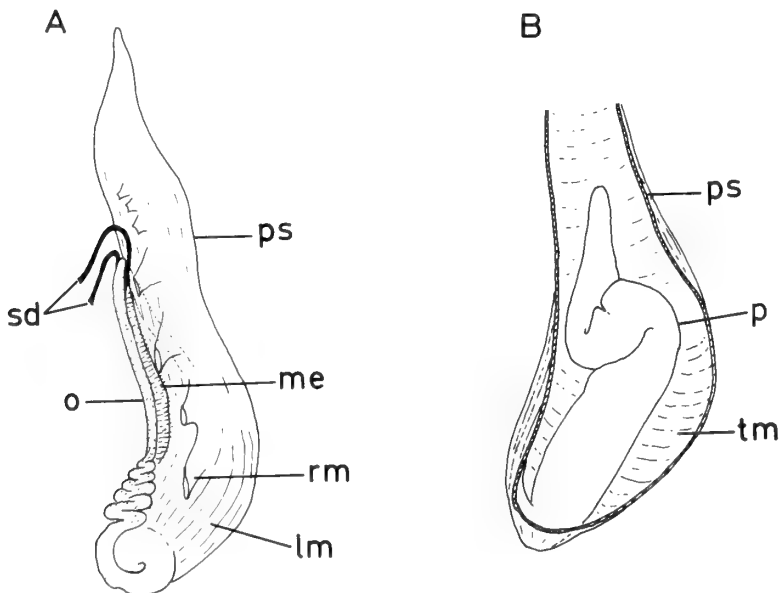


Figure 4

Morum tuberculosum. Details of retracted proboscis. A. Attachment of salivary ducts and anterior oesophagus to the proboscis sheath. B. Proboscis retracted and folded within the proboscis sheath. lm = longitudinal muscle of proboscis sheath; me = mesentery attaching oesophagus to proboscis sheath; o = oesophagus; p = proboscis; ps = proboscis sheath; rm = retractor muscle; sd = salivary duct; tm = transverse muscle of proboscis sheath.

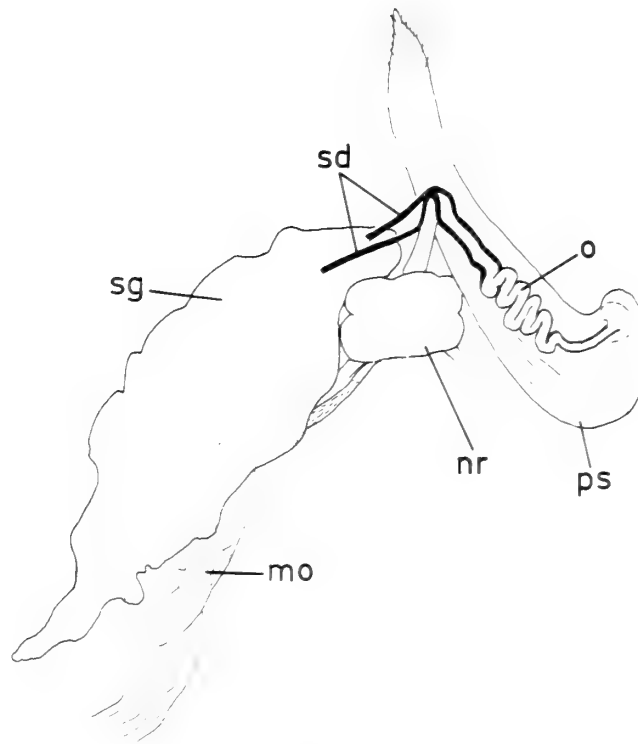


Figure 5

Morum tuberculosum. Passage of the oesophagus from the proboscis sheath through the nerve ring. mo = mid-oesophagus; nr = nerve ring; o = anterior oesophagus; ps = proboscis sheath; sd = salivary ducts; sg = salivary glands.

with strongly developed circular muscles (Figures 7, 8E). Ramifications of the salivary ducts can be traced within the salivary glands, which themselves are made up of small, closely packed acini comprised of cells densely populated by granules.

As it passes through the nerve ring, the oesophagus becomes narrow and lined by a simple epithelium without folds (Figure 8C). The wide, mid-oesophagus is lined by an extensively folded epithelium that is arranged predominantly into longitudinal pleats, but also with some transverse folds (Figures 8D, F). The posterior oesophagus is narrower, but with similar epithelial folds. The stomach is lined by similar, but larger folds. The rectum lacks an anal gland.

DISCUSSION

The alimentary anatomy of *Morum* is grossly dissimilar from that of other cassids, as may be seen by comparing Figures 2-5 with the dissection of *Phalium granulatum* (Born, 1778) (Figure 9) or with figure 1a of HUGHES & HUGHES (1981). *Morum* has a pair of dense salivary glands fused into a large mass; cassids have a distinct pair of small acinar salivary glands and a pair of huge, spongy proboscis glands. The salivary ducts of *Morum* join the

oesophagus anterior to the nerve ring and are deeply embedded in the oesophageal wall; the salivary ducts of cassids pass through the nerve ring and are not deeply embedded in the oesophageal wall. The proboscis of *Morum* can be retracted far within the proboscis sheath; the proboscis of cassids does not retract much within the level of the rhynchostome. The proboscis sheath of *Morum* is withdrawn by a few, long retractor muscles that effect complete introversion; the proboscis sheath of cassids is withdrawn by numerous shorter retractor muscles and introversion is never complete even when the proboscis is fully retracted. The middle section of the anterior oesophagus of *Morum* is attached to the proboscis sheath by a short mesentery, with the result that on retraction of the proboscis and introversion of the proboscis sheath, the anterior oesophagus is thrown into a Z-bend; the anterior oesophagus of cassids lies freely within the lumen of the proboscis sheath and remains straight when the proboscis sheath is withdrawn. The mid-oesophagus of *Morum* is lined by a predominantly longitudinally folded epithelium and passes without clear demarcation into the narrower posterior oesophagus; the mid-oesophagus of cassids forms a distinct oesophageal gland with a transversely pleated epithelium. The buccal mass and radula of *Morum* are

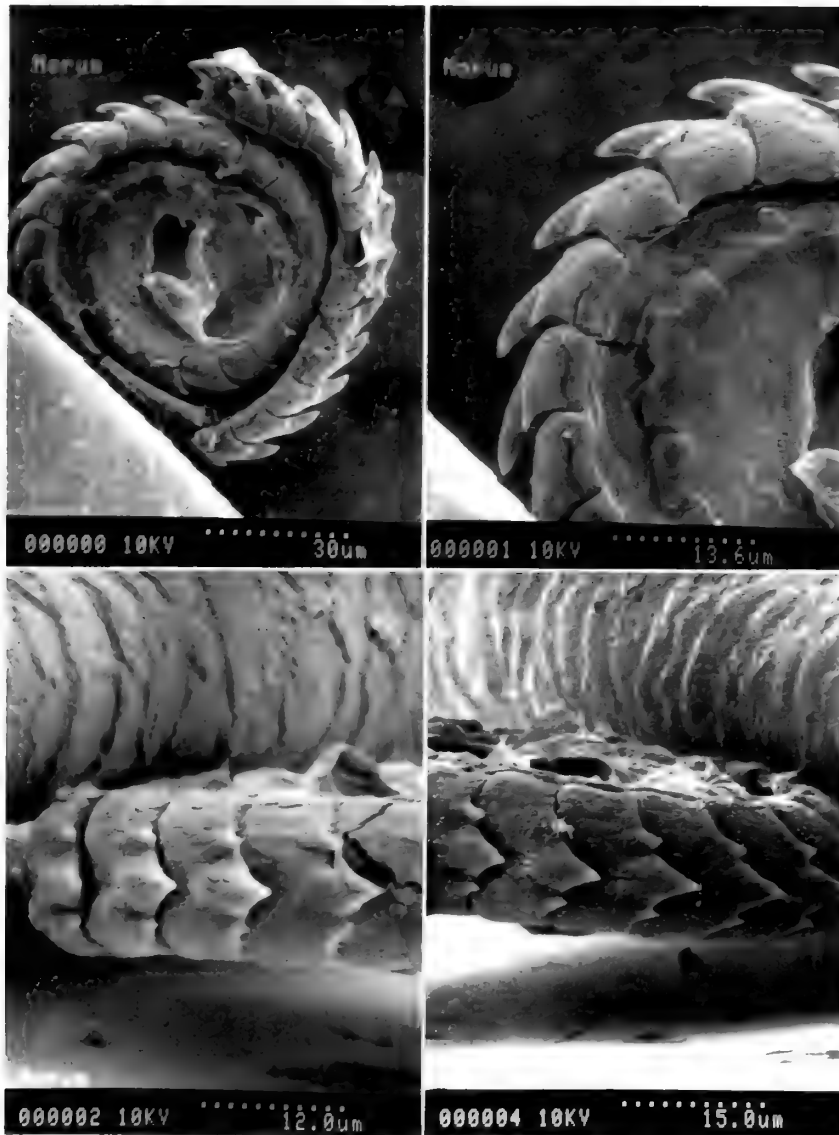


Figure 6

Morum tuberculosum. Scanning electron micrographs of the radula, taken from a specimen with a shell length of 25 mm.

microscopic and the radula has only one tooth per row; the buccal mass and radula of cassids are of normal proportions and the radula has seven teeth per row. The central tooth of *Morum* is tricuspid; the central tooth of cassids has many cusps. *Morum* lacks jaws; cassids have a pair of lateral jaws.

There are other morphological differences between *Morum* and cassids. The propodium of *Morum* forms a semi-circular shield, but there is no suggestion of a propodial shield in cassids. The siphon of *Morum* extends far beyond the siphonal canal, but does not do so in cassids.

Morum appears to be trophically distinct from the cassids. The refusal of echinoid prey, the structure of the buccal apparatus, and the absence of acid-secreting proboscis glands show that *Morum* could not drill echinoid tests in the manner that is characteristic of cassids (HUGHES & HUGHES, 1981).

Together, these facts indicate that *Morum* does not belong to the Cassidae, nor even to the Tonnacea, all of which have paired salivary and acid-secreting proboscis glands, salivary ducts running through the nerve ring, and a distinct oesophageal gland (HUGHES & HUGHES, 1981). In-

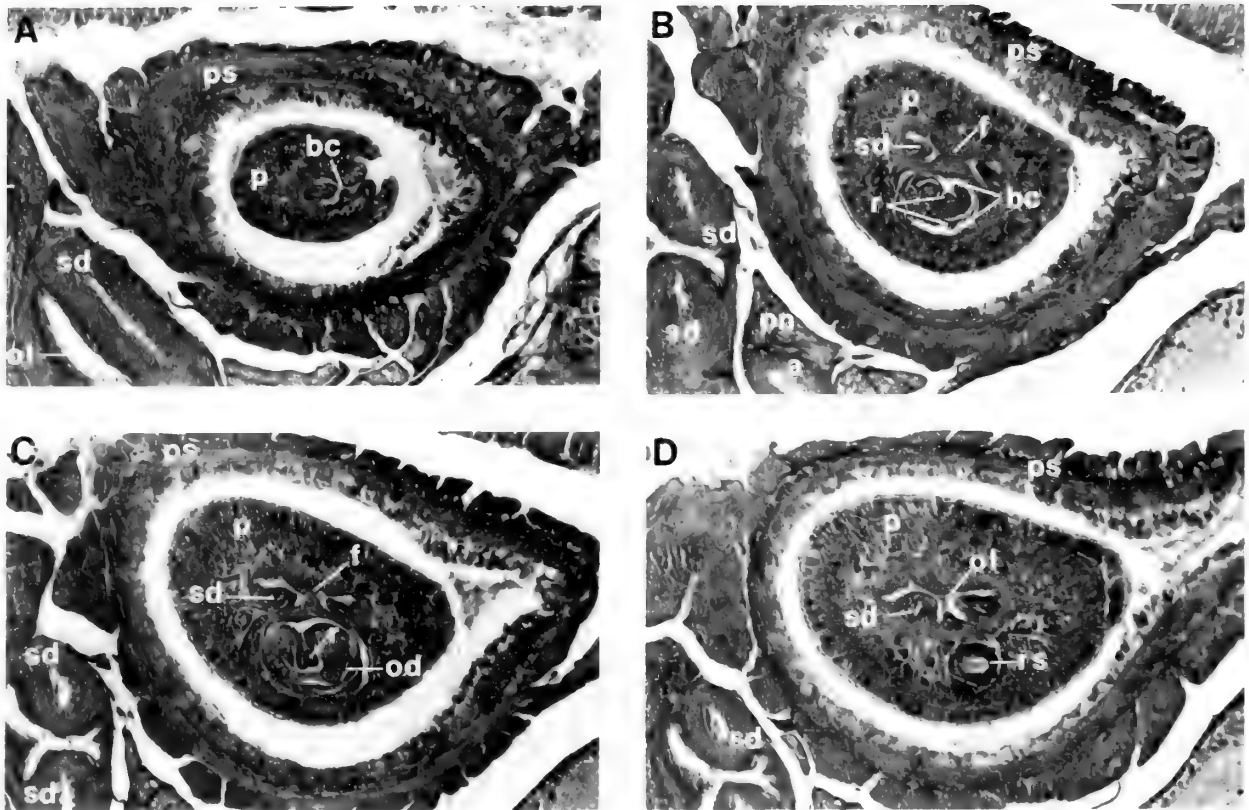


Figure 7

Morum tuberculosum. Transverse sections through the buccal apparatus. Magnification, $\times 187$. A. Immediately anterior to the tip of the odontophore; the salivary ducts have emptied into the buccal cavity slightly posterior to this section. B. The tip of the odontophore; the radula runs over both the dorsal and ventral surface of the odontophore; the salivary ducts are about to open via the ventrolateral papillae into the buccal cavity; mid-dorsal and mid-ventral folds of the oesophageal epithelium meet. C. Further behind the tip of the odontophore; the radula lies within a deep groove; the radular membrane lines the walls of the groove; the small, paired odontophoral cartilages are visible. D. Behind the odontophore; the radular sac is visible; the dorsal and ventral oesophageal folds are less prominent and do not meet. For legend see Figure 8.

deed, the position of the salivary ducts anterior to the nerve ring reveals that *Morum* has closer affinities with the Neogastropoda (PONDER, 1973) than with the Mesogastropoda, to which cassids belong. *Morum* is consistent with all other neogastropods in lacking jaws (PONDER, 1973) and shares several other features with various neogastropod families.

The mode of introversion of the proboscis sheath, the attachment of the oesophagus to the wall of the proboscis sheath, and the Z-bend of the oesophagus produced by its retraction are similar to the case with *Nassarius* (FRETTER & GRAHAM, 1962:fig. 115). A microscopic buccal apparatus is found also in some members of the Colubrariidae, Harpidae, Muricidae, and Columbariidae (PONDER, 1973). Reduction of the radula tooth row to the rachidian occurs also in the Mitridae, Volutidae, Marginellidae, Volutomitridae, and Cancellariidae, but the tricuspid cen-

tral tooth of *Morum* bears closer resemblance to that of *Harpa* (see PONDER, 1973) than to that of other genera. A long siphon extending beyond the siphonal canal is found among numerous neogastropods, notably nassariids, but also among some mesogastropods. A propodial shield is found in the Harpidae and Olividae (PONDER, 1973). The absences of a valve of Leiblein and a gland of Leiblein in *Morum* are features shared by a number of neogastropod families (PONDER, 1973). The absence of paired dorsal folds in the anterior oesophagus precludes identification of the site of torsion.

Morum bears closest resemblance, however, to the Harpidae (W. Emerson and W. Ponder, personal communications); common features include the propodial shield, long siphon, ability to autotomize the hind-tip of the foot (A. Connell and W. Liltved, personal communications), microscopic radula and single tricuspid tooth per row

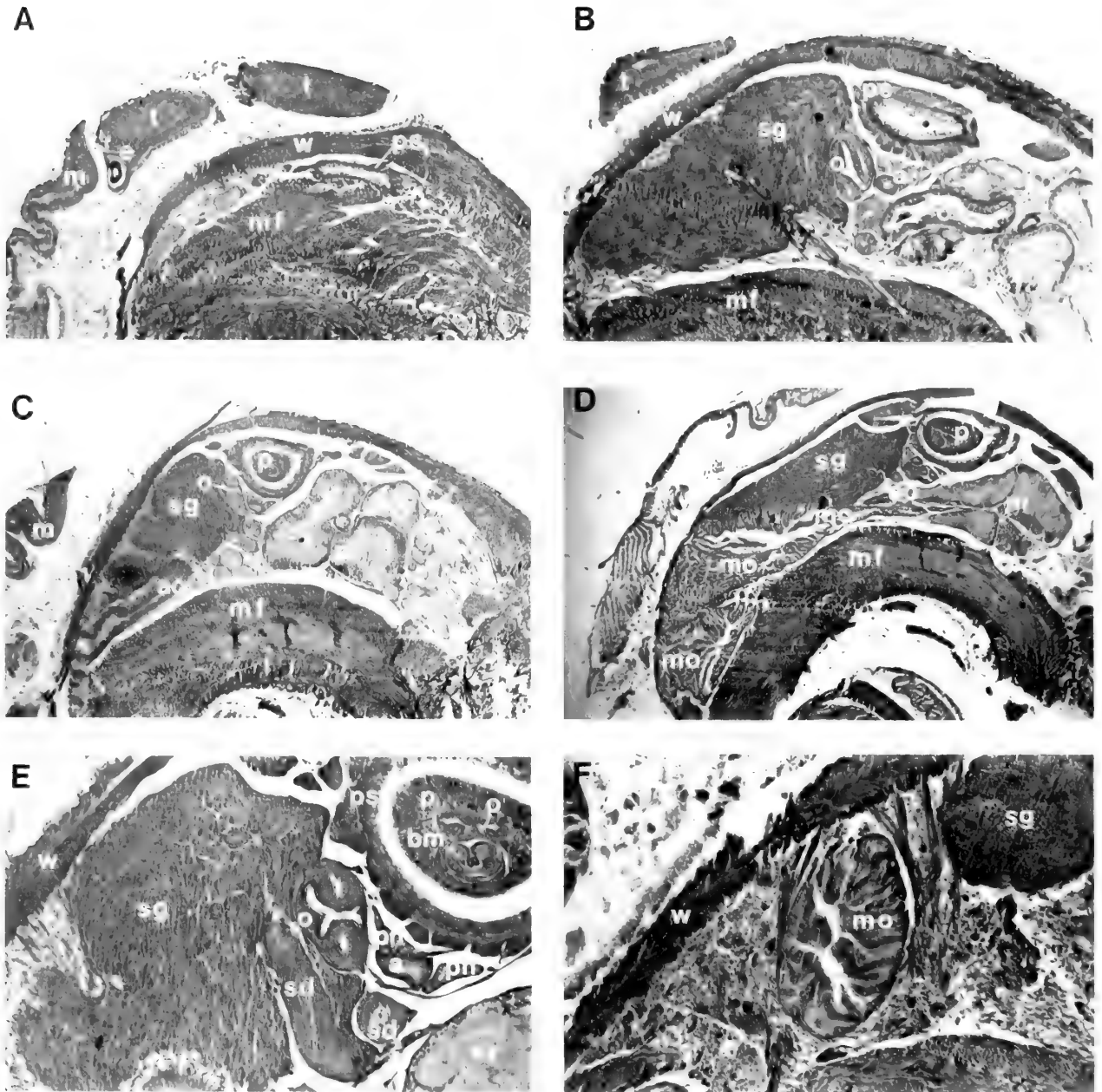


Figure 8

Morum tuberculosum. A. The tip of the proboscis sheath, close to the rhynchostome; magnification, $\times 28$. B. The anterior oesophagus entering the nerve ring; magnification, $\times 37$. C. The anterior oesophagus within the nerve ring; magnification, $\times 28$. D. The oesophagus emerging posteriorly from the nerve ring and widening into the mid-oesophagus; magnification, $\times 28$. E. One salivary duct, sectioned obliquely, is entering the anterior salivary gland, the other, sectioned transversely, serves the posterior salivary gland. The anterior oesophagus is seen with a pair of muscular salivary ducts embedded in its wall and with small dorsal and ventral folds projecting into its lumen. The oesophagus, together with the proboscis artery and proboscis nerves, is connected to the proboscis sheath by a mesentery; magnification, $\times 93$. F. The mid-oesophagus showing the extensively folded epithelium; magnification, $\times 93$. a = proboscis artery; ao = aorta; bc = buccal cavity; bm = buccal mass; e = eye; f = dorsal and ventral folds; m = mantle; mf = muscular floor of cephalic hemocoel; mo = mid-oesophagus; nr = nerve ring; o = anterior oesophagus; od = odontophore; ol = oesophageal lumen; p = proboscis; pn = proboscis nerve; ps = proboscis sheath; r = radula; rs = radular sac; sd = salivary duct; sg = salivary gland; t = cephalic tentacle; w = wall of cephalic hemocoel.

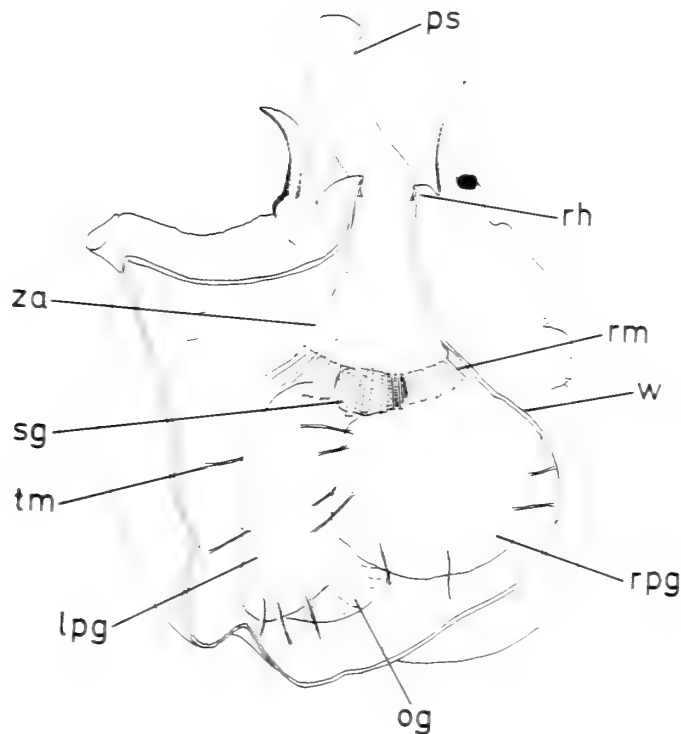


Figure 9

Phalium granulatum, showing arrangement of the partially invaginated proboscis sheath with its numerous retractor muscles, the massive proboscis glands, the small salivary glands (only one visible), and the oesophageal gland; for comparison with the foregut anatomy of *Morum tuberculosum*. lpg = left proboscis gland; og = oesophageal gland; ps = proboscis sheath; rh = rhynchostome; rm = retractor muscle; rpg = right proboscis gland; sg = salivary gland; tm = tie-muscle; w = wall of cephalic hemocoel; za = zone of attachment of proboscis sheath to body wall.

(REHDER, 1973), and lack of accessory salivary, Leiblein's and anal glands (W. Ponder, personal communication; personal observation). Preliminary dissections leave no doubt that *Morum* belongs to the Harpidae and a detailed comparison together with a taxonomic revision are underway (Hughes & Emerson, in preparation).

The feeding habits of *Morum* remain enigmatic but perhaps, like those of *Harpa* (REHDER, 1973), they involve the capture of crustaceans, using the large propodium and copious secretion of sticky mucus to envelop the prey. Certainly, *Morum* is sufficiently agile for this method of attack. The large salivary glands with their densely granular cells, together with the highly muscular salivary ducts, suggest that digestively active saliva is ejected from the proboscis. Perhaps food is ingested as a partially digested fluid. This would pass easily through the narrow part of the oesophagus at the nerve ring and would require minimal processing before entering the stomach, hence the absence of a gland of Leiblein. Fine muscle strands connecting the wide mid-oesophagus to the body wall, especially evident in *Harpa* (personal observation), indicate that this section of the gut may serve as a dilatible pump for the ingestion of fluid. The microscopic radula would

suffice to penetrate the thin arthroal membranes of the crustacean prey, allowing the injection of saliva and withdrawal of semidigested fluid.

ACKNOWLEDGMENTS

This research was generously funded by a Travel Grant from the Royal Society. It would not have come to fruition, however, without the kindness of William K. Emerson and Royce E. Hubert, who between them arranged to send me the vital specimens of *Morum tuberculosum*. Norman W. Runham, as always, gave generously of his advice and I was helped by the opinions and information freely given by Allan Connell, Bill Emerson, Bill Liltved, and Winston Ponder. Norma Blackstock made the histological preparations and Helen Hughes prepared the radula to the SEM. I thank all concerned.

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Two New Species and Genera of Aeolid Nudibranchs from the Tropical Eastern Pacific

by

TERRENCE M. GOSLINER

Department of Invertebrate Zoology, 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. Specimens of two new species of aeolid nudibranchs, *Hermosita sangria* and *Bajaeolis bertschi*, are described from the tropical eastern Pacific Ocean. Both species are placed in new genera, *Hermosita* and *Bajaeolis*, within the Facelinidae, as aspects of their external and internal morphology differ from members of closely allied genera.

INTRODUCTION

COLLECTIONS made from the Pacific and Gulf of California coasts of Baja California and from the Pacific coast of Panama have yielded specimens of two undescribed species of aeolidacean nudibranchs. This paper describes the morphology of these new taxa and discusses their systematic placement within the Aeolidacea.

Family FACELINIDAE
Subfamily FAVORININAE

Hermosita Gosliner & Behrens, gen. nov.

Diagnosis: Body elongate, limaciform. Foot corners tentacular. Rhinophores perfoliate. Cerata arranged in arches with a single row per arch. Anus cleioproctic. Nephroproct interhepatic. Salivary and oral glands simple and elongate. Masticatory border of jaws smooth. Radula uniseriate with cuspidate rachidian teeth. Central cusp of rachidian wide, with slender adjacent denticles. Reproductive system with proximal receptaculum seminis and distal bursa copulatrix. Penis simple with small, fleshy papilla on one side of apex.

Type species: *Hermosita sangria*, spec. nov.

Etymology: *Hermosita* means "beautiful little one" in Spanish.

Hermosita sangria Gosliner & Behrens, spec. nov.

(Figures 1A, 2-5A, 6; Table 1)

Coryphella sp.: BEHRENS, 1980:105, fig. 155.

Type material: Holotype: California Academy of Sciences, CASIZ 059586, approximately 52 mm (preserved), collected in 17 m of water, 0.75 km S. of Isla San Benito Oeste, Baja California, Mexico (28°20'N, 116°10'W), 31 August 1982, by Florence McAlary.

Paratypes: (1.) One specimen, CASIZ 059587, 16 mm (preserved), collected in 13 m of water, Punta San Augustino, Isla Cedros, Baja California, Mexico (28°5'N, 115°21'W), 29 August 1982, by Daniel W. Gotshall. (2.) Four specimens, CASIZ 059588, Isla San Benito, collected by James Gatewood and Marc Chamberlain. (3.) Three specimens, Division of Mollusks, National Museum of Natural History, U.S.N.M. 635838, collected with egg masses, 3-m depth, Bahía Magdalena, Baja California Sur, 30 May 1958, by Conrad Limbaugh.

Etymology: The specific epithet, *sangria*, refers to the blood red pigment present on the head, rhinophores, and cerata of this species.

Description

External morphology: The living animals (Figures 1A, 2) may reach 70 mm in length. The body is elongate and



Figure 1

Living animals. A. *Hermosita sangria*, spec. nov., specimen collected from Isla San Benito, Aug. 1984. Photo by James Gatewood. B. *Bajaeolis bertschi*, spec. nov., 27-mm specimen collected from Bahía de los Angeles, 15-m depth, Oct. 1979. Photo by Jeff Hamann.

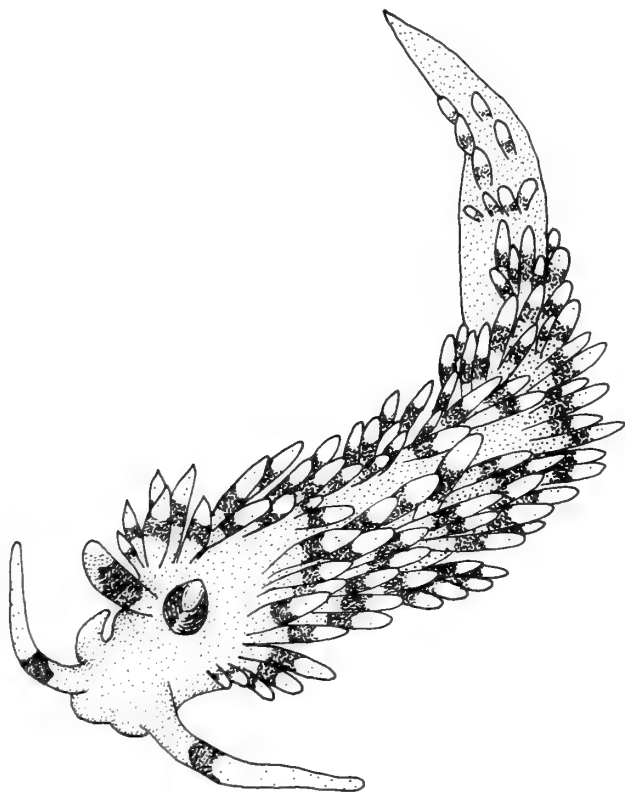


Figure 2

Hermosita sangria, spec. nov. Living animal drawn from color transparency.

graceful. The foot is wide, approximately twice the width of the notum, and tapers posteriorly to a rounded tail. The perfoliate rhinophores possess 16–22 lamellae. The oral tentacles are elongate with pointed apices. The foot corners (Figures 2, 3A) are tentacular, about $\frac{1}{3}$ – $\frac{1}{2}$ of the length of the oral tentacles. The slightly clavate cerata (Figure 3B) are semicircular in cross-section, with a flattened dorsal surface. The cavity of each ceras contains nodular digestive gland cells and terminates at an elongate, apical cnidosac. The cerata are arranged in about 8 horseshoe-shaped arches, with a single row of cerata per arch (Figure 3A). In one specimen the ceratal formula was I-17, II-16, III-16, IV-12, V-12, VI-9, VII-6, VIII-3–4. The cerata at either end of each arch are shortest while the longest are most central. The anus is cleioproctic (Figure 3A), located within the second ceratal arch (the first arch of the right posterior digestive branch). The nephroproct is situated between the first two ceratal groups, within the interhepatic space. The gonopores are located on the right side of the body, ventral to the anterior half of the first ceratal arch.

The ground color of the body is violet, which deepens to a rich vermilion red band near the middle of the cerata, foot corners, oral tentacles and rhinophores. The distal

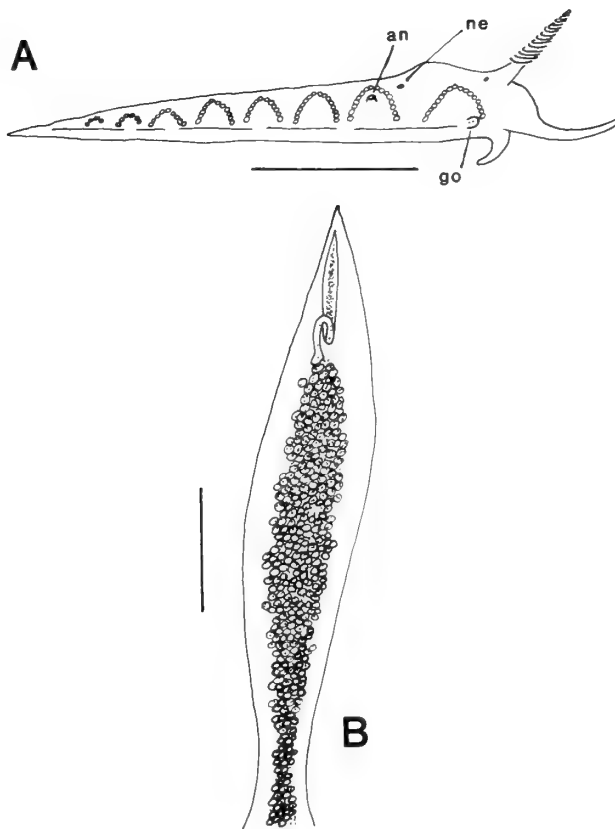


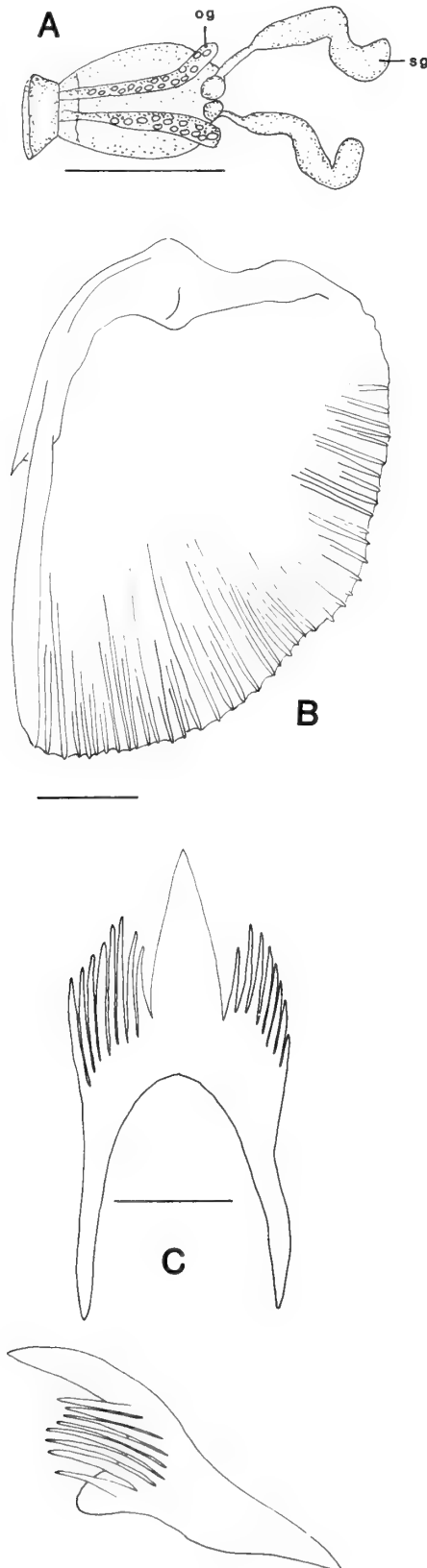
Figure 3

Hermosita sangria, spec. nov. A. Lateral view, scale = 25 mm. an = anus; go = genital orifice; ne = nephroproct. B. Detail of ceras, scale = 2.0 mm.

third of these structures is tipped with yellow, or white in some specimens.

Digestive system: The buccal mass is thick and muscular (Figure 4A). The oral glands are simple and clavate. The salivary glands are unbranched and slightly convoluted. The thick, rectangular jaws (Figure 4B) are gold in color and deeply concave. Their masticatory border is smooth, devoid of denticles. The radular formula is 26–30 \times 0.1.0. The radular teeth (Figures 4C, 5A) are thin and elongate. On either side of the prominent, triangular central cusp are 9–15 elongate, slender denticles.

Reproductive system: The reproductive system (Figure 6A) is androdiaulic. The ovotestis contains abundant diffuse acini, which empty into the short, narrow preampullary duct. The preampullary duct expands into the muscular, slightly convoluted ampulla. The ampulla narrows again to the junction of the oviduct, vas deferens, and the duct of the receptaculum seminis. The vas deferens is exceedingly short and expands abruptly into the penis. There is no distinct prostatic portion of the vas deferens, although the penis itself is lined with elongate



prostatic cells (Figure 6B). The penis empties into a separate male gonopore. On one side of the penis is a distinct fleshy papilla that was present in all specimens examined. The receptaculum seminis is lobate and irregular in outline. It inserts into the common junction by means of an elongate stalk. The oviduct is short and enters the granular albumen gland. The membrane gland consists of several distinct folds. The mucous gland comprises the bulk of the genital mass and consists of two distinct lobes that differ slightly in their color and texture. Adjacent to the female gonopore, and joining with it, is the spherical bursa copulatrix.

Egg mass: The egg mass is highly convoluted and is closely appressed to the central axis of the hydroid prey of the adults. There is a single egg per capsule.

Natural history: *Hermosita sangria* has been found exclusively on the gorgonian-like hydroid *Solanderia* sp. in a depth of 3–17 m. It is known only from the Pacific coast of Baja California, from Isla Cedros to Bahía Magdalena.

Systematic Placement of *Hermosita sangria*

Hermosita sangria is clearly placed in the Facelinidae, as the anus is cleioproctic and the uniseriate radula bears cuspidate teeth. By virtue of the fact that *Hermosita* has all cerata groups arranged in simple arches, it is considered as a member of the subfamily Favorininae, following EDMUNDS (1970) and GOSLINER (1980). *Hermosita sangria* is the only favorinid with a distal bursa copulatrix and a proximal, semi-serial receptaculum seminis. *Hermosita* is morphologically similar to members of several aeolidacean genera. Its systematic relationship to these genera requires a discussion of ancestral and derived features within the suborder.

Among the Aeolidacea, possession of a proximal receptaculum seminis and a distal bursa copulatrix represents the probable plesiomorphic (ancestral) state. This configuration is the more common condition in members of the Flabellinidae, which also possess a triseriate radula and a pleuroproctic anus (also plesiomorphic states). In more modified aeolidaceans, which have a uniseriate radula, there is usually a single, sperm storage organ, either a receptaculum or a bursa, but not both. There are a few notable exceptions to this general trend. *Noumeaella africana* (EDMUNDS, 1970), *Antonietta luteorufa* (SCHMEKEL, 1966), *Dicata odhneri* (SCHMEKEL, 1967), *Cuthona divae* (MACFARLAND, 1966, as *C. rosea*), *C. concinna* (WILLIAMS & GOSLINER, 1979), and *Babakina caprinsulensis* (MIL-

Figure 4

Hermosita sangria, spec. nov. A. Buccal mass, scale = 2.0 mm. og = oral gland; sg = salivary gland. B. Jaw. C. Radula, scale = 80 μ m.

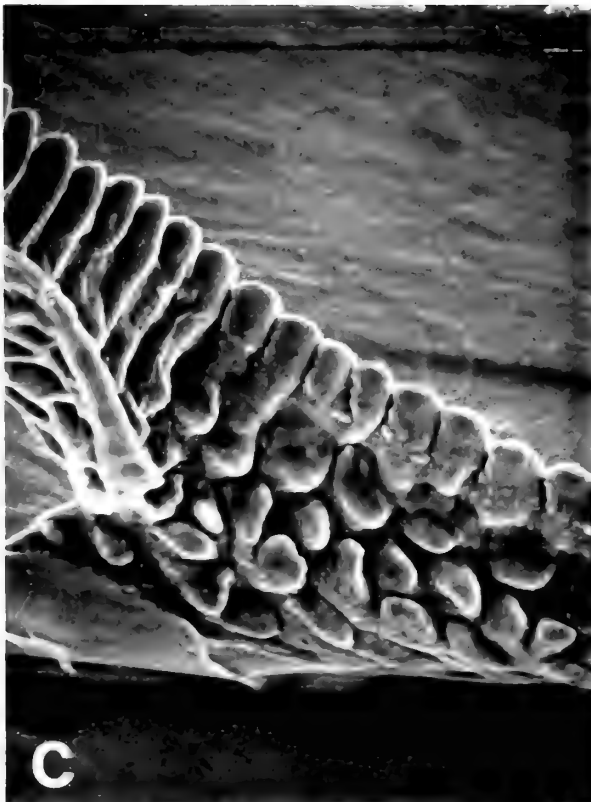


Figure 5

Scanning electron micrographs. A *Hermosita sangria*, spec. nov. Radula, $\times 500$. B-D *Bajaeolis hertschi*, spec. nov. B. Jaw, $\times 80$. C. Masticatory border, $\times 1000$. D. Radula, $\times 500$.

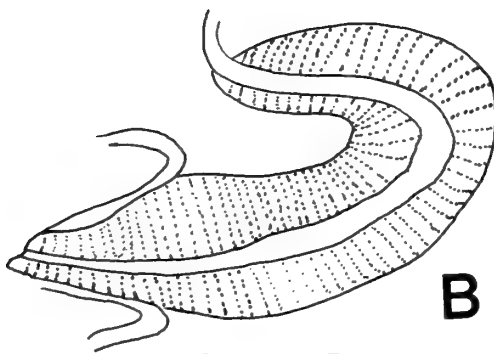
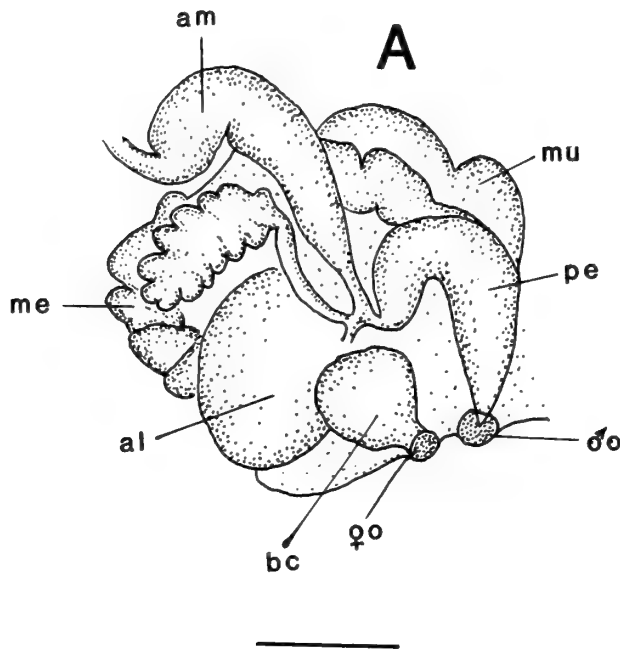


Figure 6

Hermosita sangria, spec. nov. A. Reproductive system, scale = 1.0 mm. al = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; pe = penis; rs = receptaculum seminis; ♀o = female orifice; ♂o = male orifice. B. Penis and vas deferens, scale = 0.5 mm.

LER, 1974) all possess a uniseriate radula, but have a receptaculum and a bursa. Of these, *Babakina* has a pleuroproct anus, a prominent notal brim, cerata arranged in poorly defined rows, and numerous rows of denticles on the masticatory border of the jaw. GOSLINER (1980) has stated that *Babakina* is allied to the Flabellinidae on the basis of the presence of numerous primitive features. The only apomorphy (derived feature) it possesses is a uniseriate radula. This warrants maintenance of its placement as a separate family, but in no way suggests affinities

to the Facelinidae. *Cuthona divae* and *C. concinna* possess an acleioproct anus and a penis with an elongate penial gland, unique derived features within the Eubranichidae and Tergipedidae. The three remaining taxa are members of the Facelinidae and are compared to *Hermosita* in more detail (Table 1). In all three of these taxa the receptaculum seminis is serial, the prostate is elongate, and the radular teeth have triangular denticles. In *Hermosita* the receptaculum is semi-serial, there is no distinct prostate (prostatic cells are contained in the penis [Figure 6B]), and the radular teeth bear thin, elongate denticles (as in *Herviella*). *Hermosita* is also unique in possessing a penis with an eccentric fleshy papilla.

Of sympatric aeolids, *Hermosita sangria* bears a strong external resemblance to *Flabellina iodinea* (Cooper, 1863). The two species have similar coloration, perfoliate rhinophores, and tentacular foot corners. However, in *F. iodinea* the anus is pleuroproct, the ceratal groups are elevated on notal cushions, the radula is triseriate, with numerous triangular denticles on the rachidian teeth, and there are several rows of denticles along the surface of the masticatory border.

Family FACELINIDAE
Subfamily FAVORININAE

Bajaeolis Gosliner & Behrens, gen. nov.

Diagnosis: Body elongate, limaciform. Foot corners tentacular. Rhinophores perfoliate. Cerata arranged on pedunculate arches with two rows per arch. Anus cleioproct. Nephroproct interhepatic. Salivary glands simple, oral glands highly dendritic. Masticatory border of jaw elongate with several rows of denticles. Radula uniseriate with broad, cuspidate rachidian teeth. Central cusp of rachidian small. Adjacent denticles short, triangular. Reproductive system triaulic with proximal receptaculum seminis. Penis simple, unarmed.

Type species: *Bajaeolis bertschi*, spec. nov.

Etymology: *Bajaeolis* is named for the Baja California Peninsula.

Bajaeolis bertschi Gosliner & Behrens, spec. nov.

(Figures 1B, 5B–D, 7–11; Table 2)

Type material: Holotype: California Academy of Sciences, CASIZ 059589, approximately 40 mm in life, collected in 10 m of water, off Punta La Gringa, Bahía de los Angeles, Baja California, Mexico, 6 October 1984, by Terrence M. Gosliner.

Paratypes: (1.) Three specimens, CASIZ 059590, collected in 10 m of water, off Punta La Gringa, Bahía de los Angeles, Baja California, Mexico, 6 October 1984, by Terrence M. Gosliner. (2.) One specimen, CASIZ 059591, S. end of Isla Coronado, Bahía de los Angeles, Baja California, Mexico, 2 October 1984, by Hans Bertsch. (3.)

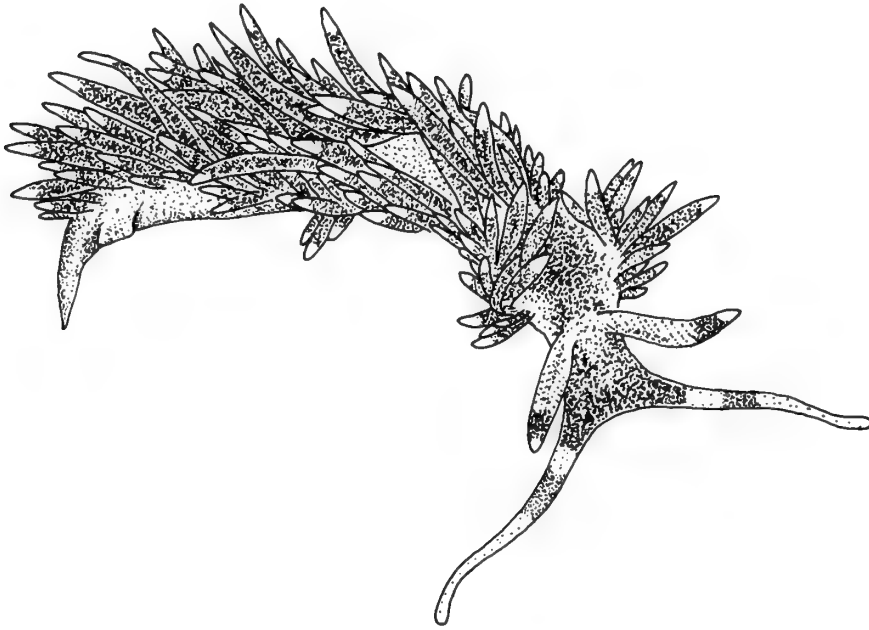


Figure 7

Bajaeolis bertschi, spec. nov. Living animal drawn from color transparency.

Two specimens, CASIZ 059592, Islas Perlas, Bahía de Panama, Panama, June 1982, by Jeff Hamann.

Etymology: *Bajaeolis bertschi* is named after our good friend and colleague, Hans Bertsch, in recognition of his contributions to the knowledge of the opisthobranch fauna of the Gulf of California.

Description

External morphology: The living animals (Figures 1B, 7) reach 40 mm in length. The body is elongate and grace-

ful. The foot is approximately equal in width to the notum and tapers posteriorly to a slightly rounded end. The rhinophores are perfoliate with 18–25 lamellae. The oral tentacles are elongate and taper to an acute apex. The foot corners (Figure 8A) are long and tentacular, $\frac{1}{3}$ – $\frac{1}{2}$ the length of the oral tentacles. The cerata are cylindrical but slightly tapered. They contain diffuse digestive gland tissue and an apical cnidosac. The cerata (Figure 8B) are arranged in 6 undulating arches per side, with a double row of cerata per arch, in all specimens observed. There is a prominent notal brim that is interrupted between the

Table 1

Comparison of *Hermosita* with other aeolid genera.

Genus	Rhinophores	Anterior ceratal cluster	Masticatory border	Vas deferens	Receptaculum seminis	Denticles of radular tooth	Penis
<i>Antoniotta</i>	Smooth	Several rows	Smooth	Elongate, prostatic, and ejaculatory	Serial	Triangular	Simple conical, unarmed
<i>Dicata</i>	Smooth	Arch	Smooth	Elongate, prostatic, and ejaculatory	Serial	Triangular	Simple conical, unarmed
<i>Hermosita</i>	Perfoliate	Arch	Smooth	Short	Semi-serial	Elongate	Simple with fleshy papilla
<i>Noumeaella</i>	Papillate	Arch	Denticulate	Elongate, prostatic, and ejaculatory	Serial	Triangular	Armed with stylet

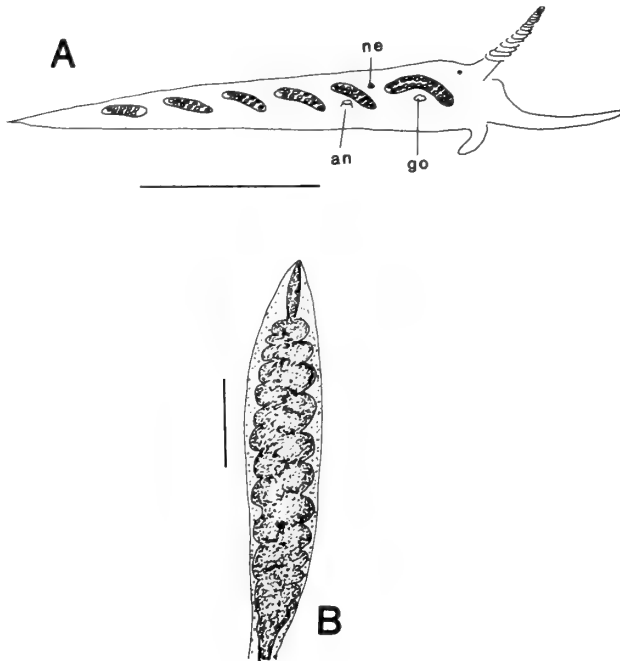


Figure 8

Bajaeolis bertschi, spec. nov. A. Lateral view, scale = 10 mm. an = anus; go = genital orifice; ne = nephroproct. B. Detail of ceras, scale = 1.0 mm.

first and second arch. Within each arch the length of the cerata increases towards its center. In one specimen the cerata formula is: I-17, II-16, III-10, IV-10, V-10, VI-8-10. There may be as many as 29 cerata in the anteriormost arch. The anus is cleioproct, located on the right side of the body, ventral to the center of the second ceratal arch. The nephroproct is located ventral to the center of the interhepatic space. The genital apertures are located within the anterior half of the first ceratal arch.

The ground color is whitish yellow, becoming red mid-dorsally. The head, notum, and cerata are covered by opaque white spots. Just below the apex of each cerata, these spots are more densely concentrated. The central core of the cerata is deep vermillion. The apex of each cerata is translucent and the white cnidosac is visible through it. The oral tentacles are a light purple. There is a darker purple or reddish band near the middle, or occasionally at the base, of the oral tentacles and subapically on the rhinophores.

Digestive system: The buccal mass is muscular (Figure 9A). The oral glands are complex, highly dendritic structures. There is a major bifurcation of each gland near the posterior limit of the buccal mass. The salivary glands are simple and clavate. The jaws (Figures 5B, 9B) are thin and rectangular with an elongate masticatory border that runs most of the length of the jaws. The masticatory border (Figure 5C) bears four or five rows of denticles each

Table 2

Comparison of *Bajaeolis* with other aeolid genera.

Genus	Rhinophores	Cerata	Masticatory border	Radula	Penis	Nephroproct	Oral glands
<i>Favorinus</i>	Smooth, with bulbous swellings or annulate	Single row per arch	Several rows of denticles	With prominent central cusp	Simple, un-armed or with stylet	Interhepatic	Absent
<i>Jason</i>	Papillate	Double row per arch. Cerata on peduncles	Smooth	Vestigial	With internal glands	Interhepatic	Simple
<i>Dondice</i>	Annulate	Double row per arch. Cerata on peduncles	Single row of denticles	With prominent central cusp	With large internal gland	Interhepatic	Absent
<i>Pteraeolidia</i>	Perfoliate	Double row anteriorly; single row posteriorly. Cerata on peduncles	Several rows of denticles	With small central cusp	With rows of conical papillae	In 2nd arch adjacent to anus	Simple
<i>Bajaeolis</i>	Perfoliate	Double row per arch. Cerata on peduncles	Several rows of denticles	With small central cusp	Simple, un-armed	Interhepatic	Dendritic
<i>Facalana</i>	Perfoliate	Double row per arch. Cerata on peduncles	"Glaucus-like" single row of denticles	With small central cusp	Leaf-like with glands along edge	?	?

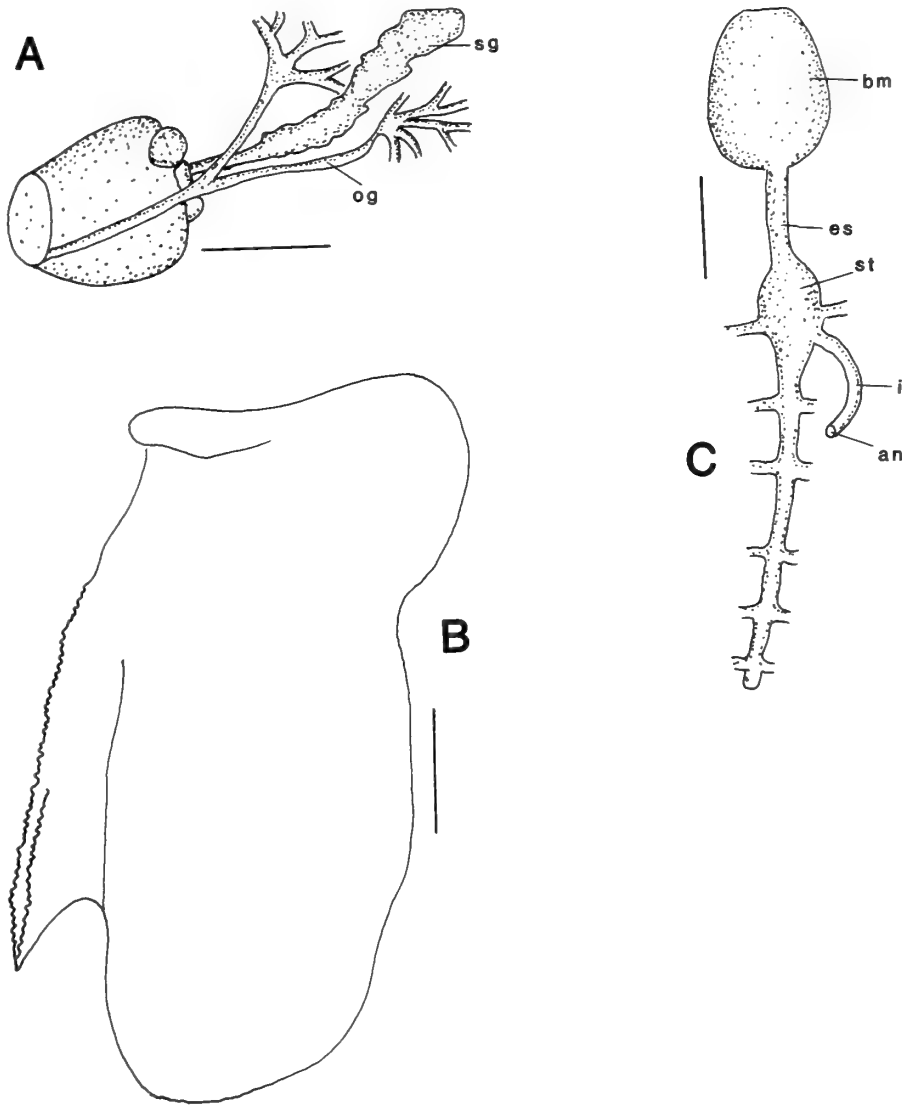


Figure 9

Bajaeolis bertschi, spec. nov. A. Buccal mass, scale = 1.0 mm. og = oral gland; sg = salivary gland. B. Jaw, scale = 0.25 mm. C. Branching of digestive system, scale = 4.0 mm. an = anus; bm = buccal mass; es = esophagus; i = intestine; st = stomach.

with 55–78 teeth. The radular formula is $13-15 \times 0.1.0$. The radular teeth (Figures 5D, 10) have a thick basal portion and possess 12–16 short, triangular denticles on either side of the short central cusp. There is a single digestive branch giving rise to each of the ceratal arches (Figure 9C).

Reproductive system: The reproductive system (Figure 11A) is essentially triauletic, with separate nidamental, vaginal, and penial pores. The ampulla is undulate and elongate. It branches into the vas deferens and the oviduct.

The vas deferens is prostatic with no distinct division between it and the penis. The penial papilla is conical and unarmed, without associated glands. The receptaculum seminis is bilobed in one specimen and undivided in a second specimen. Its elongate duct joins the oviduct, branches to the female gland mass, and continues to form the vagina. The albumen gland is granular and folded. The membrane gland consists of several lobes. The mucous gland comprises the bulk of the genital mass and consists of three distinct lobes.

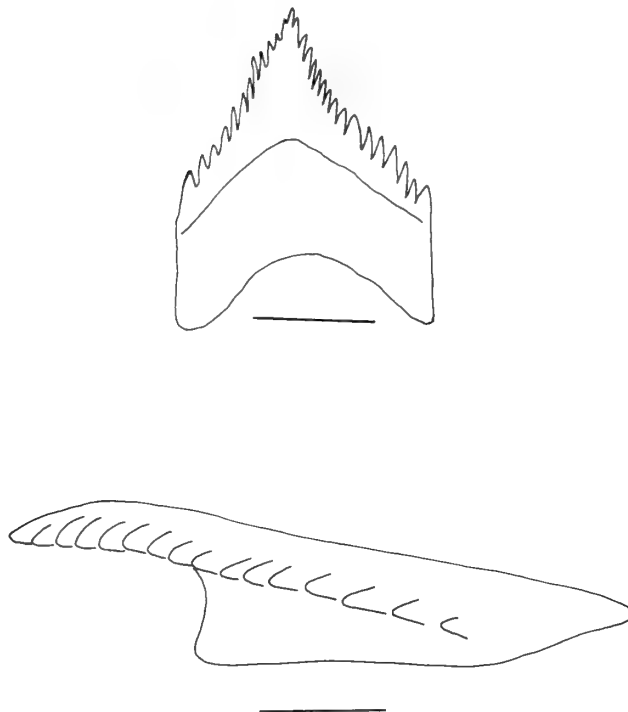


Figure 10

Bajaeolis bertschi, spec. nov. Radula. *Top*. Dorsal view, scale = 60 μ m. *Bottom*. Lateral view, scale = 30 μ m.

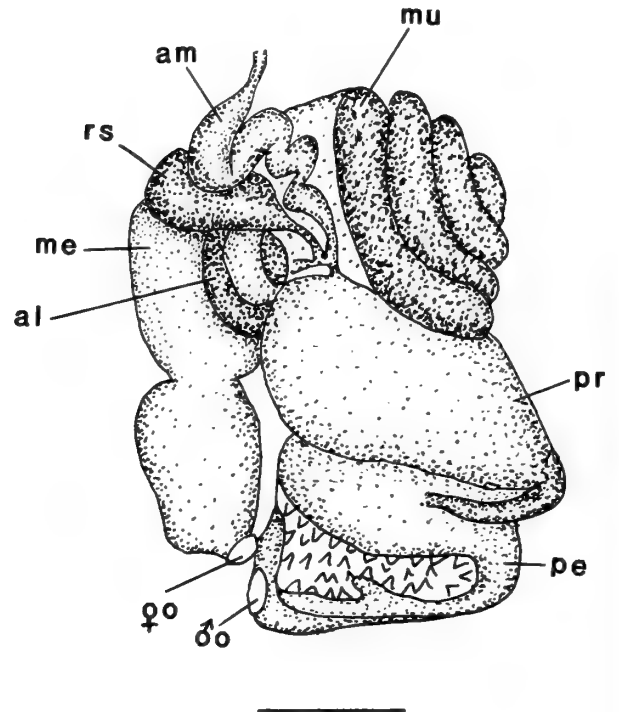


Figure 12

Pteraeolidia ianthina (Angas, 1864). Reproductive system, scale = 2.0 mm. al = albumen gland; am = ampulla; me = membrane gland; mu = mucous gland; pe = penis; pr = prostate; rs = receptaculum seminis; ♀o = female orifice; ♂o = male orifice.

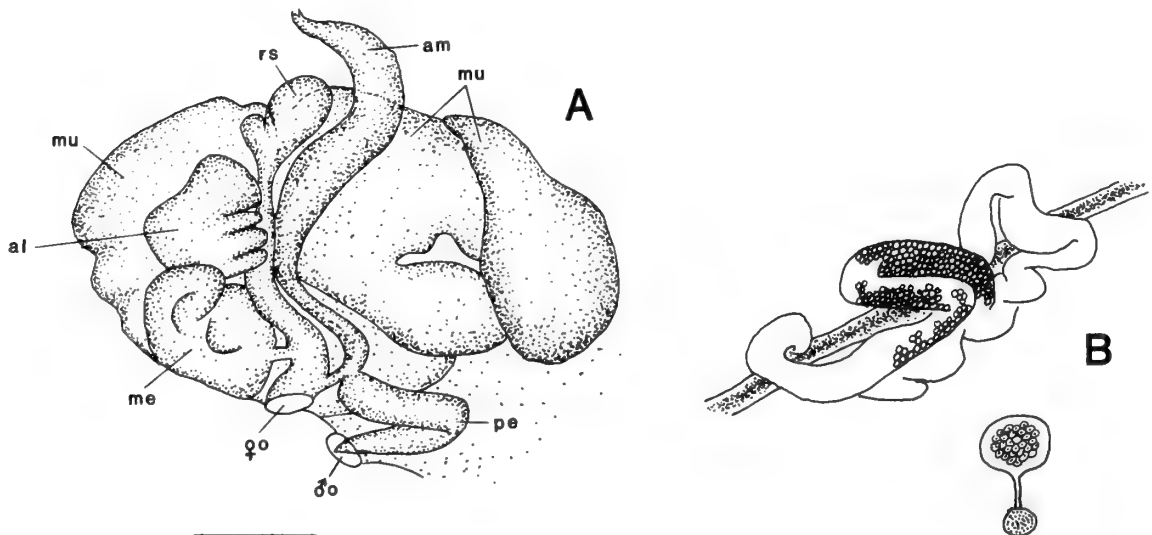


Figure 11

Bajaeolis bertschi, spec. nov. A. Reproductive system, scale = 1.0 mm. al = albumen gland; am = ampulla; me = membrane gland; mu = mucous gland; pe = penis; rs = receptaculum seminis; ♀o = female orifice; ♂o = male orifice. B. Egg mass.

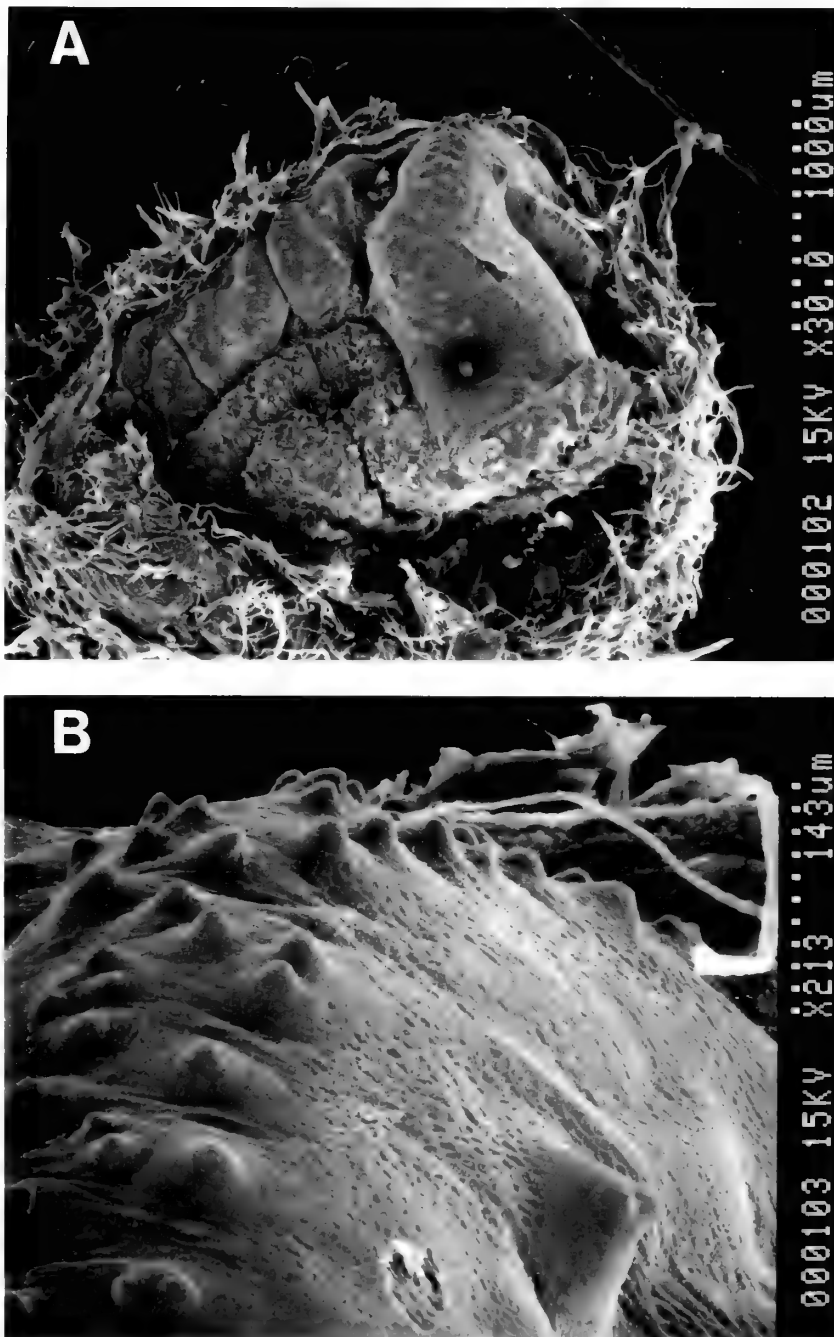


Figure 13

Pteraeolidia ianthina (Angas, 1864). Scanning electron micrographs. A. Penis. B. Detail of penial papillae.

Egg mass: The egg mass is salmon colored and highly convoluted. It is attached to the hydroid substrate along its edge, by means of a thin, transparent membrane. The mass, which is tightly packed with eggs arranged singly per capsule, is about 15 mm in length (Figure 11B).

Natural history: This species has been found exclusively upon athecate hydroids of the genus *Eudendrium*. The material from Bahía de los Angeles was collected on colonies of *E. ramosum* (Linnaeus, 1758). Specimens have been collected in shallow subtidal communities from the

Gulf of California (Bahía de los Angeles) and from the Pacific coast of Panama.

Systematic Placement of *Bajaeolis bertschi*

Bajaeolis bertschi bears similarities to members of several genera of aeolidaceans (Table 2). The uniseriate radula with cuspidate teeth, the cleioproct anus, and the nephroproct situated within the interhepatic space are characteristics of the Facelinidae. All the ceratal clusters are arranged in arches, as in members of the Favorininae. *Bajaeolis* has a double row of cerata forming each ceratal arch. This feature is exhibited by members of several genera of the Favorininae (MILLER, 1974). Of the Favorininae that have been previously described, only *Facalana pallida* Bergh, 1888, the type species of a monotypic genus, has perfoliate rhinophores, as in *Bajaeolis*. However, *F. pallida* has jaws similar in shape to those found in *Glaucus*, and there is only a single row of denticles along the masticatory border, as compared to the several rows present in *Bajaeolis*. In *Facalana* the penis is flattened and bears a row of glands along its perimeter, while in *Bajaeolis* it is simple and conical.

The only other genus within the Favorininae that has multiple rows of denticles along the masticatory border is *Favorinus*. However, *Favorinus* lacks oral glands (present study), while *Bajaeolis* is unique among described Favorininae in having dendritic oral glands. In *Favorinus* the ceratal arches contain only a single row while they are double in *Bajaeolis*.

Like *Bajaeolis*, *Pteraeolidia* possesses perfoliate rhinophores and jaws with several rows of denticles along the masticatory border. The familial placement of *Pteraeolidia* has been in dispute. MILLER (1974) suggested that *Pteraeolidia* should be included in the Glaucidae (Glaucidae + Facelinidae + Pteraeolididae of previous workers) whereas GOSLINER (1980) maintained that the external morphology and ecology of *Pteraeolidia* and *Glaucus* were sufficiently aberrant and that both genera should be placed in distinct families. RUDMAN (1982) stated that *Pteraeolidia* should be included in the Glaucidae because classification should reflect phylogeny, not ecology. Although classification certainly should reflect phylogeny, placement of organisms with derived traits in distinct taxa in no way contradicts a monophyletic classification. The acleioproct aeolid families Eubranchidae and Tergipedidae (=Cuthonidae) are phylogenetically closely allied (probably sister groups), yet tergipedids are considered distinct from eubranchids because they have a derived feature, a uniseriate rather than triseriate radula. The same situation applies to the Facelinidae, Glaucidae, and Pteraeolididae. Furthermore, in *Pteraeolidia* the nephroproct is adjacent to the anus in the second ceratal arch (BABA, 1949; FRANC, 1968; present study) while in all facelinids where it has been described the nephroproct is situated more anteriorly, in the interhepatic space. In addition to the position of the nephroproct, there are several other

significant differences between *Bajaeolis* and *Pteraeolidia*. Although both taxa have several rows of denticles along the masticatory border, the border is short in *Pteraeolidia* (GOSLINER, 1980) and elongate in *Bajaeolis*. *Bajaeolis* has dendritic oral glands that extend into the dorsal portion of the body, well beyond the posterior limit of the buccal mass. In *Pteraeolidia* (present study) the oral glands are simple, ventral, and extend posteriorly only to about the middle of the jaws. *Pteraeolidia* was described (BERGH, 1875) as having a simple unarmed penis. Re-examination of specimens in this study (Figures 12, 13) indicates that the penis is flattened, with numerous conical papillae on its surface. This contrasts markedly with the simple conical penis of *Bajaeolis*.

Bajaeolis differs significantly from all described aeolidaceans. No previously described member of the Favorininae is known to possess dendritic oral glands. The presence of perfoliate rhinophores, a masticatory border of the jaw with several rows of denticles, ceratal arches with two rows of cerata, and a simple conical penis differentiates *Bajaeolis* as a distinct genus.

Externally, this species bears a similarity in its coloration and body form to the sympatric aeolid *Flabellina stohleri* Bertsch & Ferreira, 1974. However, *F. stohleri* has a pleuroproct anus, a triseriate radula, and fewer cerata per cluster. Additionally the white surface of *F. stohleri* is in the form of closely set spots rather than specks, and purple bands are absent from the rhinophores and oral tentacles.

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Six New Species of *Trivia* from Southern Africa (Gastropoda: Triviidae)

by

WILLIAM R. LILTVED

Department of Marine Biology, South African Museum, P.O. Box 61, Cape Town 8000, South Africa

Abstract. Six new species of *Trivia* are described from the seas of southern Africa. The shells and radula are described for *T. magnidentata*, spec. nov. and *T. khanya*, spec. nov. Descriptions of only the conchological features of *T. multicostata*, spec. nov., *T. eratoides*, spec. nov., *T. virginiae*, spec. nov., and *T. lemaitrei*, spec. nov. are provided. Problems associated with the subdivision of the Triviidae are discussed.

INTRODUCTION

THE SOUTHERN and eastern Cape Province coasts of South Africa, from the shallow sub-littoral zone to depths of hundreds of meters, have yielded numerous new molluscan records and species. In an attempt to revise the much confused southern African lamellariacean fauna, I have collected material pertaining to a number of previously unknown species of *Trivia*. Although CATE (1979) presented a systematic revision of the Triviidae based on conchological features, GOSLINER & LILTVED (1982) have discussed problems with this system, in light of internal morphological criteria. However, due to the fact that much of the material examined here had been taken from the stomachs of benthic fishes, the soft parts were no longer present. No choice is left but to describe these new taxa from their shell morphology only, and in two cases the radular morphology is also provided. The subgeneric status of the six new species may only be determined once sufficient preserved material of each species is accumulated and a thorough comparative anatomical examination of the entire family is conducted (GOSLINER & LILTVED, 1982).

Trivia magnidentata Liltved, spec. nov.

(Figures 1-4)

External morphology: One individual (Figure 2) collected in 50 m off Danger Point, western Cape Province, was primarily translucent white in color. Extraordinarily fleshy mantle evenly covered with 1-mm long red dashes. Dorsal rim of mantle surrounded by larger red blotches. Siphon evenly cylindrical, recurved, and translucent white. Tentacles cylindrical and blunt at tips. Foot translucent

white, reaching approximately 40 mm when fully extended. External characters of paratype A (Figure 3) from Walker Bay (slightly to the west of Danger Point) were similar in all respects to the aforementioned individual, apart from lacking red pigmentation on its mantle's outer surface. The mantle of the Walker Bay animal was sparsely pigmented with 2.5-mm wide oval or circular black spots.

Radula (Figure 4): Radula formula, $45 \times 2.1.1.1.2$ in one individual. Rachidian broad, teeth with 9-10 sharp inwardly curved denticles on either side of the sharply pointed, evenly tapered central cusp. Inner lateral teeth with 7-8 small, outwardly curved denticles on outer face. Outer laterals arched, without denticles. Basally, innermost laterals approximately twice as wide as the outermost tooth.

Shell: Large, pyriform, somewhat inflated, tapering anteriorly. Labrum fairly narrow but solidly formed, occasionally reaching up to 2.5 mm beyond lateral plane of body whorl. Labral width normally even throughout its length, occasionally slightly more swollen medially. Labrum bisected by extremely coarse, well-defined bladlike ribs. Ribs continuing farther than just onto the body whorl, and terminating in 10-15 coarse denticles with semi-circular interstices. Anterior and posteriormost labral ribs, also strongly developed as those crossing medial labral width, not terminating as denticles, leaving these areas smooth and devoid of denticles. Eleven to nineteen medially swollen elongate teeth extend in for short distance across base, over columellar peristome, occasionally continuing across columella. Anterior and posteriormost columellar denticles merging with strong ribs that cross base

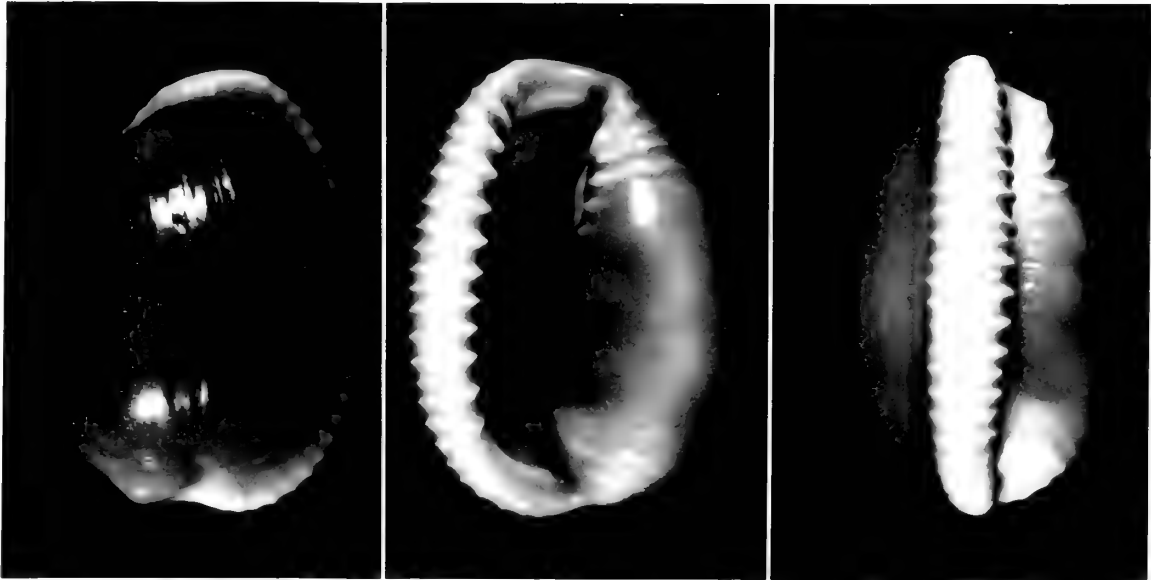


Figure 1

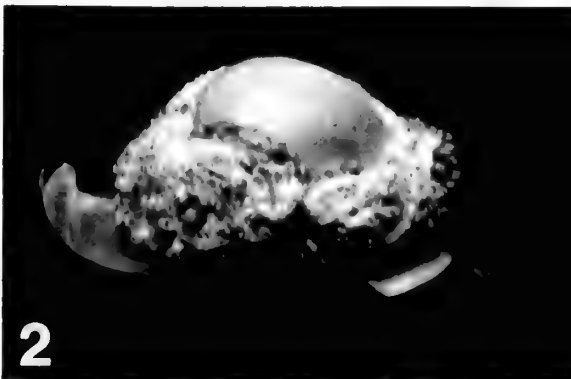
Trivia magnidentata, spec. nov. Holotype shell, 22.1 mm long. Dorsal, ventral, and lateral views.

obliquely. Occasional examples have bases that are entirely transversely crossed by ribs extending short distance up columellar margin. Fossula elongate and curved. Riblets may cross fossular area, extending downward from terminal ridge, merging with 0-5 rounded denticles. Aperture wide, widest anteriorly. Base often heavily calcified, in some cases attaining almost twice thickness of dorsum. Dorsum vaulted, occasionally with maleated texture. Shallow dorsal sulcus or darkly pigmented area may be present mid-dorsally. Spire often fairly elevated, not crossed by fine riblets extending upward from posterior end of base. Shells from the eastern Cape Province tend to be rose-colored dorsally, with heavily calcified white bases.

Shells from the western Cape are normally paler pink or white, and tend to be more lightly calcified.

Measurements:

	<u>length (mm)</u>	<u>width (mm)</u>	<u>height (mm)</u>
holotype	22.1	17.8	13.1
paratype A	20.7	16.6	13.2
paratype B	18.2	14.7	11.6
paratype C	20.9	17.2	13.9
paratype D	22.5	18.0	14.4
paratype E	17.9	15.7	17.7
paratype F	13.8	10.6	8.3
paratype G	17.9	13.5	15.6



Explanation of Figures 2 and 3

Figure 2. *Trivia magnidentata*, spec. nov. Living animal. Figure 3. *Trivia magnidentata*, spec. nov. Paratype A. Living animal.

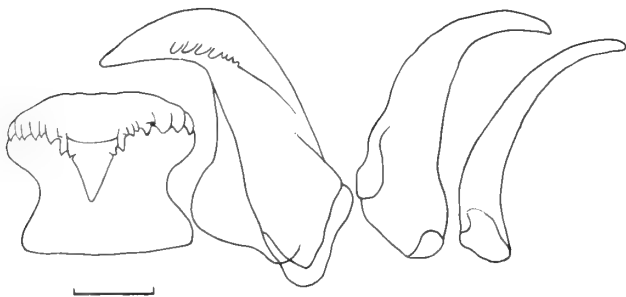


Figure 4

Trivia magnidentata, spec. nov. Half a row of radular teeth. Scale bar = 100 μ m.

Type locality: Jeffreys Bay beach (34°00'S, 25°00'E), eastern Cape Province, South Africa.

Type depositary: The holotype (SAM A36796) and seven paratypes (SAM A36797, A36798, A36799, A36800, A36801, A36802, A36803) have been deposited in the South African Museum in Cape Town.

Habitat and distribution: *Trivia magnidentata* has been observed at depths between 30 and 55 m, living in association with various species of compound tunicates. The new species has been recorded at various localities between Olifantsbos in the western Cape Province and East London in the eastern Cape Province.

Etymology: From the Latin adjective *magnus*, meaning "great," and *dentatus*, meaning "toothed," in reference to the unusual labral dentition of the shell.

Discussion: *Trivia magnidentata*, spec. nov. conchologically most closely resembles *T. rubra* (Shaw, 1909). Both species attain approximately the same size and coloration. The labral and columellar dentition of *T. magnidentata* is always far coarser than is seen in *T. rubra*. The transverse labral ribs of *T. rubra*, which are not always present, are weakly defined and seldom cross onto the body whorl. *Trivia magnidentata* has sharp bladelikey ribs that cross obliquely over the anterior and posteriormost portions of the base and extend onto the columellar margin. In extreme cases the entire base is endowed with transverse ribbing. Such anterior-posterior ribbing may be present in *T. rubra*, but is always weakly formed, somewhat indistinct, and does not extend over the columellar margin. The shell of *T. magnidentata* tends to taper more sharply anteriorly, rendering the anterior terminal longer and more rostrate than the ovate shell of *T. rubra*. The radular morphology of *T. magnidentata* differs considerably from that of *T. rubra*. The most major difference lies in the structure of the rachidian tooth. The rachidian of *T. magnidentata* is far smaller and more dorsoventrally compressed than that of *T. rubra*. It also lacks the elongate, uneven basal

portion present in the rachidian of *T. rubra*. The denticles on either side of the central cusp in *T. magnidentata* are sharper than in *T. rubra*.

When disturbed the animal was hardly able to retract into its shell. Like various other endemic southern African *Trivia*, the new species must expel water from the mantle before retracting. The water contained in the mantle may create hydrostatic pressure to give the animal additional rigidity.

Trivia khanya Liltved, spec. nov.

(Figures 5, 6)

External morphology: One freshly dead specimen trawled off Mossel Bay, eastern Cape Province, South Africa had a fleshy rust-colored mantle. Siphon white with orange tip, foot white and fleshy.

Buccal mass: Jaws consist of numerous polygonal platelets. Radula (Figure 6) formula, $39 \times 2.1.1.1.2$ in one individual. Rachidian teeth possess 5–6 rounded denticles on either side of long, fairly wide central cusp. Two innermost denticles immediately adjacent to central cusp are situated one above the other. Inner lateral teeth have 4 or 5 prominent denticles on their outer face. Outer lateral teeth are thin and arched, without denticles.

Shell: Medium sized for *Trivia*, globular to pyriform. Anterior terminal may be slightly to greatly produced, projecting only slightly. Labrum wide, normally swollen medially. Labrum bisected by even, widely spaced ribs crossing transversely from 12–14 pronounced denticles, extending just onto body whorl. Thirteen to fifteen elongate denticles are situated on calcified ridge along columella slightly convolute. Concavely produced fossula has teriormost columellar teeth extend as riblets obliquely across base. Posteriormost columellar teeth occasionally less well developed than those anteriorly situated. Columella slightly convolute. Concavely produced fossula has 5 or 6 small denticles, often formed at base of short riblets, crossing fossular area from anteriormost columellar denticles. Spire always fully visible, protruding slightly. Dorsum smooth and highly nacreous, light to dark pink, occasionally with fulvous, 2–3-mm ovoid markings situated mid-dorsally. Base fairly thickly calloused and white in color.

Measurements:

	length (mm)	width (mm)	height (mm)
holotype	15.3	14.1	11.6
paratype A	13.8	11.5	9.2
paratype B	14.1	12.4	10.1

Type locality: Off Cape Recife (34°00'S, 25°30'E), eastern Cape Province, South Africa, at 130 m.

Type depositary: The holotype (SAM A36804) and two

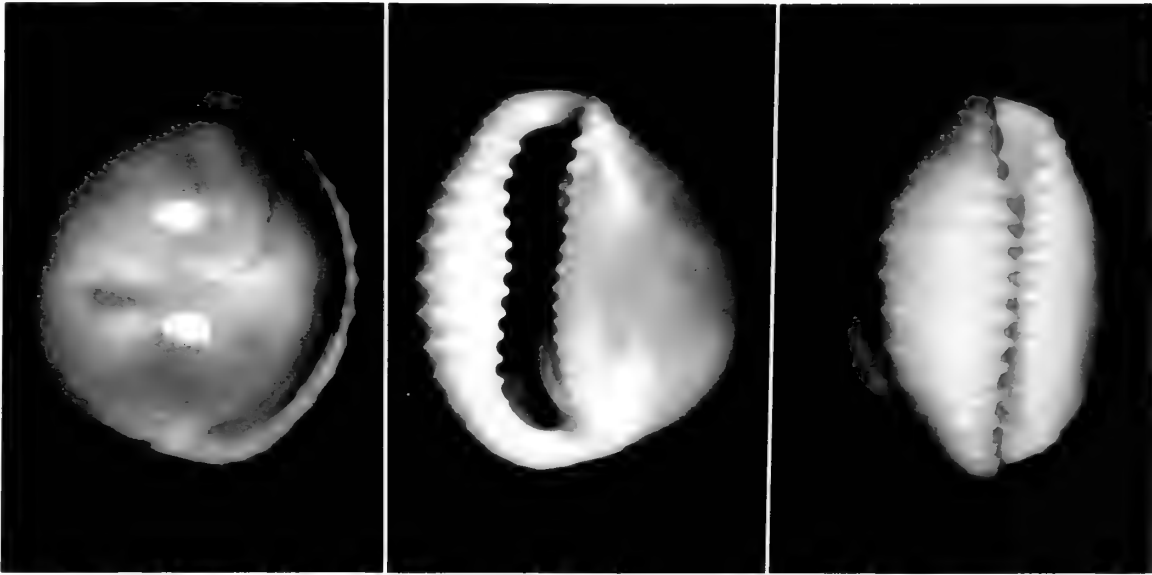


Figure 5

Trivia khanya, spec. nov. Holotype shell, 15.3 mm long. Dorsal, ventral, and lateral views.

paratypes (SAM A36805, A36806) have been deposited in the South African Museum. The type material was collected by commercial fishermen on trawlers working off the eastern Cape Province.

Habitat and distribution: The type specimens were collected from trawls over low-profile reefs off Cape Recife and Cape St. Blaize. All specimens examined were taken from ± 119 m.

Etymology: From the Zulu adjective *khanya*, meaning "to be glossy" or "bright," in reference to the highly lustrous surface of the shell.

Discussion: Globular specimens of *Trivia khanya*, spec. nov. most closely resemble *T. calvariola* Kilburn, 1980. *Trivia khanya* averages half the size of *T. calvariola* and is most often pyriform in shape when compared with the essentially spherical shell of *T. calvariola*. Shells of *T. khanya* may be various shades of pink, whereas *T. calvariola* is invariably white in color. The labrum of *T. calvariola* also is markedly more tumid than that of *T. khanya*.

The radular characteristics of *Trivia khanya* and *T. calvariola* differ markedly. Apart from appearing to have fewer rows and smaller radular teeth than *T. calvariola*, the rachidian tooth of *T. khanya* has 5 or 6 rounded denticles on either side of the central cusp, whereas *T. calvariola* has 8–11 acute denticles similarly situated. The base of the rachidian in *T. khanya* is slightly narrower than the upper half of the tooth; the base of the rachidian of *T. calvariola* far exceeds the width of the tooth's upper half. The inner lateral teeth of *T. khanya* are wider than

those of *T. calvariola* and have 4 or 5 rounded denticles as opposed to 5–8 acute, triangular denticles on the outer face. The outer lateral teeth of *T. khanya* are comparatively much wider and more arched when compared with the long slender outer laterals of *T. calvariola*.

Trivia lemaitrei Liltved, spec. nov.

(Figure 7)

Shell: Medium sized for *Trivia*, globular with vaulted dorsum. Anterior and posterior terminals very slightly produced. Labrum narrow, almost flush with body whorl, which is bisected by relatively widely spaced transverse ribs arising from 9–16 feeble denticles, in some cases only mere crenulations on labrum's inner edge. Columellar

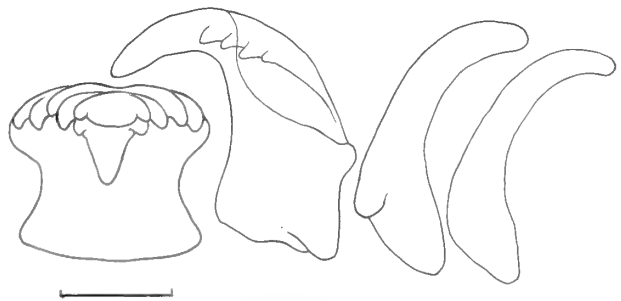


Figure 6

Trivia khanya, spec. nov. Half a row of radular teeth. Scale bar = 100 μ m.

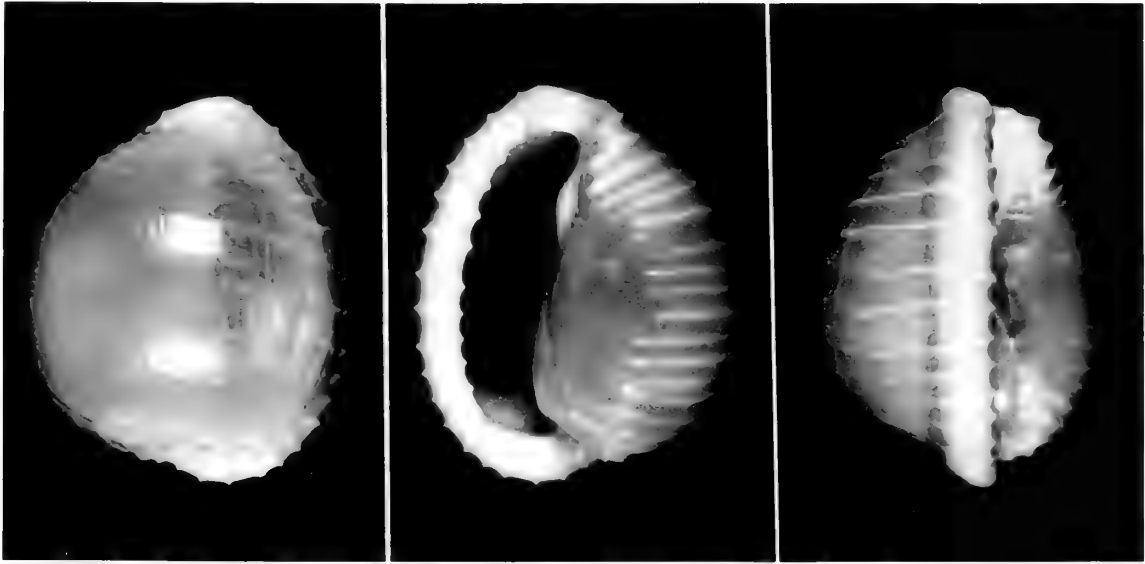


Figure 7

Trivia lemaitrei, spec. nov. Holotype shell, 12.2 mm long, dorsal, ventral, and lateral views.

peristome is edentate in all specimens. Columella deeply convolute and fossula concave, occasionally crenulate. Aperture extremely wide, widest medially. Margins unevenly transversely ribbed, occasionally extending to halfway up body whorl on either side. Ribs continue onto somewhat flattened base, where most often they dissipate medially: anterior and posteriormost ribs continue and occasionally cross peristome onto the columella. Anteriormost basal ribs elevated and bladelike. Dorsum smooth and invariably extremely thin, varying from translucent to transparent. Spire often pointedly produced, occasionally partially obscured by fine ribs. Shell varies from white to pink, occasionally with a darker pink band running along body whorl immediately adjacent to labrum.

Measurements:

	<u>length (mm)</u>	<u>width (mm)</u>	<u>height (mm)</u>
holotype	12.2	10.6	8.4
paratype A	14.1	12.9	10.7
paratype B	11.0	9.3	7.8

Type locality: Off Cape St. Blaize (34°00'S, 22°00'E), eastern Cape Province, South Africa.

Type depository: The holotype (SAM A36807) and two paratypes (SAM A36808, A36809) have been deposited in the South African Museum. The specimens were collected by fishermen on commercial trawlers on an undetermined date.

Habitat and distribution: The type specimens were taken from the stomachs of fish, *Congiopodus torvus* (Wal-

baum) and *C. spinnifer* (Smith), trawled at ± 100 m, off Cape St. Blaize, eastern Cape Province. Specimens have also been washed onto the beach at Jeffrey's Bay, eastern Cape Province, South Africa.

Etymology: The new species is named in honor of Richard Lemaitre of Somerset West, Cape Province, South Africa, who provided the holotype in addition to other type material used in this study.

Discussion: *Trivia lemaitrei*, spec. nov. conchologically most closely resembles *T. vesicularis* (Gaskoin, 1836). The transverse ribs of *T. lemaitrei* are markedly more distantly spaced than those of *T. vesicularis*. The central basal ribs of *T. lemaitrei* tend to dissipate approximately halfway across the base, whereas in *T. vesicularis* these ribs cross the base running over the columellar peristome into the aperture. The aperture of *T. lemaitrei* tends to be wider than that of *T. vesicularis* and the labrum is normally more arched. The columella of *T. lemaitrei* is also markedly more convolute than that of *T. vesicularis*. At maturity the shell of *T. vesicularis* has continuous transverse ribs crossing the dorsum, whereas in 10 specimens of *T. lemaitrei* examined, these ribs reached only approximately halfway up the body whorl on either side.

Trivia multicostata Liltved, spec. nov.

(Figure 8)

Shell: Medium sized for *Trivia*, subglobular, thin, and elongate. Anterior terminal produced, whereas posteriorly less produced. Labrum narrow and exteriorly forming

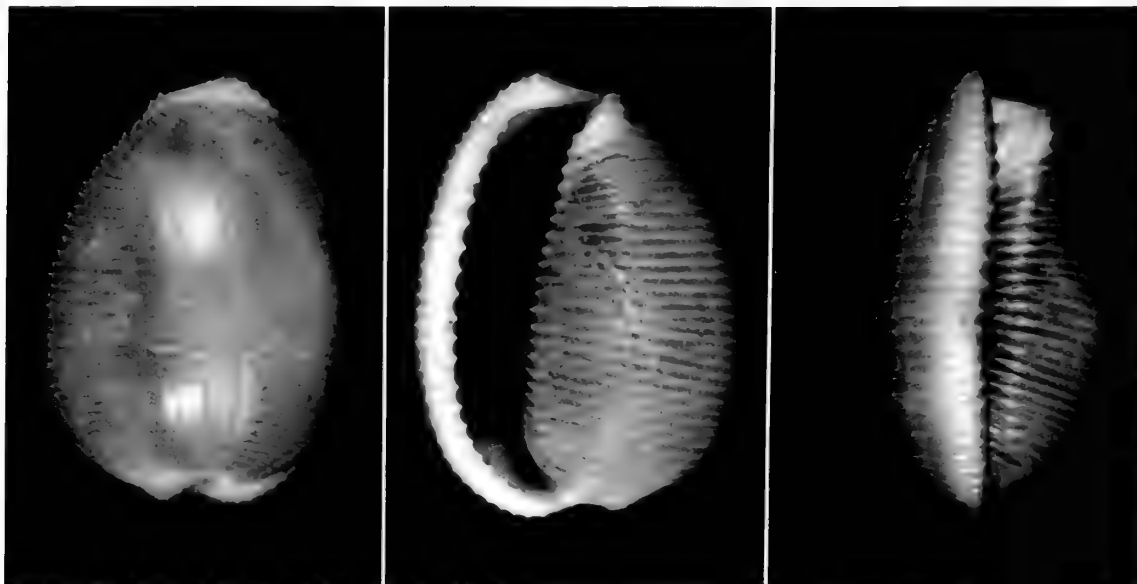


Figure 8

Trivia multicoskata, spec. nov. Holotype shell, 16.3 mm long. Dorsal, ventral, and lateral views.

continuous plane with body whorl. Fifteen to twenty-two labral denticles pointed, extremely fine, with rounded interstices. Fine, evenly spaced ribs cross labrum and extend continuously around body whorl onto columella. Dorsal sulcus or rib alternation absent mid-dorsally. Twenty to twenty-seven evenly spaced denticles present along columellar peristome, elongate calcified portions of transverse ribs extending into aperture. Columella slightly bowed, and fossular area slightly concave but minimally developed. Zero to seven fine denticles may be present in this area. Aperture dilated due to narrowness of labrum, bowed and of even width throughout its length. Spire somewhat produced and rounded, being crossed vertically by fine ribs, not obscuring it at all. Body whorl of mature shell so thin as to render it translucent and occasionally transparent. Color varies from white to pale pink.

Measurements:

	length (mm)	width (mm)	height (mm)
holotype	16.3	12.6	10.4
paratype A	12.6	10.1	8.2
paratype B	12.5	10.1	8.0

Type locality: Off Cape St. Blaize (34°00'S, 22°00'E), eastern Cape Province, South Africa.

Type depository: The holotype (SAM A36810) and two paratypes (SAM A36811, A36812) have been deposited in the South African Museum. The specimens were collected by fishermen on commercial trawlers on an undetermined date.

Habitat and distribution: The type specimens were taken from the stomachs of the fish *Congiopodus torvus* (Walbaum) and *C. spinnifer* (Smith), trawled at ± 100 m, off Cape St. Blaize, eastern Cape Province, South Africa.

Etymology: From the Latin adjective *multi*, meaning "many," and *costa*, meaning "ribbed," in reference to the numerous fine transverse ribs present on the shell.

Discussion: *Trivia multicoskata*, spec. nov. appears to be closely related to *Trivia costata* (Gmelin, 1791). Individuals of both species tend to attain a similar size and shape. *Trivia multicoskata* has a thinner, more inflated shell, which is covered with extremely fine, evenly spaced transverse ribbing. *Trivia costata* is considerably more heavily calcified and has a less vaulted dorsum with fewer ribs. The aperture of *T. multicoskata* may be nearly twice as wide as that of *T. costata*. This is essentially due to the labrum's narrowness in *T. multicoskata*. The labral denticles of *T. multicoskata* are much finer and more numerous (15–22 in *T. multicoskata*, 9–18 in *T. costata*) when compared with the strong, coarse denticles on the heavily calcified, somewhat flared labrum of *T. costata*. This also applies to the columellar denticles of *T. multicoskata*, which are weakly formed in comparison with the coarser denticles situated along a distinct calcified ridge of the columellar peristome in *T. costata*. The spire of *T. multicoskata* is more rounded and less produced than that of *T. costata*. The base of *T. multicoskata* is rounded, whereas in *T. costata* it is somewhat flattened. *Trivia costata* is normally much darker in color compared with the faint pink hue of *T. multicoskata*.

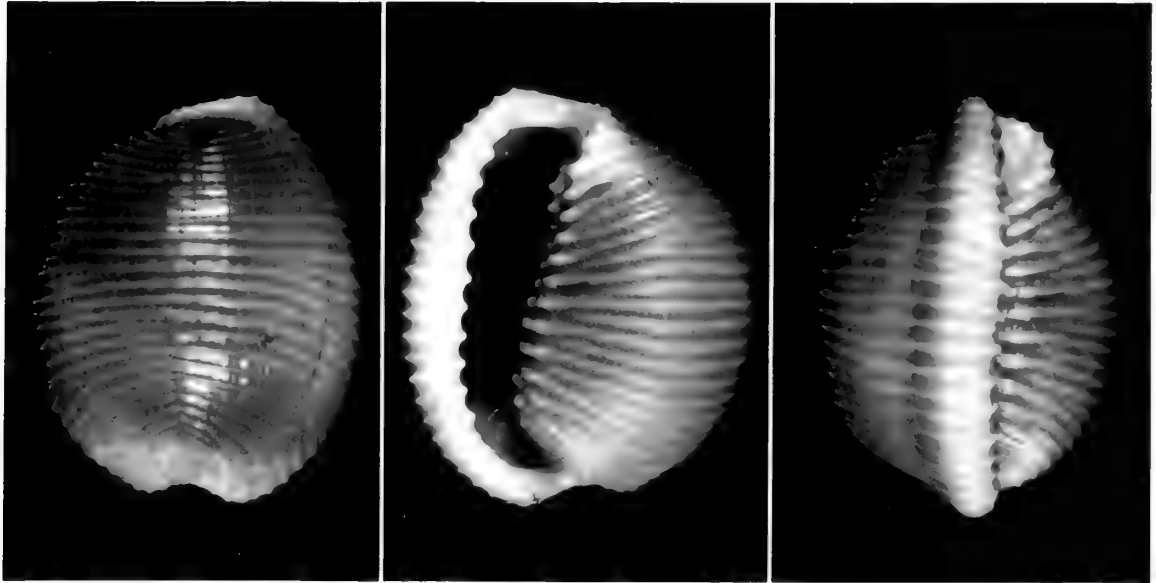


Figure 9

Trivia virginiae, spec. nov. Holotype shell, 9.8 mm long. Dorsal, ventral, and lateral views.

Trivia virginiae Liltved, spec. nov.

(Figure 9)

Shell: Medium sized for *Trivia*, spherical, thin, with terminals being only slightly produced. Labrum narrow and protrudes slightly exteriorly. Ten to fourteen fine denticles situated along inner edge of labrum, evenly spaced, pointed with wide, semicircular interstices. Fine, closely spaced ribs cross labrum and extend continuously around body whorl, over columellar peristome into aperture. Columellar denticles arise as thickened, elongate portions of transverse ribs crossing columellar peristome. Unusual secondary row of denticles occurs within aperture, forming continuous row merging with fossular denticles. Fossular area slightly convex, fossula somewhat humped. Aperture fairly wide, bowed, and dilated anteriorly. Spire produced, rounded and crossed vertically by fine ribs extending upward from small funicular callosity situated at anterior end of base adjacent to aperture. Body whorl light pink, labrum white.

Measurements:

	length (mm)	width (mm)	height (mm)
holotype	9.8	8.4	7.2
paratype A	9.2	7.8	5.9
paratype B	9.8	6.8	5.4

Type locality: Off Cape St. Blaize (34°00'S, 22°00'E), eastern Cape Province, South Africa.

Type depository: The holotype (SAM A36813) and two

paratypes (SAM A36814) have been deposited in the South African Museum. The specimens were collected by fishermen on commercial trawlers on an undetermined date.

Habitat and distribution: The type specimens were taken from the stomachs of fish, *Congiopodus torvus* (Walbaum) and *C. spinnifer* (Smith), trawled at ± 100 m, off Cape St. Blaize, eastern Cape Province, South Africa. Known only from the type locality.

Etymology: The new species is named in honor of my mother, Virginia Oosthuizen-Liltved, who first introduced me to the splendors of the natural world.

Discussion: *Trivia virginiae*, spec. nov. is most closely allied to *T. eratooides*, spec. nov. Distinguishing features are noted under discussion of the latter species.

Trivia eratooides Liltved, spec. nov.

(Figure 10)

Shell: Medium sized for *Trivia*, slender pyriform in shape. Anterior terminal greatly produced, curving slightly to left. Posteriorly, spire extends beyond posteriormost edge of labrum. Thirteen to fourteen fine-pointed denticles with semicircular interstices extend transversely as ribs, over body whorl and into aperture. Of 6 specimens examined, 3 exhibited darkly pigmented streak, giving impression of dorsal sulcus. These pigmented streaks are overlain by unbroken transverse ribs. Columellar denticles arise as elongate swollen areas on transverse ribs along columellar peristome. Normally these denticles are very sparse and

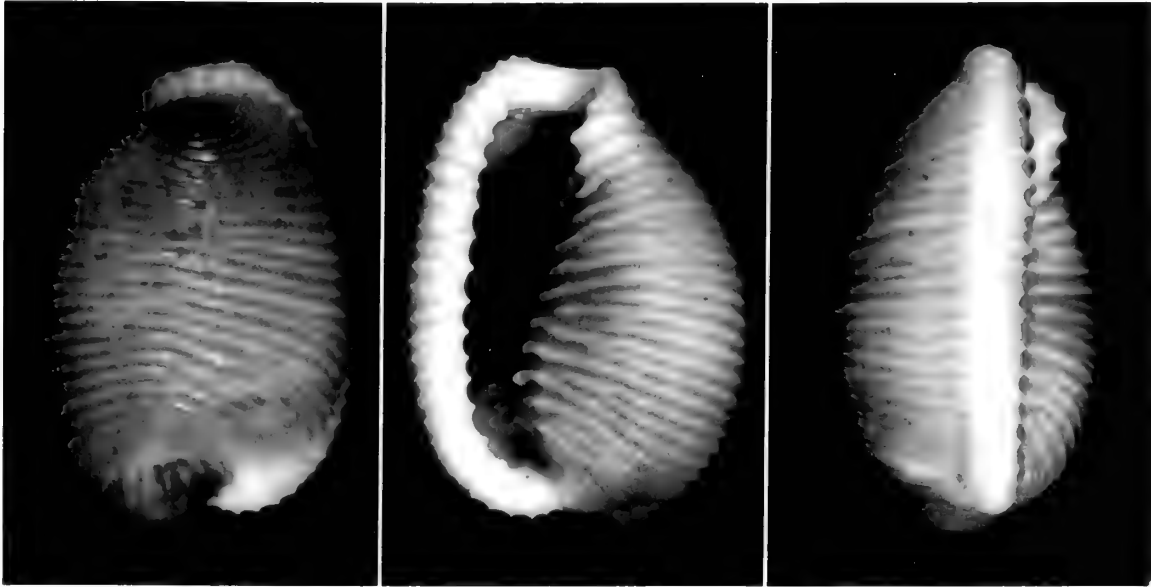


Figure 10

Trivia eratooides, spec. nov. Holotype shell, 9.7 mm long. Dorsal, ventral, and lateral views.

uneven, concentrated mainly at posterior end of aperture. Anterior terminal ridge strongly developed, somewhat "claw-like," transversely cut with bladelike ribs. Prominent, calcified ridge within aperture gives rise to pronounced secondary row of denticles forming continuous line with fossular denticles. Denticulate fossular area deeply concave, overlapped by overhanging terminal ridge. Aperture wide, anteriorly greatly dilated. Spire unusually large for species of this size. Spire apically rounded, crossed vertically by riblets extending upward from funicular area. Dorsally shell is pink to white, most often heavily calcified basally and white in color.

Measurements:

	length (mm)	width (mm)	height (mm)
holotype	9.7	7.1	5.5
paratype	9.7	6.9	5.4

Type locality: Off Cape St. Blaize (34°00'S, 22°00'E), eastern Cape Province, South Africa.

Type depository: The holotype (SAM A36815) and paratype (SAM A36816) have been deposited in the South African Museum. The specimens were collected by fishermen on commercial trawlers on an undetermined date.

Habitat and distribution: The type specimens were taken from the stomachs of fish, *Congiopodus torvus* (Walbaum) and *C. spinnifer* (Smith), trawled at ± 100 m, off Cape St. Blaize, eastern Cape Province, South Africa. Known only from the type locality.

Etymology: From *Erato*, the generic name of an allied group of Triviidae, and the suffix *-oid* from new Latin, meaning "a likeness to," reference to the superficially similar shape of the new species to the shape of shells belonging to the genus *Erato*.

Discussion: Of all endemic southern African species, *Trivia virginiae*, spec. nov. and *T. eratooides*, spec. nov. seem to be conchologically most closely allied. Initially, *T. virginiae* is separable from *T. eratooides* by the possession of a spherical shell as opposed to being slenderly pyriform in shape. The latter in addition is more heavily calcified. Characteristics of the columellar dentition in both species are particularly noteworthy. Both species similarly have two separate rows of columellar denticles, one row situated along the columellar peristome and another within the aperture, lying horizontally on the same plane as the fossula. The exterior row in *T. virginiae* is most prominently defined, whereas the inner row is less well developed. The opposite is true of *T. eratooides*, in which the exterior row lacks definition and the interior row is made up of long rugose denticles. The terminal ridge is well defined in both species, but is markedly more prominent in *T. eratooides*. The spire of *T. eratooides* is far more elevated and prominent than in *T. virginiae*. *Trivia virginiae* is generally pinkish, whereas *T. eratooides* is usually white.

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Anatomy, Distribution, Synonymy, and Systematic Relationships of *Atagema alba* (O'Donoghue, 1927) (Nudibranchia: Doridacea)

by

HANS BERTSCH¹

Biological Sciences, National University, San Diego, California 92106, U.S.A.

AND

TERRENCE M. GOSLINER

Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. We illustrate the radula (with scanning electron microscopy) and the reproductive system of *Atagema alba*. We report the occurrence of this species from northwestern Baja California, Mexico (in addition to its known distribution in southern and central California, U.S.A.), confirm the identity of *A. alba*, and contrast *A. alba* with its known congeners. We discuss the problematic nature of using the degree of elaboration of the prostatic region to distinguish the Doridinae, Archidoridinae, and Discodoridinae.

INTRODUCTION

THE OPISTHOBRANCH SPECIES of the Pacific coast of California are fairly well known, but there still remain some taxonomic problems that require resolution (BEHRENS, 1980; McDONALD & NYBAKKEN, 1981). During the past 20 years, various authors have proposed solutions to some of these (*e.g.*, STEINBERG, 1961, 1963; ROLLER, 1970; BEHRENS, 1984).

In contrast, one species has been given two synonyms in the past 20 years. Although the posthumous publication of MACFARLAND'S (1966) major monograph on western North American opisthobranchs resolved many problems, it also created duplication of scientific names. The editors of that monograph decided to publish MacFarland's names—even though they might be proliferating new synonyms—and leave it to future workers to resolve the nomenclatural problems. *Petelodoris spongicola* MacFarland, 1966, was thus introduced into the literature even though

it is an obvious synonym of *Atagema quadrimaculata* Collier, 1963 (ROLLER, 1970). The identity of *Glossodoridiformia alba* O'Donoghue, 1927, had remained in doubt, and the species overlooked by most recent workers, until McDONALD (1983:150-151) proposed that this species was synonymous with *Atagema quadrimaculata*.

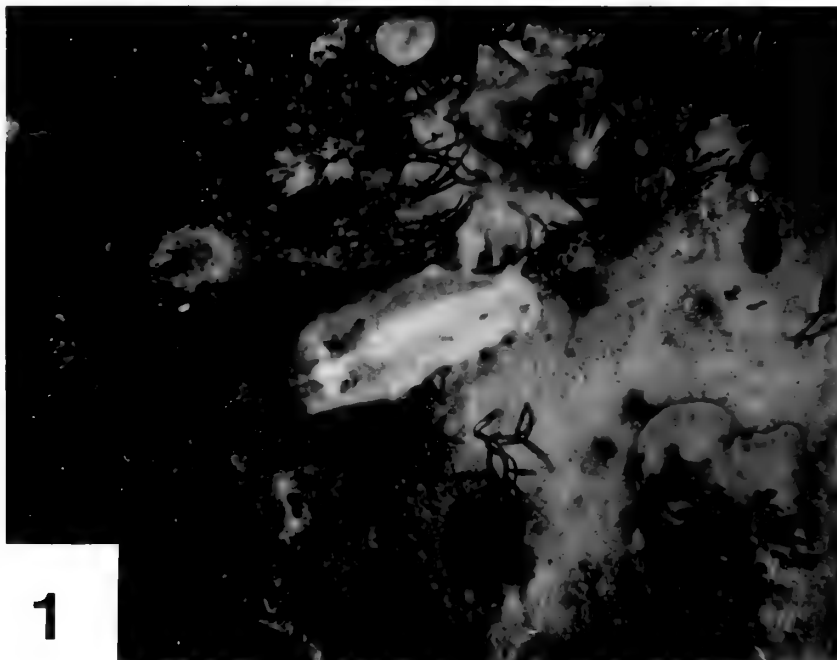
In this paper we describe aspects of the anatomy of *Atagema alba* (O'Donoghue, 1927), extend its known range into Mexican waters, discuss its synonymy and distinguishing characteristics (comparing it with both the north-eastern Pacific opisthobranch fauna and its congeners), and discuss its subfamilial placement.

ANATOMY

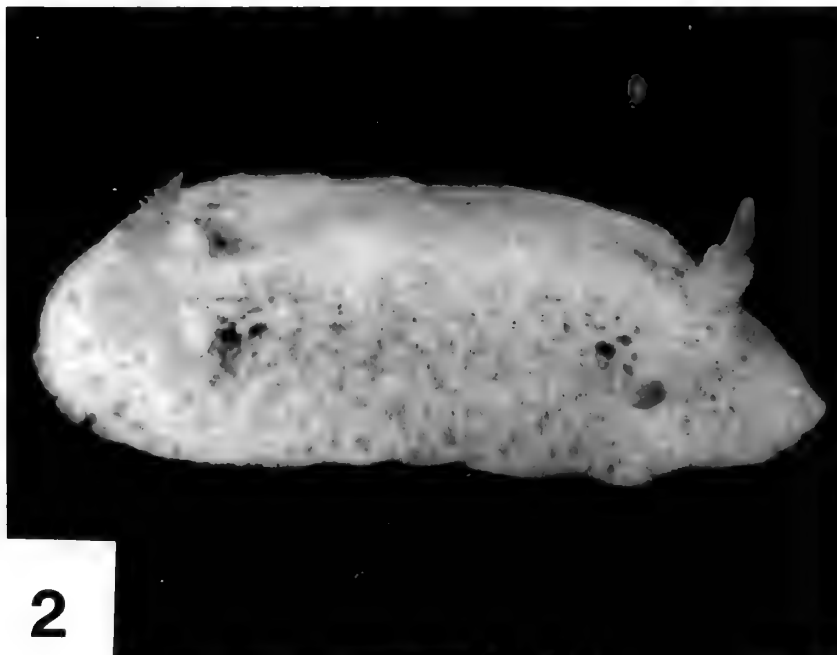
Material Examined

One specimen, 38 mm long; subtidal, 13.7 m deep, on the exposed cliff face of a pinnacle at the outer entrance of a small cove at Arbolitos, in the Punta Banda area, south of Ensenada, Baja California, Mexico (31°42'N, 116°41'W); 2 December 1984; *leg.* H. Bertsch and T. Smith. The individual (Figure 1) was on a small rocky

¹ Mailing address: 6056 Beeman Avenue, North Hollywood, CA 91606, U.S.A.



1



2

Explanation of Figures 1 and 2

Figure 1. In situ underwater photograph of *Atagema alba*, 13.7 m depth, Arbolitos, Baja California (HB photograph).

Figure 2. Close-up of *Atagema alba* collected at Arbolitos (David Mulliner photograph).

ledge on which were numerous solitary corals, *Balanophyllia elegans* Verrill, 1864. An obvious sponge food was not immediately visible; strong surge and currents prevented us from further searching.

External Anatomy

Atagema alba is an elongate dorid, strongly humped along the midline (Figure 1). It is whitish, with small black-gray flecks that give the animal a dirty appearance. The rhinophore sheaths form elevated, prominent cones around the proximal portions of each rhinophore. The branchiae project posteriorly from underneath 3 flat, posteriorly directed branchial lobes. There are broad, triangular, auriform tentacles, and a greatly exaggerated upper lobe to the bilabiate anterior foot margin.

The most diagnostic external features of this species (which O'Donoghue partly described or partly attributed to his specimen being damaged) are: the rhinophore sheath that forms a high cone (a generic character; see MACFARLAND, 1966:pl. 27, fig. 5, and our Figure 2); the broad, triangular, auriform tentacles; the extremely deep bilabiate nature of the anterior foot margin (see MACFARLAND, 1966: pl. 27, fig. 4) with an enlarged upper lobe; and the posteriorly pointing branchiae underneath 3 horizontal lobes ("giving the animal a superficial likeness to a phanerobranchiate form," O'DONOGHUE, 1927:88).

Radula

The radula consists of simply hamate, hooklike teeth (Figures 3, 4). The scanning electron micrographs illustrate the simple shape of these teeth, and the lack of any accessory denticles. The radular formula of our specimen from Mexico is 17 (26.0.26). O'Donoghue's holotype had a radular formula of 17-18 (25-26.0.25-26); Collier's specimen was 18 (18-19.0.18-19), and MacFarland's was 15 (20-23.0.20-23). The known composite radular formula of *A. alba* is 15-18 (17-26.0.17-26).

Reproductive System

The convoluted ampulla bifurcates distally into the short oviduct and elongate vas deferens. The vas deferens is round in cross section and prostatic proximally. It then narrows sharply and again widens into a muscular, ejaculatory segment. A distinct penial papilla is absent. The oviduct enters the albumen gland, the smallest portion of the female gland mass. The membrane gland is the largest portion of the mass. The mucous gland is ventral to and smaller than the membrane gland. The receptaculum seminis is saccate and muscular. From its base extend two ducts. The more proximal one enters the albumen gland near the entrance of the oviduct. The distal duct joins the duct of the thin-walled, spherical bursa copulatrix. Together these ducts form the vagina, which shares a common gonopore with the penis. The mucous gland empties

into a separate nidamental gonopore, which is located ventrally to the vaginal-penial gonopore.

DISTRIBUTION

The known distribution of *Atagema alba* is from Point Pinos, in Monterey, California (MACFARLAND, 1966), to San Diego, California (COLLIER, 1963). Our specimen represents a southern range extension of over 100 km, and the first report of the species from Mexican waters. This extension is not surprising because the fauna of the north-west coast of Baja California is part of the Californian temperate faunal province (BERTSCH, 1983, 1985; BERTSCH & JOHNSON, 1983). *Atagema alba* is now known from central and southern California and northwestern Baja California (from Monterey, California, to Arbolitos, about 15 km south of Ensenada, Baja California, Mexico). It has been found in areas of strong surf or surge, from the extreme low intertidal to the shallow subtidal zones (MCDONALD, 1983; personal observations).

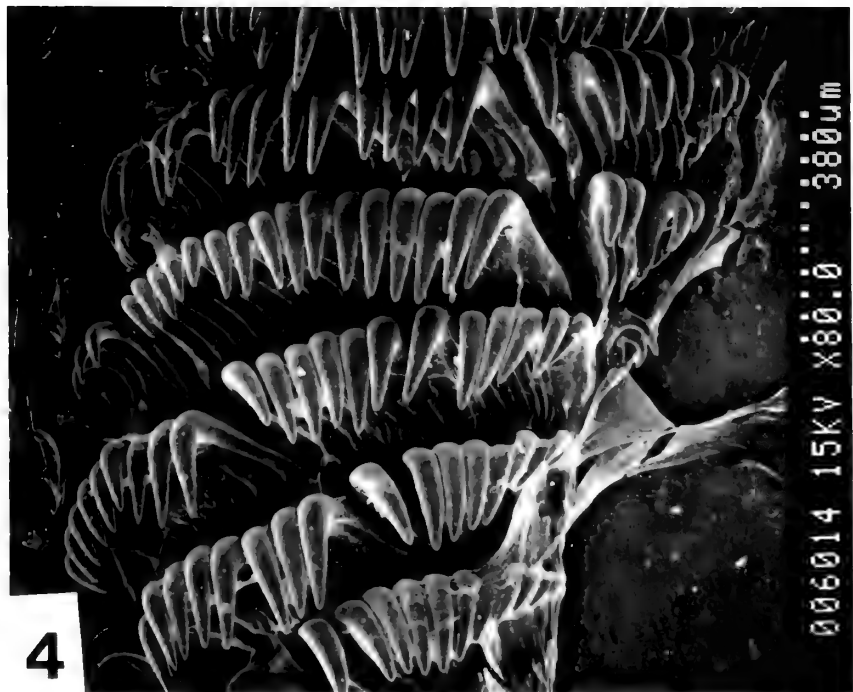
DISCUSSION

Comparison with Sympatric Doridaceans and Synonymy

Our recent collection of a specimen of *Atagema alba* prompted us to re-examine MCDONALD's (1983) proposed synonymy. He had based the synonymy on the unique branchial arrangement and on a number of traits that are referable to several species (*e.g.*, white ground color, small papillae on dorsum, and number of rhinophore lamellae). We decided to base our acceptance or rejection of his synonymy on a detailed comparison of *Atagema alba* with all other northeastern Pacific opisthobranch species (using as many anatomical characters as possible).

We were able to select 13 characteristics from O'DONOGHUE's (1927:87-89) description that could give information about the specific identity of the organism, and then compared these with all known species of opisthobranchs from the American Pacific coast (BEHRENS, 1980; MCDONALD & NYBAKKEN, 1981). *Atagema quadrimaculata* is the only species that exhibited all 13 characters.

The overwhelming concordance of *Atagema quadrimaculata* with the features described by O'Donoghue, and the incomplete agreement with any other species, led us to re-affirm the synonymy of *Glossodoridiformia alba* and *Atagema quadrimaculata*. The possibility that O'Donoghue's species has not been collected since its original description can be discarded because O'Donoghue's description fits known, recently collected specimens so well, and because the fauna of the central-southern California area is quite well known. Priority of the genus name *Atagema* necessitated the name change to *Atagema alba*. Hence, the synonymy is as follows:



Explanation of Figures 3 and 4

Figures 3, 4. Scanning electron micrographs of the radula of *Atagema alba* (specimen collected at Arbolitos). Magnification and scale on pictures (SEM's by TG).

Atagema Gray, 1850

Synonyms:

Petelodoris Bergh, 1882

Glossodoridiformia O'Donoghue, 1927

Atagema alba (O'Donoghue, 1927)

Synonyms:

Glossodoridiformia alba O'Donoghue, 1927

Atagema quadrimaculata Collier, 1963

Petelodoris spongicola MacFarland, 1966

Collier's holotype specimen of *Atagema quadrimaculata* had been deposited in the collections of the California Academy of Sciences; through an oversight, the museum number was not given in the original publication. The holotype is catalogued as CASIZ No. 018182.

Comparison with Known Congeners

Species of the genus *Atagema* occur in the northern Pacific, the southwestern Pacific, and the eastern Atlantic (including the Mediterranean). The three Atlantic species all have five lobes to the pre-branchial flaps (whereas *A. alba* has three): *Atagema gibba* Pruvot-Fol, 1951, *A. rugosa* Pruvot-Fol, 1951, and *A. africana* Pruvot-Fol, 1953. These species were described with even less information than O'Donoghue used to name *A. alba*. They are brownish, and have more teeth per half row than does *A. alba*. The fingerlike oral tentacles of *A. gibba* are different than those found in *A. alba*. THOMPSON & BROWN (1974) and PERRONE (1983) further distinguish *A. gibba* and *A. rugosa*. Studying PRUVOT-FOL's (1953:76-77) description of *A. africana* suggests that further research on additional specimens from the original locality may show that this species is synonymous with an earlier named *Atagema*.

The New Zealand *Atagema carinata* (Quoy & Gaimard, 1832) can be distinguished from *A. alba* because of its pure white color, contrasting pale yellow-orange rhinophores and gills, and broadly oval (rather than elongate) body form (WILLAN & COLEMAN, 1984).

Atagema triphylla (Bergh, 1882) (type species by monotypy of *Petelodoris*) shares a number of characteristics with *Atagema alba*: shape of radular teeth, three pre-branchial lobes, white with brown speckling color, etc. Although it has a radular formula identical to that of the specimens MacFarland used to name *Petelodoris spongicola*, the described radula and body of *A. triphylla* are smaller. Bergh indicates that *A. triphylla* has brown coloration on the fine papillae, whereas MacFarland indicates that the brown coloration is between the papillae. The only known specimen of *A. triphylla* was collected in Japan. Although some eastern Pacific species are known to occur in Japan (e.g., BABA, 1937, *Diaulula sandiegensis*), the geographic separation (*A. alba* has not been collected north of central California) and anatomical differences are sufficient to prevent synonymizing these two species based on the available information. The identity of *A. triphylla* must await recent collections of *Atagema* from Japan.

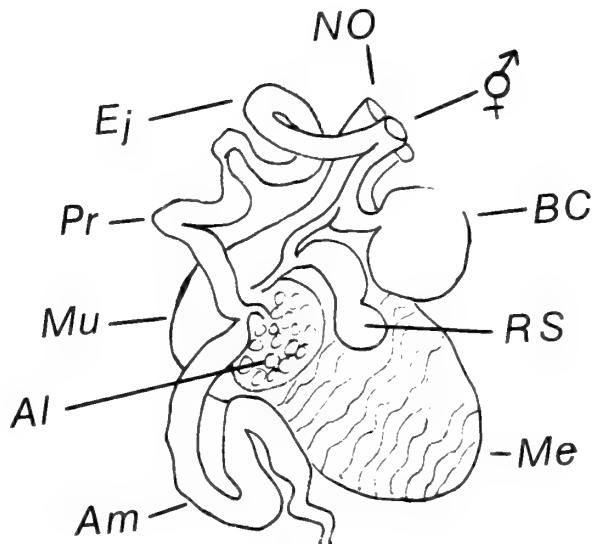


Figure 5

Reproductive system of *Atagema alba*. Al, albumen gland; Am, ampulla; BC, bursa copulatrix; Ej, ejaculatory duct; Me, membrane gland; Mu, mucous gland; NO, nidamental opening; Pr, prostate; RS, receptaculum seminis; ♀, common gonopore.

Systematic Relationships

The systematic relationships among cryptobranch doridacean nudibranchs have traditionally been a source of confusion and difference of opinion. Familial and subfamilial divisions have been based largely upon differences in reproductive anatomy (ODHNER, 1926, 1939; THIELE, 1931; BURN, 1968; FRANC, 1968; SCHMEKEL & PORTMANN, 1982). The degree of elaboration of the prostate and penial papilla has been used to distinguish between the Doridinae, Archidoridinae, and Discodoridinae.

The Doridinae was separated from the Archidoridinae by ODHNER (1926) but later (ODHNER, 1939) he combined the two subfamilies within the Doridinae. BURN (1968) transferred *Austrodoris odhneri* MacFarland, 1966, from the Doridinae to the genus *Archidoris* in the Archidoridinae. This alteration was made based on the fact that MacFarland's species possesses a prostatic region and has a small, but distinct, penial papilla. On the other hand, SCHMEKEL & PORTMANN (1982) described the reproductive system of *Archidoris pseudoargus* (Von Rapp, 1827). The specimen they depicted (fig. 7.9b) has a large penial papilla (as in *Archidoris*), but lacks a thickened prostatic region.

Atagema has been placed in the Archidoridinae by most authors (MACFARLAND, 1966, as *Petelodoris*; THOMPSON & BROWN, 1976, 1984; BEHRENS, 1980; McDONALD, 1983) but has been placed in the Doridinae by others (ODHNER, 1939; ABBOTT, 1974). *Atagema alba* has a well-differentiated, flattened prostatic region, distinct from the

narrow, non-prostatic vas deferens of *Archidoris pseudoargus*, and the prominently developed prostate of the Discodoridinae, such as *Anisodoris nobilis* (MACFARLAND, 1966:pl. 37, fig. 27).

The division of the subfamilies of the Dorididae and the distinction between the Doridinae and Archidoridinae, in particular, are certainly open to question. The fact that species that appear to be included in *Archidoris* differ in the elaboration of the prostate and penial papilla suggests that the separation of the subfamilies may be unwarranted. However, more detailed study of several taxa is required to determine the variability of these morphological characters. The type species of *Archidoris*, *Doris tuberculata* Cuvier, 1804, must be examined before meaningful conclusions can be drawn to determine subfamilial and generic limits.

ACKNOWLEDGMENTS

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A Description of a New *Helminthoglypta* s.s.
(Gastropoda: Pulmonata: Helminthoglyptidae)
from San Diego County, California

by

RICHARD L. REEDER

Faculty of Biological Science, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A.

AND

WALTER B. MILLER

Department of Ecology and Evolutionary Biology, The University of Arizona,
Tucson, Arizona 85721, U.S.A.

Abstract. A new species of land snail, *Helminthoglypta fairbanksi* Reeder & Miller, is described from San Diego County; its relationship to *H. tudiculata* (Binney, 1843) is discussed.

INTRODUCTION

FROM ABOUT 1931 UNTIL 1964, the late Wendell O. Gregg explored innumerable mountains and canyons, forested slopes and desert rock piles of central and southern California for existing populations of land snails. Many of these populations were found to be of undescribed species. During the last eight years of that period, one of us (WBM) had the good fortune to accompany Gregg on his field explorations and to acquire, shortly before his death in 1979, all of his undescribed lots of shells as well as anatomical whole mounts.

We are gradually revisiting localities to determine the current status of the populations of undescribed species as well as to obtain more detailed habitat data. One recently visited population of an undescribed species of *Helminthoglypta* in northwesternmost San Diego County was found to be thriving. It is described below.

Helminthoglypta (Helminthoglypta) fairbanksi
Reeder & Miller, spec. nov.

(Figures 1-4)

Diagnosis: A large, globose *Helminthoglypta* with the shell heavily malleated and a closed umbilicus; anatomy as in *Helminthoglypta* s.s.

Description of shell of holotype: Shell large, globose, imperforate, with conic spire. Color olive-brown with a darker brown band on the rounded shoulder. Aperture broadly elliptical with the peristome thickened and moderately reflected. Embryonic whorls $1\frac{1}{3}$ with faint indications of radial growth wrinkles. Post-embryonic whorls with increasingly prominent radial growth wrinkles which become an elaborate series of anastomosing ridges resulting in profuse malleation on the penultimate and body whorls, the malleations being elongate radially and continuing onto the base of the shell. Diameter 34.3 mm, height 12.3 mm, number of whorls $5\frac{3}{4}$.

Reproductive anatomy: The reproductive anatomy is typical of the subgenus with a capacious atrial sac with a large dart sac at its proximal end. There are two mucous glands with mucous bulbs, the ducts of which unite to form a single duct before entering the upper end of the atrial sac. The spermatheca is large, spherical, with a long duct and a long spermathecal diverticulum originating about midway along the length of the duct. The penis and epiphallus form a continuous duct, the epiphallus with a caecum of moderate length. The penis is divided into a long upper penis and a short lower penis, the former being a double-walled tube. The proximal half of the upper penis is wide, tapering to its junction with the epiphallus

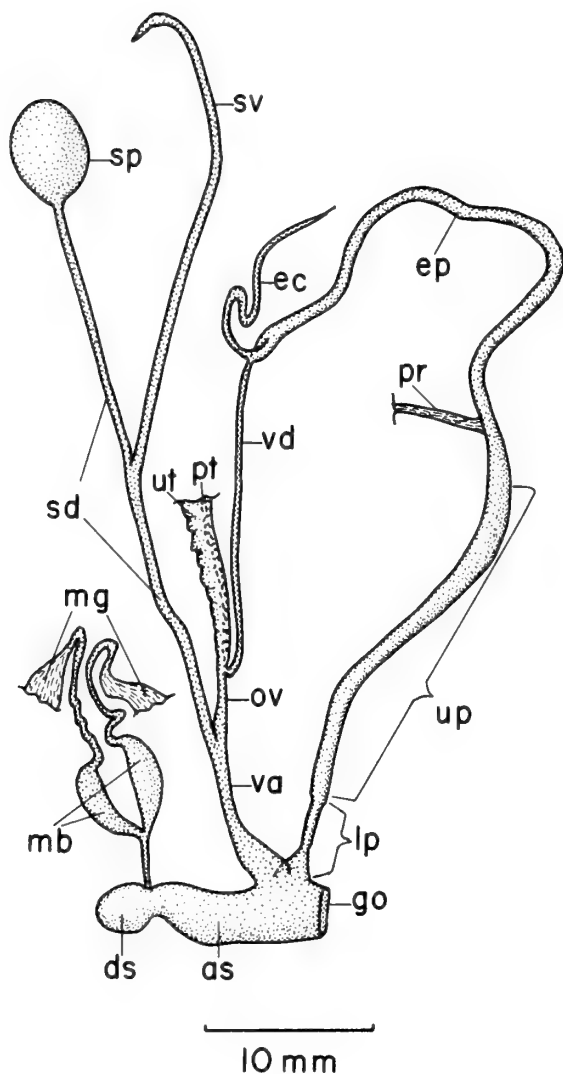


Figure 1

Portion of reproductive system of *Helminthoglypta fairbanksi* Reeder & Miller prepared from projection of stained whole mount of holotype SBMNH no. 34002. as = atrial sac; ds = dart sac; ec = epiphallallic caecum; ep = epiphallus; go = genital orifice; lp = lower part of penis; mb = mucous gland bulbs; mg = mucous gland membranes; ov = oviduct; pr = penial retractor muscle; pt = prostate; sd = spermathecal duct; sp = spermatheca; sv = spermathecal diverticulum; up = upper part of penis; ut = uterus; va = vagina; vd = vas deferens.

and tapering also to the more narrow distal half of the upper penis. The lower penis is of similar diameter to the distal half of the upper penis. The vas deferens passes around the dart apparatus and the penial retractor muscle inserts on the epiphallus. Measurements of distinctive structures are as follows:

penis	28.3 mm
epiphallus	37.8 mm
epiphallallic caecum	17.0 mm
spermathecal duct	32.5 mm
spermathecal diverticulum	32.3 mm

Variations in paratypes: A total of 15 adult and 15 immature shells was examined. The largest adult paratype measures 34.2 mm in diameter and 25.6 mm in height, and the smallest measures 29.1 mm and 23.5 mm respectively. All of the specimens examined exhibit the marked malleation described for the holotype. One adult and one juvenile show a few faint, incised spiral lines on the third whorl. Three adults and nine juveniles show isolated areas of thinner ridges forming small, somewhat circular patterns superimposed on the larger ridges of the principal sculpture. These areas are confined to the body whorl.

Disposition of types: Holotype: Santa Barbara Museum of Natural History no. 34002. Paratypes: The Academy of Natural Sciences of Philadelphia no. 359671; U.S. National Museum no. 849003; W. B. Miller collection nos. 4184, 7442, 7444; R. L. Reeder collection no. 569; H. L. Fairbanks collection no. 460.

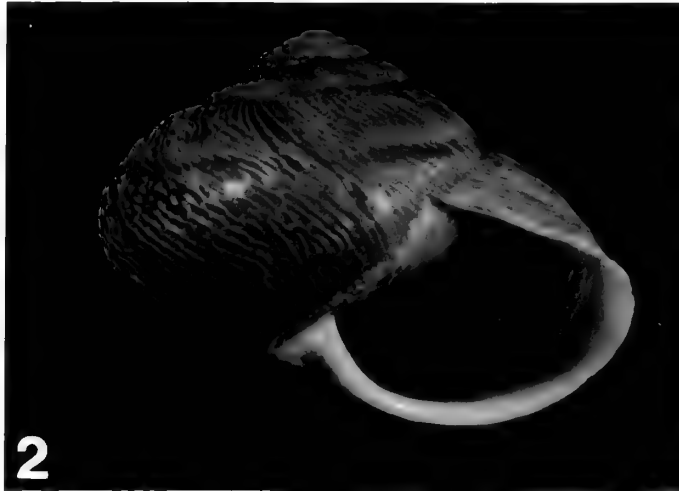
Type locality: San Diego County, California; oak woodlands along DeLuz Creek and adjacent to DeLuz Road from 1.0 to 1.7 miles (1.6–2.7 km) south of DeLuz; 33°25.5'N, 117°19.4'W; elevation 90 m (300 ft).

Discussion: *Helminthoglypta fairbanksi* is most closely related to *H. tudiculata* (Binney, 1843) from which it differs only in shell characters, namely its prominently raised wrinkles around each malleation, and its consistently closed umbilicus. Although *H. tudiculata* is common in other parts of San Diego County and in nearby Riverside County (e.g., Dripping Spring), no populations showing intergrading characters between *H. fairbanksi* and *H. tudiculata* have ever been found. *H. fairbanksi* has apparently speciated in isolation along the watershed of DeLuz Creek and Cottonwood Creek where it is sympatric with *H. traskii traskii* (Newcomb, 1861).

Distribution and habitat: In addition to the type locality south of DeLuz, *Helminthoglypta fairbanksi* has been found along the northwest side of DeLuz Creek, 0.2 miles (0.32 km) north of DeLuz and a few miles northwest of DeLuz at a point 4.2 miles (6.8 km) SE of Tenaja Campground, 3.2 miles (5.2 km) northwest of DeLuz Road and Tenaja truck trail.

Vegetation at the type locality consisted principally of *Quercus agrifolia* and *Rhus diversiloba*.

Etymology: This species is named for H. Lee Fairbanks, friend and colleague who accompanied us in our efforts to obtain additional live specimens.



Explanation of Figures 2 to 4

Helminthoglypta fairbanksi Reeder & Miller, spec. nov. Shell of holotype, SBMNH no. 34002; diameter 34.3 mm.
Figure 2. Aperture view. Figure 3. Apical view. Figure 4. Umbilical view.

ACKNOWLEDGMENTS

We are indebted to the late Wendell O. Gregg for friendship, specimens, and first pointing out the uniqueness of many snail populations in southern California. We thank also our colleagues Lee Fairbanks for help in collecting

and Susan J. McKee for photographs and excellent help in the lab. We are also indebted to the University of Tulsa for providing funds for field work and to The University of Arizona for providing laboratory space.

NOTES, INFORMATION & NEWS

Western Australian Museum Holdings

The benthic fauna of the North West Shelf of northwestern Australia was virtually unknown until recently. In 1979 the Australian Commonwealth Scientific and Industrial Organization (CSIRO) began a survey of the shelf and slope with the goal of determining the potential for commercial fisheries in the area. A number of cruises was made from 1979 to 1984 on the chartered research vessel *Soela*. The W.A. Museum was fortunate to have marine biologists on several of the *Soela* cruises. A wide variety of animals, including over 100 species of mollusks, was collected and all have full collecting data.

The staff of the W.A. Museum have recently become aware of a number of people throughout the world who have obtained a specimen or two, primarily of *Perotrochus*, but also *Teramachia* and others, from "North-western Australia" and are intending to describe new species. Such descriptions will not be based on the full range of material that is available and will inevitably overlap one another. We wish to draw attention of malacologists throughout the world to the W.A. Museum's holdings of deepwater mollusks from the North West Shelf. The specimens are available for examination by reputable scientists in any country. They can be loaned to any museum on the list of recognized institutions maintained by the Australian government. Colleagues may contact Dr. Fred E. Wells, W.A. Museum, Francis Street, Perth, Western Australia 6000, Australia, for specimens or information on what groups are being currently studied.

International Commission on Zoological Nomenclature

The following Opinion of potential interest to our readers has been published by the ICZN in the *Bulletin of Zoological Nomenclature*, volume 42, part 4, on 6 December 1985:

Opinion No. 1366 (p. 359). *Mactra sachalinensis* Schrenk, 1862 (Mollusca, Bivalvia): conserved.

California Malacozoological Society

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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.

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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*. As a partial expression of our gratitude, the names 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 member of the new patronage groups 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, ed-

itor'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.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on 25 September 1985, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 29 of *The Veliger*. For affiliate members of the Society, the subscription rate for Volume 29 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.

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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. 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:

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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.

BOOKS, PERIODICALS & PAMPHLETS

Monograph of Living Chitons (Mollusca: Polyplacophora).

Volume 1, Order Neoloricata: Lepidopleurina

by PIET KAAS & RICHARD A. VAN BELLE. 1985. E. J. Brill Publisher: Leiden. 240 pp.; 95 figs., 45 maps. Bound, 98 guilders (about \$31.00 U.S.).

This long-awaited volume is the first in a series of 10 volumes that will cover all Recent Polyplacophora. Since the publication of H. A. Pilsbry's classic work on the Polyplacophora (1892-1894. *Manual of Conchology*, Vols. 14 and 15 [in part]), there has been no comprehensive taxonomic review of the chitons. At last we will have access to a review not only of the prolific descriptive period of Gray, Sowerby, and Reeve, but the numerous nomenclatural contributions of the 20th century contributors including Thiele, Ashby, May, Iredale, Hull, Leloup, Kaas, Ferreira, and others. Kaas & Van Belle have obviously made great effort to obtain and study type material and additional specimens, and their work will be invaluable because of their diligence.

This first volume covers the suborder Lepidopleurina, which includes the families Leptochitonidae, Hanleyidae, and Afossochitonidae. Of the 83 species included, seven species are described as new. The volume begins with a general introduction to the Polyplacophora followed by a lengthy systematic section, distributional maps, a bibliography, and an index. The introduction fails to note important literature of the last two decades; not even mentioned are the significant reviews pertaining to polyplacophoran physiology and behavior (P. R. Boyle. 1977. *Oceanogr. Mar. Biol. Ann. Rev.* 15:461-509) or reproduction and development (J. S. Pearse. 1979. *Reproduction of Marine Invertebrates* 5:27-85). There is no evaluation of the taxonomic characters.

Most of the chitons in this volume are placed in the genus *Leptochiton* Gray (72 species). Many of these species were formerly considered as *Lepidopleurus* Risso, which Kaas & Van Belle reserve for only two species, *L. cajetanus* (Poli) and *L. scrippsianus* Ferreira. *Parachiton* Thiele and *Pilsbryella* Nierstrasz are used as subgenera of *Leptochiton*; *Terenochiton* Iredale is listed as a synonym of *Leptochiton* s.s. The confusing taxonomic status of *Hanleya* species is clarified; *Laminoplax dalli* (Kaas) is considered conspecific with *H. hanleyi*, and the genus *Laminoplax* Ferreira must be considered a junior synonym of *Hanleya*.

In spite of the title, one quickly realizes that this series is not a monograph but an extensive revision (*sensu* E. Mayr. 1969. *Principles of Systematic Zoology*. p. 261). As the authors mention, this series is an extension of their

previous work (1980. *Catalogue of Living Chitons*). Synonymies and descriptions are presented, but the volume suffers from the lack of an evolutionary perspective. Species within a subgenus are entered geographically, not phylogenetically; differential diagnoses and comments on evolutionary relationships are, for the most part, totally lacking. There is virtually no discussion about the family, generic, and subgeneric categories used. Taxonomic keys to species and sections to record specimens examined are conspicuously absent. The location of type specimens of junior synonyms are occasionally omitted.

Kaas & Van Belle should have been more attentive to standard taxonomic procedures and the International Code of Zoological Nomenclature (ICZN). For example, some authorship inconsistencies may confuse biologists who turn to this work for the correct citation of a name. In their treatment of *Leptochiton curvatus* (p. 96), a Carpenter manuscript name, the author in the heading is noted as "Carpenter MS, Pilsbry, 1892," a form that violates ICZN Recommendation 51B. In the synonymy, the author is listed as "(Carpenter MS) Pilsbry, 1892," leading one to believe that Pilsbry is the proper author, while in the plate caption (p. 97) authorship is recorded as "Carpenter in Pilsbry, 1892," the form recommended by the ICZN. Other MS name situations in the volume may be equally confusing. When introducing some of the new species, Kaas & Van Belle simply note that the species are different and they violate ICZN Recommendation 13A by not providing a comparison with other species. These types of errors, along with some typographical errors, are unfortunate and it is hoped that more care will be taken during the production of future volumes which, prior to publication, should be reviewed by other malacologists and carefully edited.

Many of the illustrations in this volume are superb line drawings done by the highly talented senior author. Some of the figures are copies from the literature; a few of these are practically useless and detract from the otherwise high standard set by the authors. The figures for most species include drawings of the whole animal, isolated valves, girdle elements, and a portion of the radula.

Regardless of the negative comments presented above, this series will be without doubt one of the most important 20th-century contributions to the field of chiton systematics. It contains a wealth of taxonomic information, some of it taken from obscure publications not readily available to most workers. Kaas & Van Belle are to be congratulated for having undertaken a monumental work that is not likely to be duplicated for many years to come. Hopefully, future volumes will provide more complete coverage of the taxa and will be reviewed by authorities prior to

publication. For those interested in chitons, this work is certainly the taxonomic reference of the future and it should be included in all malacological libraries.

Robert C. Bullock

Biology of Opisthobranch Molluscs. Volume II

by T. E. THOMPSON & G. H. BROWN. 1984. The Ray Society: London. Monograph No. 156:229 pp.

This fine volume completes the systematic account of the British opisthobranch mollusks begun by Dr. Thompson (1976. *Biology of Opisthobranch Molluscs. I*). The authors discuss 108 species of British nudibranchs; there are dichotomous species keys for all 4 suborders of Nudibranchia and descriptions of the characteristics of the higher taxonomic categories (e.g., families and genera) of the British species. These descriptions usually distinguish closely related taxa.

The presentation of each species is clear and uniform: major synonyms, external living characteristics, some internal anatomy (nearly always the radula, with other parts described variously), comments on life history (usually feeding and spawning records), and distribution. Some species are also given a discussion of taxonomic or other problems.

There are color drawings of 95 species, black-and-white line drawings of all species treated, scanning electron micrographs of the radulae of 14 species, and black-and-white camera lucida drawings of the radulae of nearly all the species (some are so rare their radulae are unknown). Although these are placed in different sections of the book, it is relatively easy to find the various drawings while reading the text. Often similar (or phylogenetically related) species are grouped on one plate or figure. This reviewer especially liked the radular descriptions: the illustrations are informative and often several radular formulae are given, showing the "intraspecific and ontogenetic radular variation in opisthobranch systematics" (*Syst. Zool.* 25:117-122). The distributional maps indicate occurrences in the British Isles only. Usually the text carefully separates valid, spurious, or questionable distributional records found in older publications.

At the end of the book is a partial survey of the opisthobranch literature published between 1976 and 1982 (rarely 1983). As in the main section, there is an emphasis on publications dealing with Atlantic species. The survey is a useful entry to the literature, but heed the authors' caveat, "A substantial quantity remains."

This is an excellent book, although there are the inevitable minor complaints: other opisthobranch specialists will disagree with some of the authors' various supra-specific taxonomic uses, arguments, or statements (e.g., Cadlinidae; *Coryphella/Flabellina*); the confusing *Cumanotus* discussion perhaps inadvisedly proposed a new specific name without a "proper" description (similar sug-

gestions regarding *Cumanotus beaumonti* and *Ancula pacifica/A. gibbosa* were published by McDonald in 1983); and regrettably a number of U.S. Pacific coast records or publications (e.g., *Tenellia adspersa*) are not included. However, conflicting interpretive judgments are essential to the advancement of scientific understanding, and do not detract from the data and biological information that the authors present for these 108 species of northeast Atlantic nudibranchs.

In this volume, Thompson & Brown have admirably, concisely, and clearly described what is known (and unknown) about the British nudibranchs.

Hans Bertsch

World-wide Snails:

Biogeographical Studies on Non-marine Mollusca

edited by ALAN SOLEM & A. C. VAN BRUGGEN. 1984. E. J. Brill/Dr. W. Backhuys: Leiden. x + 289 pp.

This volume contains selected papers from the Colloquium on Non-marine Mollusc Biogeography held at the 8th International Malacological Congress in Budapest, 1983. In terms of this book, "non-marine" almost means "terrestrial"; out of 19 papers, only three and part of another are concerned with freshwater snails. All of the contributions represent hands-on, sleeves-rolled-up malacology; there are no armchair speculators here. Many of the papers present the core of long-term or monographic studies by their authors. Those that involve phylogenetic analysis generally adhere to the principle of grouping by synapomorphy. More than half mention geology or geologic processes, either as setting or as agents influencing distribution of snails.

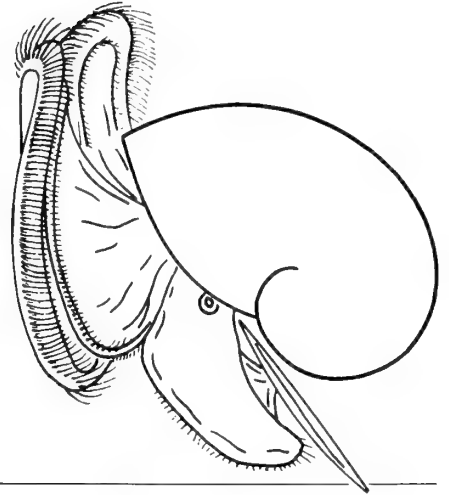
The question perhaps implicit in this volume's existence, and articulated in the introduction by Solem, is: why should biogeographers in general be interested in non-marine mollusks? What does this group of some 35,000 species have to contribute to a contemporary biogeography heavily derived from plant and vertebrate studies? There is the seeming paradox that fossil snails of Eocene age or older can usually be assigned to extant families, yet Recent species-arrays exist that undoubtedly owe their existence to radiation in the last few tens or hundreds of Kyr. While a number of factors combine to keep sympatric diversity low, except in a few favored places like the North Island of New Zealand, allopatric diversity may be exceptionally high. Solem's "A world model of land snail diversity and abundance," which predicts that the median range for all land snail species will prove to be less than 50 km, should be required reading for anyone contemplating the serious study of snail geography.

Non-malacological biogeographers could use the volume to check on their assumptions, too.

B. Roth

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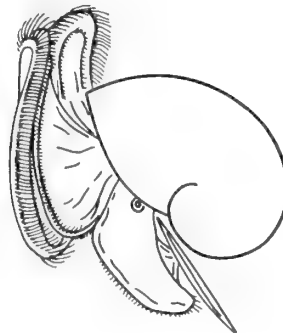
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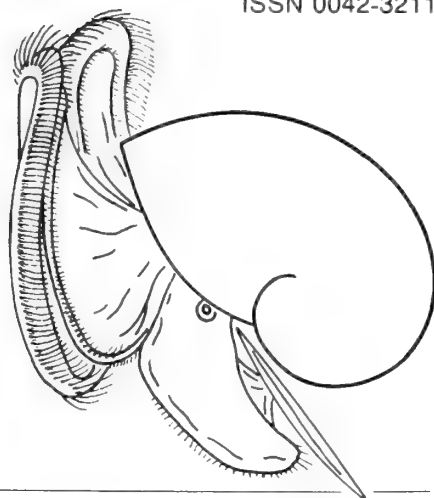
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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

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.

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This issue of *The Veliger* is dedicated
to the memory and many contributions of
Donald Putnam Abbott
(1920–1986)

Donald Putnam Abbott (1920-1986)

DONALD PUTNAM ABBOTT, Stanford University Professor Emeritus of Biology, died of cancer in Honolulu, Hawaii, on 18 January 1986. He was 65 years old. Dr. Abbott had retired in 1982, after 32 years on the faculty of Stanford University, and moved to Hawaii with his wife Isabella, who is a professor of botany at the University of Hawaii. He had planned to devote himself to his studies of the biology of ascidian tunicates, and to his inquiries into the origins of the chordates and of the mollusks. And until several months before his death he was able to do so, combining these endeavors with wide and long-postponed travels.

Donald Abbott was born and raised in Chicago. In 1937, at the age of 16, he left Chicago and headed west, eventually making his way to Hawaii. One can only imagine the impact this extraordinary journey must have had on him, as that city youth crossed the West of the late Depression and finally traded Chicago for the Hawaii of those pre-war times. But one thing is clear: for Abbott, his journey and its consequences were already part of a whole life of voyages, of quests. He entered the University of Hawaii in the fall of 1937, and received his bachelor's degree there in zoology in 1941. When the outbreak of war cut short Abbott's graduate studies, he helped instruct at the University, and in 1943 he enlisted in the army for the duration of the war. In 1943, too, he married his college classmate, Isabella Aiona. After his discharge from the army, Abbott attended the University of California at Berkeley. There, he received his master's degree in 1948 and his doctorate in 1950. He studied at Berkeley under the legendary S. F. Light and then, upon Light's death, completed his dissertation with Ralph Smith.

In 1950 Abbott joined the faculty of Stanford University's Hopkins Marine Station, and he remained with Stanford for his entire career. The year-round faculty at that seaside lab was small and fine—for a long time just Don Abbott, Lawrence Blinks, Rolf Bolin, and C. B. van Niel—and the influx of summer faculty and researchers annually enhanced even this superb nucleus. At Hopkins, Abbott developed his summer course in invertebrate zoology. From the course's dawn fieldtrips, all-morning lectures, and all-afternoon labs emerged a generation of zoologists who would be acquainted not only with comparative biology as a science but also with the animals themselves as the best of all teachers: "The animal is always right!" was virtually the course's slogan.

Abbott taught his course with breathtaking intensity

and with such clarity that one's lecture notes seem to carry his very tone of voice years later. One particularly memorable lecture was his expansive summary of crustacean types, replete with seventeen multicolored blackboard drawings, to which many of us still turn to make sense of the regions and appendages of crustacean bodies. In the afternoons Abbott took his own place at the lab-bench among his students; even as the rest of us flagged, he continued his day of careful and indefatigable observation. He showed us what stamina meant! Many of us found his example on these occasions to be exactly what we needed; as we gained our own stamina and commitment, the richness and invigorating pleasure of invertebrate zoology seemed to open itself just naturally to us. Over the three decades that he taught this course, Abbott compiled a large portfolio of working drawings. "Sketches," he preferred to call them, but in fact they are extraordinary in revealing the organisms depicted, in demonstrating how to share what one sees, and in their sheer beauty. Galen H. Hilgard, who was one of Abbott's graduate students, is currently editing and preparing a collection of these drawings for publication.

Donald Abbott was also one of the founding faculty and driving forces of the famous "spring course" in the 1960's and 1970's at Hopkins Marine Station. He felt that the best way to learn about marine biology was to do it, and so the entire Hopkins faculty of that time joined together each spring to teach about 25 undergraduates from the Stanford campus. The course's subject differed from year to year: for example, it might be a taxon such as *Tegula funebris*, or a topic such as DDT's effects in the sea. After some introductory lectures to get their bearings, students warily ventured into research projects on that year's subject. They worked for some two months under professorial care and with one another's encouragement. At the end of the course, at a two-day symposium, the students, many of them transformed into apprentice biologists by the experience of the course, formally presented and discussed the results of their work. And then, beyond the course itself, many students carried their work on to publication, virtually all with Dr. Abbott's attentive help through this daunting further experience. It was in this way that *The Veliger* published, as three special supplements, undergraduate research reports from the Stanford spring course. The spring course soon became nationally famous for the caliber of its teaching and of its students' efforts, and it has now inspired many others of

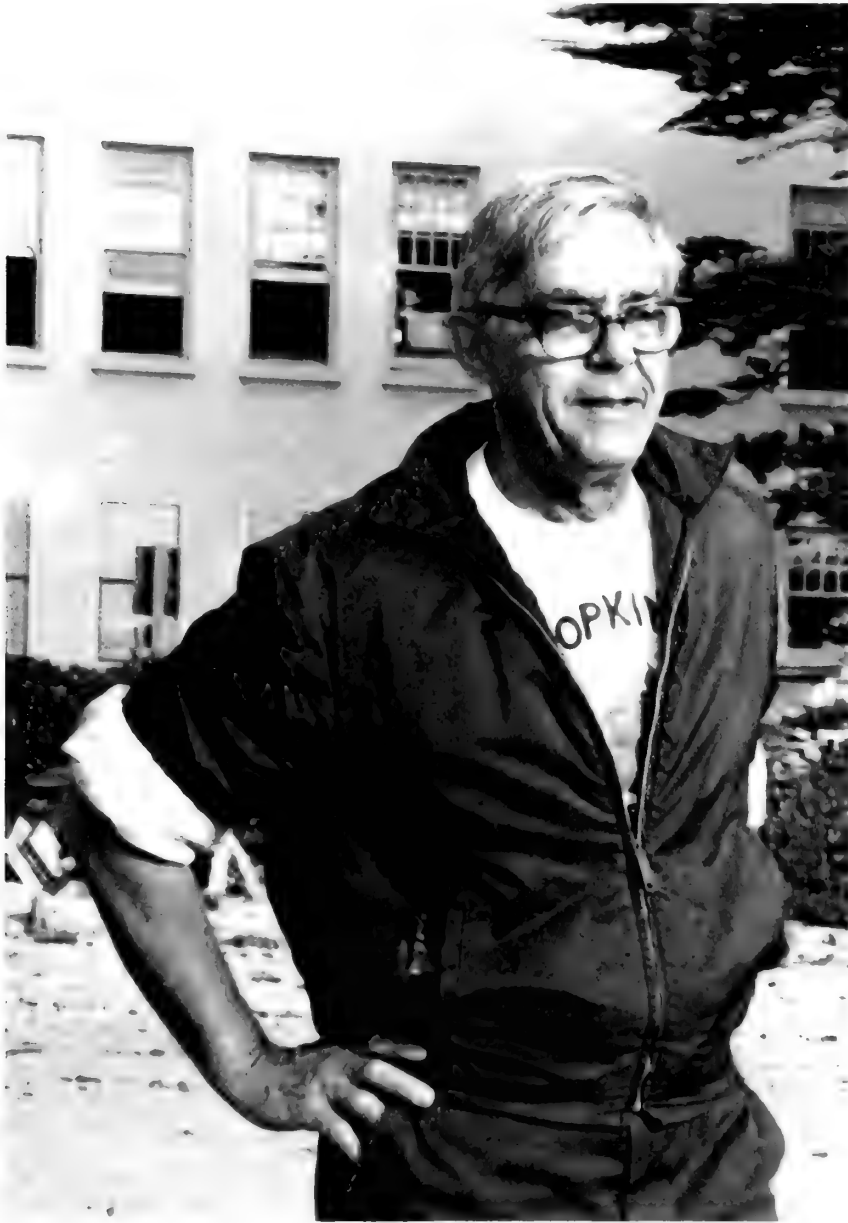


Figure 1

Don Abbott at Hopkins Marine Station during the summer of 1982. (Photo: Galen Kent Howard)

its kind. Abbott threw himself into these spring courses. He called each one "a whole new expedition."

Twenty-six doctoral and 10 master's students studied principally with Dr. Abbott, and he was the mentor, as well, of many more. His students' research topics were of a remarkable variety, but nearly always they addressed an issue in organismic biology, in the biology of evolutionary and ecological diversity—in "natural history." They expressed his persuasion that one must make sense

of biological processes by comprehending their relationships to whole organisms. In this style and perspective, he was in the tradition of the great naturalists, both at Hopkins Marine Station and when leading research trips abroad. In this latter role Abbott was chief scientist on several expeditionary cruises of the research ships *Te Vega* and *Proteus*. These cruises took him and many students to the Indian Ocean, the southwest Pacific, Hawaiian waters, the coast of British Columbia, Baja California, and the

Pacific coast of tropical America. And in his own studies, Abbott conducted especially notable expeditionary work on Ifaluk Atoll in the Caroline Islands, in the Philippines, on the Galápagos Islands, and in Chile.

His sojourn on Ifaluk Atoll in 1953 was surely the “naturalist’s voyage” of Donald Abbott’s life. With Marston Bates, he recounted the magic of it in their book, *Coral Island*. From June to November that year Abbott and a few other researchers lived among the 260 inhabitants of that little atoll and studied the natural history of the atoll and “the natural history of Micronesian man.” He had long since been captivated by the tropical Pacific; the experience of Ifaluk perfected its spell. He was already an accomplished young biologist; he returned from Ifaluk a seasoned naturalist, tested and proved by weeks of continuous fieldwork on a coral reef. Without an experience of that kind, he would later declare, “no biologist ought to consider himself fully educated.” And he returned profoundly moved by what he had learned about Oceanic alternatives to Western ways. His life thereafter was infused by the possibilities of these alternatives. He had always favored, as he later wrote, “cooperative inquiry into nature and man, rather than competitive struggle for individual achievement and fame.” Now, among Ifalukians and among his fellow scientists there, he had seen this ideal realized in that tiny and remote place. He wore what he learned there as surely in his heart as he did the Ifalukian porpoises tattooed on his thigh.

On his way home to California from Ifaluk, Abbott was struck down by polio, so badly that his life hung in the balance. Though he recovered gradually from the worst of it, he then faced the likelihood that he would never walk again. With enormous patience and effort, he regained his mobility. But even after the success of this comeback, the ordeal gave his outlook on life an urgency that never left him. Even though he eventually was well again, that slight limp could not help but remind him of his terribly close call, and he responded to this reminder with a drive that characterized all his subsequent work and with the personal intensity that all of us around him felt.

“I feel sorry,” Abbott once wrote, “for the man who isn’t wholeheartedly devoted to at least one thing in the realm of man or nature.” His own wholehearted devotion was for ascidians. His publications about them are papers of singular elegance. For example, his doctoral thesis, published in 1953, presented a lucid and now classic description of morphogenesis in the buds of the ascidian *Metandrocarpa taylora*. With his student Winona Trason he described in 1968 the spectacular ascidians *Ritterella rubra* and *Distaplia smithi*. Abbott and Jeffrey Johnson in 1972 at last sorted out the tangle that had confounded efforts to tell *Styela montereyensis* from “*Styela barnharti*” (actually *S. clava*, but confused, beyond that, with *S. plicata*). In fact, the two now seem almost unmistakable—now that Abbott and Johnson have shown us how to look

at them! In 1954 and again in 1975, Abbott prepared the urochordate keys for “Light’s Manual,” *Intertidal Invertebrates of the Central California Coast*. In the last few years he undertook a thorough review and revision of the genus *Ascidia*. When he died, he was in the midst of this endeavor, and he also had neared completion of an account of the ascidians of the Hawaiian reefs, to which he had returned so happily in retirement.

In the late 1970’s Abbott teamed with Eugene Haderlie and various chapter-contributors to write “the big book,” *Intertidal Invertebrates of California*. The photographer R. H. Morris provided many of the photographs for this book. This splendid volume, which was published in 1980, immediately became an indispensable reference for all West Coast zoologists. “We’ll only put in natural history,” Abbott once declared. But for him, of course, “natural history” ran the gamut from DNA to ecosystems ecology—whatever good work could be related sensibly to the life of the organism in its environment; and so the species accounts quickly became encyclopedic surveys of just about any aspect at all of the biology of the organisms in the book.

The surveys were encyclopedic, but often scanty, because we know so little about so many inhabitants of our shores. And so, as much as it is an account of what we do know, the big book is also a guide to the questions we might ask next about the species it describes. For in an epoch of uncertain answers, Abbott stressed the significance of *questions themselves*. His inquiries about research characteristically began not with “What are you doing?” but rather with “What are you asking?” He taught how to pose questions, how to press and sustain them, how to adapt them to one’s organisms, and how to recognize the organisms’ subtle answers. He taught this as a skill of paramount value—the means by which one really could become an investigative reporter of nature.

Beyond his own publications, Abbott dedicated himself to work on which his students and colleagues sought his help. Where others might have expected credit in the titles, he chose, rather, to let his own (often crucial) contributions to others’ work simply be acknowledged as they saw fit. A list of papers recording his help—even just those acknowledging it with that special tone reserved for particular gratitude—would be tremendously long. Perhaps to his relief out of modesty, these paeons are scattered beyond retrieval throughout the literature of current invertebrate biology. And these are merely the explicit signs of an implicit presence of far wider magnitude: he taught and advised and encouraged his students and colleagues with truly untold generosity. From students’ papers in the Hopkins spring course to colleagues’ papers in ascidian biology, manuscripts fairly poured through his scrutiny. He had uncanny skill in locating the weak observation, the uncertain interpretation. He edited and even reorganized papers with deft tact. He pressed that ultimate condensation, the table and the graph, insisting on clarity.

And then—the transformed paper published—he would congratulate the author wholeheartedly. How many can the world hold like that? No wonder so many acknowledgments so often have a ring of special thanks.

Abbott was without peer in the care and accuracy of his teaching and research. As his students, we would try our utmost to imitate his standards and be glad to approach them from time to time. But then, too, his curiosity scarcely had horizons; he was constantly inquiring. He was a naturalist of ideas, and he delighted in romping far from his home “professional” terrain. As conversations spun out into the evening, he was apt to rise to any subject—“the nature of art, the meaning of ‘importance,’ the impact of the individual on history, and man’s place in the cosmos,” as he once summed it up. And he would just as likely go on to grapple with any giant social ill and to solve it by some impossibly rational scheme. Perhaps these ardent explorations best revealed why he once said “scientific research is the last refuge of the romantic.”

Donald Abbott was preeminently a teacher. He shared his ideas and insights with his fellow biologists as he did with his students: directly, unreservedly, and in person. His way was one of friendship, of humane engagement, of going beyond curiosity to real caring about others and

about their work, of “cooperative inquiry into nature and man,” of uncommon generosity. That is what it came to: generosity. Beyond the zoology that he taught us and the example of uncompromising care and of intellectual stamina that he set for us, beyond the fertile questions and ideas—beyond all that, we flourished in his generosity.

We flourished, and so did his family. From their first acquaintance in that undergraduate biology class, Don and Izzie carried their shared work in science as a special bond throughout their married life. He was immensely proud of her professional accomplishments and thoroughly dedicated to her distinguished career as a phycologist. He delighted in the opportunities they had to combine their separate specialities in joint research and teaching. Their daughter, Ann Kaiue Abbott, grew up nurtured by devoted parents. Don loved to tell of special moments they had all shared in her childhood; the mantelpiece at home held the many odd stones and coral carvings that Don and Ann had found or made together. In their home, we joined the pleasure of our science with the happiness of their family.

Todd Newberry
Michael Hadfield

Name Changes in the "Acmaeidae"

by

DAVID R. LINDBERG

Museum of Paleontology, University of California, Berkeley, California 94720, U.S.A.

Abstract. Major changes at the familial and generic level in the "Acmaeidae" are introduced here. These changes are necessary because morphological convergence in limpet taxa has been greatly underestimated, and the previous classifications have failed to recognize many of the distinct lineages in the taxon. Three new taxonomic changes are presented and discussed: (1) The division of the family Acmaeidae into two families, the Acmaeidae, which contains the genera *Acmaea* and *Pectinodonta*, and the Lottiidae, which includes the remaining genera previously assigned to the family Acmaeidae. (2) The synonymization of the genus *Collisella* with the senior synonym *Lottia*. (3) The restriction of the genus *Notoacmea* to Australian and New Zealand species and the referral of the remaining species to the genus *Tectura*.

INTRODUCTION

NAME CHANGES of well-known or well-studied taxa always generate skepticism, resentment, and frustration in the biological community. Moreover, they add another entry for bibliographic searches and create longer, more elaborate synonymies. However, as the understanding of phylogenies increases, the necessary name changes must be made. And because the valid name is determined by rules of nomenclature, the correct name may not be our "favorite."

Detailed studies of members of the family Acmaeidae Forbes, 1850, show that phylogenetic relationships are poorly reflected in the current classification and that a thorough revision of the group is needed. Three contributions toward that revision have appeared (LINDBERG, 1981a, 1983; LINDBERG & MCLEAN, 1981). Much of this work is synthesized and incorporated in the forthcoming *The Archaeogastropoda of the Northeastern Pacific* (J. H. McLean & D. R. Lindberg). Also appearing in that volume are radical changes in patellacean taxonomy at the generic and familial levels. Because of the constraints of the systematic format in that work, it was not possible to discuss in detail all the factors involved in many of these changes. Therefore, I present here discussion of three of the more disconcerting changes: (1) the division of the family Acmaeidae into two families, the Acmaeidae Forbes, 1850, and the Lottiidae Gray, 1840; (2) the synonymization of the genus *Collisella* Dall, 1871, with the senior synonym *Lottia* Sowerby, 1834; and (3) the transfer of eastern Pacific limpets from the genus *Notoacmea* Iredale, 1915, to the genus *Tectura* Gray, 1847. Reasons for the

chronic taxonomic confusion in these limpets are also discussed. It is hoped that these explanations will ease the tension during the transition. A summary of name changes proposed here for the northwest Pacific "Acmaeidae" is presented in Table 1.

LOTTIIDAE GRAY, 1840, AND ACMAEIDAE FORBES, 1850

There always has been something enigmatic about *Acmaea mitra* Rathke, 1833, the type species of the genus *Acmaea* Eschscholtz. IREDALE (1915) proposed four genera for the New Zealand acmaeid fauna because he could not find any similarities between the New Zealand species and the northeastern Pacific type species. Had Iredale compared any of the New Zealand species to any other northeastern Pacific species, he would have found at least two apomorphic characters in either shell morphology, shell structure, radula configuration, or radular basal plate morphology shared between the species in hand. In 1950 J. A. Shotwell found that *A. mitra* was an exception to a general trend in shell morphology relative to height in the intertidal zone in northeastern Pacific "*Acmaea*" (SHOTWELL, 1950). More recently, MARGOLIN (1964) has pointed out that, unlike other low intertidal "acmaeids," *A. mitra* does not have an escape response from the predatory starfish *Pisaster ochraceus* (Brandt, 1835).

Although there has been little general agreement among patellacean systematists, almost all workers have restricted the usage of the genus *Acmaea*. *Acmaea* was one of four names intended to include all patellaceans with a single

Table 1
Summary of name changes for the northwest Pacific "Acmaeidae."

Old classification (LINDBERG, 1981b)	New classification
Family Acmaeidae Forbes, 1850	Family Acmaeidae Forbes, 1850
<i>Acmaea mitra</i> Rathke, 1833	<i>Acmaea mitra</i> Rathke, 1833
	Family Lottiidae Gray, 1840
<i>Acmaea funiculata</i> (Carpenter, 1864)	<i>Niveotectura funiculata</i> (Carpenter, 1864) ¹
<i>Acmaea apicina</i> Dall, 1879	<i>Erginus apicina</i> (Dall, 1879) ¹
<i>Problacmaea moskalevi</i> Golikov & Kussakin, 1972	<i>Erginus moskalevi</i> (Golikov & Kussakin, 1972) ¹
<i>Problacmaea sybaritica</i> (Dall, 1871)	<i>Erginus sybaritica</i> (Dall, 1871) ¹
<i>Lottia gigantea</i> Sowerby, 1834	<i>Lottia gigantea</i> Sowerby, 1834
<i>Collisella pelta</i> (Rathke, 1833)	<i>Lottia pelta</i> (Rathke, 1833)
<i>Collisella digitalis</i> (Rathke, 1833)	<i>Lottia digitalis</i> (Rathke, 1833)
<i>Collisella paradigitalis</i> (Fritchman, 1960)	<i>Lottia strigatella</i> (Carpenter, 1864)
<i>Collisella conus</i> (Test, 1945)	<i>Lottia conus</i> (Test, 1945)
<i>Collisella limatula</i> (Carpenter, 1864)	<i>Lottia limatula</i> (Carpenter, 1864)
<i>Collisella ochracea</i> (Dall, 1871)	<i>Lottia ochracea</i> (Dall, 1871)
<i>Collisella triangularis</i> (Carpenter, 1864)	<i>Lottia triangularis</i> (Carpenter, 1864)
<i>Collisella instabilis</i> (Gould, 1846)	<i>Lottia instabilis</i> (Gould, 1846)
<i>Collisella alveus</i> (Conrad, 1831)	<i>Lottia alveus</i> (Conrad, 1831)
<i>Collisella asmi</i> (Middendorff, 1847)	<i>Lottia asmi</i> (Middendorff, 1847)
<i>Collisella borealis</i> Lindberg, 1982	<i>Lottia borealis</i> (Lindberg, 1982)
<i>Tectura rosacea</i> (Carpenter, 1864)	<i>Tectura rosacea</i> (Carpenter, 1864)
<i>Notoacmea testudinalis</i> (Müller, 1776)	<i>Tectura testudinalis</i> (Müller, 1776)
<i>Notoacmea scutum</i> (Rathke, 1833)	<i>Tectura scutum</i> (Rathke, 1833)
<i>Notoacmea persona</i> (Rathke, 1833)	<i>Tectura persona</i> (Rathke, 1833)
<i>Notoacmea fenestrata</i> (Reeve, 1855)	<i>Tectura fenestrata</i> (Reeve, 1855)
<i>Notoacmea paleacea</i> (Gould, 1853)	<i>Tectura paleacea</i> (Gould, 1853)
<i>Notoacmea depicta</i> (Hinds, 1842)	<i>Tectura depicta</i> (Hinds, 1842)
" <i>Notoacmea</i> " <i>insessa</i> (Hinds, 1842) ²	
" <i>Collisella</i> " <i>scabra</i> (Gould, 1846) ²	

¹ See LINDBERG, 1983.

² Generic classification will be discussed elsewhere; "*N.*" *insessa* is a member of the family Lottiidae, "*C.*" *scabra* is not.

gill in the nuchal cavity. After 40 years of indiscriminate use of *Acmaea* and the other three names (*Lottia*; *Patelloida* Quoy & Gaimard, 1834; and *Tectura* Gray, 1847), DALL (1871) first revised the Acmaeidae, based on shells, radulae, and external anatomy of 32 species. He was the first to define subgenera, based primarily on radular characters. After this initial splitting, generic and subgeneric names proliferated in the family. The increasingly restricted use of the name *Acmaea* s.s. results in a current definition that usually includes fewer than five species. However, as discussed below, *Acmaea* is monotypic. And not only is *A. mitra* the only species, it is also distinct at the familial level from all other putative intertidal acmaeids; the relatives of *A. mitra* are in the subtidal, not the intertidal.

MACCLINTOCK (1967:75) was the first to point out that *Acmaea mitra* and members of the predominately subtidal family Lepetidae Gray, 1857, belong to the same shell-structure group (his group 15): "no other patelloid currently classed in the family Acmaeidae is known to have a shell structure similar to that of *A. mitra*." But how could *A. mitra* be related to blind, gill-less, subtidal lim-

pets with bizarre radulae? An important pattern was recognized when members of the patellacean genus *Pectinodonta* Dall, 1882, were found to also be members of shell structure group 15 (LINDBERG, 1981a). Members of the genus *Pectinodonta* are blind, gill-bearing, subtidal limpets with bizarre radulae. However, there are important plesiomorphic characters shared by *A. mitra* and species of *Pectinodonta*. Besides shell structure, both share three pairs of lateral teeth arranged in a posteriorly diverging \wedge -shape, identical ventral plate morphology, a lack of marginal teeth, and similar gross anatomy and shell morphology. The major differences between the two taxa are the lack of eyes and the multicuspoid third lateral teeth of *Pectinodonta*. The lack of eyes in abyssal species is common in marine mollusks and other invertebrates, and a similar multicuspoid modification of the third lateral teeth for feeding on wood is also known in *Potamacmaea* (PEILE, 1922) from southwest Asia, a member of the subfamily Patelloidinae (OLIVER, 1926) (Lindberg, unpublished observation). Thus, the differences between *Acmaea* and *Pectinodonta* are minor compared to the differences between these two taxa and the other members of the family "Ac-

maeidae." Moreover, the similarities between these two white-shelled genera and the white-shelled Lepetidae are becoming apparent as the progenetic nature of the Lepetidae is recognized (McLean & Lindberg, in preparation).

Restriction of the genus *Acmaea* to a single species and the newly recognized phylogenetic relationship between *Acmaea*, *Pectinodonta*, and the Lepetidae, which constitute distinct taxa of the familial category (*i.e.*, Lepetidae and Pectinodontinae Pilsbry, 1891), necessitate a reconsideration of the family Acmaeidae and its place in classification. The family Acmaeidae must be redefined to reflect more accurately the phylogeny of its clade. The family is, therefore, redefined to include two subfamilies, the Acmaeinae and the Pectinodontinae. The type genera are the only genera referred to these subfamilies. The Lepetidae are maintained as previously defined by McLEAN (1966) and MOSKALEV (1977). Those taxa previously assigned to the family Acmaeidae that are not members of shell-structure group 15 are referred to the family Lottiidae Gray, 1840 (type genus *Lottia* Sowerby, 1834), the oldest available name for this clade. The shells of members of the families Lottiidae, Lepetidae, and Acmaeidae always have radial and concentric crossed-lamellar layers in juxtaposition. In the families Lepetidae and Acmaeidae, a foliated layer is always present dorsal of the concentric crossed-lamellar layer; the Lottiidae lack a foliated layer.

Lottia Sowerby, 1834, *vs.* *Collisella* Dall, 1871

In 1833 J. E. Gray proposed the genus *Lottia*, diagnosing it as follows: "[*Lottia*] must be extremely perplexing to those systematists who attend only to the form of the shells without paying any regard to its animal inhabitant. The shells of *Patella* and *Lottia* do not in the least differ in external form, and yet their animals belong to very different orders, the one having the branchiae placed around the foot as in chitons, and the other having them placed on the side of the neck, like the Fissurellae, from which indeed it chiefly differs in having only one branchia" (GRAY, 1833:800). From this description it is clear that Gray recognized the distinctness of the clade that has been subsequently known as the Acmaeidae. In a 4-yr period (1830 to 1834) other names in this group were introduced: *Tecture* by AUDOUIN & MILNE-EDWARDS (1830), *Acmaea* by ESCHSCHOLTZ (1833), *Lottia* by GRAY (1833), and *Patelloida* by QUOY & GAIMARD (1834). Although the respective type species differed in radular characters, distinctions were not made at the time. It remained for DALL (1871) to recognize their differences.

In 1871 W. H. Dall proposed the subgenus *Collisella* (type species *Acmaea pelta* Rathke, 1833) for those acmaeid limpets with a single pair of reduced marginal teeth (uncini) and a ctenidium (DALL, 1871). In the late 1940's Japanese workers had begun to use *Collisella* as a full genus based on radular and shell characters. McLEAN (1966) followed this trend, recognizing *Collisella* at the generic level based on radular, shell, and ecological cri-

teria. Many subsequent workers followed this usage, and with the publication of *Light's Manual* (SMITH & CARLTON, 1975), the use of *Collisella* became well-established in literature on northeastern Pacific intertidal species.

Although Gray originally diagnosed the genus *Lottia* by the single gill in the nuchal cavity, this distinction was lost because he failed to provide an indication of the taxon (Article 16; ICZN, 1964). SOWERBY (1834) validated *Lottia* when he published a description of the genus and illustrations of four species, *L. gigantea*, *L. antillarum*, *L. testudinaria*, and *L. radians*. When Sowerby illustrated *L. gigantea* he had no idea that the animal that inhabited the shell also had a secondary gill. He used the genus *Lottia* in Gray's original sense, for those limpets with a nuchal cavity gill rather than a secondary gill. It was J. G. Cooper who in 1860 first brought to P. P. Carpenter's attention the presence of both a nuchal cavity gill and a secondary gill in this enigmatic species. CARPENTER (1860) proposed the genus *Tecturella* for this species with both "acmaeid" and patellid gill characters. However, *Tecturella* was a homonym of *Tecturella* Stimpson, 1853, a genus of polychaete worms. In 1861 Carpenter proposed *Tecturina*, possibly as a replacement name for *Tecturella* (CARPENTER, 1861), but failed to diagnose the genus and thus *Tecturina* must be regarded as a *nomen nudum*. Carpenter had one more go at it in 1866 when he proposed the genus *Lecania*; however, he had realized by 1864 (CARPENTER, 1864:650) that the genus *Lottia* was available for this species because of SOWERBY's (1834) illustration of *L. gigantea*, and thus he published *Lecania* in synonymy with *Lottia*. Therefore, *Lecania* is Carpenter's second *nomen nudum* for the taxon. It is also a homonym for *Lecania* Macquart, 1839, a genus of Diptera. CARPENTER (1866:344) did, however, establish *L. gigantea* as the type species of *Lottia* by subsequent monotypy. GRAY's (1847) designation of *Acmaea scutum* Rathke, 1833, as the type species of *Lottia* was not valid because *A. scutum* was not a species assigned by Sowerby to *Lottia* in his validation of Gray's name. Thus, the genus *Lottia* became restricted from Gray's original usage for limpets with a nuchal cavity gill to those with both a nuchal cavity gill and a secondary gill.

With the restriction of the genus *Acmaea* to limpets with conical, white shells and three pairs of radular teeth, the genus *Collisella* became the genus of choice for those limpets with a radular morphology identical to that of *Lottia*, but which lack secondary gills. Because gill morphology was considered to be the most conservative character in patellacean systematics, the obvious similarity between members of the genus *Collisella* and *L. gigantea* was never addressed.

LINDBERG & McLEAN (1981) described four new species of *Lottia* from the Galápagos Islands. Although there was little similarity between these species and the large Californian *L. gigantea*, they pointed out that all five species shared a common shell structure, radula configu-

ration, and secondary gill morphology. Moreover, they pointed out that secondary gill morphology was not as conservative as once thought, and that shell structure was a much more reliable character. "Acmaeid" limpets with secondary gills have subsequently been found in the boreal, Panamic, and Caribbean regions (LINDBERG, 1983; personal observation). Moreover, these species belong to different shell-structure and radular groups, which strongly suggests that secondary gills have evolved in many different lineages and are, therefore, convergent characters. The obvious questions are: from what lineage did *L. gigantea* evolve, and is presence of a secondary gill a character of generic importance in this clade?

The answer to the first part of the question was furnished by comparing the anatomy and allozymes of *Lottia gigantea* to other California *Collisella* species. The results show that *L. gigantea* is very closely related to *Collisella limatula* (Carpenter, 1864) (SLY, 1984; Lindberg & SLY, in preparation). Moreover, *L. gigantea*, *C. limatula*, and *Collisella strigatella* (Carpenter, 1864) are more closely related to one another than they are to *Collisella pelta*, the type species of the genus *Collisella*. There is little doubt that *L. gigantea* is derived from *C. limatula* or from a common ancestor. Based on the fossil record of southern California and northern Baja California this speciation event occurred within the last 250,000 yr (Lindberg, unpublished data).

Thus, *Lottia gigantea* is the product of a recent speciation event within the *Collisella* group and is more closely related to some *Collisella* species than some *Collisella* species are to each other. The unique characters of *L. gigantea* all appear to be associated with the evolution of its territorial behavior (see STIMPSON, 1970, and WRIGHT, 1982, for a description of territorial behavior). The low profile shell with its strongly anterior apex forms a plowlike anterior slope that the limpet uses to push intruders out of its territory. The large size of this species, a common feature of territorial species (GHISELIN, 1974:142), undoubtedly presented problems of respiratory surface area to body volume, and the secondary gill was the evolutionary solution. These few autapomorphic characters are far outweighed by the symplesiomorphies in radular morphology, internal anatomy, shell structure, and external pigmentation.

The synonymizing of *Lottia* with *Collisella* has larger ramifications because *Lottia* is the senior synonym and all the species presently assigned to the genus *Collisella* should be assigned to *Lottia*. In many ways it is appropriate for *Lottia* to become the correct name for this diverse clade of limpets. After all, this usage exactly expresses the original intentions of J. E. Gray, who first recognized the group.

Tectura Gray, 1847, or *Notoacmea* Iredale, 1915

Notoacmea (type species, by original designation, *Pateloida pileopsis* Quoy & Gaimard, 1834) was proposed by IREDALE (1915) for several Australian species that were

not referable to genera that he had earlier described. Although the criteria for the establishment of this genus were poorly defined, the name was adopted by Australian, New Zealand, and Japanese workers for fine-ribbed, thin-shelled species that lacked radular marginal teeth.

GRANT (1937:15) was the first worker to assign some of the northeastern Pacific "acmaeids" to *Notoacmea*, which she considered as a subgenus of *Acmaea*. FRITCHMAN (1961) adopted Grant's classification and published subgeneric assignments for many of the northeastern Pacific species. MCLEAN (1966) also used *Notoacmea* as a subgenus and then later (MCLEAN, 1969) considered *Notoacmea* as a full genus. However, there are problems with the use of *Notoacmea* for species outside the austral region. All new world "*Notoacmea*" have MACCLINTOCK's (1967) shell-structure group 1, whereas most of the *Notoacmea* of Australia and New Zealand have group 4.

In his study of the shell structure of the patellaceans, MACCLINTOCK (1967) found that shell-structure group 4 (includes group 5 also) were restricted to Australia and New Zealand. Those species with this unique shell structure include the type species of *Notoacmea* as well as the nominal genera *Atalacmea* Iredale, 1915, and *Conacmea* Oliver, 1926. Nowhere else in the world has this shell-structure type been found in either fossil or Recent species. Although it is apparently derived from shell-structure group 1 by a simple transposing of the radial crossed-lamellar layer to either side of the myostracum, it has a very limited biogeographical distribution.

I have earlier pointed out the problems with the use of *Notoacmea* for eastern Pacific species (LINDBERG, 1976, 1981b). However, a solution to this problem was not forthcoming because of the confusing character states found in several different groups of patellaceans for which the radula lacked marginal teeth. LINDBERG & MCLEAN (1981) established that it was possible to distinguish some of the groups by examining the complexity of the radular basal plates in different shell-structure groups (see also GRANT, 1937:14). They also pointed out that some eastern Pacific "*Notoacmea*" had thicker, more prominently ribbed shells than the typical *Notoacmea* of the austral region. As shell structure and radula configuration became known for additional eastern Pacific species, it was readily apparent that a clade of "acmaeids," convergent in radular morphology with *Notoacmea* in the austral region, was extant in the North Pacific, North Atlantic, and Caribbean regions. The determination of the correct name for this clade concerns us here.

Several type species are members of this clade, including *Notoacmea scopulina* Oliver, 1926 (*Subacmea* Oliver, 1926), *Patella testudinalis* Müller, 1776 (*Testudinalia* Moskalev, 1966), and *Patella virginea* Müller, 1776 (*Tectura* Gray, 1847). Although *Tectura* is the senior synonym for this clade, it was also the most unlikely genus given its current usage.

The concept of *Tectura* has most recently been restricted to small subtidal limpets with light-colored shells marked

with red or pink rays and with faint radial ribbing. The radular teeth of these species are approximately equal in size and shape; marginal teeth are lacking. There is a single gill in the nuchal cavity and members of this genus belong to shell-structure group 1. Previously, there have been only two species that were unquestionably members of this group, *T. virginea* and *T. rosacea* (Carpenter, 1864). Both are subtidal species and are associated with coralline algae. It is now recognized that equal development of the lateral teeth is a common adaptation of subtidal coralline-feeding species and that species with this radular type occur in almost every shell-structure group in the family Lottiidae (McLEAN, 1966; LINDBERG, 1981b, 1983; LINDBERG & McLEAN, 1981). It is, therefore, regarded as a convergent character in the family and of little use in systematics. This is also true of shell morphology and coloration of subtidal coralline-feeding species (LINDBERG, 1983). However, the more conservative (plesiomorphic) characters of *T. virginea* and *T. rosacea*, those of shell structure, gill morphology, and radular basal plate morphology, clearly indicate that these species are members of the clade that we have previously called "*Notoacmea*."

Although it may be difficult for some workers to imagine *Tectura virginea* and the large, dark *Tectura scutum* as members of the same genus, similar contrasts exist in most other "acmaeid" taxa. For example, consider *Lottia triangularis* (Carpenter, 1864) and *L. pelta*. *Lottia triangularis* is a small white-shelled, subtidal species with lateral teeth of equal size and shape. *Lottia pelta*, in contrast, is a large, dark-shelled intertidal species with lateral teeth unequal in size and shape. However, both have complex basal plate morphologies, identical shell structure, one pair of marginal teeth, similar gill morphologies, etc., and there is no doubt that *L. triangularis* and *L. pelta* are members of the same clade. The differences between them exist because of adaptations to differences in their habitat not their phylogeny. This is the same situation that occurs in the genus *Tectura*; however, here the type species is the derived subtidal species, not one of the larger, more typical intertidal species.

It is unclear whether the genus *Tectura* as used here is worldwide in distribution or restricted to the Northern Hemisphere. Species groups, with similar radulae and shell structures, have been previously recognized in the Southern Hemisphere (e.g., *Subacmea* and *Conacmea*). However, given the tremendous amount of convergence that occurs in the Lottiidae, it is doubtful that these groupings represent clades. It is unlikely that further study of shells or radulae will yield characters that elucidate phylogenetic relationships in and between regional groups of *Tectura* s.l.; further division of the genus will need to be based on anatomical and biochemical characters.

DISCUSSION

Name changes in the Patellacea have been suggested with increasing frequency over the past 15 yr. After almost 100

yr of usage as a principal genus in the superfamily, *Acmaea* has now become restricted to a single species. Genera that replaced *Acmaea* have themselves been replaced or redefined. Superficially, it appears that "splitting" in the Patellacea has reached epidemic proportions. Why has this occurred?

The main reason for the drastic reallocation and arrangement of the Patellacea is directly due to underestimation of convergence in the taxon. The first worker to provide an insight into the convergence in the superfamily was MACCLINTOCK (1967). MacClintock described seven shell structural types in the "Acmaeidae." When he compared gill and radular morphologies with shell structure data, some significant trends became apparent. MacClintock attempted to interpret these trends, but was hampered by a confusing and inaccurate systematic literature.

When limpets are grouped by shell structure, the convergence in radular, gill, and shell characters becomes readily apparent, and usually, these convergences are directly correlated to habitat and (or) history of the taxon. The reason these relationships (and the numerous distinct taxa) were not previously recognized has been due to: (1) the extremely simple morphology of the shell, and (2) the mistaken belief that gill characters were conservative.

The simple shell morphology of the Patellacea has been a problem since the time of Lamarck and Linné. In the late 1700's all mollusks with a limpetlike shell were assigned to the genus *Patella*. As studies were conducted, many taxa were removed from the genus (e.g., *Siphonaria* Sowerby, 1823; *Fissurella* Bruguiere, 1789; *Diodora* Gray, 1821; *Hipponix* DeFrance, 1819; *Capulus* Montfort, 1810; etc.) (see POWELL, 1973:84). The "acmaeids" were one of the last groups to be removed. In this early period there was no attempt to diagnose the patellacean groups on their own characters. They were, and in some cases remain, the residual taxa that are left when non-members are identified and removed. Thus, we have been left with a form taxon, composed of numerous lineages.

It is no accident of history that J. E. Gray is associated with all three taxa discussed above; Gray examined the animals, rather than simply their shells. Every study of a patellacean group that has considered more than shell morphology has led to a better understanding and more taxonomic divisions. Analogous situations have occurred in many other molluscan groups. Consider the genus *Trochus*, *sensu* Linné, 1758. We no longer consider *Trochus* to be the principal genus in the Trochidae with a worldwide distribution. Instead, we recognize numerous genera, including *Tegula* Lesson, 1835, *Calliostoma* Swainson, 1840, and *Margarites* Gray, 1847, in the northeastern Pacific; *Cantharidus* Montfort, 1810, *Monodonta* Lamarck, 1799, and *Gibbula* Risso, 1826, in the northeastern Atlantic; and *Austrocochlea* Fischer, 1885, *Umboonium* Link, 1807, *Phasianotrochus* Fischer, 1885, and *Chlorodiloma* Pilsbry, 1889, in the austral region. Today, *Trochus* is restricted to the Indo-Pacific and its definition no longer includes

the vast majority of the trochid species. Similar changes are now occurring in the Patellacea.

ACKNOWLEDGMENTS

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A New Species of *Adontorhina* (Bivalvia: Thyasiridae) from the Northeast Pacific, with Notes on *Adontorhina cyclia* Berry, 1947

by

PAUL H. SCOTT

Department of Invertebrate Zoology, Santa Barbara Museum of Natural History,
2259 Puesta del Sol Road, Santa Barbara, California 93105, U.S.A.

Abstract. A minute bivalve, *Adontorhina sphaericosa* Scott, spec. nov. (Thyasiridae), is described from Boca de Quadra, Alaska. The new species occurs from 95 to 330 m in two fjords in southeast Alaska, at 165 m in British Columbia, and from 204 to 458 m on the continental slope of Oregon. The morphologic relationship and familial placement of three thyasirids, *Adontorhina*, *Axinulus*, and *Leptaxinus*, are discussed. Diagnostic characters separating these three genera are proposed and illustrations of the primary type specimens are included. A revised description and new records of *Adontorhina cyclia* Berry, 1947, are reported, including a major northern range extension to the Bering Sea, Alaska. The gross anatomy for both species of *Adontorhina* is described and illustrated.

INTRODUCTION

WHILE INVESTIGATING the mollusks of the Boca de Quadra fjord, Alaska, a new thyasirid was discovered. Subsequent study of material from British Columbia and the continental slope of Oregon yielded the same species. Generic placement proved difficult due to the paucity of literature on the three minute thyasirid genera *Adontorhina* Berry, 1947, *Axinulus* Verrill & Bush, 1898, and *Leptaxinus* Verrill & Bush, 1898. All species in the genera have small, white shells with poorly developed dentition. The previously published accounts do not elucidate the differences between these conchologically similar genera. Examination of the primary type material was illuminating, with the new species belonging to *Adontorhina*. The new species of *Adontorhina* is here described and an expanded description of *A. cyclia* Berry, 1947, is provided, along with new distributional and habitat records.

CONVENTIONS AND ABBREVIATIONS

The following treatment includes a description of the two species of *Adontorhina*, with information on type specimens and localities, and notes on distribution and habitat. All taxonomic references are listed in the bibliography.

The following are abbreviations of institutions used in the text: CAS, California Academy of Sciences; LACM, Los Angeles County Museum of Natural History; MCZ,

Museum of Comparative Zoology; NMC, National Museum of Canada; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; USNM, United States National Museum of Natural History.

TAXONOMIC ACCOUNT

Family THYASIRIDAE Dall, 1901

Subfamily AXINOPSINAE Bernard, 1983

Adontorhina Berry, 1947

(Type species: *Adontorhina cyclia* Berry, 1947; by original designation)

Shell small, fragile, orbiculoid to spheroid; beaks prosogyrous and moderately prominent; periostracum thin, adherent, silky to highly polished; ligament internal, resting on a narrow shelf posterior to the beaks; hinge plate narrow to moderately wide, composed of two sections, one section extending anterior to the beaks, the other section located centrally along the posterodorsal margin; without true teeth but with minute granules along the hinge plates that intermesh much like mammalian molars, granules varying between specimens from weakly to strongly expressed; pallial line entire [emended BERRY, 1947:260].

The systematic relationships of *Adontorhina* have been questioned by some investigators. BERRY (1947) was un-

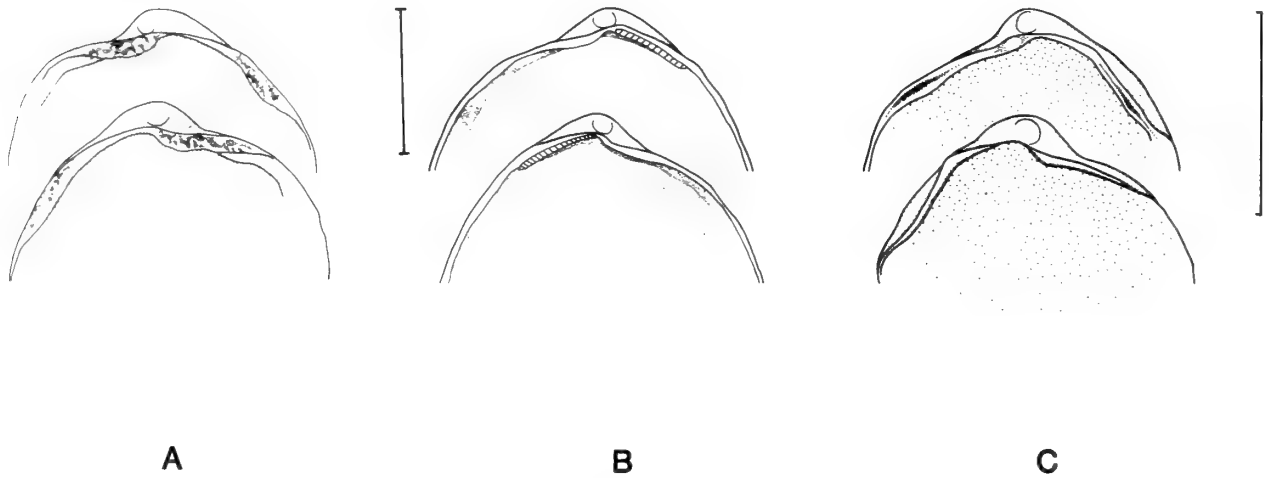


Figure 1

Hinge plates of minute thyasirids. A. *Adontorhina cyclia*, paratype, MCZ 165903. B. *Axinulus brevis*, holotype, USNM 159873. C. *Leptaxinus minutus*, holotype, USNM 45686. Scale bars = 1 mm.

certain about his placement of *Adontorhina* into the family Thyasiridae. *Adontorhina cyclia* was described from the Lower Pleistocene ("Hilltop Quarry," San Pedro, California) and the lack of soft parts and the unusual hinge may have caused the confusion. HERTLEIN & GRANT (1972) considered that the granular hinge plate and the lack of a radial sulcus precluded placement in the Thyasiridae. My recent inspection of the soft parts of *Adontorhina cyclia* and *Adontorhina sphaericosa* further adds to the uncertainty. While the two species have arborescent digestive glands characteristic of Thyasiridae (ALLEN, 1958; BERNARD, 1972, 1979), they have only a single demibranch per ctenidium, a character of the Lucinidae (ALLEN, 1958). Inspection of the ctenidia of *Axinulus careyi* Bernard, 1979, also showed a single demibranch, as well as a lucinid "heel" on the foot. I am continuing to study the anatomy of minute "thyasirids" in order to further define family characters. Until such a study is complete, I feel *Adontorhina* and *Axinulus* are best retained in the Thyasiridae.

A thorough treatment of the minute thyasirid genera has not been published in this century. *Adontorhina*, *Axinulus*, and *Leptaxinus* all have small fragile shells with a weakly expressed hinge. DALL (1901) included a cursory comment on *Leptaxinus*, "shell like *Axinulus*, but with distinct lateral teeth." He placed *Axinulus* as a subgenus of *Thyasira* Lamarck, 1818, "with the dorsal areas obsolete" (DALL, 1901). A relationship between *Adontorhina* and *Axinulus* is alluded to by KEEN & COAN (1974). BERNARD (1979) mentioned the difficulty in separating *Axinulus* and *Leptaxinus*, and considered *Axinulus careyi* as intermediate between these two genera. CHAVAN (1969) discussed all three genera but did not give diagnostic characters to easily separate them.

Although a complete revision of these genera is not within the scope of this paper, examination of type material of the type species of the three genera yielded the following distinctions. *Adontorhina cyclia* Berry, 1947, has a narrow to broad hinge plate with a unique granular appearance. Anteriorly, the hinge granules are distinct, and weakly to moderately expressed posteriorly (Figure 1A). *Axinulus brevis* Verrill & Bush, 1898, has a narrow hinge plate that is smooth and edentulous (Figure 1B), although a minute hinge tubercle beneath the beak may be present in some species of *Axinulus*. The hinge plate of *Leptaxinus minutus* Verrill & Bush, 1898, is narrow but not simple; the right valve has a small tubercle beneath the beak, which fits into a corresponding notch in the left valve. The right valve also has long anterior and posterior lateral grooves into which the dorsal shell margin of the left valve is seated (Figure 1C).

Adontorhina sphaericosa Scott, spec. nov.

(Figures 2-5, 9A, 12, 13)

Description: Exterior: Shell small (<2 mm), thin, fragile, white to transparent, highly inflated; periostracum thin, adherent, highly polished; surface smooth except for low irregular incremental growth striae visible under high magnification; beaks central, inflated, slightly prosogyrate; lunule weakly expressed, not demarcated by a line or ridge; escutcheon wide, deep, well defined, extending from beaks to posterodorsal margin; outline suborbiculate, anteroventral margin slightly drawn out; strongly adherent red-brown mud present along the anterior and posterior dorsal margins of many specimens.

Interior: Hinge plate narrow to moderately wide, edentulous with irregular granules; hinge plate with two dis-

tinct sections: (1) an anterior plate extending from just posterior of the beaks to three-fourths of the way to the anterior margin, and (2) a posterior plate centrally located along the posterodorsal margin not extending to beaks or posterior margin; ligament internal, long, narrow, reddish-brown, extending from the anterior hinge plate to the posterior hinge plate; adductor muscle scars moderately to weakly impressed, ovate, sub-equal in size; pallial line entire, thin, moderately to weakly impressed.

Gross anatomy: Mantle thin, transparent, margins thickened; mantle fusion limited to a small section ventral to the single posterior opening; anterior adductor muscle large, elongate, ventral edge slightly curved inward of the mantle margin; posterior adductor muscle very small, sub-ovate, continuous with mantle margin; foot elongate, vermiform, with bulbous distal section; each ctenidium consisting of a single demibranch; mouth very large; labial palps of moderate size for family; digestive gland and gonadal tissue forming a single mass of arborescent tufts; rectum located dorsally between the ctenidia, visible only in dorsal view, extending from beaks to the posterior adductor muscle; renal tissue ventral of rectum between the ctenidia, with distinct concretions.

Type locality: Boca de Quadra fjord, southeast Alaska, 55°10.2'N, 130°37.5'W, 280 m depth, in 90% silt and clay, Coll. Robert Cimberg, September 1981.

Type measurements (mm) and deposition:

	Length	Height	Width (sv = single valve)	Depository
Holotype	1.6	1.6	1.3	SBMNH 33911
Paratypes	1.5	1.5	1.2	SBMNH 33910
	1.2	1.2	0.9	SBMNH 33910
	1.6	1.6	1.2	SBMNH 33910
	1.3	1.3	0.6 (sv)	SBMNH 33910
	1.4	1.4	0.6 (sv)	SBMNH 33910
	1.5	1.5	0.7 (sv)	SBMNH 33910
	1.3	1.3	0.6 (sv)	SBMNH 33910
	1.4	1.4	0.7 (sv)	SBMNH 33910
	1.4	1.4	0.6 (sv)	SBMNH 33910
	1.3	1.3	0.6 (sv)	SBMNH 33910
Paratypes	1.4	1.5	1.2	CAS 057048
	1.5	1.5	1.2	CAS 057048
	1.4	1.3	1.0	CAS 057048
Paratypes	1.6	1.6	1.2	LACM 2087
	1.5	1.5	1.3	LACM 2087
	1.4	1.4	1.1	LACM 2087
Paratypes	1.5	1.5	1.1	NMC 92606
	1.5	1.6	1.2	NMC 92606
	1.5	1.5	1.1	NMC 92606
Paratypes	1.4	1.4	1.0	USNM 847155
	1.5	1.6	1.3	USNM 847155
	1.4	1.4	1.1	USNM 847155

Etymology: The specific name is derived from the Greek

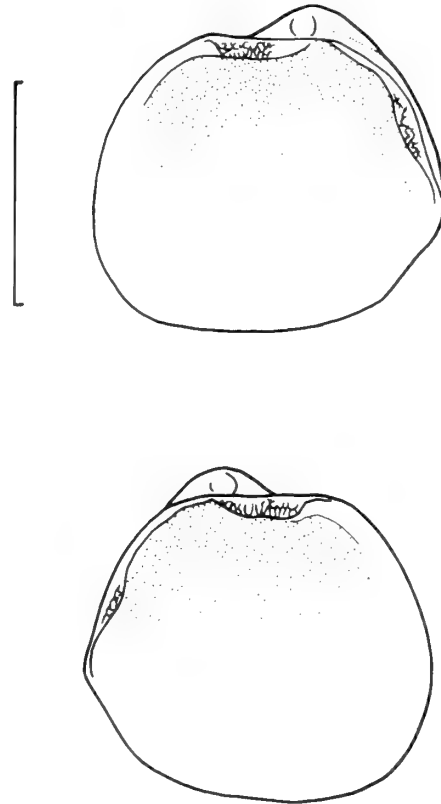


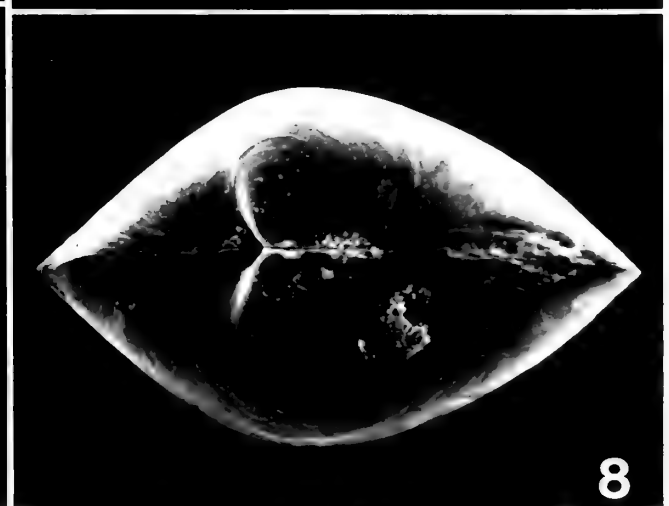
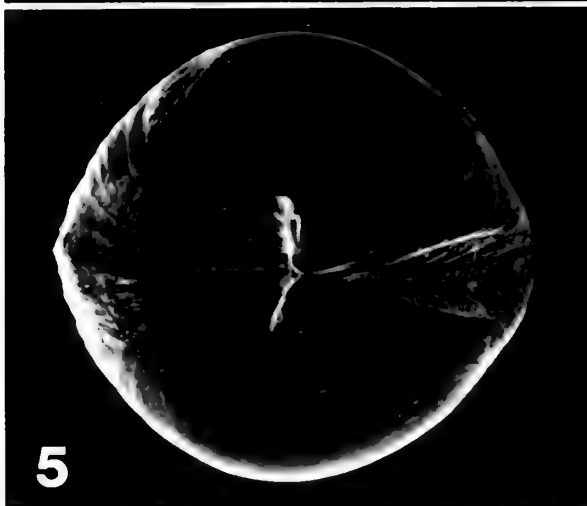
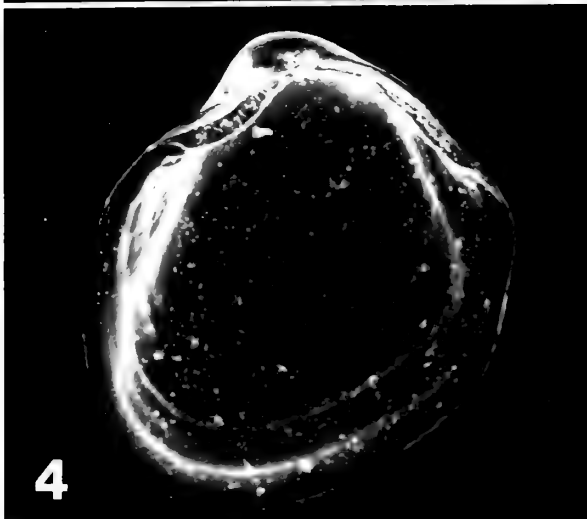
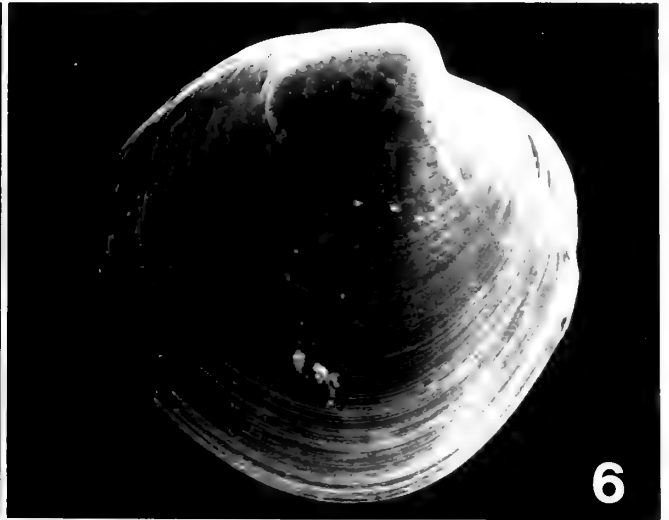
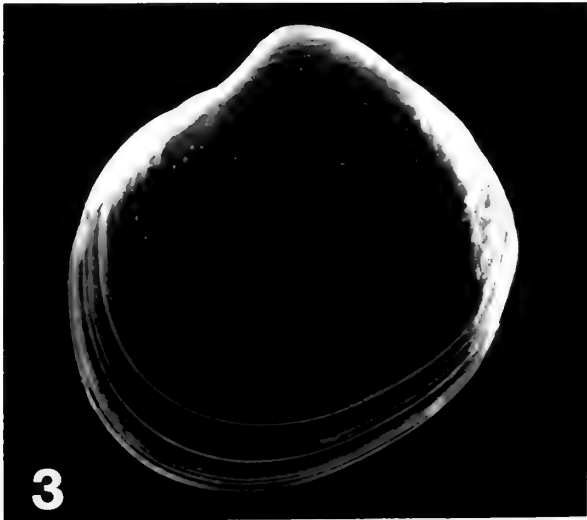
Figure 2

Internal view of left and right valves of *Adontorhina sphaericosa* Scott, holotype, SBMNH 33911, Boca de Quadra, Alaska. Scale bar = 1 mm.

sphairikos, referring to the inflated, spheroid shape of the shell.

Material examined: 65 lots from Alaska, 1 lot from British Columbia, 14 lots from Oregon; approximately 350 total specimens.

Distribution and habitat: Smeaton Bay, Alaska (55°18.5'N, 130°45.8'W, SBMNH 34041); Boca de Quadra, Alaska (55°10.2'N, 130°37.5'W, SBMNH 34042); British Columbia, Canada (48°43.8'N, 123°20.5'W, SBMNH 34043); and off Newport, Oregon (43°48.7'N, 124°50.5'W, SBMNH 34044). *Adontorhina sphaericosa* has yet to be found off Washington although the species probably occurs there. Lack of sampling at the proper depth or damage of this fragile species during collection or processing may account for the absence of specimens. Known depth distribution is from 95 to 330 m in Alaska, 165 m in British Columbia, and from 204 to 458 m in Oregon. *Adontorhina sphaericosa* has been found only in fine sediments ranging from 81 to 95% silt and clay. Bottom temperatures at stations where the species



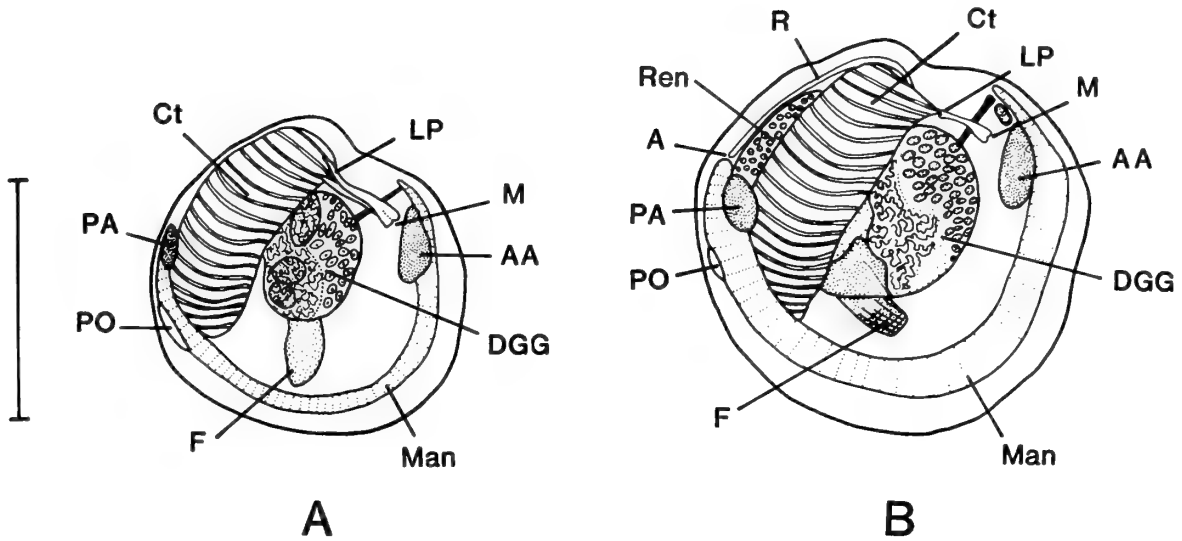


Figure 9

Gross anatomy. A. *Adontorhina sphaericosa*, SBMNH 34040, Boca de Quadra, Alaska. B. *Adontorhina cyclia*, SBMNH 34039, off Coos Bay, Oregon. Key: A, anus; AA, anterior adductor muscle; Ct, ctenidium; DGG, digestive gland-gonad; F, foot; LP, labial palps; M, mouth; Man, mantle; PA, posterior adductor muscle; PO, posterior opening; R, rectum; Ren, renal tissue. Scale bar = 1 mm.

was found ranged from 4° to 7°C in Alaska (VTN, 1980, 1981) and from 5° to 7.5°C in Oregon waters (R. E. Ruff, personal communication, 1984).

Comparison: *Adontorhina sphaericosa* is easily differentiated from *A. cyclia* by the well-defined escutcheon and the extreme inflation of the valves of the former species. Juvenile specimens of *A. sphaericosa* are less inflated than adults but do exhibit a distinct escutcheon.

Adontorhina cyclia Berry, 1947

(Figures 1A, 9B, 6–11)

BERRY, 1947:260–261, plate 1, figures 1, 2; HOWARD, 1952: 5; JONES, 1965:127–141, figure 1; HERTLEIN & GRANT, 1972:254; BERNARD, 1983:30.

Description (expanded BERRY, 1947): Exterior: Shell

small (<3 mm), thin, fragile, white to transparent; moderately inflated; periostracum thin, adherent, silky to shiny; surface smooth except for incremental striae visible under high magnification; beaks slightly anterior of center, moderately inflated, slightly prosogyrate; lunule weakly expressed, not demarcated by a line or ridge; escutcheon faintly impressed, visible only under high magnification; anterodorsal margin almost straight, perpendicular to beaks; posterodorsal margin straight to gently curved; in some specimens, a very slight radial undulation extending from posterior of beaks to posterior margin; strongly adherent red-brown mud present along the anterior and dorsal margins of many specimens.

Interior: Hinge plate narrow to moderately wide, edentulous with irregular granules weakly to strongly expressed; hinge plate composed of two sections: (1) an anterior plate of variable length extending from under beaks

Explanation of Figures 3 to 8

Figures 3–5. Scanning electron micrographs of three specimens of *Adontorhina sphaericosa* from southeast Alaska.

Figure 3. External view of left valve, Boca de Quadra, Alaska; length = 1.55 mm, height = 1.53 mm.

Figure 4. Internal view of right valve, Boca de Quadra, Alaska; length = 1.50 mm, height = 1.70 mm.

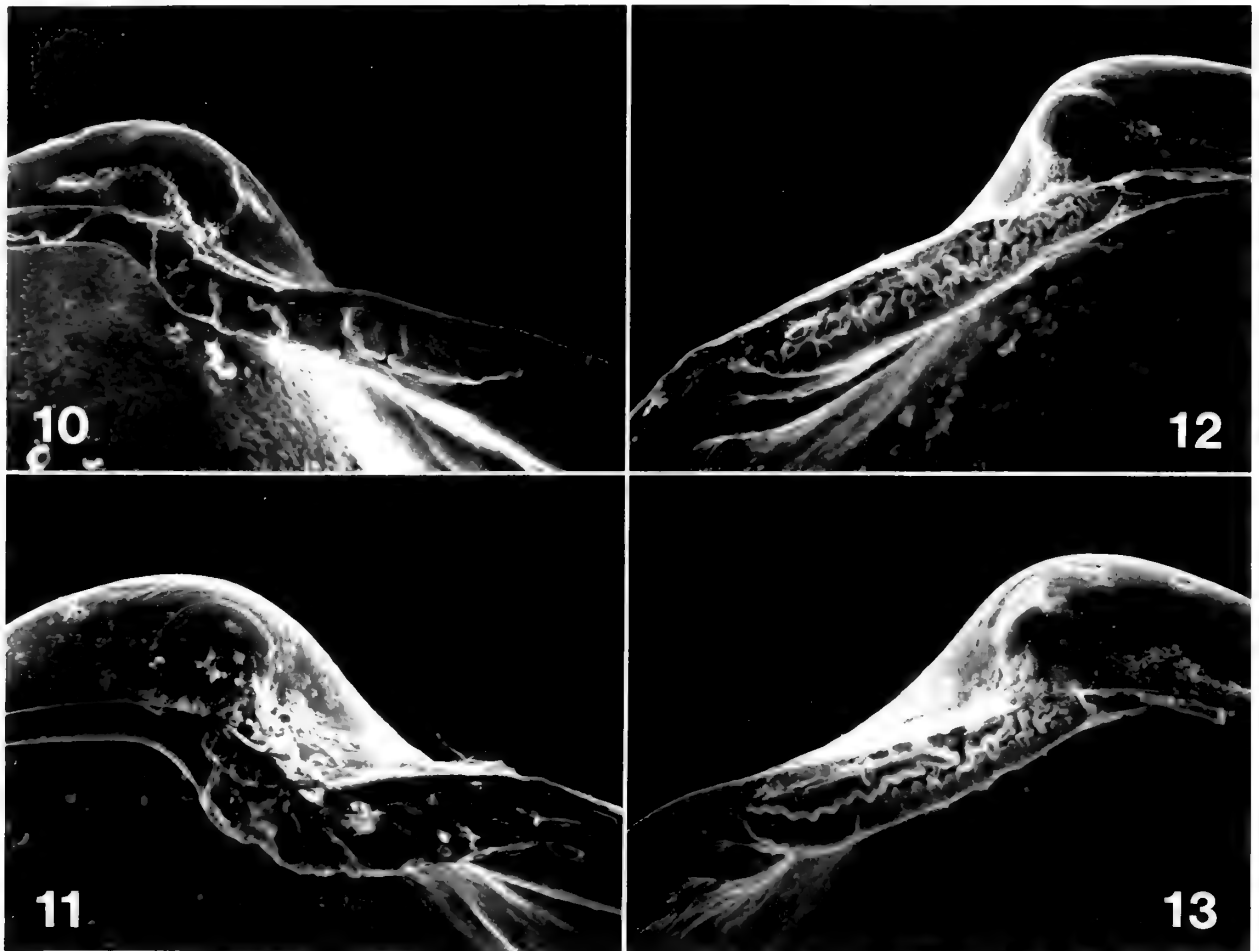
Figure 5. Dorsal view of both valves, Smeaton Bay, Alaska; length = 1.73 mm.

Figures 6–8. Scanning electron micrographs of three specimens of *Adontorhina cyclia* Berry, 1947, from southeast Alaska.

Figure 6. External view of right valve, Smeaton Bay, Alaska; length = 2.05 mm, height = 2.07 mm.

Figure 7. Internal view of right valve, Smeaton Bay, Alaska; length = 1.80 mm, height = 1.87 mm.

Figure 8. Dorsal view of both valves, Smeaton Bay, Alaska; length = 2.00 mm.



Explanation of Figures 10 to 13

Scanning electron micrographs showing details of the anterior hinge plates of *Adontorhina* from Alaska and Oregon.

Figure 10. Left valve of *Adontorhina cyclia*, off Coos Bay, Oregon; 120 \times . Note narrow, obscure hinge plate.

Figure 11. Left valve of *Adontorhina cyclia*, Smeaton Bay, Alaska; 120 \times . Note wide, thickened hinge plate.

Figure 12. Right valve of *Adontorhina sphaericosa*, Boca de Quadra, Alaska; 90 \times . Note fine hinge granules.

Figure 13. Right valve of *Adontorhina sphaericosa*, Boca de Quadra, Alaska; 90 \times . Note long, heavy, lamellar hinge plate.

to anywhere from one-fourth to three-fourths of the way to the anterodorsal margin, (2) a posterior plate weakly defined to obscure, when present centrally located along the posterodorsal margin, granules obscure on posterior plate; ligament internal, long, narrow, extending between anterior hinge plate and posterior hinge plate; adductor scars weakly impressed, ovate/elongate, subequal in size; pallial line thin, entire, weakly impressed.

Gross anatomy: Mantle thin, transparent, margins thickened; mantle fusion limited to a small region ventral to the single posterior opening; anterior adductor muscle large, elongate, ventrally curved inward from the mantle margin; posterior adductor muscle small, subovate, con-

tinuous with mantle margin; foot elongate, vermiform, without bulbous distal section; each ctenidium consisting of a single demibranch; mouth large; labial palps very reduced; digestive gland and gonadal tissue forming a single mass of arborescent tufts; rectum dorsal to the ctenidia, extending posteriorly from the beaks and curving along the dorsal margin; anus slightly dorsal of posterior adductor muscle; renal tissue directly ventral of the rectum, with distinct concretions.

Material examined: Holotype, 4 paratype lots; 1 lot from Mexico; 17 lots from California, including 4 lots from San Pedro Pleistocene; 50 lots from Oregon; 136 lots from Alaska; approximately 2300 total specimens.

Type locality: Lower Pleistocene, "Hilltop Quarry," San Pedro, Los Angeles County, California (33°45.3'N, 118°18.3'W).

Location of type material: Holotype: CAS 61460, 1 left valve (from Stanford Univ. Paleo. Type Coll. LSJU 7865, ex S. S. Berry Coll. 10404). Paratypes: SBMNH 34033 (from S. S. Berry Coll. 10405); USNM Paleontology 560376; CAS 044002 (from Stanford Univ. Paleo. Type Coll. LSJU 7865); SDNHM Paleontology 320, 321, 0639, 04312 and 04313 (each valve in lot given a separate number); MCZ 16590; no paratypes were deposited at the Paleontological Research Institute (P. Hoover, personal communication) or California Institute of Technology (G. Kennedy, personal communication) contrary to BERRY (1947); paratype deposited in E. P. Chace collection not found.

Distribution and habitat: Bering Sea, Alaska (58°36.0'N, 174°56.0'W, LACM 60-26.27) to Guadalupe Island, Baja California, Mexico (29°09'N, 118°17'W, LACM 51-44), one live specimen was also collected in the Gulf of California off Bahia de Los Angeles, Baja California, Mexico (28°53'40"N, 113°32'45"W, LACM 36-53). Depth distribution in southern California is from 11.6 to 1886 m (JONES, 1965; JONES & THOMPSON, in press). *Adontorhina cyclia* has been collected from 36 to 116 m in Oregon and from 22 to 330 m in Alaska. The records from northern waters are not as extensive as the southern California data in JONES (1965). The depth range in the northern localities may be considerably expanded when additional samples are collected and identified. As expected by a species with a broad depth distribution, *A. cyclia* is able to live in a variety of sediments. JONES (1965) reports the species in sand to clayey silt with the highest densities at 40–60% silt and clay. Bottom temperatures at depths less than 600 m range from 9.3 to 15.4°C in southern California (JONES, 1965), 7.9° to 8.9°C in Oregon (R. E. Ruff, personal communication, 1984), and 5° to 7°C in Alaska (VTN, 1980, 1981).

An additional fossil locality is Timms Point, San Pedro, Los Angeles County, California (LACM Invert. Paleo. 130-6 and 130-7) in Timms Point Silt; Pleistocene.

DISCUSSION

Although *Adontorhina cyclia* is a common component of the infauna at continental shelf and slope depths from Oregon to Alaska, this is the first report of the species from these regions. It is probable that the species has been confused with the juveniles of the numerically dominant *Axinopsida serricata* (Carpenter, 1864). Externally the two species are superficially similar, each being small, white, fragile and orbicular. However, *Adontorhina cyclia* is more inflated and exhibits a nearly straight anterodorsal margin. Internally the hinge structure is completely different, with *Adontorhina cyclia* possessing an edentulous, granular hinge plate, and with *Axinopsida serricata* having a distinct

pseudocardinal tooth in the right valve and a corresponding pit in the left valve.

Adontorhina sphaericosa and *Adontorhina cyclia* occurred together at 16 stations in southeast Alaska. Both species were found at 7 stations in Boca de Quadra fjord in depths from 95 to 330 m, and at 9 stations in Smeaton Bay in depths from 148 to 265 m. Densities were approximately 20/m² for each species at these stations. Other common thyasirid species at these stations include *Axinopsida serricata* (Carpenter, 1864) and *Thyasira gouldii* (Philippi, 1845).

The hinge plate of both species of *Adontorhina* is exceedingly variable. Specimens of *A. cyclia* can vary from having a narrow, obscure anterior plate (Figure 10) to a moderately wide, thickened anterior plate (Figure 11). The "granules" of *A. sphaericosa* vary greatly among specimens. They can be very numerous and small (Figure 12) or coalesced into long lamellar plates (Figure 13). In all specimens of *Adontorhina* I have observed, no two hinge plates exhibited the same granule pattern. The unique qualities of the hinge granules of each specimen is indeed very reminiscent of the individual variations in human fingerprints.

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Descriptions of Two New Gastropods of the Trichotropidae from Kerguelen and Crozet Islands (South Indian Ocean)

by

ANDERS WARÉN

Swedish Museum of Natural History, Box 50007, S-10405 Stockholm, Sweden

PATRICK M. ARNAUD

Station Marine d'Endoume (CNRS-UA.41), F-13007 Marseille, France

AND

JAIME R. CANTERA

Departamento de Biología, Universidad del Valle, Cali, Colombia

Abstract. Two new species of prosobranchs, *Torellia lanata* and *T. (Neoconcha) angulifera*, are described from Kerguelen and Crozet islands. The two species are compared to all previously described Antarctic trichotropids and to some similar species from other areas. *Neoconcha vestita* Smith, 1907, is transferred to *Torellia* and given a new name, *T. (N.) smithi*, because of homonymy with *T. vestita* Jeffreys, 1867. The larval development in some species of *Torellia* is discussed.

INTRODUCTION

THE FAMILY TRICHOTROPIDAE Gray, 1850, is today represented by several common species in Arctic and Antarctic areas, both in deep and shallow waters. In tropical areas, however, the family is rare and restricted to depths below 100–200 m with two rare exceptions: *Separatista helicoides* (Gmelin, 1791), which lives associated with a polychaete (HABE, 1962:76), and *Lippistes cornea* (Gmelin, 1791), of which the biology is unknown. As far as is known, trichotropid species are ciliary feeders (YONGE, 1962; GRAHAM, 1954) and hermaphrodites. They have a well developed pseudoproboscis that is actually a drawn-out lower lip. Other good characters for recognizing the family are: an operculum with strongly corroded apical or lateral nucleus, usually a hairy periostracum, and distinct sculpture of close set, sharp riblets, smaller than the spiral ribs. A wide umbilicus is usually present and most genera have a well developed siphonal canal, which, how-

ever, is poorly developed or absent in *Torellia* and a few other groups.

The two species described below were found in connection with work on the Antarctic molluscan fauna by two of us (P.M.A. and J.R.C.) and revisory work on the family Trichotropidae by the third one (A.W.).

SYSTEMATICS

Family TRICHOTROPIDAE Gray, 1850

Genus *Torellia* Jeffreys, 1867

Type species: *Torellia vestita* Jeffreys, 1867, by monotypy.

Diagnosis: Trichotropidae with a low-spired shell of 2–4 evenly rounded teleoconch whorls of evenly increasing diameter. Siphonal canal poorly developed or absent. Peri-

ostracum well developed, sometimes more solid than the shell, usually hairy.

Torellia lanata Warén, Arnaud & Cantera

(Figures 1, 2, 13, 21–24)

Neoconcha sp. 1: CANTERA & ARNAUD, 1985:57.

Material (for station data, cf. CANTERA & ARNAUD, 1985):

- Ker (1964): Ch.1: 1 specimen.
- Cruise MD.03 (1974): CB.7: 2 specimens (and 1 empty shell); CB.50: 1; CP.58: (2); CP.59: 11, including holotype; CB.61: 2; CB.62: 3; CP.72: 1 (1).
- Cruise MD.04 (1975): DC.8: (1); CP.13: 4; DC.37: 1; CB.60: 1; CP.61: 2; CP.92: 2; CP.182: (1); CP.226: 2; CP.285: (1).
- Cruise MD.30 (1982): CP.64: 1; DC.202: (1).

Deposition: Holotype (from MD.03-CP.59) and paratypes in Museum National d'Histoire Naturelle, Paris (no catalogue numbers assigned); paratypes in British Museum (Natural History), London (BMNH 1985163), and U.S. National Museum, Washington (USNM 859004).

Type locality: The holotype is from "Marion-Dufresne" cruise MD.03; CP.59, 43°59.2'S, 70°01.9'E, 158 m, 16 April 1974, SE of Kerguelen Is.

Distribution: Collected live between 165 and 465 m at Crozet Is. (NW of Ile des Pingouins and between Ile aux Cochons and Ile de la Possession), and between 60 and 585 m around Kerguelen Is. (mixed bottoms with calcareous sand, diatomaceous mud, basaltic gravel and boulders).

Description: Shell: Large for the family, rather fragile, inflated, white and covered by a thick, woolly, cream-colored or beige periostracum. Larval shell (Figures 21, 22) not very distinctly set off; sculptured by sharp, distinct spiral lines and less distinct, curved axial riblets; consisting of 2.5 whorls, diameter 1.6–1.8 mm. Holotype (unusually large) with 3.1 teleoconch whorls of rapidly increasing diameter. Initial part of teleoconch with about 10 narrow spiral ribs and weaker but more close-set incremental lines, together giving this part of shell a reticulated appearance. Periostracum later thickens, partly concealing the less sharp sculpture here. Initial part of teleoconch evenly rounded, later cross sections of whorls more polygonal: two keels between sutures, two keels infraperipherally, one sharp (80°) periumbilical keel forming lower corner of aperture. Keels emphasized by triangular periostracal tufts. Suture deep, channeled, partly filled by periostracum that may also cover lower part of preceding whorl. Thin parietal callus and straight columella formed by inner lip. Umbilicus broad and deep, more so in adults. Periostracum of numerous, high incremental lamellae of an opaque core and a thicker mucus-resembling outer layer (almost invisible when dry) gives

the shell a thick and woolly appearance when wet contrasting with the thin, fragile-appearing shell when dry (Figures 1, 2).

Dimensions: Height of the shell 21.5 mm, diameter 22.3 mm; height of the aperture 14.2 mm, breadth 12.5 mm (holotype).

Soft parts: Tentacles short, stout, of the same length as the breadth of the snout, eyes on basal bulges of the outer sides. Penis simple, finger-shaped, flattened, curved backwards. Pseudoproboscis large, kept in a large cavity between head and foot. Hermaphrodite. Foot small. Operculum semicircular, with the curved side facing the columella and a lateral nucleus that is corroded away in adult specimens. Radula, see Figure 13.

Remarks: *Torellia lanata* resembles *T. insignis* Smith, 1915, and *T. planispira* Smith, 1915, in having strong periostracal keels. It differs, however, from the first-mentioned by having a distinct angle in the lower corner of the aperture and from the latter by having a higher spire. It differs also from *T. insignis* in having a proportionally broader radula and different shape of the radular teeth (cf. figure of *T. smithi*, which closely resembles *T. insignis*). Another difference is the larval shell, which in *T. insignis*, *T. smithi*, and *T. planispira* consists of 1.3 spirally striated whorls of a diameter of 2.0–2.2 mm. *Torellia antarctica* (Thiele, 1912) (Figures 4, 5), which was based on a very young specimen with only slightly more than one postlarval whorl, differs by having strong spiral ridges on this first whorl and a larval shell of a diameter of 1.5 mm consisting of 1.5 whorl. THIELE (1912:plate 15, figure 21) figured the radula of *T. antarctica*. This figure looks rather different compared with Figures 11–14, but as mentioned before, his single specimen was very young and a corresponding change in radular morphology with age is discussed below (Discussion, Systematic Position).

Torellia (Neoconcha) angulifera

Warén, Arnaud & Cantera

(Figures 3, 8, 14–16, 23, 24)

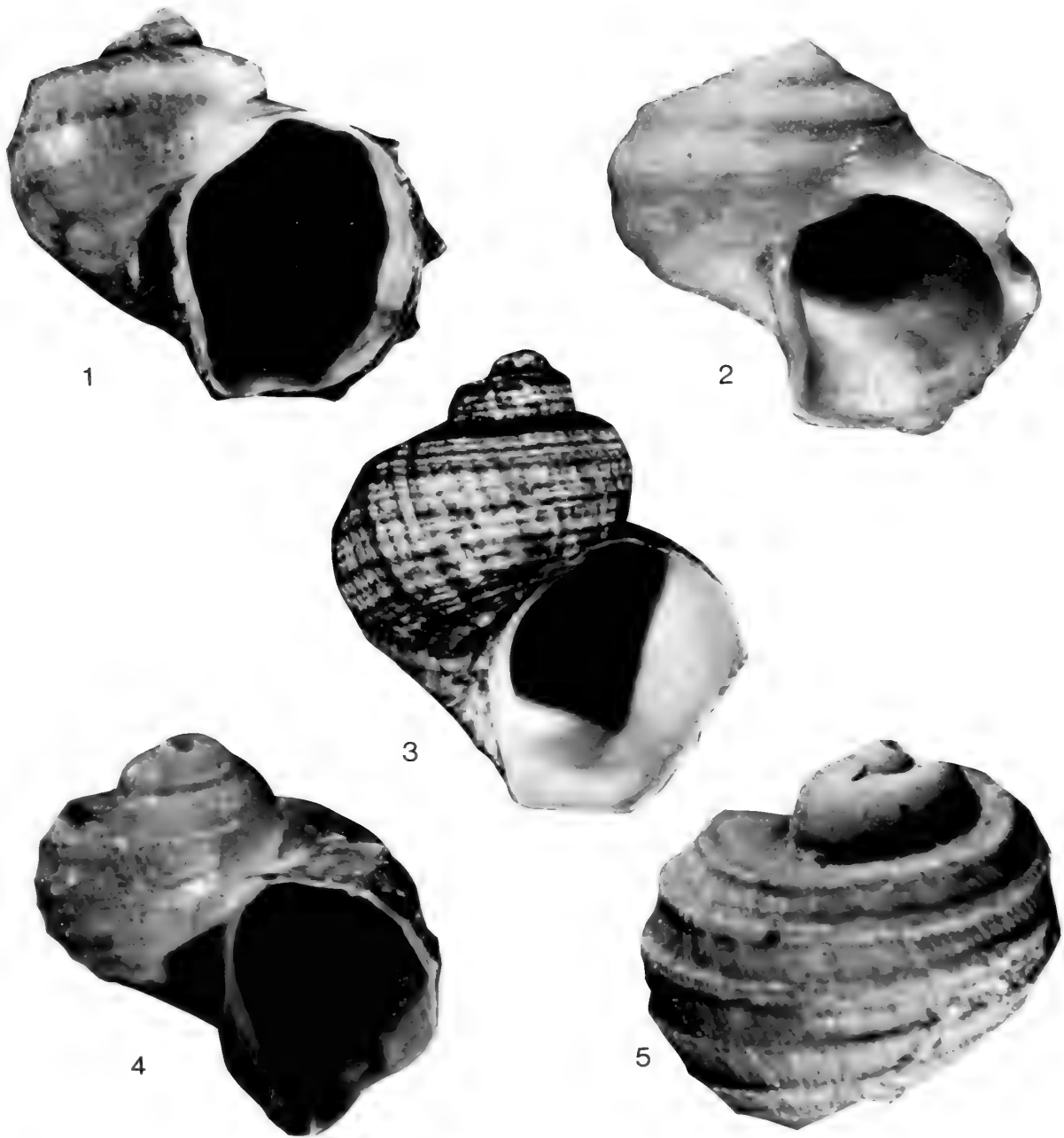
Antitrichotropis antarctica, non Thiele, 1912: CANTERA & ARNAUD, 1985:56.

Material (for station data, cf. CANTERA & ARNAUD, 1985):

- Cruise MD.04 (1975): BB.9: (1 empty shell); DC.218: 1 (holotype); BB.219–220: (1).
- Cruise MD.30 (1982): DC.24: 2 (5); CP.28: (1); DC.60: 1 (4); DC.205: (6); DC.229: (2); DC.258: (3).

Deposition: Holotype (from MD.04-DC.218) and paratypes in Museum National d'Histoire Naturelle, Paris (no catalogue numbers assigned); paratypes in British Museum (Natural History), London (BMNH 1985164), and U.S. National Museum, Washington (USNM 859005).

Type locality: The holotype is from "Marion-Dufresne"



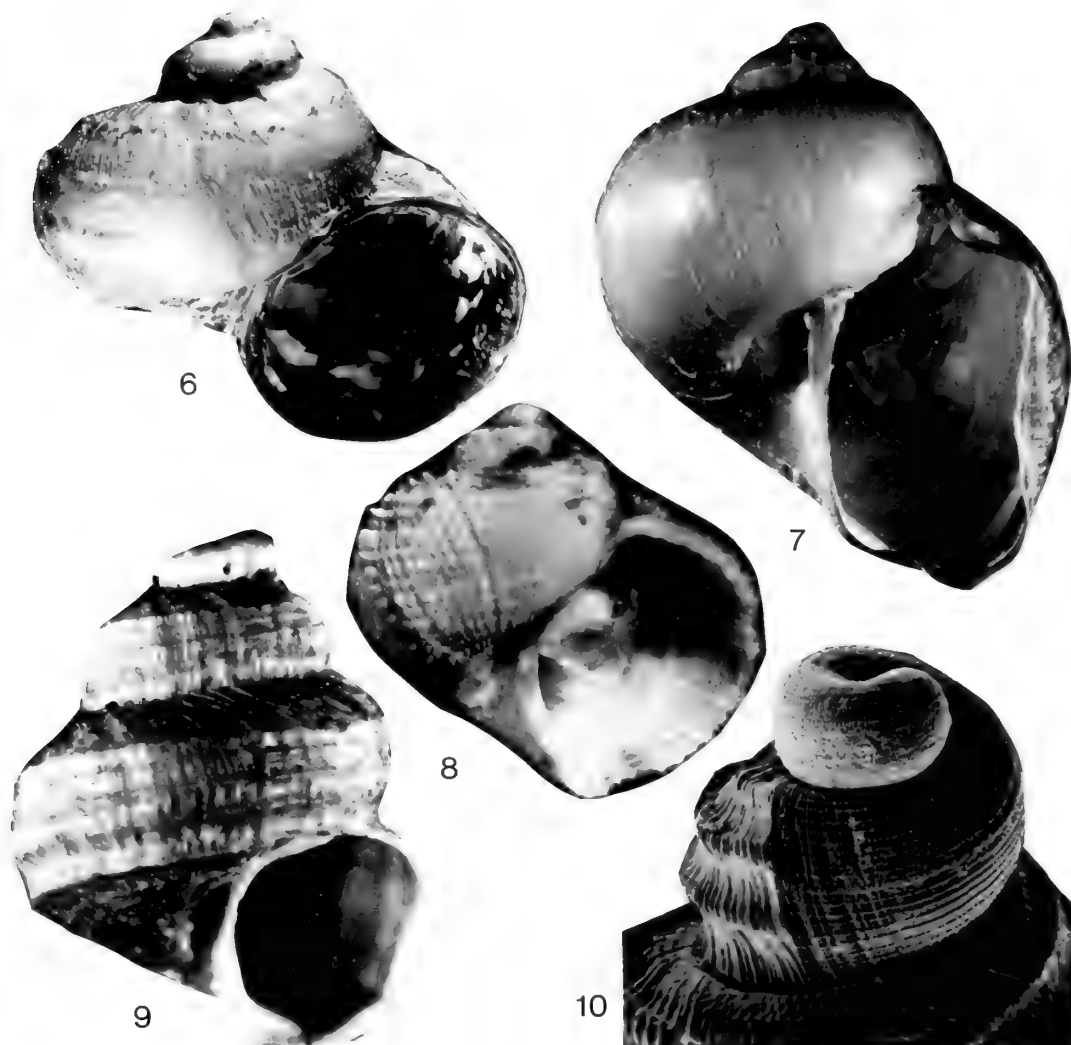
Explanation of Figures 1 to 5

Figure 1. *Torellia (Torellia) lanata*, spec. nov., MD.03-CP.59, SE Kerguelen Islands. Diameter 18.2 mm.

Figure 2. *Torellia (T.) lanata*, wet specimen, MD.03-CP.59. Diameter 21 mm.

Figure 3. *Torellia (Neoconcha) angulifera*, spec. nov., MD.04-DC.218, NNE Kerguelen Islands. Height 10.6 mm, holotype.

Figures 4 and 5. *Torellia (N.) antarctica* (Thiele, 1912), syntypes, Zoologisches Museum der Humboldt Universität, Berlin, registration number 63023. Diameters 2.7 and 2.3 mm, respectively.



Explanation of Figures 6 to 10

Figure 6. *Torellia (Neoconcha) insignis* Smith, 1915, Terre Adélie, Antarctica, SE of Curie Island, 110-130 m. Diameter 21.9 mm.

Figure 7. *Torellia (N.) smithi*, nom. nov., Terre Adélie, Antarctica, between Cap Bernard and Curie Island, 139-140 m. Diameter 14 mm.

Figure 8. *Torellia (N.) angulifera*, MD.30-DC.24, Crozet Islands, wet specimen showing periostracum. Diameter 7.3 mm.

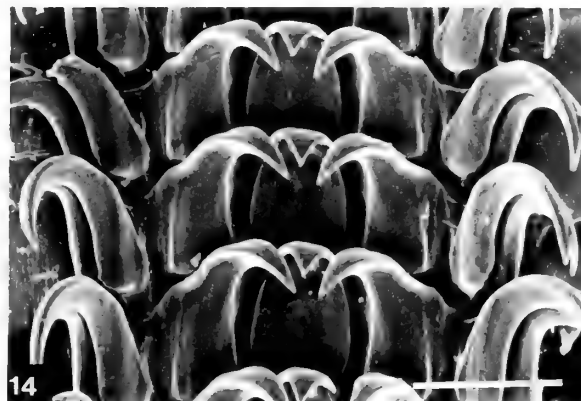
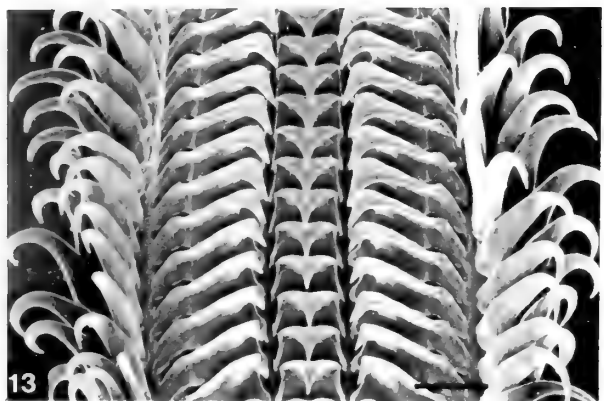
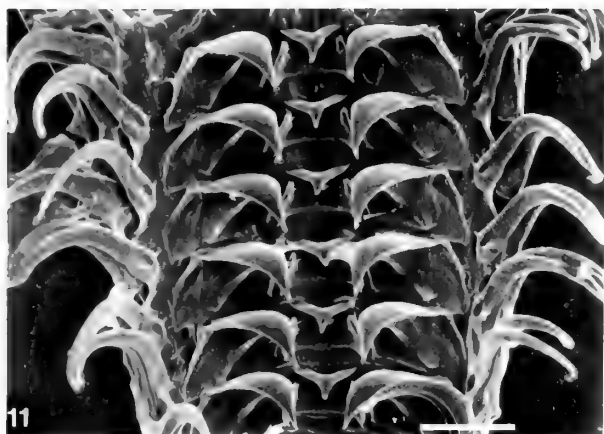
Figure 9. *Torellia japonica* (Okutani, 1964), holotype, Tokyo University Museum, registration number RM 8824. Height 5.97 mm.

Figure 10. *Trichotropis conica* Möller, Greenland. Height of section shown 1.15 mm.

cruise MD.04-DC.218, 48°19.3'S, 70°09.0'E, NNE of Kerguelen Is., 128 m, 10 March 1975.

Distribution: Collected live between 105 and 115 m at Crozet Is. (SE of Ile des Apôtres and NW of Ile des Pingouins) and at 128 m NNE of Kerguelen Is. (on a mixed bottom of pebbles and gravel, and on mud rich in diatoms and foraminifers).

Description: Shell: Medium size for the family, white, with a thin brown periostracum, high spire and indication of siphonal canal. Larval shell (Figures 15, 16) of 2.5 whorls, diameter of 1.6 mm, sculptured by evenly arched indistinct axial ribs and less distinct spiral lines. Whorls evenly rounded, covered by periostracum and demarcated from the teleoconch only by a change in sculpture. Holotype with 2.5-3 (apex corroded) postlarval whorls



Explanation of Figures 11 to 14

Figure 11. *Torellia (Torellia) vestita* Jeffreys, 1867, radula, Bay of Biscay.

Figure 12. *Torellia (Neoconcha) smithi*, radula, from specimen in Figure 7.

Figure 13. *Torellia (T.) lanata*, radula, from holotype.

Figure 14. *Torellia (N.) angulifera*, radula, from a paratype. Scale lines = 0.1 mm.

sculptured by about 7 (on the first one) to 16 (just above the outer lip) spiral cords of varied strength and much more close-set, oblique, sharp growth lines. Whorls usually evenly rounded, sometimes with a shoulderlike sub-sutural area demarcated by an angulation along part of spire. Aperture rounded with distinct siphonal corner and solid columella. Parietal callus thin.

Dimensions: Height of the shell 10.6 mm, diameter 9.6 mm; height of the aperture 6.8 mm, breadth 5.9 mm.

Soft parts: Similar to those of *Torellia lanata*; pseudoproboscis and its cavity somewhat smaller. Operculum with more apical nucleus. Radula, see Figure 14.

Remarks: The only trichotropid known to us that bears any resemblance to *Torellia angulifera* is *Haloceras japonicus* Okutani, 1964 (Figure 9), from deep water, NE of Miyake-Jima (Honshu, Japan). However, the type species of *Haloceras* Dall, 1889, is not a trichotropid (A.W., un-

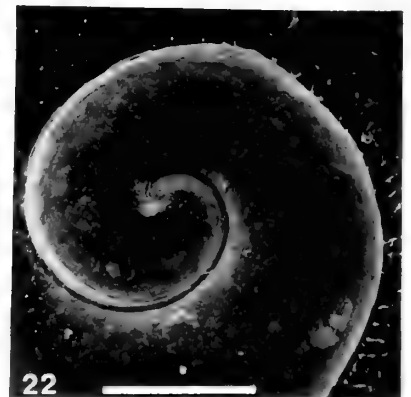
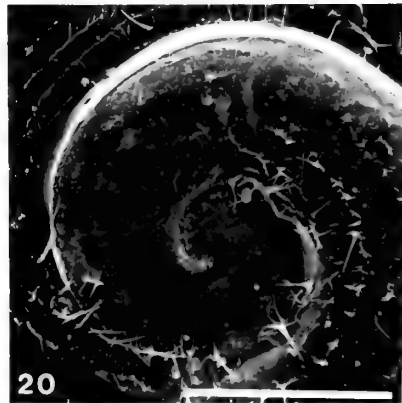
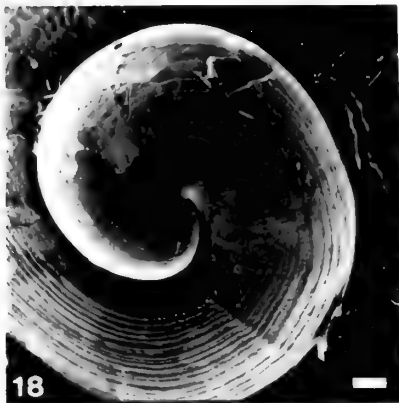
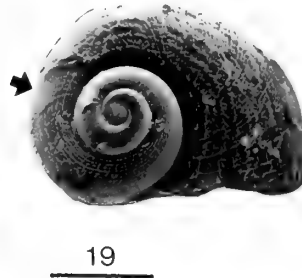
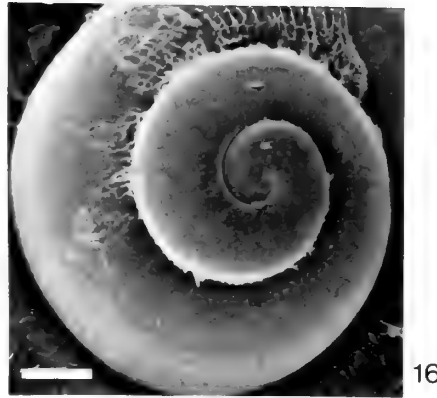
published). From shell characters we believe that *H. japonicus* can be included in *Torellia* and that it is related to *T. angulifera*. Our new species differs, however, in having a proportionally higher aperture and no keel delimiting the basal area. *Torellia japonica* also has a much smaller apical angle.

Torellia antarctica differs in having a larval shell of only 1.5 whorl and by having stronger spiral keels on the first teleoconch whorl (cf. Figures 4, 5).

DISCUSSION

Systematic Position

About 40 generic names have been proposed in, or transferred to, the Trichotropidae. Most of these names are based on species belonging to the family, and separation of genera is difficult. About six species have been



Explanation of Figures 15 to 22

Figures 15 and 16. *Torellia (Neoconcha) angulifera*, MD.03-CP.59, Kerguelen Islands.

Figures 17 and 18. *Torellia (N.) smithi*, apex of specimen in Figure 7.

Figures 19 and 20. *Torellia vestita* Jeffreys, 1867, Bay of Biscay.

Figures 21 and 22. *Torellia (Torellia) lanata*, MD.03-CP.59, Kerguelen Islands.

Figures with odd numbers show the apical whorls at approximately the same magnification. Even-numbered figures are more magnified to show initial whorls. Scale lines: odd numbers = 0.25 mm, even numbers = 0.10 mm.

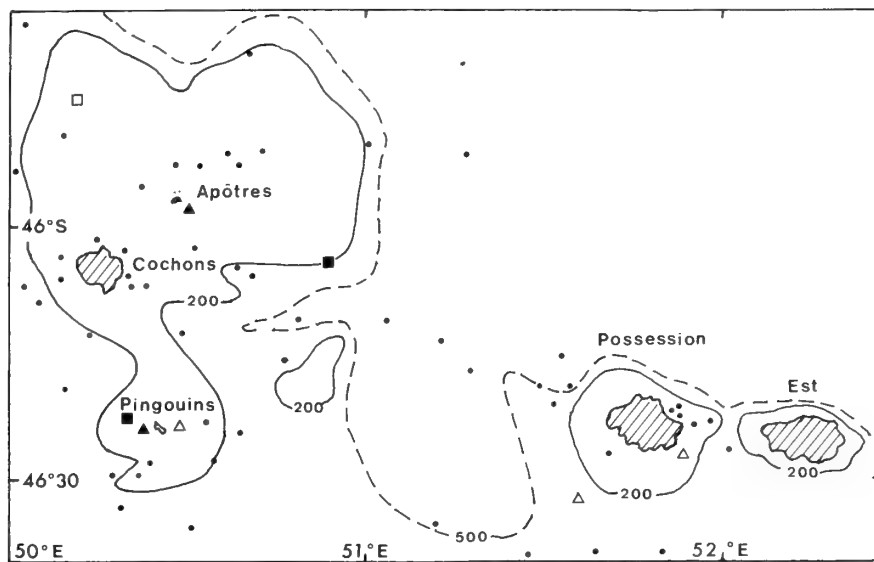


Figure 23

Distribution of *Torellia lanata* (triangles) and *T. angulifera* (squares) around Crozet Islands. Open triangles and squares indicate empty shells only. Black dots indicate negative evidence for both species.

described anatomically in some detail (EALES, 1923; GRAHAM, 1954; YONGE, 1962; DELL & PONDER, 1964), but gaps in the knowledge of other groups make it difficult to use this information. Examination of radulae of about 20 species scattered throughout the family gave no direct indication that radular characteristics can be used to any great extent.

The only direct connection between variation in different shell characters is that a reduction of height of the spire also leads to a reduction of the development of the siphonal canal. This can be seen in the *Torellia* species discussed here, in *Lippistes* Montfort, in *Zelippistes* Suter, and in the closely related Capulidae.

Low-spired species with a poorly developed or no siphonal canal have usually been incorporated in the genus *Torellia* Jeffreys, 1867, with the exception of some Antarctic species for which the following genera have been suggested:

Trichoconcha Smith, 1907. Type species: *T. mirabilis* Smith, 1907 (by monotypy).

Neoconcha Smith, 1907. Type species: *N. vestita* Smith, 1907 C.O.D.).

Antitrichotropis Powell, 1951. Type species: *Trichotropis antarctica* Thiele, 1912 (not Melvill & Standen, 1912) (O.D.).

Discotrichoconcha Powell, 1951. Type species: *D. cornea* Powell, 1951 (O.D.).

Trichoconcha was separated from "*Trichotropis* and *Velutina*" by SMITH (1907) because of unspecified differences

in the shell but was not compared with *Torellia*. EALES (1923) remarked that it is very similar to *Torellia* and it was considered a subgenus of *Torellia* by THIELE (1929). One remarkable feature of *Trichoconcha mirabilis* noted by EALES (1923) is that it has a green radula. However, the radula of *Torellia vestita* Jeffreys, 1867, the type species of *Torellia*, is also green. We are not aware of this coloration in any other trichotropid. Similarity in both the configuration and color of these radulae, as pointed out by EALES (1923), prompts us to consider *Trichoconcha* a synonym of *Torellia*.

Neoconcha was erected without comparison with other trichotropid genera. It was maintained as a distinct genus by THIELE (1929) because of radular differences from *Torellia* (cf. Figures 11, 12). It is true that the radulae of the type species of the two genera are different and that the same type of radula as in *Torellia vestita* occurs also in *Torellia angulifera* (Figure 14) and *Neoconcha insignis* Smith, 1907. However, *Trichotropis planispira* Smith, 1915, has a radula intermediate between *Torellia* and *Neoconcha*, and because of this and similarities in shell characters, we cannot do more than keep *Neoconcha* as a subgenus of *Torellia*. This in turn will necessitate a name change of *N. vestita* Smith, because of secondary homonymy with *Torellia vestita* Jeffreys, 1867, and we suggest *Torellia (Neoconcha) smithi*, nom. nov., to replace it.

Antitrichotropis was suggested by POWELL (1951) because of "being depressed turbanate" and lacking denticles on the lateral teeth. THIELE (1929) had placed the type species, *Trichotropis antarctica*, in *Trichotropis* because of

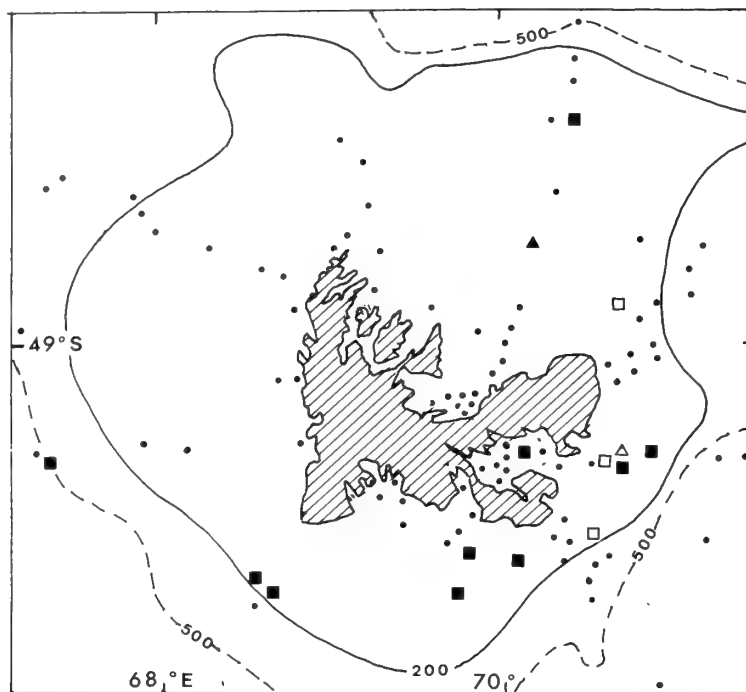


Figure 24

Distribution of *Torellia lanata* and *T. angulifera* around Kerguelen Islands. For explanation, see Figure 23.

similarities in the radula, e.g., denticles on the central tooth. However, young specimens of *Torellia*, of a size comparable with the holotype of *Trichotropis antarctica*, also have central teeth with denticles; here, it is a juvenile character that disappears with age (A.W., unpublished). The radula of adult *Trichotropis antarctica* is not known, but similarities in the shell with *Torellia angulifera* and in radular morphology with *T. vestita* indicate that it will prove to belong to *Torellia*, probably to the subgenus *Neoconcha*.

The monotypic genus *Discotrichoconcha* was erected by POWELL (1951) because of the flat shell and small size of the type species. So far, no living specimen has been found and the soft parts are unknown. It is, therefore, difficult to contradict Powell's statement that the differences mentioned necessitate this genus. The only possibility is to compare the variation of shell characters known in *Torellia*. In addition to the species discussed here, *Torellia* contains: *Torellia ammonia* Dall, 1919, *Torellia orientalis* (Schepman, 1909), *Torellia pacifica* Okutani, 1980, and *Torellia vallonina* Dall, 1919. *Torellia millestriata* Okutani, 1964, is omitted from this comparison because it seems to be related to *Haloceras* Dall, judging from our examination of the type specimen, but no soft parts are known.

Comparison shows that the spire of *Discotrichoconcha* is actually more depressed than in other species of *Torellia* and the aperture is distinctly broader than high. The larval shell, however, is of the same type as in other species

of *Torellia*—low, rounded, and with a fine spiral sculpture—and different from that of other trichotropid genera. Therefore, we consider *Discotrichoconcha* a subgenus of *Torellia*, but examination of soft parts will probably show it to be a synonym.

Two additional Antarctic species should be mentioned here. *Lippistes exilis* Powell, 1958, has been examined. Powell's holotype is an old worn shell with no trace left of periostracum, but in the same report POWELL (1958) also recorded a specimen of *Trichoconcha planispira* that we have examined. This specimen turned out to be conspecific with *L. exilis*, but had a strongly axially wrinkled periostracum, with a single periostracum keel just above the periphery. The two specimens were collected off Enderby and McRobertson islands, about 60°E. They do not belong to *Lippistes* (which has a strongly sculptured, flat larval shell with a distinct labial varix), but fit well in *Torellia*, at least from shell characters. The second species to be commented on is *Lacuna wandelensis* Lamy, 1905. It was placed in *Antitrichotropis* by POWELL (1951) but belongs to the Littorinidae (Warén & Arnaud, unpublished data).

Interpretation of the Larval Shell

THORSON (1935) described the reproduction of *Trichotropis borealis* Broderip & Sowerby, 1829, and *T. conica* Möller, 1842. These species deposit egg capsules with 12–

20 eggs, which develop directly to larvae that hatch in the crawling stage. The larval shell also clearly indicates this, consisting of 1.5 whorl of a diameter somewhat less than 1 mm and clearly demarcated from the teleoconch (Figure 10). A similar, but more depressed and rounded larval shell, is also present in *Torellia mirabilis*, *T. smithi* (Figures 17, 18), *T. insignis*, *T. antarctica*, *T. planispira*, and *T. cornea*, and it seems obvious that these species have direct development. In the two species here described, as well as in *T. vestita*, the larval shell morphology is different. It consists of about 2.5 whorls, but the diameter is still about 1.5 mm. This size corresponds with the smallest specimens found among 150 specimens of *T. vestita* from the NE Atlantic. Therefore, one should expect planktotrophic larval development in these species. This, however, is contradicted by two facts: (1) there is no clear demarcation of protoconch 1 (Figures 15, 16, 19–22) and (2) the larval shell has a periostracum similar to that of the teleoconch. Similar conditions have been observed in the Buccinidae (BOUCHET & WARÉN, 1985) in species in which the eggs develop to a shelled veliger larva that stays for a long time in the egg capsule, feeding on other eggs or embryos or on a rich supply of nourishment that fills out the capsule. During this time of development several additional whorls are formed; they are covered by periostracum and not distinctly demarcated from the protoconch 1. (This mode of development differs from the classical case of adelphophagy, where the initial part of the larval shell is formed very late.) Whether the species of *Torellia* with a multispiral larval shell have planktotrophic larvae or direct development as described above can presently not be inferred.

ACKNOWLEDGMENTS

All the material of both *Torellia lanata* and *T. angulifera* has been obtained thanks to the logistic and financial support of Terres Australes et Antarctiques Françaises, Paris. We want also to direct our thanks to Ms. Kathie Way, British Museum (Natur. Hist.), London; Dr. Rudolf Kilius, Zoologisches Museum an der Humboldt-Universität, Berlin; and Dr. Philippe Bouchet, Museum National d'Histoire naturelle, Paris, who loaned types and other specimens, and prepared the SEM photos at Centre de Microscopie, CNRS, Paris. Catherine Lamb kindly corrected the English.

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A New Species of *Sonorella*
(Gastropoda: Pulmonata: Helminthoglyptidae)
from Sonora, Mexico

by

EDNA NARANJO-GARCÍA AND WALTER B. MILLER

Department of Ecology and Evolutionary Biology, University of Arizona,
Tucson, Arizona 85721, U.S.A.

Abstract. A new species of *Sonorella* from Sonora, Mexico, is described, and a new locality for *Sonorella magdalenensis* is recorded.

INTRODUCTION

DURING THE PERIOD 1965 TO 1967, one of us (W.B.M.) conducted extensive explorations of northern Sonora in order to discover possible populations of *Sonorella* and to determine the southern limit of distribution of the genus (MILLER, 1965, 1967a, b). Subsequently, malacological investigations in Sonora were suspended until our interest was re-kindled in September 1983 when two students from the University of Arizona, Russell Duncan and Jennifer Titley, discovered a population of *Sonorella magdalenensis* (Stearns, 1890) along the Agua Fria river. In November 1984, we undertook an expedition to that locality, in the region of Rancho La Brisca, and we were able to obtain over two dozen live adult, active specimens. Examination of the reproductive systems determined that we were dealing with a mixture of two sympatric species, *Sonorella magdalenensis* (Stearns, 1890) and a new species described below.

DESCRIPTION

Family HELMINTHOGLYPTIDAE Pilsbry, 1939

Sonorella Pilsbry, 1900

Sonorella aguafriensis

Naranjo-García & Miller, spec. nov.

(Figures 1, 2)

Description of shell of holotype: Shell depressed, globose, heliciform, thin, glossy, light brown with a chestnut spiral band on the round shoulder, the umbilicus narrow, contained about 7 times in the diameter and about $\frac{1}{4}$ covered by the reflected columellar lip. First part of the embryonic shell smooth, followed by growth wrinkles and

hyphenlike papillae arranged in descending spiral threads over the growth wrinkles, for 1 to $1\frac{1}{2}$ whorls. Following whorls with growth wrinkles and rounded papillae, the latter gradually disappearing; the body whorl with radial growth wrinkles only. Body whorl descending to the oblique aperture which is ovate-lunate and wider than high; parietal callus thin; peristome slightly reflected (Figure 1).

Reproductive system: The upper part of the reproductive system is typical of the genus. The penis contains a short verge slightly narrower at its beginning than at its tip. The verge is somewhat undulated at the sides and terminates with a wide conical tip; it is slightly less than $\frac{1}{3}$ as long as the penis. A penial sheath covers the lower region of the penis. Epiphallus thin, the distal part as well as the epiphallic caecum enveloped by connective tissue attached to the penial sheath; the epiphallic caecum very short. Vagina approximately same length as the penis; the lower $\frac{2}{3}$ of the vagina wider than the upper $\frac{1}{3}$, becoming slender to the point of junction with the spermathecal duct (Figure 2).

Type locality: West bank of Río Agua Fria, Sonora, Mexico, about 1 km upstream from Rancho La Brisca installations, 30°24.3'N and 110°32.5'W. The site is in a small canyon running north-south, with scattered volcanic rocks on the slope above the river. The vegetation is riparian with *Prosopis juliflora*, *Opuntia* sp., *Salix* sp., *Nicotiana glauca*, *Morus* sp., *Fraxinus velutina*, *Juglans major*, *Baccharis sarothroides*, and *Platanus wrightii*.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. SBMNH 34074. Paratypes: National Museum of Natural History, Smithsonian Insti-

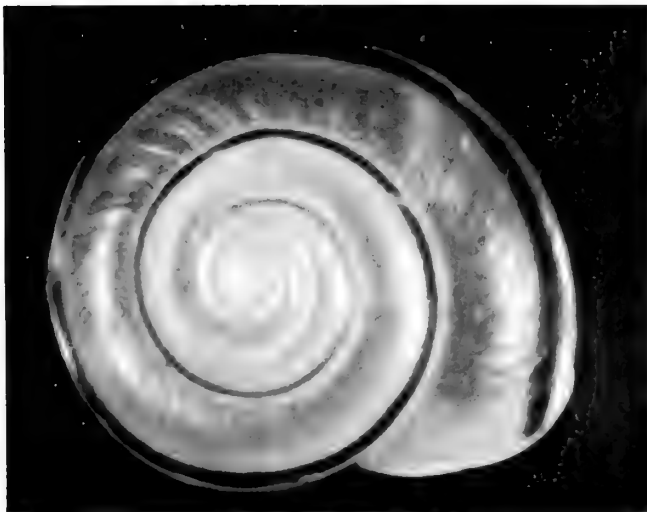


Figure 1

Sonorella aguafriensis Naranjo-García & Miller, spec. nov. Shell of holotype, SBMNH 34074. Top, apertural view; middle, apical view; bottom, umbilical view.

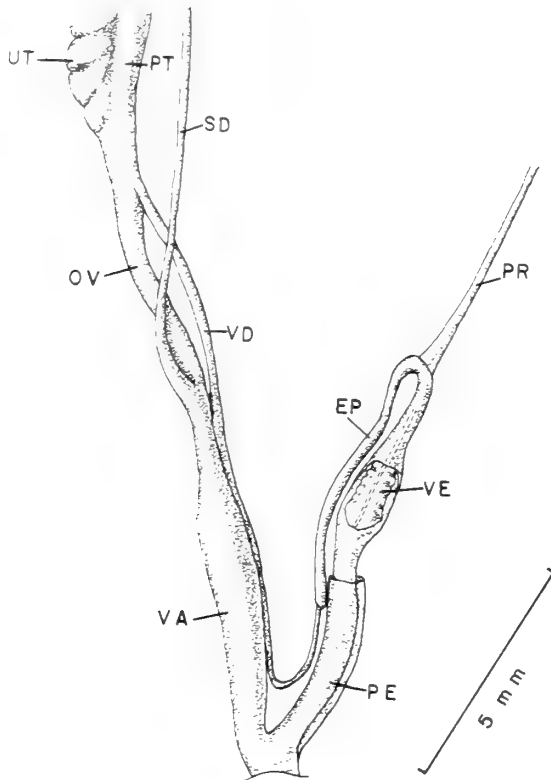


Figure 2

Lower reproductive system, *Sonorella aquafriensis*, spec. nov. Holotype, SBMNH 34074. EP, epiphallus; OV, free oviduct; PE, penis; PR, penial retractor muscle; PT, prostate; SD, spermathecal duct; UT, uterus; VA, vagina; VD, vas deferens; VE, verge.

tution No. USNM 859003, Academy of Natural Sciences of Philadelphia No. ANSP 359974, Field Museum of Natural History No. FMNH 212879, University of Texas at El Paso No. UTEP 9384, Universidad Nacional Autónoma de México Colección Malacológica No. 1201, Edna Naranjo-García collection No. 408, Walter B. Miller collection No. 7453.

Etymology: This species is named after the river along which it lives, Río Agua Fría.

DISCUSSION

Sonorella aquafriensis belongs to the *Sonorella binneyi* complex (BEQUAERT & MILLER, 1973:111); it is probably most closely related to *Sonorella sitiens sitiens* Pilsbry & Ferriss, 1915. The verge of *S. aquafriensis* has the same general shape as that of *S. s. sitiens* but is consistently more slender (Figure 2). *Sonorella aquafriensis* has a shorter spermathecal duct than *S. s. sitiens*; the vagina of *S. aquafriensis* has a shape similar to that of *S. s. sitiens*, but the slender region is longer than in *S. s. sitiens*. In *S. aquafriensis* the vagina and the penis are approximately of the same length, whereas in *S. s. sitiens* the vagina is shorter than the penis. The embryonic shell of *S. aquafriensis* has a sculpture of growth wrinkles with superimposed papillae, whereas that of *S. s. sitiens* is smooth. The measurements of the 17 paratypes varied only slightly from those of the holotype, with the shell heights ranging from 8.2 to 9.3 mm with a mean of 8.8 mm, and the maximum diameter 15.0 to 16.8 mm with a mean of 15.7 mm. All of the embryonic shells have hyphenlike papillae descending as spiral threads over the growth wrinkles, although in some of them these threads become faint near the shoulder.

ACKNOWLEDGMENTS

We wish to express our thanks to James Hoffman, friend and colleague, for helping us in the field, and to the Consejo Nacional de Ciencia y Tecnología for grant support to one of us (E.N.-G.).

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Observations on the Range and Natural History of *Monadenia setosa* (Gastropoda: Pulmonata) in the Klamath Mountains, California, and the Taxonomy of Some Related Species

by

BARRY ROTH

Department of Invertebrate Zoology, Santa Barbara Museum of Natural History,
Santa Barbara, California 93105, U.S.A.

AND

PETER H. PRESSLEY

Department of Invertebrate Zoology, California Academy of Sciences,
San Francisco, California 94118, U.S.A.

Abstract. *Monadenia (Monadenia) setosa* occurs mainly in riparian corridors with dense deciduous understory in Trinity County, California, U.S.A. Eastward, *Monadenia (Shastelixa) churchi*, which within the range of *M. setosa* is restricted to open hillside habitats, occupies streamside habitats. On the north and west, *M. setosa* is replaced by *Monadenia (Monadenia) fidelis*, with a narrow zone of intergradation. One population, with a density of 0.11 snail/m², was monitored over an annual cycle. Capture of marked individuals departed significantly from randomness. Widely varying population estimates reflected irregular snail activity patterns. Reproductive maturity apparently occurs at different seasons of the year; early growth is probably rapid, slowing as maturity is approached. Feeding occurs on the ground and on the trunks of trees with smooth bark. Both adults and juveniles occur on the ground and also climb vertical surfaces. Beetle and possible rodent predation occur; the latter may often be unsuccessful. Limited home ranges, probably related to available shelter, may exist. *Monadenia (Monadenia) callipeplus* of the Scott River drainage represents a parallel development of a bristly shell surface. *Monadenia (Monadenia) scottiana* is elevated from a subspecies of *M. fidelis* to species rank. *Monadenia chaceana* is restored to species rank and assigned to the subgenus *Monadenia* s.s.

INTRODUCTION

LITTLE PUBLISHED INFORMATION exists on the ecology or life history of snails of the New World helicacean family Helminthoglyptidae. The most extensive contributions are those by VAN DER LAAN (1971, 1975a, b, 1980) on what he called *Helminthoglypta arrosa* (actually the distinct species *H. stiversiana* [Cooper, 1875]; ROTH, 1982) and the accounts of a 1978 field study of *Monadenia (Monadenia) setosa* Talmadge, 1952, in the Shasta-Trinity National Forest, California, U.S.A., for the U.S. Forest Service (ROTH, 1978; ROTH & ENG, 1980). In contrast to *H.*

stiversiana, which occurs in large numbers in a relatively uniform habitat (coastal *Lupinus* scrub), *M. setosa* is a species of cryptic habits, occurring in low densities in a structurally complex forest habitat.

The 1978 study of *Monadenia setosa* included drainages that are tributary to the Trinity River from Italian Creek (secs. 14, 23, T. 5 N, R. 7 E, Humboldt Base and Meridian) to Manzanita Creek (secs. 32, 33, T. 34 N, R. 12 W, Mount Diablo Base and Meridian), all in Trinity County, California. *Monadenia setosa* was found living in the canyon of Swede Creek, and empty shells in the drain-

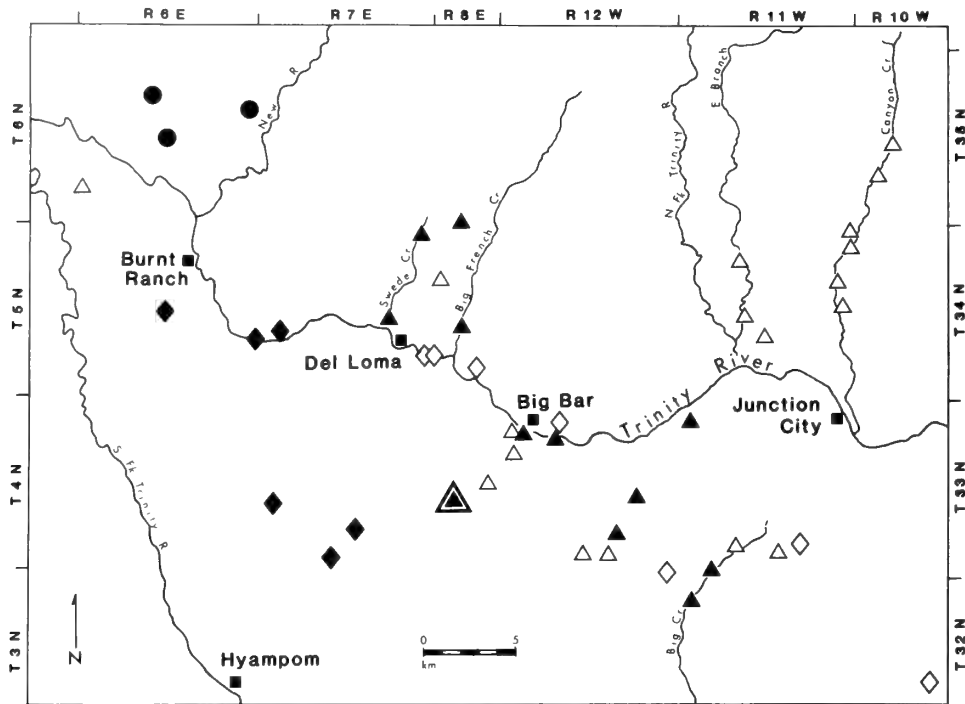


Figure 1

Location of sampling stations and distribution of *Monadenia* species. Solid triangles, *M. setosa*; solid circles, *M. fidelis*; solid diamonds, *M. fidelis*-*M. setosa* intergrades; open diamonds, *M. churchi*; open triangles, no *Monadenia* present. Large triangle, Bidden Creek monitoring site.

ages of Little Swede and Big French creeks. The finding of juvenile snails under loose bark of standing dead trunks of broadleaf trees, while adults were found on the ground, led to the suggestion that standing broadleaf deadwood, as a special juvenile habitat, might be a limiting resource. The species was reported to be restricted to riparian corridors with dense, mixed hardwood understory, either on canyon slopes or streamside benches. Only empty shells were found on the surface of talus slopes away from the watercourses; these shells were assumed to have been displaced from elsewhere. Drier slopes with an oak-madronne-douglas fir association supported a different assemblage of mollusks, without *M. setosa*. These findings were used in an interim management plan adopted in 1979 by the Shasta-Trinity National Forest (ROTH & ENG, 1980).

The present paper reports the results of additional field study of *Monadenia setosa* sponsored by the Forest Service in 1981-1982. The area of consideration was expanded to include the zone of Big French Creek identified as probable habitat in the interim management plan, regions of suitable habitat on the south side of the Trinity River and subsidiary drainages south to Hayfork Creek, and drainage divides north of Swede Creek and Big French Creek. This resulted in extending the known range of *M. setosa* to the north, east, and south (Figure 1).

One selected *Monadenia setosa* population was studied

in the field at approximately 3-wk intervals over a complete annual cycle. The study included (1) an estimate of population size by mark-and-recapture technique, (2) size data for estimates of population age structure, individual life-span, and age at reproductive maturity, (3) observation of site selection by adults and juveniles to test the apparent dependence on standing deadwood suggested by the 1978 study, (4) records of individual movement and daily and seasonal activity patterns, (5) observations on feeding, and (6) an estimate of the possible effect of vegetational succession on *M. setosa* habitat.

Reproductive activity was watched for but was not observed, nor were egg clutches seen in the field.

Monadenia callipeplus Berry, 1940, was sampled at its type locality, Tompkins Creek near the Scott River, and dissected to determine whether *M. callipeplus* might be merely a remote occurrence of *M. setosa*. The reproductive systems of *M. callipeplus* and *M. scottiana* Berry, 1940, are illustrated herein and the taxonomic status of these species discussed.

The Office of Endangered Species of the U.S. Fish and Wildlife Service regards *Monadenia setosa* as a "candidate species" for Endangered or Threatened status (*Federal Register*, 49:21674, 22 May 1984). *Monadenia setosa* is officially listed as a rare species in Section 670.5, Title 14, California Administrative Code.

SETTING

The Klamath Mountains occupy a region between the Pacific Ocean and the southern end of the Cascade Range; on the southeast they are bordered by the Great Valley of California and on the southwest by the northern California Coast Ranges. They consist of old (early Paleozoic through Jurassic), complexly abutted rock suites and, to judge by the general absence of younger marine sediments, have included positive land area for much of Mesozoic and probably all of Cenozoic time (DAVIS *et al.*, 1978). The Klamath region is unique in terms of plant geography, having "... one of the most highly complex vegetation patterns in North America Into this area extend and meet in a complexly interdigitating pattern, various types of vegetation which form the prevailing climaxes of other areas. All western plant formations dominated by trees occur in the Klamath Region, as in no other area. Those forest formations that are of most highly mixed tree-stratum composition and are thought most to resemble Arcto-Tertiary forests in the West occur in this region—the redwood forests and mixed evergreen forests. Of these the mixed evergreen forest is the link between two major fractions of western forest vegetation—the coniferous forests, and the sclerophyll and oak-pine woodland grouping. The Klamath Region has also an exceedingly rich flora for its latitude; it is a center of floristic diversity and narrow endemism . . . , and many plant genera have maximum numbers of species in the West, including endemics, occurring there" (WHITTAKER, 1961:5-6).

In the area studied the prevailing climax is the Mixed Evergreen Forest of MUNZ & KECK (1959): mixed forests with two-level canopies of larger coniferous trees—douglas fir (*Pseudotsuga menziesii*) and yellow pine (*Pinus ponderosa*)—and smaller broadleaf-evergreen or sclerophyllous trees (*Lithocarpus densiflora*, *Arbutus menziesii*, *Castanopsis chrysophylla*, and *Quercus chrysolepis*). Deciduous trees (*Acer macrophyllum* and *A. circinatum*, *Cornus* sp., *Quercus kelloggii*, and others) are also present, mainly along watercourses. WHITTAKER (1961) observed that in relation to moisture the canopy changes from mesic stands in which the coniferous stratum is dense and deciduous trees may outnumber sclerophylls, through stands in which the conifers are scattered in open growth above a dense sclerophyll stratum, to more xeric stands in which both strata are open and pines (*P. ponderosa* for the most part) replace *Pseudotsuga* as the principal conifers. Particularly in some of the steeper canyons in the study area (for example, the canyon of Swede Creek described by ROTH & ENG, 1980) the transition from riparian facies with dense deciduous understory to open stands is quite abrupt, or at least gradational over a few tens of meters, with individual understory species occupying rather well-defined zones parallel to streams.

On a regional scale, the density of conifers increases and that of sclerophylls decreases toward the more humid

environments nearer the coast; *Pseudotsuga* becomes more prevalent and, finally, beyond the limits of the study area, there is gradation into the coastal *Sequoia* forest. Toward the drier interior, *Pseudotsuga* declines, the sclerophyll strata become more open, and the mixed evergreen forests grade into pine-oak foothill woodland (WHITTAKER, 1961). The effects of complex local topography, interacting with these regional trends, produce a mosaic of vegetational types, as readily seen on Forest Service timber-type maps.

DISTRIBUTION STUDY

Methods

The distribution of all land mollusks was investigated in an area roughly defined by Ripstein Campground, north of Junction City (on the NE), Hawkins Creek (NW), Hyampom (SW), and Hayfork Summit (SE), with additional study along Hayfork Creek as far south as Natural Bridge Picnic Area (Figure 1) (approximately 123°00'–123°30'W longitude by 40°37.5'–40°52.5'N latitude). The westernmost stations, on Hawkins Creek and Hennessy Ridge, are in Six Rivers National Forest and were searched to confirm the observation that *Monadenia setosa* does not extend this far west. More specific search, focusing only on the distribution of *Monadenia*, was also carried out, and additional findings by Forest Service personnel and W. B. Miller of the University of Arizona are included in the range report. All stations are in the watershed of the Trinity River and its tributary streams, including New River. Mollusks were located using standard field techniques: visual search in areas of likely looking cover, in brushpiles, around and under logs, in rock crevices and rockslides (down to the level where soil left no more crawl-space for mollusks), and so forth. Where field inspection showed minute shells to be present, leaf litter was collected and sifted in the laboratory for micromollusks. Reports on other species of mollusks beside *M. setosa*, molluscan faunal associations, and descriptions of new species are being presented elsewhere (ROTH & PRESSLEY, 1983, and in preparation; ROTH, 1985a, b).

Field work was conducted from September 1980 to October 1981 with at least some sampling during every month of the year. Spring and autumn were the most productive times. Locations of sites yielding mollusks are listed by section, township, and range in the Appendix. Also included are sites surveyed from May to September 1978, in drainages that are tributary to the Trinity River from Italian Creek to Manzanita Creek (ROTH, 1978). Localities were categorized as being either (A) within the zone of dense deciduous understory, or (B) in stands of open growth.

Results

Of the 38 general sampling stations occupied, 11 yielded *Monadenia setosa*. Figure 1 presents the species' distribution as shown by all material examined. This is a sub-

stantial extension of known range over the distribution shown by the 1978 study.

New marginal stations defining the range are Localities 2, 3, 4, 11, 12, 19, and 30 (see Appendix for locality descriptions). Only empty shells were found at the northernmost station, Loc. 2, but there is no reason to doubt that the species lives there. In addition to the stations cited, earlier in 1980 Forest Service personnel found *Monadenia setosa* in SE¼ sec. 6, T. 33 N, R. 11 W (near Eagle Creek); SE¼ sec. 22, T. 33 N, R. 12 W (drainage of Big Bar Creek); and perhaps also sec. 14, T. 33 N, R. 12 W (Big Bar Creek; specimen not seen by us).

Repeated search east of the Limestone Creek and Big Creek localities (Locs. 11, 12) yielded no *Monadenia setosa*, so this probably approximates the southeastern limit of its range. Negative results were also obtained north of the Trinity River along Canyon Creek, the North Fork of the Trinity, and Big French Creek north of Loc. 30, even in apparently suitable habitat. At many of the eastern localities, *M. setosa* is absent but *Monadenia churchi* Hanna & Smith, 1933, is present in ecologically analogous situations. A few kilometers south of Loc. 11, Big Creek flows through lightly forested foothills and debouches into Hayfork Valley, where the appropriate riparian habitat is lacking. Search along tributaries of Hayfork Creek, entering Hayfork Valley from the south, produced *M. churchi* but no *M. setosa*.

West of the localities cited, no typical *Monadenia setosa* have been found. The areas of Hawkins Creek, Hennessy Ridge, and New River yielded *Monadenia fidelis* (Gray, 1834). At Don Juan Creek, Cedar Flat, and McDonald Creek above Burnt Ranch occur *M. fidelis* with a partially matte base and light scattering of bristles on the shell. This may be a zone of past or present genetic exchange between *M. fidelis* and *M. setosa*. Further analysis is needed to show whether simple intergradation or secondary contact and hybridization are present; the narrowness of the zone and its apparent distinctness suggest the latter. Shells taken by Forest Service personnel at Clark Creek (sec. 19, T. 4 N, R. 7 E), Hyampom Creek (sec. 27, T. 4 N, R. 7 E), and a fork of Corral Creek (sec. 33, T. 4 N, R. 7 E) are of similar character and may represent a southern continuation of the hybrid zone.

Discussion

Except for Hayfork Valley on the south, the boundaries of the range of *Monadenia setosa* do not coincide with any obvious topographic or vegetational discontinuities. As noted above under "Setting," the region is gradational between humid coastal-subcoastal forest and the more arid interior. Geologically, all localities with typical *M. setosa* fall within a varied belt of Paleozoic and Triassic metamorphic rocks (see IRWIN, 1960:plate 1). Localities with *M. fidelis* or the suspected hybrids are on the chiefly granitic terrane of the Ironside Mountain batholith. To the east, the belt mapped as pre-Silurian (?) schists has yield-

ed neither species. It is not clear how this underlying geology might affect the distribution of snail species.

Monadenia setosa lies on the eastern edge of the subgenus *Monadenia*, *sensu stricto* (compare map in ROTH, 1981:figure 1). East of the range of *M. setosa*, *Monadenia churchi*, which within the range of *M. setosa* is restricted to open stands and exposed slopes, comes to inhabit riparian corridors with deciduous understory. *Monadenia churchi* belongs to the inland subgenus *Shastelixa* (ROTH, 1981:figure 1) and its range extends eastward around the head of the Sacramento Valley. It is undoubtedly more tolerant of xeric conditions than *M. setosa*. Up to a certain threshold (possibly having to do with temperature range) *M. setosa* may be competitively superior in riparian woodland situations and exclude *M. churchi* from this habitat. However, except for some work on the agonistic behavior of slugs (ROLLO & WELLINGTON, 1977, 1979), little is known about land mollusk interactions that could lead to competitive exclusion.

In terms of thermal parameters (mean annual temperature and mean annual range of temperature), the subgenera *Monadenia* s.s. and *Shastelixa* show little overlap (ROTH, 1981:figure 18). (Note that on this graph of thermal ranges, Big Bar is the station defining the "continental" corner of the *Monadenia* s.s. polygon.) Evidence for the relationship between temperature and distribution in *Monadenia* is also discussed by ROTH (1981).

MONITORING STUDY

Methods

Following a preliminary reconnaissance in early September 1980, a 1044-m² study site was selected on the lower reaches of Bidden Creek in the SE¼ sec. 19, T. 4 N, R. 8 E (Humboldt Base and Meridian). This site presents a considerable variety of microhabitats within a riparian woodland facies and supports a substantial population of *Monadenia setosa*. The study site extends on either side of Bidden Creek, which here flows at a low gradient a few hundred meters from its confluence with Corral Creek. The site is bounded on the north by a steep bank and on the south by a low bank rising to a cleared and graded campsite. Outside the riparian corridor the vegetation is mixed evergreen forest with douglas fir, white fir, giant chinquapin, and canyon oak.

Major features of the site were mapped at a scale of 1:100 with a Brunton compass and range finder (Figure 2a). Within the site the predominant trees are alders (*Alnus rhombifolia*), with douglas fir and black oak (*Quercus kelloggii*) less numerous. Standing deadwood, mostly alder, is present and there are logs and large branches on the ground. These remained virtually in place over the course of the study. Shrubs, mostly vine maple (*Acer circinatum*) with slim, multiple trunks, are also present.

Most of the area of the study site is gravelly stream terrace, well drained and covered with a layer of leaf-

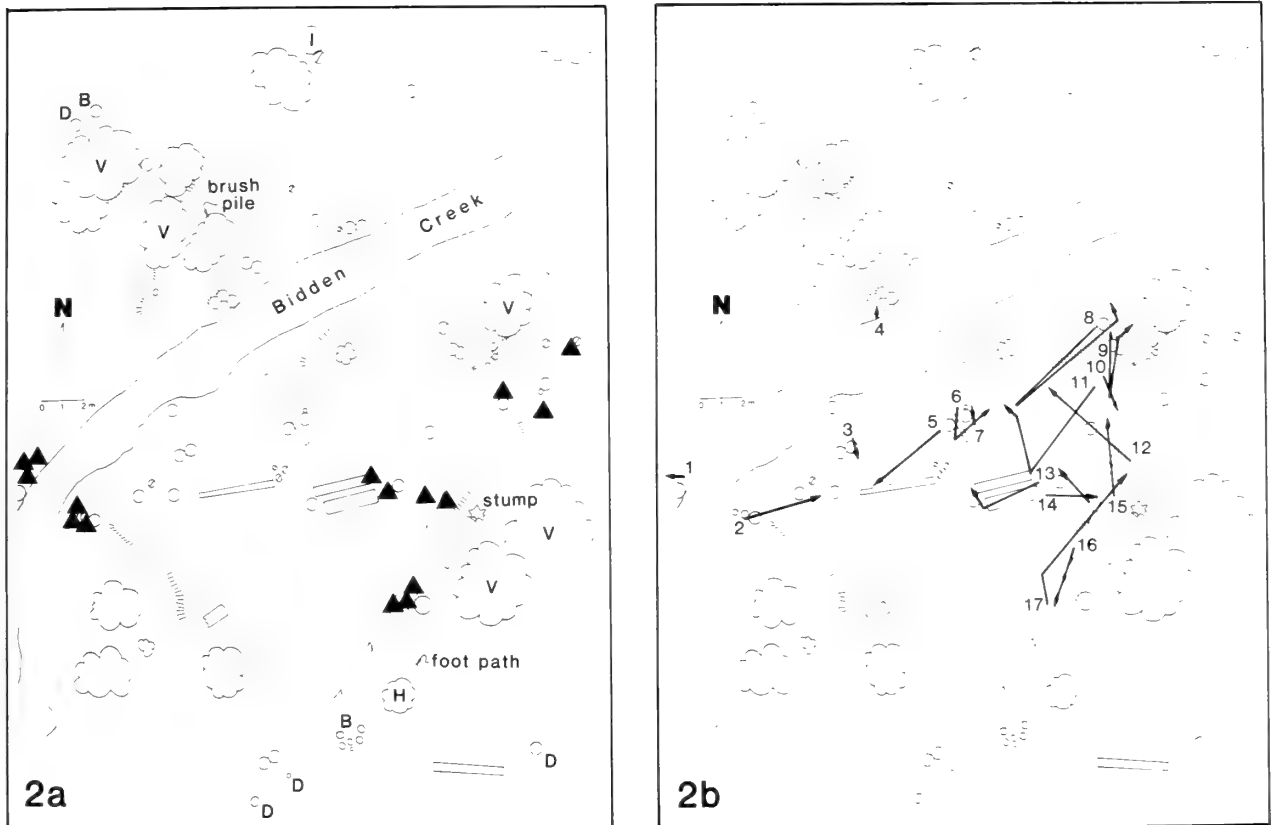


Figure 2

Map of monitoring site on Bidden Creek. Figure 2a. Distribution of snail captures (solid triangles) on a typical sampling occasion, 8 May 1981. B, black oak, *Quercus kelloggii*; D, douglas fir, *Pseudotsuga menziesii*; H, California hazel, *Corylus cornuta* var. *californica*; I, incense cedar, *Calocedrus decurrens*; V, vine maple, *Acer circinatum*; unlettered circles, alder, *Alnus rhombifolia*; slashed circles, standing dead trunks. Rectangular forms are logs and large branches on ground. Figure 2b. Locations of multiple captures during monitoring study; arrows connect successive captures of numbered snails.

mold—thus agreeing with preferred *Monadenia setosa* habitat as determined by ROTH & ENG (1980). Water flowed over much of the area episodically during winter 1980–1981, but the site was not subjected to extreme flushing action. Hatched areas on the map outline 1–3 m high, downstream-trending piles of cobble- to small boulder-sized metavolcanic rocks, most with the rounded edges of stream cobbles. The piles are probably the result of past mining operations. Rocks in the top half-meter are loose, but the lower ones are more or less silted in; many crevices remain and provide mollusk shelter, especially for the big slug *Ariolimax columbianus* (Gould, 1851). The rock piles are moderately overgrown by shrubs, but most of the trees in the site grow on the unencumbered stream terrace.

A mark-release-recapture study was carried out with sampling at approximately 3-wk intervals beginning 24 October 1980. The site was searched systematically with

flashlights in the first 2 h after dark. In order not to affect the sampling properties of the site, the search was made without disrupting rock piles or other potential shelter. Snails were individually tagged on the shell with numbers in India ink covered by a daub of clear nail polish. When necessary, the shell was dried first with a jet of compressed air. This tagging method does not appreciably alter the image of the shell and, thus, should not have affected the probability of recapture or predation. After marking, the snails were returned to their original site and orientation. Snails found sealed to the substrate were marked in place.

Altogether, 68 snails were captured and marked; 19 of these were recaptured at least once. For each capture the following were recorded: location, substratum, state of activity and orientation, shell diameter in mm, number of whorls (counted by the method of PILSBRY, 1939), whether adult (with reflected lip) or juvenile, and distance from nearest active neighbor. Capture sites were marked in the

Table 1

Data from mark-release-recapture study and parameters from Jolly's stochastic multiple-recapture analysis.

Day	Date	No. in sample	No. released	Proportion of recaptures	No. marked snails at risk ¹	Total population ¹
1	24 Oct 80	2	2	—	—	—
2	25 Oct 80	10	10	0	0	—
3	27 Apr 81	5	5	0	11.67	—
4	8 May 81	17	16	0.118	23.33	198.3
5	9 May 81	2	2	0	14.00	—
6	10 May 81	8	8	0.500	52.00	104.0
7	26 May 81	6	6	0.333	74.00	222.0
8	27 May 81	12	11	0.417	93.00	223.2
9	28 Jun 81	1	1	0	—	—
10	2 Oct 81	16	16	0.313	21.00	67.2
11	3 Oct 81	5	5	0.600	15.50	25.8
12	4 Oct 81	12	—	0.583	—	—

Calculated by method of JOLLY (1965).

field with aluminum nursery tags; on subsequent recapture, the horizontal distance from the last release was measured.

Population size was estimated by linear regression of the percentage of recaptures in a given session's sample versus the total number of snails marked. Extrapolating the regression equation to the 100% level gives an estimate of population size (HADFIELD & MOUNTAIN, 1980). Jolly's stochastic multiple-recapture method (JOLLY, 1965) gave problematic results probably influenced by snail activity and sheltering habits.

Capture records of 8–10 May 1981 and of 2–4 October 1981 were pooled to produce two estimates of shell-size frequency in the population. Size-frequency distribution was examined as an indicator of population age structure.

Results and Discussion

Population size: Linear regression analysis gives a population estimate of 112 snails. The equation is $y = 0.959x - 6.962$ with a correlation of $r = 0.760$. For the 1044-m² study site, this translates into a density of 0.11 snail m⁻². The regression method, assuming as it does a constant population size with no dilution (birth and immigration) or loss (death and emigration), provides a simple but mechanical estimate; it states, in effect, that if the calculated linear relationship were to hold good, then 112 snails would represent 100% of the population.

Table 1 presents the data of the mark-release-recapture study and population estimates based on Jolly's multiple-recapture method. No captures were made from November 1980 through March 1981 and July through September 1981, reflecting winter and summer inactivity periods. These dates are omitted from the analysis; the calculations

are not affected. A much larger population is indicated in May than in October 1981, even though the number of captures remained similar. Either massive mortality or emigration between the spring and autumn sampling could have produced such results. However, the October samplings showed no other evidence of heavy mortality, such as empty shells. There were no scouring floods in this interval and extensive emigration seems improbable, given the apparent tendency for snails to occupy a limited home range over the course of a year (see below, "Substratum, location, and mobility"). Summer, with the onset of hot and dry conditions, is an unlikely time for snail dispersal to increase. ROLLO & WELLINGTON (1981) have demonstrated increased sheltering behavior by slugs at this time, and the summer drop in the number of active *Monadenia setosa* observed probably represents the same seasonal trend. Search during May, when fresh vegetation was extensive at the study site, may have been less efficient than in October, when the vegetation was sparse and beaten down; but marked and unmarked snails should not have been differentially affected.

A variance test for the randomness of recapture (SOUTHWOOD, 1966:77) yielded a probability much less than 0.001. It seems likely that visual search without disruption of the substrate detects mostly active snails and that these do not represent a random sample of the population at large. The wide range of estimates for successive dates (8 May, 198 snails, versus 10 May, 104 snails; and 2 October, 67 snails, versus 3 October, 26 snails) further indicates the limitations of this method: it is implausible that the population should have decreased by 50% overnight.

The probability of a snail's being active on a given night may not be independent of its state of activity on the preceding night. If, for example, a foraging snail tends to feed to satiation on one night then retire to shelter for one or several days while digesting the meal, its probability of recapture during that period will be lowered. If, on the other hand, foraging is stimulated by a particular combination of microclimatic variables, and the key combination occurs at different times in different microhabitats within the study site, then foraging by individual snails (or "neighborhood groups" of snails) may be highly clumped in time. The first situation will tend to raise the population estimate (fewer recaptures on the second of two close sampling dates), and the second, conceivably, to lower it (more recaptures of the same snails).

The complexity of snail activity patterns tends to violate the assumption of equal catchability. PARR *et al.* (1968), HEATWOLE & HEATWOLE (1978), and HADFIELD & MOUNTAIN (1980) reported similar problems in applying capture-recapture methods to snail populations. A program of greater sampling intensity might overcome the influence of irregular snail activity.

Growth and age: Pooled data on whorl number from 8–10 May 1981 and 2–4 October 1981 are presented in

Figure 3. "Adult" shells are defined as those with a reflected lip at the aperture. Formation of a reflected lip often, although not invariably, coincides with reproductive maturity in land snails. WILLIAMSON (1979) recorded that some *Cepaea hortensis* with reflected lips proved on dissection to have poorly developed genitalia while others had fully developed reproductive organs. *Theba pisana* may be reproductively mature while still in the phase of active shell growth (COWIE, 1984). However, in *Monadenia setosa* dissected by us, all those with a reflected lip, and none of those without, have had fully developed genitalia.

Once a reflected lip is formed, the shell does not increase in diameter or whorl number, so that shell size ceases to be an indicator of age. The tendency for individual *Monadenia setosa* to occupy a home range subjects each one to an individual regime of shell erosion and wear. Thus, periostracal wear, used by WILLIAMSON (1979) for *Cepaea*, is of doubtful use as an age indicator.

May and October distributions are strongly skewed toward high whorl counts, both when the whole samples are considered and when adult shells are excluded. Adult shells in these samples have 5.7 or more whorls; a 5.6-whorl adult was captured in October 1980. There is extensive overlap between adult and juvenile shells in the range of 5.7 whorls and above.

Probability paper analysis (HARDING, 1949) of juvenile shells in the May and October samples does not clearly resolve any separate size classes, probably owing to small sample size. With the assumption of equal rates of mortality and immigration-emigration for adults as for juveniles, and no anomalous years intervening, the data in Figure 3 imply at least as many year-classes of adults present as there are of juveniles. There may well be more; adult *Cepaea* age-classes for up to 5 yr after lip reflection have been detected (WILLIAMSON, 1979), and 10-yr-old *Helix pomatia* are probably not uncommon in natural populations (POLLARD *et al.*, 1977). VAN DER LAAN (1971) reported 6–10-yr longevity in *Helminthoglypta stiversiana*. SOLEM & CHRISTENSEN (1984) reported camaenid species with >8-yr longevity, and more than five year-classes of adults in a population.

Two autumn and six spring captures were in the process of secreting a reflected lip. If maturation and lip reflection coincide in *Monadenia setosa*, the onset of reproductive maturity is not tied to one season. Early summer reproductive activity has been recorded for the species (ROTH & ENG, 1980). It is not known whether individuals forming reflected lips in May mate and lay eggs the following June and July, although this seems plausible. Perhaps individuals forming reflected lips in October are capable of mating and oviposition that autumn and winter. A scattered (or bimodal?) timing of reproduction might be strategic in a region like the Klamaths where the duration and severity of seasons are varied and unpredictable. Alternatively, individuals forming reflected lips in the autumn may not become reproductive until the following spring.

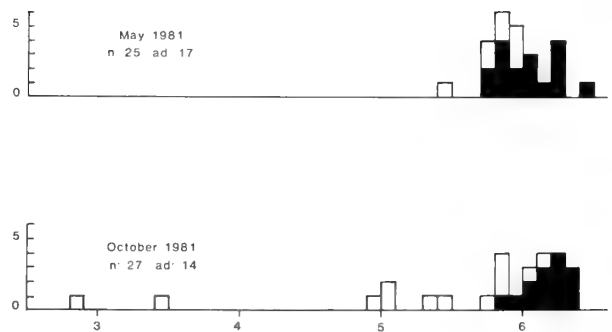


Figure 3

Number of individuals (ordinate) and whorl number (abscissa) in May and October 1981 samples. Adults (ad) indicated by solid bars.

Two individuals added reflected lips between the times of first and subsequent capture. Snail No. 3 had no reflected lip on 25 October 1980, but had begun to secrete one on 25 May 1981; whorl number was 5.8 on both occasions. Snail No. 30 had no reflected lip on 8 May 1981 but had one on 2 October 1981, adding 0.2 whorl in the interval. Snail No. 7 had 5.5 whorls on 25 October 1980, and 5.7 whorls on 2 October 1981, with no reflected lip added. Snails Nos. 43 and 44 are recorded as having the last quarter-inch of whorl clean on 27 May 1981, implying fresh growth, but nothing more than relative timing can be inferred.

These very limited size-frequency and growth data shed little light on population age structure. The paucity of small individuals (fewer than five whorls) suggests three possible interpretations: (1) they are present at the site but not effectively detected by our search method; (2) little recruitment by reproduction has taken place recently at the study site; or (3) individuals pass through the small size range very quickly, after which growth slows to more nearly the observed values.

The earlier study of *Monadenia setosa* (ROTH & ENG, 1980) indicated differences in site selection by juveniles and adults; the present study did not entirely corroborate those results (see below, "Substratum, location, and mobility"). But except for noting the possibility that, merely by being smaller, the young individuals were more easily overlooked, there is no way to judge the correctness of the first interpretation. The second interpretation, low recruitment, may be supported by the fact that the 2 yr preceding the beginning of this study were unusually dry. Heavy egg and (or) juvenile mortality, or reduced mating may have occurred. In *Helminthoglypta stiversiana*, copulation rate and egg production are correlated with rainfall (VAN DER LAAN, 1980).

Taken as average, the observed growth rates would imply an interval of 9 to 18 yr from hatching to maximum size. We strongly suspect that earlier growth is more rapid. Terrarium-raised *Monadenia fidelis beryllica* attained

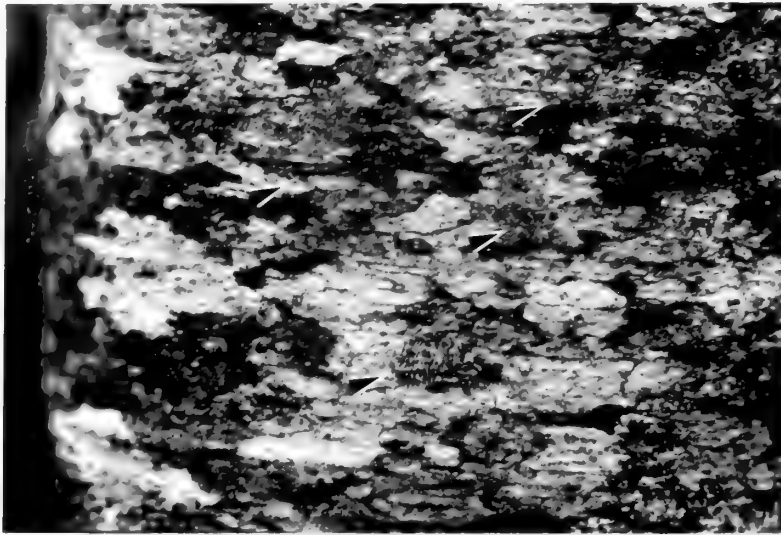


Figure 4

Radular scrapings of *Monadenia setosa* on lichen on alder trunk (arrows).

maturity in 5 yr (records in California Academy of Sciences). The time to maturity is 1–3 yr in *Cepaea hortensis* (WOLDA, 1970; WILLIAMSON, 1979), 6.9 yr in *Achatinella mustelina* (HADFIELD & MOUNTAIN, 1980), 3–6 yr in *Caracolus carocollus* (HEATWOLE & HEATWOLE, 1978), and 3.0–3.75 yr in *Helminthoglypta stiversiana* (VAN DER LAAN, 1971). Some Australian camaenids become functional males after 2 yr (SOLEM & CHRISTENSEN, 1984). Ontogenetic variation in growth rate is a recognized phenomenon in pulmonate mollusks, sometimes related to the state of development of the gonad (WILBUR & OWEN, 1964). HADFIELD & MOUNTAIN (1980) found a relatively constant rate of growth in the Hawaiian tree snail *Achatinella mustelina* over a size range of about 6 to 18 mm length. The factors influencing growth pattern may differ between tropical and temperate environments.

Substratum, location, and mobility: Of 92 captures at the study site for which substrata were recorded, 30 were on the soil or leafmold of the ground itself. Nineteen were on the bark of alders from 0.25 to 7 m above the ground, 29 were on other objects, either stalks or twigs (14), logs or deadfalls (8), or rocks (7); four were in rockpiles, four under objects on the ground, and three under the bark of standing deadwood. Three were recorded as “in leafmold,” as opposed to crawling on top of it.

In the mixed evergreen forest east and upslope from the study site, snails were observed in douglas fir needles on loose soil, at the edge of a decaying log, in a cavity under a decayed stump, and in depressions in the ground.

Some feeding takes place on smooth trunks of alder. Six snails were observed to be rasping the bark, and many trunks showed extensive marks of radular scraping (Fig-

ure 4). In each case the food was one or more species of the mosaic of encrusting lichens. No snails or feeding tracks were seen on larger trunks with furrowed bark. Feeding was also observed on the ground, with the food items being the petiole of a violet, a dendritic lichen attached to a twig (two cases), and an unidentified stalk. Nearly all snails observed on alder trunks were either extended or crawling, even if not feeding.

Small snails, less than 10 mm in diameter, were found on the ground on moss (1), on bark under a deadfall (2), and about 2.5 mm deep in leafmold (1). Snails between 10 and 20 mm in diameter were found feeding on alder bark 1–2 m above the ground (2), or in a rockpile (1). ROTH & ENG (1980) indicated that the preferred habitat of juveniles under 9 mm in diameter was under the bark of standing deadwood, but our results indicate a broader range of site selection by small snails. The three specimens found under the bark of standing deadwood during this study were 29.7, 29.6, and 26.4 mm in diameter; the first two were adults, the third was immature.

Figure 2a plots the locations of individual *Monadenia setosa* on a typical search occasion, 8 May 1981. In Figure 2b, straight lines connect the locations of successive captures over the course of the study. This convention is not meant to suggest that this is all the movement these snails have undergone. Rather, it is a minimum estimate, because a snail could be recaptured near its original capture site after having ranged much farther away. The 3-wk sampling interval is too coarse to pick up variation in short-term movement (*cf.* experiments of COWIE, 1980); the observations do not, therefore, bear directly on the dispersive potential of the species but rather illustrate the tendency for individual snails to remain within a limited

part of the total habitable zone available to them. In the course of a single night's wandering, an individual snail can (and probably often does) travel farther than the distance between captures many months apart. Snail No. 9, for instance, was closer on the night of 3 October 1981 to its original (October 1980) site of capture than to its position when found the preceding night.

Not surprisingly, the perennial stream Bidden Creek was not crossed by any snails in the course of the study. Perhaps more significantly, the semicircular low bench on the north side of the creek remained devoid of snails throughout the study, although apparently offering suitable habitat. This plus the pattern of captures and recaptures indicate that the snails are not uniformly dispersed through their environment and that their distribution at any one time reflects historical factors and, probably, the tendency for *Monadenia setosa* to occupy a narrow home range. Several species of snails and slugs restrict their activities to limited areas (HEATWOLE & HEATWOLE, 1978) or return to specific sites after periods of activity (POTTS, 1975; COOK, 1979; ROLLO & WELLINGTON, 1981). Recapture tracks of snails Nos. 1, 6-9, and 13 show association over time with specific shelter sites such as clumps of trees or logs on the ground. Snail No. 5 may have changed its association from an alder clump at its first capture in April 1981 to a downed log 3-4 m southwest the following October. Snail No. 2 may have shifted from one alder clump to another between May and October 1981.

The pattern of movement seems explicable in terms of the behavior under experimental conditions of the snails and slugs investigated by ROLLO & WELLINGTON (1981). These workers found that slugs (*Ariolimax columbianus*) were capable of long-term homing to a shelter, probably by chemosensory means. Individual slugs tended to home to one of several available shelters, even when all shelters had been occupied by slugs of the same species. Homing is, therefore, probably more complex than simple response to odor.

ROLLO & WELLINGTON (1981:figure 2) detected a seasonal trend in sheltering behavior, apparently related to the severity of the microclimate. Hot, dry weather can kill exposed mollusks (although snails, with shells that can be sealed against desiccation, are less vulnerable than slugs), and there is more risk in wandering far from shelter when conditions tend toward dryness. The summer drop in the number of active snails observed at the study site probably reflects the same phenomenon in *Monadenia setosa*. Similarly, in open conifer-sclerophyll stands, where suitable shelter is sparse and of small extent, homing behavior that intensifies with dryness (up to a point where the "preferred" strategy is to seal down and wait) may be significant to survival.

Balanced against the homing proclivity must be a dispersal tendency, although at this point the tradeoff cannot be specified. As ROLLO & WELLINGTON (1981:255) note,

"no habitat remains favourable indefinitely, and animals must be capable of abandoning those that deteriorate and discovering new favourable areas." In their study, slugs vacated shelters that became fouled by dead individuals, as well as those that became dry or partly flooded.

Less dispersal would be expected in stressed or marginal habitats (POTTS, 1975). Occurring as it does on the east edge of the range of its subgenus, *Monadenia setosa* may encounter marginal conditions more often than, for example, *M. fidelis* populations in the heart of the range. Reduced dispersal under such conditions must intensify genetic isolation and probably in many cases contributes to differentiation and speciation as in *M. setosa* and *M. callipeplus*.

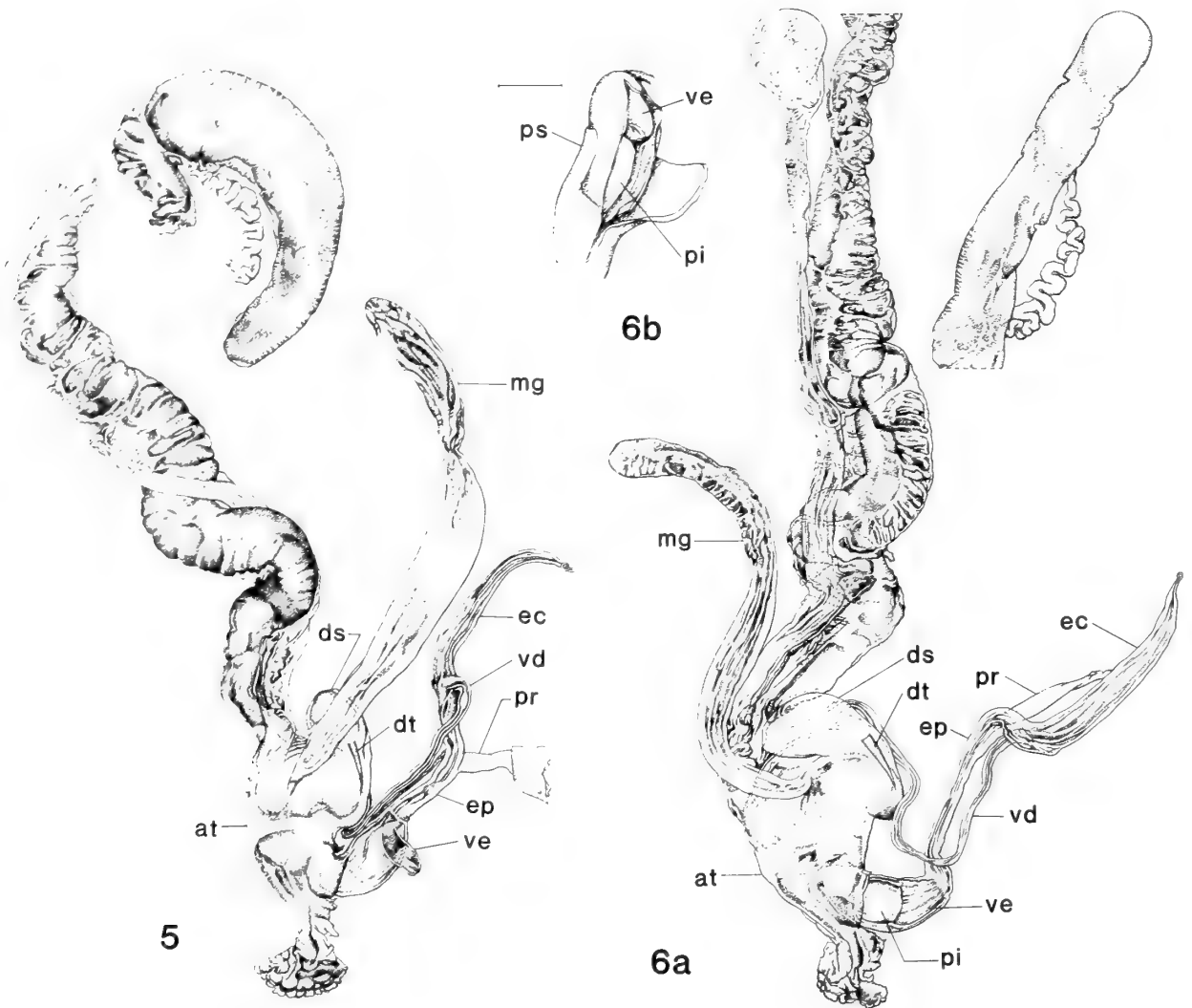
Predation: Evidence of two kinds of predation on *Monadenia setosa* was obtained. On 27 May 1981, snail No. 49 was found apparently freshly killed or stunned by a lampyrid beetle larva (*Ellychnia californica* Motschulsky; det. D. H. Kavanaugh, California Academy of Sciences). This species is commonly found inside dead snail shells in California and in the laboratory kills and devours *Helix aspersa* (Roth, personal observations). The snail was base-up on the ground, the animal withdrawn into its shell with just the tail tip showing, and the larva in the soil just beneath it. The snail showed no response to touch.

The upper limb of the aperture of many *Monadenia setosa* specimens shows small, frequently paired, indentations that suggest nipping by rodent teeth. Similarly indented growth lines occur on the body whorl of other shells. These must represent snails that escaped predation. Rodents may pick up the snails by the lip of the aperture, encounter some repugnatorial secretions of the mantle collar, and drop the snails. ROTH & ENG (1980) previously reported probable rodent or shrew predation and insect parasitization.

COMPARISON OF *MONADENIA SETOSA* AND *M. CALLIPEPLUS*

The original description and the few available museum specimens of *Monadenia (Monadenia) callipeplus* Berry, 1940, from Tompkins Creek (a tributary of the Scott River not far above the latter's confluence with the Klamath River) were similar enough to *M. setosa* to raise the question of whether it represented a remote occurrence of the same species.

On 27-28 April 1981, we found living *Monadenia callipeplus* sparingly among loose, dry black oak and canyon oak leaves and twigs on rocky ground, on the cliff at the south side of the mouth of Tompkins Creek. This locality is about 1.6 km downstream (east) from the original finding of *M. callipeplus* (according to BERRY, 1940) but is connected with it by a continuous corridor of similar habitat, so there is no reason to doubt the identification. The type specimen of *M. callipeplus* was also taken among dry leaves and sticks. We also collected a sample of *Monadenia*



Explanation of Figures 5 and 6

Figure 5. Genitalia of *Monadenia callipeplus*.

Figures 6a and b. Genitalia of *Monadenia scottiana*. Figure 6b. Detail of penis, opened to show pilaster and verge. at, atrium; ds, dart sac; dt, dart; ec, epiphallic caecum; ep, epiphallus; mg,

mucus gland; pi, penial pilaster; pr, penial retractor muscle; ps, penial sheath; vd, vas deferens; ve, verge.

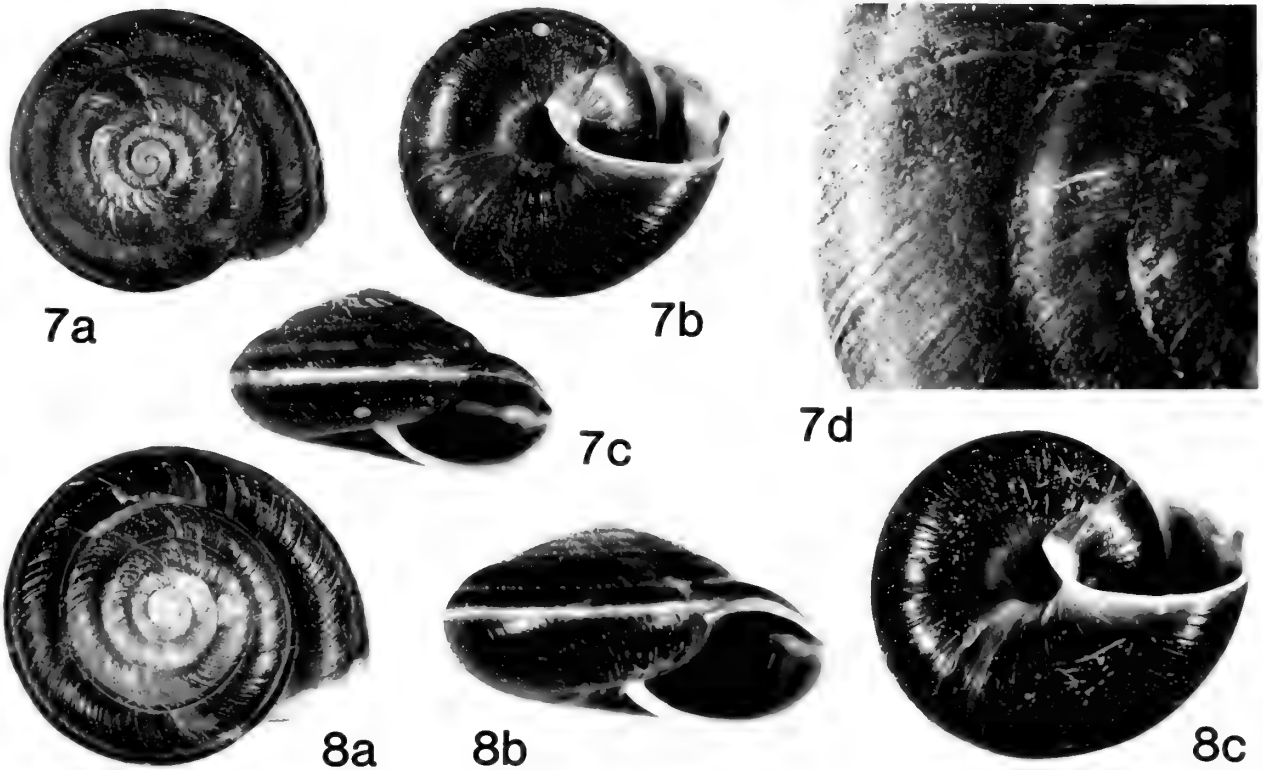
Scale bar = 2.2 mm for Figures 5 and 6a; 2.5 mm for Figure 6b.

(*Monadenia*) *scottiana* Berry, 1940, at Spring Flat campground on the Scott River, about 4.0 km south of Tompkins Creek. This proved useful in the interpretation of *M. callipeplus*, as described below.

The living animal of *Monadenia callipeplus* is slender and creamy buff with black shading on the dorsal tubercles. This is in contrast to the dark gray to black body of *M. setosa* with its brick-red to salmon colored tubercles. The mantle over the lung is buff with about 40% of its area covered by black maculations.

A stained whole mount of the genitalia was prepared by the method of GREGG (1959) (Figure 5). The basic

structure of the genitalia is that of the subgenus *Monadenia* s.s. The flagellum (=epiphallic caecum, ec) is shorter than the penis plus the epiphallus, slightly curved but not spirally coiled except for a minute single coil at the distal end. The atrium (at) is small for the subgenus. The dart sac (ds) is proportionally large and contains a 2-mm, tusk-shaped dart (dt). The upper chamber of the penis is fig-shaped, wider below, with its cavity almost filled by a large, subcylindrical verge (ve) that is slightly wider at its free end; the free end is compressed with two labiate flaps, one on either side of the terminal meatus. The penial retractor muscle (pr) is broad and short; it inserts near



Explanation of Figures 7 and 8

Figure 7. Shell of *Monadenia callipeplus*. Figures 7a-c. Top, basal, and apertural views, $\times 1.5$. Figure 7d. Detail of periostracal surface, $\times 7.5$.

Figure 8. Shell of *Monadenia scottiana*. Figures 8a-c. Top, apertural, and basal views, $\times 1.5$.

the middle of the epiphallus. The lumen of the vas deferens (vd) is dilated into a 1-mm ovate cavity about 0.75 mm from its insertion on the epiphallus. The lower, duct-like part of the mucus gland (mg) is stout; the lowest portion runs over the surface of the atrium to an insertion at the base of the dart sac.

Monadenia callipeplus is smaller than *M. setosa*. The shell (Figures 7a-d) is 22.5–25.3 mm in diameter in adults, compared to a mean of about 30 mm for *M. setosa*, although the smallest *M. setosa* examined (Loc. 2), at 23.7 and 24.1 mm, are smaller than the largest *M. callipeplus*. The umbilicus of *M. callipeplus* is proportionally somewhat larger (mean, $0.117 \times$ shell diameter); this difference is barely apparent without caliper measurement. The yellowish band below the periphery is brighter (*i.e.*, less obscured by periostracum) than in *M. setosa*. The periphery is subcarinate, the surface matte on the spire and base, and the periostracum bears short translucent setae and associated wrinkling, as described in detail by BERRY (1940).

These conchological distinctions by themselves would not be considered grounds for taxonomic separation of

Monadenia callipeplus from *M. setosa*. The genital differences are more important and, by analogy with genital differences in other *Monadenia* species (ROTH, 1981), indicate that *M. callipeplus* and *M. setosa* are separate species. The verge of *M. callipeplus* differs from that of *M. setosa* (ROTH & ENG, 1980:figure 3A) in its terminal compression and presence of flaps. Because of its function in copulation, the verge is probably a good indicator of specific difference. In two sympatric *Monadenia* species in the Shasta Lake region, ROTH (1981) found that the main genital difference was in the shape of the verge. Other points of distinction include the large dart sac of *M. callipeplus*, its small atrium, and the proportionally longer flagellum.

The taxon described as *Monadenia fidelis scottiana* BERRY, 1940, occurs at neighboring sites to *M. callipeplus* (BERRY, 1940) (Figures 8a-c). It is similar but has a shiny, dark brown periostracum, fine, discontinuous, incised spiral lines, and sparse, blunt papillation on the spire. No periostracal setae are present, but on the spire and base of some juvenile specimens there are fine, oblique, raised lines of periostracum, similar to those in *M. fidelis* from

west of the range of *M. setosa*. BERRY (1940) mentioned specimens with papillation on the base as well. The genitalia (Figures 6a, b) show most of the typical characters of *Monadenia* s.s. The epiphallus (ep) is slender and the verge (ve) in the upper chamber of the penis is very large, obconic, with the free end larger in diameter than the base (Figure 6a). The basal chamber of the penis is deeply invaginated into the atrium. A single large pilaster (pi), with its distal end abutting the flat end of the verge, extends into the basal chamber on the side of the penis opposite the vagina. The penial retractor muscle (pr) inserts on the distal one-third of the epiphallus. The dart sac (ds) is large. On the wall of the atrium (at) below the dart sac there is a heavily staining, apparently glandular patch. The mucus gland (mg) is free from the atrium for most of its length, only the extreme lower portion being adnate. The atrium is not conspicuously small. These characters are constant in the two specimens dissected. They indicate that the taxon is distinct from *M. callipeplus* and from *M. fidelis* as well. It is accordingly raised here to species rank, *M. scottiana*.

Another species from the same general region is *Monadenia chaceana* Berry, 1940, of the Shasta River Canyon. ROTH (1981) mistakenly associated this species with *Monadenia (Shastelix) troglodytes* Hanna & Smith, 1933; but anatomical mounts made available by W. B. Miller show that *M. chaceana* is a member of *Monadenia* s.s. In two specimens from near the confluence of the Shasta and Klamath rivers, Siskiyou county (WBM 5172), the flagellum is about as long as the penis plus the epiphallus, tapering distally to a slender, subcylindrical tip. Both atrium and dart sac are smaller than in *M. scottiana*; the dart sac is shorter in proportion to the atrium. As in *M. scottiana* there is a heavily staining patch below the dart sac. The summit of the penis is markedly broader than the epiphallus. The verge in the upper penial chamber is convexly conical, and the meatus subterminal. Below the verge, the median wall of the chamber is thickened. The penial retractor muscle is slender and longer than the flagellum. The spermathecal duct is much more slender than in *M. scottiana*, in which it is somewhat cavernous for its entire length.

Monadenia callipeplus, *M. scottiana*, and *M. chaceana* are all similar in size and shape of the shell, but no intermediate populations are known. Zones of hybridization or intergradation, if they exist, must be very narrow. We interpret these three taxa as autochthonous (locally evolving, rather than immigrating) species, arising under conditions of isolation along the eastern edge of the range of *Monadenia* s.s. As one moves farther from the coast, mesic habitats become less extensive and more likely to be broken up into a series of habitat islands whose isolation persists for many generations. *Monadenia callipeplus* is, therefore, probably more closely related to its neighboring species *M. scottiana* and *M. chaceana* than it is to *M. setosa*. Because a transparent, unornamented periostracum is be-

lieved to be the ancestral condition in *Monadenia* (ROTH, 1981), periostracal setae must be separately evolved in *M. callipeplus* and *M. setosa* and not indicative of a direct patristic relationship.

The scenario presented here for the speciation of *Monadenia callipeplus*, *M. scottiana*, and *M. chaceana* probably applies also in the case of *M. setosa* (cf. ROTH & ENG, 1980:15). The narrow zone of apparent intergradation along the western margin of the range of *M. setosa* indicates that genetic isolation from *M. fidelis* is not complete.

MANAGEMENT IMPLICATIONS

This study revealed that there are a number of more or less discontinuous zones of riparian understory that support populations of *Monadenia setosa*. If the Bidden Creek monitoring site is taken as an example (and it may be more nearly an optimum), population densities of 0.11 snail/m² may exist in many of these zones. Lesser densities may be present on slopes of mixed evergreen forest away from the riparian corridors. In every case the presence of snails seems to depend on the availability of suitable microhabitat: physical shelter in which the animals can withstand seasonal climatic fluctuations.

The low rates of growth observed suggest that recovery from any population catastrophe would be slow. The tendency for snails to occupy a limited home range and to forage in specific areas indicates that repopulation from adjacent areas would be slow and subject to chance. It is quite possible that the population on the lower benches of Swede Creek, where the species was first collected (TALMADGE, 1952), then sampled by other biologists, has not yet recovered from such sampling. In consequence, the earlier field study (ROTH, 1978; ROTH & ENG, 1980) probably underestimated the abundance of the species as a whole, even for the part of the range then known.

The pattern of captures in the monitoring study shows that May and October are the months of greatest activity. Search at any other time of year is likely to underestimate numbers or lead to the conclusion that snails are absent from a site where they do in fact occur. Early morning and after dark are the best times to detect active snails. Discovery of either *Monadenia fidelis* or *M. churchi* at a site is circumstantial evidence that *M. setosa* does not occur there; these species have never been found microsympatrically.

The fortunes of *Monadenia setosa* are tied to the availability of mesic habitat. The shading, temperature- and humidity-regulating qualities of riparian woodland with its dense understory are crucial. Appropriate physical niches exist here and there in open stands of mixed conifer-sclerophyll forest but cannot be counted on to be as extensive, as stable, or capable of supporting large snail populations as the riparian corridors.

The question of vegetational succession can be viewed in the same terms. The critical factors are probably not

the plant species per se but the related physical conditions: moisture retention, leafmold on the ground, shade, and temperature modulation. Any opening up of shading understory could be expected to favor *Monadenia churchi* and its associated species. Advanced stages of forest decadence favor *M. setosa* and its associated species because of increased availability of protective cover (as around and under deadfalls and brushpiles) and enhanced slope stability.

Before targeting a particular area of understory for protection and excluding others, a careful search under optimal seasonal conditions should be made to determine the presence and deployment of viable *Monadenia setosa* populations. In general, the conclusions of the 1978 study regarding substrate, shelter, and forest decadence conditions still hold, although the present study indicates (1) that juvenile dependence on standing deadwood was overestimated and (2) that there is limited occurrence outside of riparian corridors.

ACKNOWLEDGMENTS

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- fork Summit, ctr. sec. 21, T. 32 N, R. 10 W (B). *11. Big Creek, along Big Creek Road 0.25 mi N of intersection with Forest Service Road 4N16, N ctr. sec. 6, T. 32 N, R. 11 W (A). *12. Limestone Creek 0.125 mi upstream from confluence with Big Creek, SE¼ NE¼ sec. 31, T. 33 N, R. 11 W (A). 13. Small stream by road along E branch of N Fork Trinity River, SW¼ SW¼ sec. 16, T. 34 N, R. 11 W (A). 14. Manzanita Creek, N and S of Calif. Hwy. 299 bridge, NE¼ NE¼ sec. 5, T. 33 N, R. 12 W (A). 15. E branch of N Fork Trinity River at road crossing, SE¼ SE¼ sec. 5, T. 34 N, R. 11 W (A). 16. Near head of Big Bar Creek at Forest Service Road 4N16, NW cor. SE¼ sec. 27, T. 33 N, R. 12 W (A). 17. Don Juan Creek, for 0.25 mi N of Calif. Hwy. 299, SW¼ sec. 20, T. 5 N, R. 7 E (A). 18. E bank Cedar Flat Creek, SE¼ SW¼ sec. 19, T. 5 N, R. 7 E (A). *19. Banks of Swede Creek between Calif. Hwy. 299 and Olsson Ranch, NE¼ sec. 23, T. 5 N, R. 7 E (A) [type locality of *M. setosa*]. 20. Limestone rockslide N of Calif. Hwy. 299, 0.4 road mi E of Del Loma, NE¼ SE¼ sec. 25, T. 5 N, R. 7 E (B). 21. Upper and lower riparian benches, E side Canyon Creek, NE¼ NE¼ sec. 30, T. 35 N, R. 10 W (A). 22. Natural Bridge, SE¼ sec. 33, T. 31 N, R. 11 W (A). 23. 3.9 mi W of Trinity River bridge at Big Bar, rockslides N of Calif. Hwy. 299 (B). 24. Limestone outcrop near mouth of Manzanita Creek at Calif. Hwy. 299, NE¼ NE¼ sec. 5, T. 33 N, R. 12 W (B). 25. Hawkins Creek drainage along Forest Service Road 7N01, NW¼ NW¼ sec. 22, T. 6 N, R. 6 E (B). 26. Soldier Creek Loop, NE¼ SW¼ sec. 27, T. 33 N, R. 11 W (B). *27. S side Trinity River 0.125 mi E of confluence of Price Creek, SW¼ NE¼ sec. 5, T. 33 N, R. 12 W (A). 28. New River drainage, NW¼ NE¼ sec. 13, T. 6 N, R. 6 E (A). *29. Hill slope E of Bidden Creek N of Forest Service Road 4N47, SW¼ SE¼ sec. 19, T. 4 N, R. 8 E (B). *30. W bank Big French Creek, first large terrace N of Calif. Hwy. 299, NE¼ SW¼ sec. 20, T. 5 N, R. 8 E (A). 31. Bell Creek, SW¼ SE¼ sec. 12, T. 6 N, R. 6 E (A). 32. Madden Creek, up trail 300 yd from washed out bridge, ctr. SW¼ sec. 21, T. 6 N, R. 5 E (A). 33. Hawkins Creek above confluence with unnamed tributary stream, NW¼ SE¼ sec. 9, T. 6 N, R. 6 E (A). 34. Unnamed creek tributary to Eltapom Creek, ctr. NW¼ sec. 36, T. 4 N, R. 6 E (A). 35. South-facing pebbly talus slope E of mouth of Little Swede Creek, SW¼ NW¼ sec. 24, T. 5 N, R. 7 E (B). *36. Little Swede Creek, SW¼ NW¼ sec. 24, T. 5 N, R. 7 E (A). 37. Hennessy Ridge Road, 2.3 mi up from start of Forest Service Road 6N12, ctr. SW¼ sec. 30, T. 6 N, R. 6 E (A). 38. Hillside W of Swede Creek between Calif. Hwy. 299 and Olsson Ranch, NW¼ NE¼ sec. 23, T. 5 N, R. 7 E (B).

APPENDIX: LOCALITIES

Localities yielding land mollusks in the course of this study are listed below; they are characterized as either (A) within the zone of dense deciduous understory or (B) in stands of open growth. *Monadenia setosa* was found at localities marked by an asterisk (*). Localities with range west (W) are located with reference to Mount Diablo Base and Meridian; localities with range east (E) are located with reference to Humboldt Base and Meridian.

1. Springs by Forest Service Road 5N16, E of Barnum Ridge, SE¼ SE¼ sec. 7, T. 5 N, R. 8 E (B). *2. Limestone talus slope W of Forest Service Road 5N16, SW¼ sec. 32, T. 6 N, R. 8 E (B). *3. Drainage of Swede Creek from seep areas at head of crossing of Big Mountain Road, NE¼ sec. 1 to NW¼ sec. 13, T. 5 N, R. 7 E (A). *4. Bidden Creek, north of Forest Service Road 4N47, SW¼ SE¼ sec. 19, T. 4 N, R. 8 E (A). 5. Unnamed creek tributary to McDonald Creek at Forest Service Road 60 S of Burnt Ranch, NW¼ sec. 22, T. 5 N, R. 6 E (A). *6. Unnamed Creek along Forest Service Road 4N16 at first switchback S of Big Bar, SE¼ SW¼ sec. 6, T. 4 N, R. 8 E (A). 7. Mud Spring, NE¼ NW¼ sec. 21, T. 4 N, R. 8 E (B). 8. Near head of Price Creek at Forest Service Road 4N16, ctr. sec. 28, T. 33 N, R. 12 W (A). 9. Unnamed creek tributary to Packers Creek at Forest Service Road 4N16, SW¼ NE¼ sec. 36, T. 33 N, R. 12 W (A). 10. Roadside spring creek on Calif. Hwy. 3 NE of Hay-

Food Selection and Nocturnal Behavior of the Land Snail *Monadenia hillebrandi mariposa* A. G. Smith (Pulmonata: Helminthoglyptidae)

by

KATALIN SZLAVECZ

Department of Systematic Zoology and Ecology, Eötvös University,
Puskin u. 3, H-1088, Budapest, Hungary

Abstract. Some aspects of the natural history of an endemic Californian snail, *Monadenia hillebrandi mariposa*, were studied. Analyses of feces and laboratory experiments were carried out to observe the food selection and nocturnal behavior of the animals. Larger animals tend to spend more time crawling, less time feeding, and travel longer distances than smaller ones, although larger animals exhibited high individual variability. The snails feed on both living and dead plant material. They have a broad diet, but seem to prefer certain food items, especially leaf litter. In this aspect they are similar to other terrestrial gastropod species reported in the literature.

INTRODUCTION

LITTLE IS KNOWN about the natural history and ecology of endemic Californian snails. The taxonomy of the western North American genus *Monadenia* has been extensively studied by PILSBRY (1939) and by ROTH (1981), who divided the genus into three subgenera based upon shell morphology, reproductive anatomy, and area of distribution. One of these subgenera, *Corynadenia* Berry, 1940, occurs in California only and has long attracted the interest of malacologists and private shell collectors (HANNA & SMITH, 1954). Recent collections of these snails indicate that various aspects of their ecology and evolution deserve further attention as well. Live specimens of some species were first found only a few years ago. Often, populations of the same species occur in isolated areas, resulting in a divergence of many morphological characters. This raises questions about their taxonomy, ecology, and evolution (PRESSLEY, 1983; ROTH, personal communication).

Monadenia (Corynadenia) hillebrandi mariposa A. G. Smith, 1957, has been found on limestone outcrops of the western foothills of the Sierra Nevada Mountains (SMITH, 1957). It is a rock crevice dwelling species. Its yearly activity is restricted to a few months in the spring and fall. In the winter and summer the animals crawl deep

into the cracks of the rocks and hibernate or aestivate respectively, thus avoiding the harshness of the physical environment. *Monadenia h. mariposa* is cryptic, hiding in crevices during the daytime and crawling on the surface only at night or on rainy days. Apart from these observations nothing is known of the feeding habits, nocturnal behavior, reproduction, or life history of the species. Based upon laboratory experiments and analyses of feces, this paper makes contributions to the natural history of the species, focusing on its diet and nocturnal behavior.

MATERIALS AND METHODS

Snails were collected during the night of 23 April 1982 from a limestone outcrop in the Stanislaus National Forest (California, Mariposa County, NW $\frac{1}{4}$ sec. 29, T. 2 S, R. 18 E, Mount Diablo Base and Meridian, elevation: 800 m). All individuals collected were actively crawling and (or) foraging on the surface of the rocks. A total of 31 individuals (13 adults and 18 juveniles) was found. Snails with well-expressed lips were considered as adults. From the time of collection to the end of the experiments every individual was treated in the same way.

The snails were taken to the laboratory where they were weighed and their maximum shell diameter measured (Figure 1).

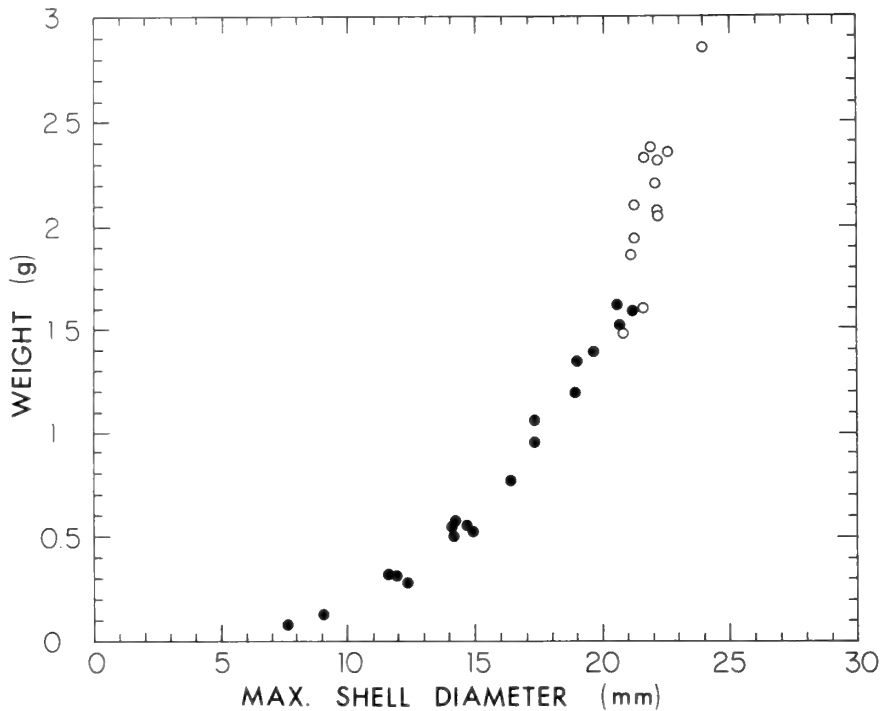


Figure 1

Relationship between maximum shell diameter and live weight of *Monadenia hillebrandi mariposa*. Filled circles, juveniles; open circles, adults.

Potential food resources in the form of living and dead plant material were also collected from the outcrop, and included the following. Living material: mosses (a mixture of *Grimmia trichophylla* Greville and *Rhytidiadelphus* sp.), a lichen (*Evernia prunastri* [L.] Acharius), *Selaginella hansenii* Hieronymus, grasses (a mixture of *Bromus tectorum* L. and *B. diandrus* Roth), an herb (*Phacelia imbricata* Greene), and pieces of limestone with algae growing on their surfaces. Dead material: bay litter (litter material only of *Umbellularia californica* [Hooker & Arnott] Nuttall), shrub litter (a litter mixture of buck rush, *Ceanothus cuneatus* [Hooker] Nuttall, service berry, *Amelanchier alnifolia* Munz, and interior live oak, *Quercus wislizenii* A. De Candolle), and pine litter (needle litter of digger pine, *Pinus sabiniana* Douglas).

Living plants and leaf litter accumulations were usually distributed in distinct patches in the field. Algae, mosses, and lichens were growing on rock surfaces.

In the laboratory, living plants were maintained in flower pots and the leaf litter was stored in plastic bags in a refrigerator.

The animals were kept in the laboratory at 13°C from 0700 to 1845 h, and at 10°C from 1845 to 0700 h at a 12L:12D photoperiod. They were fed with a dry cereal mixture of seven grains (wheat, barley, triticale, rice, rye,

oats, and millet), which they readily accepted. Wet paper towels provided the necessary moisture. The animals were starved for 48 h before the onset of each experiment.

Laboratory Experiments

All the experiments were conducted in separate plastic boxes of 40 × 27 × 16 cm size. Excess amounts of the nine different food types were placed along the edges of the boxes. Observations on the behavior of the animals were made at night between 2000 and 0600 h. Each individual was checked every 20 min using a dim flashlight and its behavior was recorded. The experiments were conducted on three consecutive nights with each animal. Thus, a total of 90 records was made for each specimen.

Three categories (feeding, crawling, and resting) were used to describe the nocturnal activity of the snails. HAMILTON & WELLINGTON (1981b) and NEWELL (1966) used the same categories when observing the behavior of terrestrial slugs, although Newell also recorded mating behavior. This latter activity could be omitted in the present case, however, because the animals were kept individually.

Crawling distances were determined by tracing the snails' mucous trail with a marking pen on a plastic sheet placed over the top of each box. Trails on the sides and

the lid of the box were also included. The total length of the trail was measured by using a map tracer. Crawling distances were measured during only one night for each animal.

The experiments were conducted during May 1982, a time of the year when snails were also active in the wild.

Analyses of Feces

To gain information about the natural diet of the animals, fecal analysis was carried out. Feces were obtained from the animals collected on 23 April 1982. Immediately after collection the snails were placed into individual containers lined with a wet paper towel to provide moisture. No food was given to the animals for 72 h. The feces produced during this time were collected from the boxes and microscopically examined. The animals, deprived of any other food source, started to rasp on the paper towel, which gradually appeared in their feces. Eventually the entire fecal material contained nothing but paper towel, mucus and (or) liver string. Feces without any trace of natural food were not included in the analysis.

The few samples of feces found in the field when the animals were collected were also analyzed.

Each sample was spread on microscope slides, covered with glycerine, and examined under a binocular microscope. The large particle size range and unidentifiable remnants prevented the quantitative evaluation used by WILLIAMSON & CAMERON (1976), in which each component was given a score ranging between 0 and 10. However, the relative amounts of "green material" (including algae, moss, lichens, pieces of green leaves, etc.) and "brown material" (including leaf litter, senescent moss, lichen, herb leaves, pieces of twigs, and soil) were compared. Thus, the following seven categories were established based on the relative amounts of green and brown material:

- B = G if the brown:green ratio was 1:1
- B > G (and G > B) if the brown:green (green:brown) ratio was between 1:1 and 2:1
- B ≫ G (and G ≫ B) if the brown:green (green:brown) ratio was between 2:1 and 5:1
- B ≫≫ G (and G ≫≫ B) if the brown:green (green:brown) ratio was greater than 5:1.

Digestive gland feces (liver string), which consist of fine brown particles originating from intracellular digestion, were not included in this evaluation.

RESULTS

Nocturnal Activity in the Laboratory

Twenty-eight animals emerged and were active (that is, spent most of their time feeding and [or] crawling) during all three nights. The three individuals that behaved differently were mostly resting or did not emerge at all. It is possible that they suffered some damage during col-

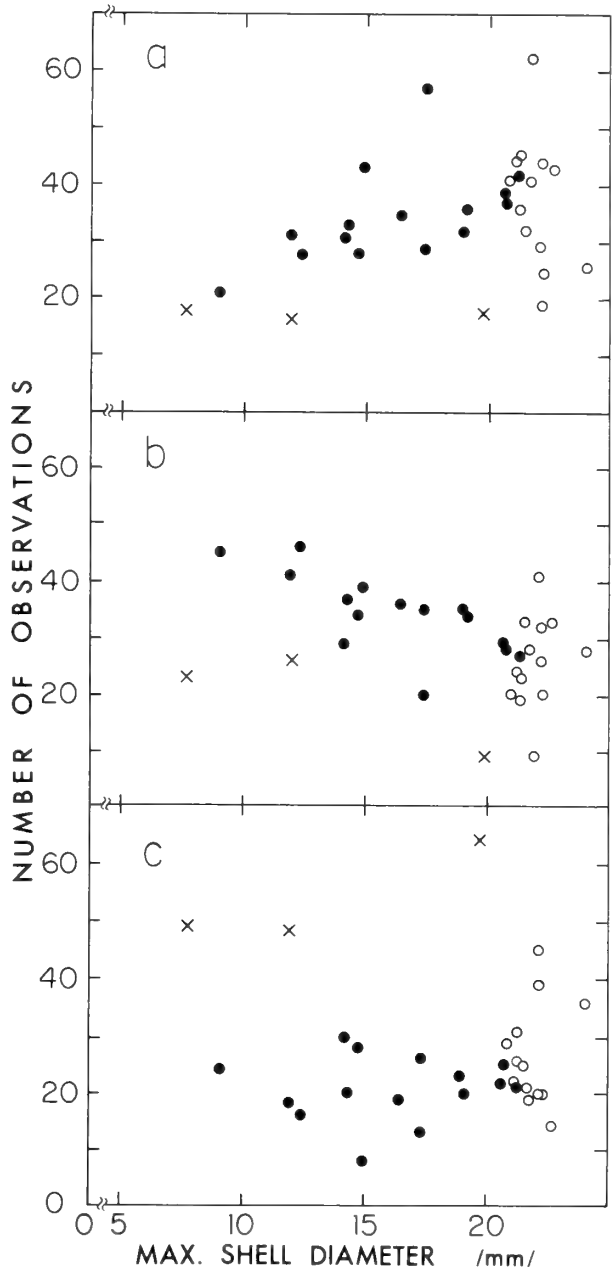


Figure 2

Relationship between size and three types of activity of *Monadenia h. mariposa*. a, crawling; b, feeding; c, resting. Filled circles, juveniles; open circles, adults; crosses, individuals that were not active each of the three nights.

lecting or handling in the laboratory. However, it is also possible that this is normal. In RICHARDSON'S (1975) experiments 80% of the snail population was active each night.

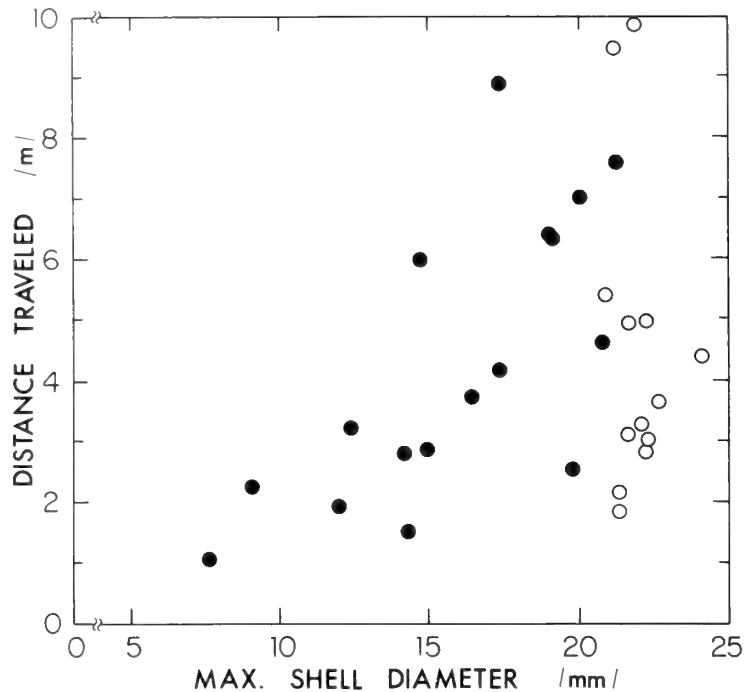


Figure 3

Relationship between size and crawling distances of *Monadenia h. mariposa*. Filled circles, juveniles; open circles, adults.

The active snails were either crawling or feeding. They moved not only among food items but often crawled on the walls and the tops of the boxes as well. The snails frequently followed their own slime trails. Looped paths were also observed. These behaviors can be associated with orientation, although trail following may also lower energetic costs by reducing the mucus production needed for movement (ROLLO & WELLINGTON, 1981; HALL, 1973). The snails frequently lifted their heads and waved their tentacles, indicating that *Monadenia h. mariposa* may also use olfactory cues to orient.

The moving and feeding activities were interrupted by periods of rest that varied in length between a few minutes and hours. During long resting periods the animals often defecated.

The scores (numbers of observations of each individual during the three nights) for each type of activity are shown in Figure 2. There was a positive correlation ($r_s = 0.34$, $P < 0.05$, Spearman rank correlation test) between size and crawling scores, and a negative one ($r_s = -0.36$, $P < 0.05$) between size and feeding scores. The correlation, however, was weak in both cases. This was mostly due to the high variation of scores for adults. There was no significant correlation between maximum shell diameter and resting scores. The correlation between feeding and crawling scores was not significant either.

When the activities of adults and juveniles were compared, only the feeding scores yielded a significant difference (Mann-Whitney U test, two-tailed).

Crawling distances (Figure 3) varied between 1 and 10 m per night. The range of the values for the adults again was large. The correlation coefficient ($r = 0.37$) was still significant at the 0.05 level. For juveniles only the correlation coefficient was much higher ($r = 0.68$, $P < 0.01$). Crawling distances were measured only one night with each individual.

Food Selection in the Laboratory

Figure 4a shows the total number of times animals were observed feeding on each food type. Although the snails accepted many different kinds of food, they were clearly selective ($\chi^2 = 268.9$, $P < 0.001$). Shrub and bay litter were ranked first and second respectively. The animals were frequently observed rasping on the xylem parts of small twigs. Grass and pine litter were the least selected.

The food selection of adults and juveniles (Figure 4b) was significantly different ($\chi^2 = 47.60$, $P < 0.01$). This, however, was entirely due to the difference between scores given for the stones with algae. If this category, which was ranked seventh when all scores were combined, were excluded from the χ^2 test, then there was no significant difference between the food selection of adults and juveniles.

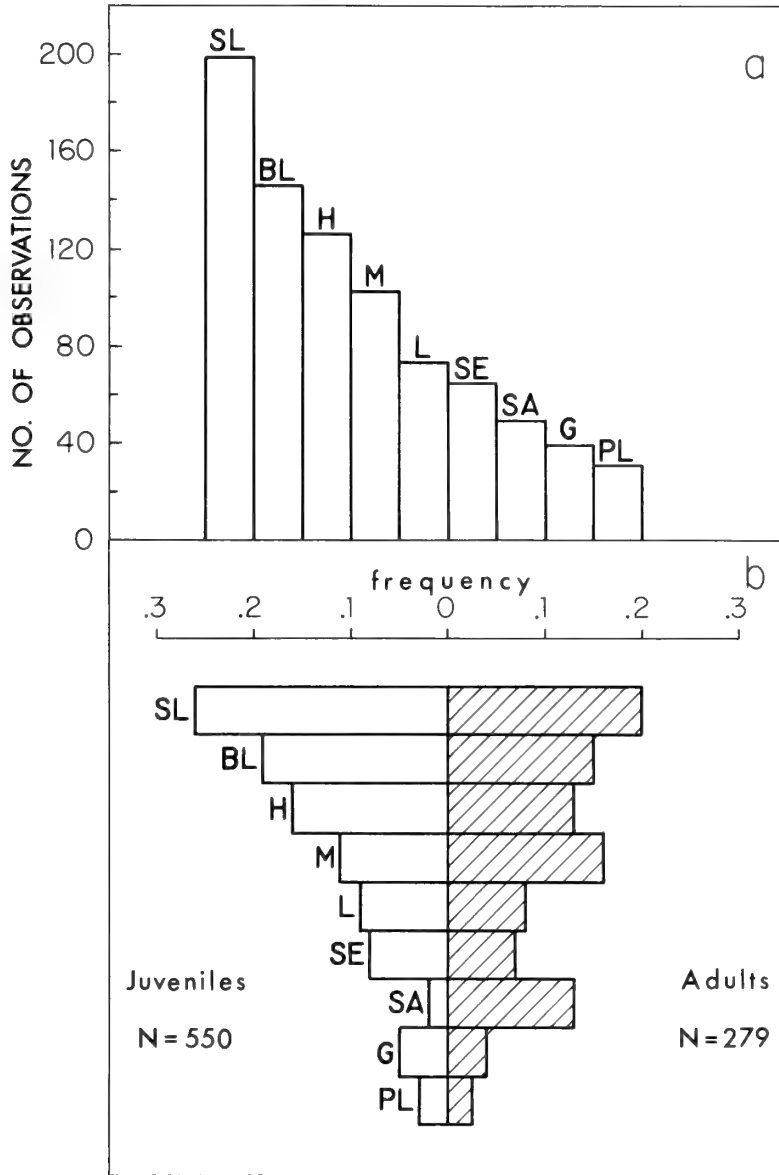


Figure 4

Food selection of *Monadenia h. mariposa* in the laboratory. a. All data combined. b. Adults and juveniles separately. Abbreviations: SL, shrub litter; BL, bay litter; H, herb; M, moss; L, lichen; SE, *Selaginella*; SA, stone with algae; G, grass; PL, pine litter.

Analyses of Feces

A total of 135 samples of feces was examined. Of these, 34 samples were disregarded, as they contained nothing but digestive gland feces, mucus, and (or) paper towel, indicating that the gut was empty. The remaining 101 samples were then analyzed mostly qualitatively. These contained food items the snails had selected in their nat-

ural habitat. Attempts were made to identify only the moss and lichen components. The ones that could be determined at least to genus level included the mosses *Rhytidiadelphus* sp. and *Grimmia trichophylla* Greville, and the lichens *Leptogium* sp. and *Physcia* sp.

The results (Figure 5a) showed that, although most of the samples contained green and brown material, the latter highly dominated in the feces ($\chi^2 = 45.76, P < 0.001$).

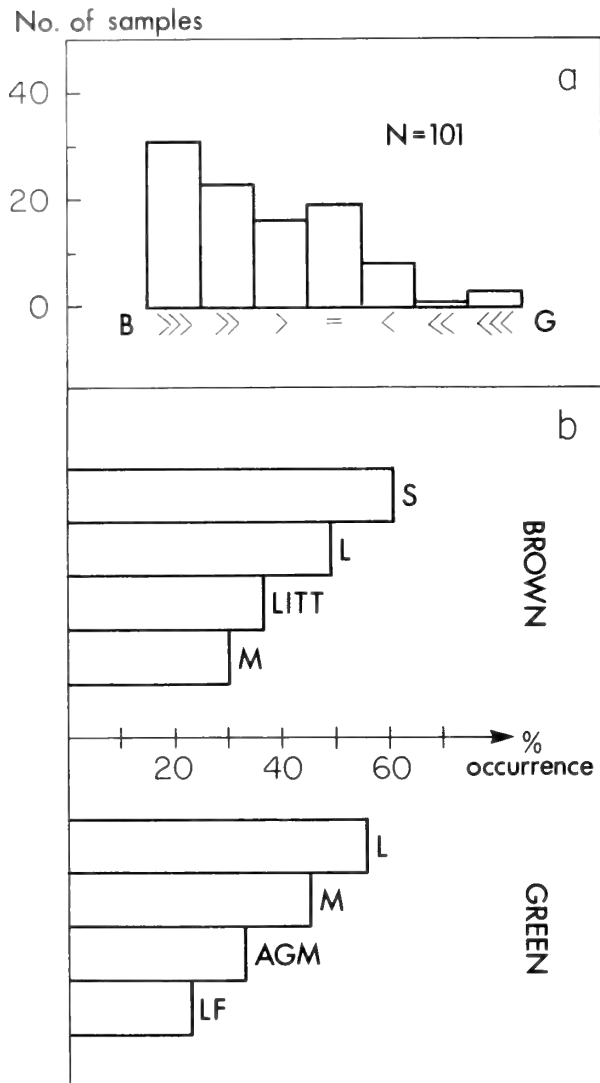


Figure 5

a. Comparison between the brown and green parts of the feces of *Monadenia h. mariposa*. See "Methods" for explanation of each category. b. The percentage occurrence of the major components in the fecal material. Abbreviations: S, soil; L, lichen; LITT, litter material; senescent leaves; M, moss; AGM, amorphous green material; LF, leaf fragments of higher plants.

The percentage occurrence of different food types is given in Figure 5b. Lichens were highly ranked in both the brown and green categories. Soil occurred in 61% of the samples and its relative amount was also high. In 12 samples the entire feces contained nothing but soil. The occurrence of white mineral particles (either quartz or limestone) was also high (47%).

Other plant material not shown in Figure 5b included (the number of samples are given in parentheses): flower

remnants (1) and seeds (2). The following animal matter was also found in a few samples: insect wings (2), a coleopteran thorax and leg (1), pieces of radula (2), and white spherical material that looked like eggs (6).

Digestive gland feces ("liver string") was found together with gut feces in only 28 samples. In the other cases in which it occurred, the feces contained only paper towel or mucus (the 34 disregarded samples). This supports RICHARDSON's (1975) finding that intracellular digestion, which results in liver string production, becomes more important in the metabolism of the snails when they feed on food of low digestibility or starve.

DISCUSSION

The results in Figures 2a and 3 indicate that larger animals tend to crawl more (that is, they spend more time crawling and travel greater distances) than smaller ones. VAN DER LAAN (1971) found that larger specimens of *Helminthoglypta arrosa* moved farther than smaller ones. In the experiments of HAMILTON & WELLINGTON (1981a), dispersing individuals of *Arion ater* were significantly heavier than non-dispersers, although this was not the case for large-bodied *Ariolimax columbianus*. Larger animals may have relatively larger stored energy reserves (HEATWOLE & HEATWOLE, 1978) and, therefore, may be able to travel greater distances than smaller ones. They are also more likely to survive unfavorable conditions. In a study investigating Puerto Rican camaenid snails, HEATWOLE & HEATWOLE (1978) found that the survival of adult *Caracolus carocollis* during dry periods and food shortages was much higher than that of the juveniles. VAN DER LAAN (1975b) also reported that the smallest individuals of *Helminthoglypta arrosa* suffered the highest mortality under dry conditions. It is the individuals of larger and, therefore, less vulnerable size that may be responsible for the dispersal of a population. It is also possible that larger animals have larger home ranges. More information is needed about the homing behavior and dispersability of *Monadenia* to resolve the problem. Small individuals probably have to spend more time feeding, especially because the active period of the population is strongly restricted by climatic factors throughout the year.

The nocturnal behavior of *Monadenia h. mariposa* shows high individual variability. It is particularly remarkable among adults that are of similar size. In their case it may be related to various activities of reproduction (searching for mates, egg production, etc.). Long-term studies of movement by other species of snails have also shown high variability among individuals in distances traveled (*Helminthoglypta arrosa*: VAN DER LAAN, 1971; *Littorina irrorata*: HAMILTON, 1978). LOMNICKI (1969), studying adult members of a *Helix pomatia* population, distinguished between "wide ranging" and "narrow ranging" individuals in terms of their mobility. In the present study the small sample size prevented any attempt to determine a frequency distribution for the different types of activity.

From both the feeding experiments and the analyses of feces it is obvious that *Monadenia h. mariposa* is neither an obligate herbivore nor a detritivore, although dead plant material comprises the majority of its diet. Most studies investigating terrestrial gastropod diets agree that snails and slugs consume fresh as well as dead plant material (e.g., BOYCOTT, 1934; CHATFIELD, 1976; JENNINGS & BARKHAM, 1975; WOLDA *et al.*, 1971), but many of these gastropods have strong preferences for certain types of dead plant material (e.g., RICHARDSON, 1975; VAN DER LAAN, 1975a; CHATFIELD, 1976; MASON, 1970).

There are two major factors that may determine the acceptance of a plant material once encountered: texture and taste. For snails the most important components of the former are the "roughness" and the "toughness" of the external surface. As in the findings of GRIME *et al.* (1968) for *Cepaea nemoralis*, epidermal hairs have no influence on the acceptance of certain food items by *Monadenia h. mariposa*. The herb *Phacelia imbricata* is densely covered with hairs and yet ranked third in the feeding preference. Hairy plant remnants were found in the fecal samples as well. Although *Selaginella hansenii* ranked only sixth, the spines on the tips of the leaves did not protect them from being eaten, and the snails easily crawled across the plant. GRIME *et al.* (1968) also found that hard external surfaces act as a barrier for *Cepaea nemoralis*. In the present investigation *M. h. mariposa* was never observed rasping on the leathery leaves of interior live oak that were in the shrub litter. *Monadenia setosa* Talmadge, a closely related species, also refused oak-leaf litter which is part of its natural substrate (ROTH & ENG, 1980), and oak leaves were not consumed by most of the slug species studied by JENNINGS & BARKHAM (1975). Oak leaves are also known to contain a high percentage of tannins that act as a defensive agent against herbivory (FEENY, 1970; SATCHEL & LOWE, 1967). This may be another reason why *M. h. mariposa* refused to feed on them.

The high rank of the bay litter is somewhat surprising. The bay tree produces essential oils. The exact role of these aromatic compounds is not known, although according to KRAMER & KOZLOWSKI (1979), they may be important in attracting pollinators or repelling herbivores. The only other study in which a gastropod was reported utilizing California bay laurel as a food source is that of INGRAM & HAND (1949), who observed the slug *Ariolimax columbianus* feeding on the fruit of the bay tree.

Grasses were generally refused by *Monadenia h. mariposa*. This is in agreement with most of the studies investigating snail diet (RICHARDSON, 1975; WOLDA *et al.*, 1971; VAN DER LAAN, 1975a; INGRAM & PETERSON, 1947). One exception is the study by WILLIAMSON & CAMERON (1976), in which *Cepaea nemoralis* ate some grass, consisting mostly of senescent blades. The grass and pine litter, which were least selected, were found on the edges of the outcrop. Often it is grassland that separates the limestone outcrops on which snail populations occur.

It is difficult to understand the diets of terrestrial gastropods, because little is known about their nutritional needs. Nonetheless, CHATFIELD (1973), WILLIAMSON & CAMERON (1976), and RICHTER (1976) reported the highest growth rate of juvenile gastropods on a mixed diet. Snail diets may certainly change due to seasonal availability of food types (CHATFIELD, 1976; WILLIAMSON & CAMERON, 1976; WOLDA *et al.*, 1971; VAN DER LAAN, 1975a; RICHTER, 1979). Also, in the case of *Monadenia h. mariposa*, diet probably depends on the local food availability, which may differ on the various limestone outcrops.

The analysis of feces, which reflects food choice in the natural habitat, resulted in a higher rank of certain food items, especially lichens and algae, as compared to the laboratory observations on the food selection by *Monadenia h. mariposa*. This, and the high occurrence of white particles in the feces, indicate that the animals may readily rasp anything they encounter on the surface of the rocks. GRIME & BLYTHE (1969) reported that the feces of *Helicigona lapicida* and *Cepaea nemoralis* individuals collected from limestone outcrops contained a large proportion of lichens.

The very few cases in which animal matter was found in the feces seem to be the result of accidental ingestion as has been found in other studies (WILLIAMSON & CAMERON, 1976; RICHARDSON, 1975; WOLDA *et al.*, 1971; HEATWOLE & HEATWOLE, 1978).

The frequent occurrence of the soil in the feces is somewhat surprising. It is not known how snails utilize it, although several hypotheses have been put forward concerning soil as a "grinding agent" (STOREY, 1970), a calcium source, or a food source (WILLIAMSON & CAMERON, 1976). The first hypothesis seems unlikely for *Monadenia h. mariposa*. It would be difficult to explain the large (sometimes 100%) amount of soil in the feces if its function were solely to help break up plant material. It is possible, however, that snails are able to extract some nutrients, or utilize the microorganisms that live in the soil. Soil seems to be an important food source for the land snail *Helicella virgata* as well. POMEROY (1969) has found that this snail in South Australia mostly feeds by scraping the surface of the topsoil.

Because of the broad diet and the usually abundant food supply, many authors think that food is not an important factor determining either the occurrence or the density of terrestrial gastropods (BOYCOTT, 1934; WOLDA *et al.*, 1971; WILLIAMSON & CAMERON, 1976). The snail population of the south-facing slope of the Winnats Pass in Derbyshire, England, where a large proportion of the limestone is exposed bare surface, is an exception. The density of the snail population there appears to be limited by food (GRIME & BLYTHE, 1969). Clearly, long-term field observations and experiments are necessary to clarify the situation in the case of *Monadenia h. mariposa* and other related snails.

In summary, for the habits investigated in this study, *Monadenia hillebrandi mariposa* fits fairly well into the general picture we have about terrestrial gastropods. Their nocturnal behavior is similar to what has been described for other snail and slug species. They have a broad diet but still show selectivity. They feed on both living and dead plant material, but tend to prefer the latter.

ACKNOWLEDGMENTS

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Zoogeographic Affinities of Prosobranch Gastropods of Offshore Coral Reefs in Northwestern Australia

by

FRED E. WELLS

Western Australian Museum, Perth 6000, Western Australia

Abstract. One hundred seventy-two species of 20 families of prosobranch gastropods are recorded from offshore reefs in northern Western Australia. Of these, 58 species are known only from the offshore reefs and have not been collected along the mainland coast of the state. This parallels the Queensland situation where the fauna of the Great Barrier Reef is also different from the mainland fauna and suggests that there is no need to separate offshore areas into separate provinces.

At least 91% of the 172 species also occur in Queensland, strengthening the contention that the shallow-water inshore areas of Queensland should be considered, along with the northern coast of Western Australia, as part of a single Tropical Australian Province.

INTRODUCTION

THE SHALLOW-WATER MARINE FAUNA of Western Australia can be divided into three regions: a tropical north coast that runs northeast from North West Cape; a south coast east of Cape Leeuwin with a temperate fauna that is continuous with the remainder of southern Australia; and a west-coast-overlap zone between Cape Leeuwin and North West Cape where the tropical and temperate faunas are mixed in varying proportions. About 10% or less of the mollusks occurring in Western Australia are endemic to the state; most have at least part of their distributions in the west-coast-overlap area (WILSON & GILLET, 1971; WILSON & STEVENSON, 1977; WELLS, 1980).

The fauna of the north coast of Western Australia is almost entirely tropical. Of 327 species of prosobranch gastropods recorded north of North West Cape by WELLS (1980) only three were classified as temperate species and 16 as endemic to Western Australia. No major faunal limits are found on the north coast; instead, species gradually drop out as latitude increases. North West Cape, at the northern extreme of the west-coast-overlap zone is the major southern limit for tropical species; of the 230 species that reach North West Cape, 90 have their southernmost known distribution in the area (WELLS, 1980). For mollusks the north coast of Western Australia is thus best considered as a single zoogeographic area.

The question of how the fauna of northwestern Aus-

tralia relates to that of the remainder of northern Australia has been more controversial. HEDLEY (1926) divided tropical Australia into a Solanderian province east of Cape York and a Dampierian province extending from the Houtman Abrolhos-Geraldton area of Western Australia to Cape York. This was subsequently modified by WHITLEY (1932), who subdivided the Queensland shallow-water fauna into a Banksian province along the coast and the Solanderian fauna on the offshore Great Barrier Reef. The division of Australia's tropical coast into two provinces was followed by CLARK (1946), based on an analysis of echinoderm distributions, a division agreed to by MARSH (1976). However, ENDEAN (1957), also based on an echinoderm study, suggested that the Banksian (inshore) area of Queensland should be included with the Dampierian area in a single Tropical Australian Province. ENDEAN (1957) considered that the echinoderm fauna of the Great Barrier Reef was distinct from that of the mainland Queensland coast. Working on mollusks, WILSON & STEVENSON (1977) and WELLS (1980) considered that there were insufficient grounds for separating the Dampierian fauna of northwestern Australia from the eastern Australian fauna.

The above analyses for Western Australia have been based largely on specimens collected along the mainland coast; very little material has been available from offshore areas until recently. The offshore mollusks available con-

sisted primarily of a series of records of beach material collected at Browse Island by D. C. Laurenson in 1971. In 1978 Dr. B. R. Wilson visited Ashmore Reef and Seringapatam Reef on the Russian research vessel *Bogorov* for a one-week period and recorded 42 species of mollusks (WILSON, 1985). In 1982 a Western Australian Museum party collected intensively at Rowley Shoals and a second expedition went to Scott Reef and Seringapatam in 1984. These visits to offshore areas, though limited, resulted in significant new records of mollusks (and other marine organisms) from Western Australia. However, the mollusks collected range over the entire phylum and are beyond the taxonomic capabilities of any single individual to identify reliably. The analysis of distribution patterns of gastropods (WELLS, 1980) was based on 20 prosobranch families best represented in the Western Australian Museum collections and best known taxonomically. The same 20 families are analyzed in the present paper, which has three objectives: to record in the literature new finds in Western Australia of these 20 families; to use the new information to help clarify zoogeographic relationships in northern Australia; and to draw the attention of other malacologists to the fact that there are additional new records for Western Australia in groups not discussed here.

THE OFFSHORE REEFS

Rowley Shoals, Scott Reef, and Seringapatam Reef (Figure 1) were considered by FAIRBRIDGE (1950) as the most perfect examples of shelf atolls in Australia. They are on the outer continental shelf 250 km or more from the nearest part of the continental mainland. Two areas of the continental shelf were described in the region by CARRIGY & FAIRBRIDGE (1954): the Rowley Shelf, on which the Rowley Shoals are located, extends offshore from North West Cape to the Leveque Rise, which extends northwest from Cape Leveque, and the Sahul Shelf, on which Scott Reef and Seringapatam Atoll are located, from the Leveque Rise to the Londonderry Rise off the Northern Territory. The atolls rise almost vertically to the surface from depths of up to 500 m. The continental shelf is deep in this area and there is evidence of recent subsidence (CARRIGY & FAIRBRIDGE, 1954), with the atolls being formed by rapidly growing columns of coral; there is no evidence of a volcanic origin (FAIRBRIDGE, 1950).

There are three reefs at Rowley Shoals (Mermaid Reef, Clerke Reef, and Imperieuse Reef) separated by 30–40 km of ocean. The reefs are 16–18 km long on the north-south axis and are pear shaped with the southern end being larger. The maximum width is 8–10 km. Scott Reef is a double reef with a circular reef 16 km in diameter in the north and a 27-km-wide horseshoe-shaped reef in the south. The two reefs are separated by a narrow channel with depths of up to 600 m. Seringapatam Reef is a small reef north of Scott Reef, with a maximum dimension of 10 km.

The reefs all have intertidal reef flats up to 2 km across

enclosing large lagoons. One or more channels through the reefs are present, usually near the northeastern corners. The reef flats on the western sides, from where the prevailing swell comes, are broader than on the eastern sides. The reef flats are low and drop off quickly into the seaward slope. Spring tides at Rowley Shoals were estimated to have a range of 5 m. After the tide reaches to the level of the reef flat, water in the lagoon is trapped and can exit only through the channels. This results in water within the lagoon being trapped at a level up to 2 m higher than the surrounding ocean at low tide. Tides are semidiurnal. The lagoons are shallow, with sand bottoms and maximum depths of about 50 m. Isolated coral patches within the lagoons reach near to the surface at low tide. Unvegetated sand cays are present on some reefs but are absent on others.

MATERIALS AND METHODS

The Rowley Shoals Expedition was conducted in July 1982, with seven full days at the Shoals, six at Clerke Reef, and one at Mermaid Reef. The Scott Reef Expedition was undertaken in September 1984, with 10 days in the Scott Reef area, nine at Scott Reef and one at Seringapatam Reef. On both occasions the 18-m rock-lobster fishing vessel *Piscean* was chartered out of Broome for the trip. The trips were timed to coincide with a sequence of spring tides. Specimens were collected in as many ways as possible: snorkelling, scuba diving, limited dredging, intertidal collecting, and searching the strand line of the intertidal sand cays. The *Piscean* was moved about and anchored in different areas to provide access to as many habitats as possible, including the seaward slope of the reefs, reef crest, reef flat, lagoon areas, and intertidal sand cays. At Clerke Reef and Scott Reef, all of the above habitats were sampled. At Mermaid Reef and Seringapatam, only the reef flat was sampled.

Living specimens were preserved in 10% buffered formalin and later were transferred to 70% alcohol. Dead shells were retained in cloth bags. All specimens were sorted in the laboratory, labelled and identified. Specimens of all species from each reef were retained and catalogued and are in the collections of the Western Australian Museum.

Queensland occurrences of the species in Table 1 are largely derived from the published literature, in particular WILSON & GILLET (1979) and ROBERTSON (1981). Other sources used were ABBOTT (1960, 1961), BURGESS (1970), CERNOHORSKY (1976, 1984), HINTON (1980), and ZEIGLER & PORRECA (1969). In some cases the collections of the Western Australian Museum have Queensland material for species not recorded in the literature from Queensland. When the literature search had been completed and the Western Australian Museum collections examined, the collections of the Australian Museum, Sydney, were searched for species still not recorded from Queensland.

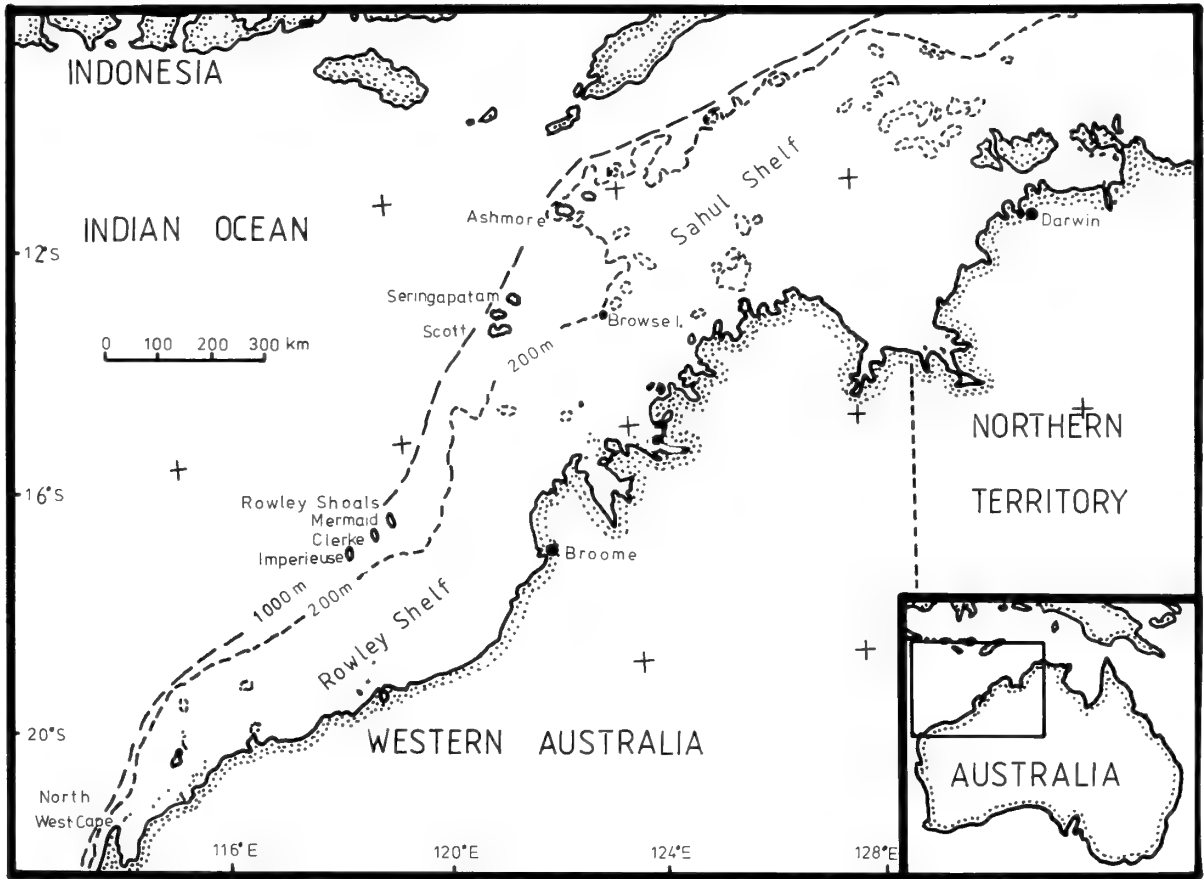


Figure 1

Map of northwestern Australia showing the locations of the offshore reefs.

RESULTS

The species of the 20 prosobranch families considered here that were collected on the Rowley Shoals and Scott Reef expeditions are listed in Table 1. Also listed are records for these species at the other offshore areas of Ashmore Reef and Browse Island and their occurrence in Queensland. A total of 172 species of the 20 families was collected, with about half of the total number of mollusk species recorded during the two trips. Of the 172 species, 58 (34%) have been recorded in Western Australia only on the offshore islands. One hundred and fifty-six (91%) are also known from Queensland. All are Indo-west Pacific species; none is restricted to Western Australia.

The trips were of too limited a duration to examine in detail differences between the fauna of the various reefs. Of the 172 species collected at Scott Reef and (or) Rowley Shoals, 74 were found at both. Many of the species recorded at only one of the two were recorded as single individuals or as only a few specimens. There were some clear differences in the molluscan faunas of Scott Reef

and Rowley Shoals. *Strombus luhuanus*, for example, was common on an intertidal sandflat at Scott Reef and *Conus quercinus* was abundant on reef platforms; neither was collected at Rowley Shoals. Two colonies of *Cassis cornuta* were found at Scott Reef, but only a single individual has been found at Rowley Shoals (G. Sartori, personal communication). *Hebra horrida* and *Nassarius papillosus* were common at Rowley Shoals but were not recorded at Scott Reef. These records indicate that there are some differences in the fauna that are natural reflections of available habitats.

A second, and more easily visible, source of faunal difference is human predation. Several species of giant clams were recorded at Rowley Shoals: *Tridacna gigas* (Linnaeus, 1758), *T. crocea* Lamarck, 1819, *T. squamosa* Lamarck, 1819, *T. maxima* (Röding, 1798), and *Hippopus hippopus* (Linnaeus, 1758). *Tridacna maxima* was recorded as a juvenile individual. *Tridacna gigas*, while not common, was seen at a number of localities and at least 15 individuals were observed, including several on the reef

Table 1

Species of 20 families of prosobranch gastropods recorded from coral reef areas off the northwestern Australian coast.

Species	Known in W.A. only from offshore reefs	Reef area					Queens- land
		Rowley Shoals	Scott	Seringa- patam	Ashmore	Browse	
Family HALIOTIDAE							
<i>Haliotis asinina</i> Linnaeus, 1758		x			x		x
<i>Haliotis ovina</i> Gmelin, 1791		x	x	x			x
<i>Haliotis</i> cf. <i>H. planata</i> (Sowerby, 1833)	x	x					—
Family TROCHIDAE							
<i>Angaria delphinus</i> (Linnaeus, 1758)			x	x			x
<i>Clanculus atropurpureus</i> (Gould, 1849)		x					x
<i>Tectus fenestratus</i> (Gmelin, 1791)					x		x
<i>Tectus pyramis</i> (Born, 1778)		x	x	x	x	x	x
<i>Tectus</i> cf. <i>T. triserialis</i> Lamarck, 1822	x	x					x
<i>Trochus hanleyanus</i> Reeve, 1843		x					x
<i>Trochus histrio</i> Reeve, 1842	x	x			x		x
<i>Trochus maculatus</i> Linnaeus, 1758		x	x	x	x		x
Family TURBINIDAE							
<i>Astraea rhodostoma</i> (Lamarck, 1822)	x	x					x
<i>Turbo argyrostomus</i> Linnaeus, 1758		x	x	x			x
<i>Turbo chryostomus</i> Linnaeus, 1758	x	x	x	x	x	x	x
<i>Turbo petholatus</i> Linnaeus, 1758			x				x
<i>Turbo</i> cf. <i>T. radiatus</i> Gmelin, 1790	x	x					x
Family NERITIDAE							
<i>Nerita albicilla</i> Linnaeus, 1758		x	x	x			x
<i>Nerita plicata</i> Linnaeus, 1758		x	x	x			x
<i>Nerita polita</i> Linnaeus, 1758		x	x	x			x
Family LITTORINIDAE							
<i>Littorina undulata</i> Gray, 1839		x	x	x			x
Family STROMBIDAE							
<i>Lambis chiragra</i> (Linnaeus, 1758)		x	x	x			x
<i>Lambis lambis</i> (Linnaeus, 1758)			x	x	x		x
<i>Lambis truncata</i> (Humphrey, 1786)	x	x	x				x
<i>Strombus dentatus</i> Linnaeus, 1758	x		x				—
<i>Strombus gibberulus</i> Linnaeus, 1758		x	x		x		x
<i>Strombus latissimus</i> Linnaeus, 1758	x		x				x
<i>Strombus lentiginosus</i> Linnaeus, 1758	x	x	x	x			x
<i>Strombus luhuanus</i> Linnaeus, 1758	x	x	x			x	x
<i>Strombus mutabilis</i> Swainson, 1821		x	x		x		x
<i>Strombus pipus</i> Röding, 1798	x				x		x
Family NATICIDAE							
<i>Natica bougei</i> Sowerby, 1908	x		x				x
<i>Natica gualtieriana</i> (Récluz, 1844)		x	x				x
<i>Natica robillardi</i> Sowerby, 1893	x	x					x
<i>Polinices melanostomus</i> (Gmelin, 1791)		x	x		x		x
<i>Polinices powisiana</i> (Récluz, 1844)				x			x
<i>Polinices pyriformis</i> (Récluz, 1844)		x	x	x			x
Family CYPRAEIDAE							
<i>Cypraea annulus</i> Linnaeus, 1758			x	x	x		x
<i>Cypraea arabica</i> Linnaeus, 1758			x	x	x		x
<i>Cypraea asellus</i> Linnaeus, 1758		x		x			x
<i>Cypraea caputserpentis</i> Linnaeus, 1758		x	x	x	x	x	x
<i>Cypraea carneola</i> Linnaeus, 1758		x	x		x	x	x
<i>Cypraea chinensis</i> Gmelin, 1791			x		x		x
<i>Cypraea depressa</i> Gray, 1824	x	x	x	x			—

Table 1
Continued.

Species	Known in W.A. only from offshore reefs	Reef area					Queens- land
		Rowley Shoals	Scott	Seringa- patam	Ashmore	Browse	
<i>Cypraea erosa</i> Linnaeus, 1758		x	x	x	x	x	x
<i>Cypraea helvola</i> Linnaeus, 1758		x			x		x
<i>Cypraea hirundo</i> Linnaeus, 1758		x	x				x
<i>Cypraea histrio</i> Linnaeus, 1758		x	x	x		x	x
<i>Cypraea isabella</i> Linnaeus, 1758		x	x	x	x		x
<i>Cypraea kieneri</i> Hidalgo, 1906			x				x
<i>Cypraea labrolineata</i> Gaskoin, 1848			x		x	x	x
<i>Cypraea lynx</i> Linnaeus, 1758		x	x		x	x	x
<i>Cypraea moneta</i> Linnaeus, 1758		x	x	x	x	x	x
<i>Cypraea nucleus</i> Linnaeus, 1758		x				x	x
<i>Cypraea poraria</i> Linnaeus, 1758		x					x
<i>Cypraea staphylaea</i> Linnaeus, 1758			x			x	x
<i>Cypraea talpa</i> Linnaeus, 1758			x				x
<i>Cypraea testudinaria</i> Linnaeus, 1758	x			x		x	x
<i>Cypraea tigris</i> Linnaeus, 1758		x	x	x	x	x	x
<i>Cypraea vitellus</i> Linnaeus, 1758		x	x	x	x	x	x
Family CASSIDAE							
<i>Casmaria erinaceus</i> (Linnaeus, 1758)		x	x	x	x		x
<i>Cassis cornuta</i> (Linnaeus, 1758)			x				x
<i>Cypraecassis rufa</i> (Linnaeus, 1758)	x		x				x
Family TONNIDAE							
<i>Malea pomum</i> (Linnaeus, 1758)			x				x
<i>Tonna perdx</i> (Linnaeus, 1758)		x	x				x
Family MURICIDAE							
<i>Chicoreus brunneus</i> (Link, 1807)			x				x
Family THAIDIDAE							
<i>Drupa grossularia</i> (Röding, 1798)			x	x			x
<i>Drupa morum</i> (Röding, 1798)			x	x			x
<i>Drupa ricinus</i> (Linnaeus, 1758)		x	x				x
<i>Drupa rubusidaeus</i> Röding, 1798		x	x	x			x
<i>Drupella cornus</i> (Röding, 1798)		x	x	x			x
<i>Maculotriron serriale</i> (Deshayes, 1834)		x	x				x
<i>Mancinella tuberosa</i> (Röding, 1798)		x	x	x			x
<i>Morula biconica</i> Blainville, 1832	x	x	x	x			x
<i>Morula fiscella</i> (Gmelin, 1790)	x	x	x	x			x
<i>Morula granulata</i> (Duclos, 1832)		x	x	x			x
<i>Morula nodicostata</i> (Pease, 1868)		x	x	x			x
<i>Morula spinosa</i> (H. & A. Adams, 1853)		x	x	x			x
<i>Morula uva</i> (Röding, 1798)		x	x		x		x
<i>Muricodrupa funiculus</i> (Wood, 1828)		x					—
<i>Nassa francolina</i> (Bruguère, 1789)			x				—
<i>Thais aculeata</i> (Deshayes, 1844)			x				x
<i>Thais armigera</i> (Link, 1807)	x		x	x			x
Family COLUMBELLIDAE							
<i>Pyrene punctata</i> (Bruguère, 1789)			x				x
<i>Pyrene testudinaria</i> (Link, 1807)		x					x
<i>Pyrene turturina</i> (Lamarck, 1822)			x				x
<i>Pyrene varians</i> (Sowerby, 1832)		x	x				x
Family NASSARIIDAE							
<i>Hebra horrida</i> (Dunker, 1847)		x					x
<i>Nassarius albescens</i> (Dunker, 1846)		x	x	x			x
<i>Nassarius gaudiosus</i> (Hinds, 1844)		x	x				x

Table 1
Continued.

Species	Known in W.A. only from offshore reefs	Reef area					Queens- land
		Rowley Shoals	Scott	Seringa- patam	Ashmore	Browse	
<i>Nassarius granifer</i> (Kiener, 1834)	x	x					x
<i>Nassarius papillosus</i> (Linnaeus, 1758)	x	x					x
Family FASCIOLARIIDAE							
<i>Fusinus undatus</i> Gmelin, 1790			x				—
<i>Latirus craticulatus</i> (Linnaeus, 1758)	x	x	x		x		—
<i>Latirus nodatus</i> (Gmelin, 1790)	x	x	x				x
<i>Latirus polygonus</i> (Gmelin, 1790)		x					x
<i>Latirus turritus</i> (Gmelin, 1790)		x	x				x
<i>Latrolagena smaragdula</i> (Linnaeus, 1758)	x	x	x	x		x	x
<i>Peristernia fastigatum</i> (Reeve, 1847)	x	x					x
<i>Peristernia nassatula</i> (Lamarck, 1822)	x	x	x				x
<i>Peristernia ustulatus</i> (Reeve, 1847)			x				—
<i>Pleuroploca filamentosa</i> (Röding, 1798)		x	x	x	x		x
Family OLIVIDAE							
<i>Oliva annulata</i> (Gmelin, 1791)	x	x	x	x			x
<i>Oliva caerulea</i> (Röding, 1798)		x					x
<i>Oliva</i> cf. <i>O. panniculata</i> Duclos, 1835	x		x				—
<i>Oliva tessellata</i> Lamarck, 1811	x		x				x
<i>Oliva textilina</i> Lamarck, 1811	x		x				x
Family MITRIDAE							
<i>Mitra chysalis</i> Reeve, 1844				x			x
<i>Mitra chrysostoma</i> Broderip, 1836	x		x				x
<i>Mitra cucumerina</i> Lamarck, 1811	x		x				x
<i>Mitra decurtata</i> Reeve, 1844	x		x	x			—
<i>Mitra imperialis</i> Röding, 1798			x				
<i>Mitra litterata</i> Lamarck, 1811		x	x	x			x
<i>Mitra mitra</i> (Linnaeus, 1758)			x	x			x
<i>Mitra paupercula</i> (Linnaeus, 1758)	x	x	x	x			x
<i>Mitra rubritincta</i> Reeve, 1844	x		x				—
<i>Mitra stictica</i> (Link, 1807)			x				x
<i>Neocancilla papilio</i> (Link, 1807)	x	x	x				x
<i>Pterygia dactylus</i> (Linnaeus, 1767)	x			x			x
<i>Pterygia nucea</i> (Gmelin, 1791)	x		x				x
Family COSTELLARIIDAE							
<i>Vexillum cadaverosum</i> Reeve, 1844			x				x
<i>Vexillum consanguineum</i> (Reeve, 1845)	x		x				x
<i>Vexillum deshayesi</i> Reeve, 1844			x				x
<i>Vexillum exasperatum</i> Gmelin, 1791	x		x				x
<i>Vexillum granosum</i> (Gmelin, 1790)	x		x				x
<i>Vexillum</i> cf. <i>V. rosea</i> Broderip, 1836			x				—
<i>Vexillum sanguisugum</i> Linnaeus, 1758	x		x				x
<i>Vexillum semicostatatum</i> Anton, 1839	x		x				—
<i>Vexillum speciosum</i> (Reeve, 1844)			x				—
<i>Vexillum</i> cf. <i>V. turrigerum</i> (Reeve, 1845)	x	x	x				x
<i>Vexillum zelotypum</i> (Reeve, 1845)			x				—
Family VOLUTIDAE							
None							
Family CONIDAE							
<i>Conus arenatus</i> Hwass in Bruguière, 1792		x	x	x			x
<i>Conus balteatus</i> Sowerby, 1833	x	x					x
<i>Conus capitaneus</i> Linnaeus, 1758		x	x				x
<i>Conus catus</i> Hwass in Bruguière, 1792		x					x

Table 1
Continued.

Species	Known in W.A. only from offshore reefs	Reef area					Queens- land
		Rowley Shoals	Scott	Seringa- patam	Ashmore	Browse	
<i>Conus ceylanensis</i> Hwass in Bruguière, 1792			x			x	x
<i>Conus chaldeus</i> (Röding, 1798)		x	x	x			x
<i>Conus coronatus</i> Gmelin, 1791		x	x	x			x
<i>Conus distans</i> Hwass in Bruguière, 1792	x	x	x	x		x	x
<i>Conus ebraeus</i> Linnaeus, 1758		x	x	x	x		x
<i>Conus eburneus</i> Hwass in Bruguière, 1792		x	x	x			x
<i>Conus flavidus</i> Lamarck, 1810		x				x	x
<i>Conus glans</i> Hwass in Bruguière, 1792		x					x
<i>Conus imperialis</i> Linnaeus, 1758	x	x	x	x			x
<i>Conus legatus</i> Lamarck, 1810	x		x				x
<i>Conus leopardus</i> (Röding, 1798)	x	x	x				x
<i>Conus litoglyptus</i> Hwass in Bruguière, 1792	x		x				x
<i>Conus litteratus</i> Linnaeus, 1758	x					x	x
<i>Conus lividus</i> Hwass in Bruguière, 1792		x	x	x			x
<i>Conus marmoreus</i> Linnaeus, 1758		x	x				x
<i>Conus miles</i> Linnaeus, 1758		x	x				x
<i>Conus miliaris</i> Hwass in Bruguière, 1792			x				x
<i>Conus mitratus</i> Hwass in Bruguière, 1792	x		x				x
<i>Conus musicus</i> Hwass in Bruguière, 1792	x		x				x
<i>Conus omaria</i> Hwass in Bruguière, 1792		x					x
<i>Conus pulicarius</i> Hwass in Bruguière, 1792		x	x	x	x		x
<i>Conus quercinus</i> Solander, 1786	x		x				x
<i>Conus rattus</i> Hwass in Bruguière, 1792		x	x			x	x
<i>Conus sponsalis</i> Hwass in Bruguière, 1792		x	x	x			x
<i>Conus striatus</i> Linnaeus, 1758			x	x			x
<i>Conus sugillatus</i> Reeve, 1844			x	x			x
<i>Conus tessulatus</i> Born, 1780			x				x
<i>Conus vexillum</i> Gmelin, 1791			x				x
<i>Conus vitulinus</i> Hwass in Bruguière, 1792	x					x	x
Family TEREBRIDAE							
<i>Hastula albula</i> Menke, 1843	x		x				—
<i>Terebra affinis</i> Gray, 1834		x	x		x		x
<i>Terebra areolata</i> (Linnaeus, 1758)			x				x
<i>Terebra crenulata</i> (Linnaeus, 1758)		x	x				x
<i>Terebra dimidiata</i> (Linnaeus, 1758)		x					x
<i>Terebra felina</i> (Dillwyn, 1817)		x	x				x
<i>Terebra guttata</i> (Röding, 1798)	x		x				x
<i>Terebra maculata</i> (Linnaeus, 1758)		x	x				x
<i>Terebra nebulosa</i> (Sowerby, 1825)		x	x				x

flat. At Rowley Shoals giant clams were abundant on the reef flat, with *T. crocea*, *T. squamosa*, and *H. hippopus* being the most common. Indonesian fishermen are not permitted on Rowley Shoals and the area has been visited by Australian charter boats on a regular basis during only the last five years. In contrast Scott Reef is regularly visited by Indonesian fishermen who collect giant clams as a food source. Only three *T. gigas* were seen at Scott Reef, all by scuba diving in the lagoon. *Tridacna crocea*, a small species that is apparently not fished, is common on the reef flat, but other giant clams are not. Shells of *Trochus*, especially *T. niloticus* were also rare at Scott Reef com-

pared to Rowley Shoals. These are also fished by the Indonesians.

Table 2 compares the numbers of mollusk species of the 20 prosobranch families recorded from the offshore reefs with records from the mainland coast of northern Western Australia. Data from the mainland coast are largely from WELLS (1980), modified somewhat by a few distributional records made since that paper was published. Of the 336 species of these families known from north Western Australia, only 115 (34%) are known from both the mainland coast and the offshore reefs. The in-shore mainland fauna is twice as large as that known from

Table 2

Relationships of gastropod species from mainland localities and offshore reefs in northwestern Australia. Data for mainland species based on WELLS (1980).

	Mainland		Offshore reefs	
	No.	%	No.	%
Restricted to area	221	66	58	34
Known from mainland and offshore	115	34	114	66
Total	336	100	172	100

the offshore reefs. Clearly, additional collecting will increase the number of species known from offshore reefs, but the fauna is relatively restricted, and quite distinct from that farther inshore.

Not only is the offshore area distinct in terms of species composition but it differs in relative composition. Many of the species that have been reported both inshore and offshore have been found at only one or a few mainland localities but are abundant offshore. *Conus miles*, for example, has been recorded as isolated individuals at only five widely scattered localities along the entire mainland coast, but was common on reef platforms on Rowley Shoals and Scott Reef.

DISCUSSION

The collections from the offshore reefs of northern Western Australia have several interesting features. The fauna is limited by a lack of habitat diversity, although more species will no doubt be found as collecting proceeds. The fauna is typical of that of Indo-west Pacific offshore reef areas. Of the 172 species reported here, 102 were listed by MAES (1967) from the Cocos-Keeling Islands (Indian Ocean) and 84 from Chagos (Indian Ocean) by SHEPPARD (1984). Diversity in the 20 families examined is similar to that recorded for the two other Indian Ocean reef systems.

The series of offshore reefs extending from southern Indonesia to northern Australia provides a ready accessibility of the area for species with planktonic larval stages (MARSH, 1976; MARSH & MARSHALL, 1983), and families with this type of reproductive strategy are diverse on the offshore reefs. Volutes and muricids are common along the mainland shore, but only a single species was recorded from the offshore reefs. At least some species of both groups lack planktonic larval stages (WILSON & GILLET, 1971; RADWIN & D'ATTILIO, 1976) and are thus prevented from reaching the offshore reefs.

At least 91% of the species recorded here also occur in Queensland; none is endemic to Western Australia. This strengthens the argument presented by ENDEAN (1957) and supported by WILSON & STEVENSON (1977) and

WELLS (1980) that the waters of tropical Australia should be considered as a single Tropical Australian Province. However, ENDEAN (1957) considered the mainland echinoderm fauna of Queensland to be quite separate from that of the Great Barrier Reef, sufficiently so in fact to consider them as separate zoogeographic units. There has been no similar comparison of inshore and offshore mollusks in Queensland. The data presented here, even though preliminary, clearly show that there is a relatively small overlap of mainland and offshore mollusks in Western Australia, paralleling the situation described by ENDEAN (1957). However, the distinct nature of the mainland and offshore faunas is a result of habitat differences, not zoogeographical patterns, and there is no need to separate the mainland and offshore faunas of Western Australia into differing zoogeographical areas. This suggests that the Banksian province of Queensland should also be considered as part of the Tropical Australian Province, and not as a separate entity.

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Burrowing Performance of Some Tropical Pacific Gastropods

by

GEERAT J. VERMEIJ AND EDITH ZIPSER

Department of Zoology, University of Maryland, College Park, Maryland 20742, U.S.A.

Abstract. The burrowing performance of 33 gastropod species from Guam, Mariana Islands, was assessed in a substrate of moderately coarse loose sand by calculating the burrowing rate index (BRI), defined as the cube root of the animal's mass in grams divided by the time in minutes necessary to achieve complete burial. Rapid burrowing (BRI 1.0 or higher) characterized only three species, and was associated with a large foot and a smooth shell. Despite the mechanical advantages of a wedge shape, species with a conical outline (as exemplified in the genus *Conus*) were slow burrowers (BRI 0.54 or less) and had a narrow aperture and a small foot. The slowest burrowers were high-spired or narrow-apertured species usually possessing spiral or axial sculpture on the shell's exterior.

With the possible exception of ratchet sculpture (ribs whose anterior flanks are less steep than the posterior flanks), no shell characteristic is diagnostic of rapid burrowing. Frequent convergence to the *Oliva* and *Conus* forms cannot be interpreted to imply functional convergence for rapid locomotion.

The burrowing performance of gastropods is comparable to that of pelecypods. We speculate that burrowing is generally ineffective as a method of escape from predators, but is instead effective in preventing detection by enemies.

INTRODUCTION

ACTIVE BURROWING in unconsolidated sediments is a common mode of life in marine gastropods. Well over half the gastropod species in shallow-water assemblages from sand and mud habitats in the tropical Indo-west-Pacific region are burrowers belonging to many prosobranch and opisthobranch families. In contrast to crawling, which has been studied extensively (MILLER, 1974; LINSLEY, 1978; PALMER, 1980; KENT, 1983; DIMMOCK, 1985), burrowing in gastropods has received comparatively little attention. Of the available studies, those of SIGNOR (1982a, b, 1983) are unique in that they provide comparative data on burrowing performance and on the way in which shell shape influences burrowing ability. His work deals only with high-spired species, however, and no large-scale survey of burrowing in gastropods comparable to STANLEY's (1970) study of pelecypods has been undertaken to date.

In this paper we present data on the burrowing performance of 33 shallow-water gastropods from sandy habitats in Guam, the southernmost of the Mariana Islands in the tropical western Pacific. We undertook this survey with three questions in mind. First, how much can be inferred about burrowing in fossil gastropods from a knowledge of the relationship between shell form and bur-

rowing in a geometrically diverse array of living species? In particular, can the frequent convergence to the *Conus* and *Oliva* forms be attributed to selection for high burrowing performance? Second, how does the performance of gastropods compare with that of other burrowing invertebrates, notably the well-studied pelecypods? Finally, how effective is burrowing as a method of escape from predators?

Burrowing performance may be enhanced by several features of the gastropod shell. Rapid burrowing may be achieved either by reducing drag or by increasing power, or both. Drag is minimized by a streamlined shell, characterized by a wedgelike anterior end, a smooth exterior, and a gently curving or straight lateral profile. This morphology promotes the movement of sedimentary particles backward along the shell surface and prevents particles from being carried along by the moving animal. In order to prevent back slippage during burrowing, some burrowers have evolved cuesta or ratchet sculpture in which the anterior flanks of exterior ridges are less steep than the posterior flanks (STANLEY, 1969, 1970; SCHMALFUSS, 1978; SAVAZZI, 1981, 1982; SIGNOR, 1982a, b, 1983). Power in gastropods is provided by the foot. A large foot, associated with a broad aperture or the internalization of the shell,

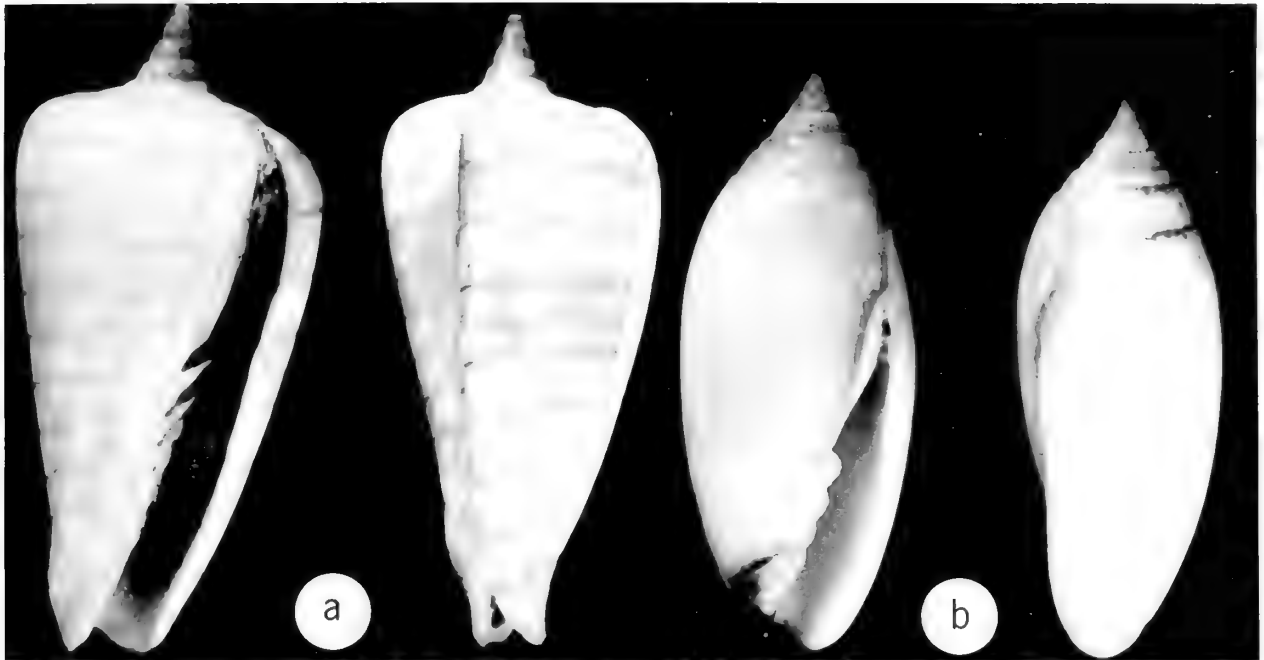


Figure 1

Shells of two species of *Imbricaria*. a. A specimen of *I. conularis*, 15.8 mm long, viewed from the aperture (left) and laterally (right). b. A specimen of *I. olivaeformis*, 12.7 mm long, viewed from the aperture (left) and laterally (right). Photographs and plate composition by Roy Kropp.

should therefore characterize rapid burrowers (SIGNOR, 1982a, b, 1983). In short, the highest rates of burrowing should be associated with conical, smooth, ratcheted, or large-apertured shells.

MATERIALS AND METHODS

Gastropods of 33 species were collected during July and August, 1984, in sandy habitats at five sites in Guam, ranging from the intertidal zone to a depth of 12 m. They were maintained at the University of Guam Marine Laboratory in running seawater in aquaria and allowed to bury in sand for periods not exceeding three days before burrowing performance was measured.

All burrowing trials were staged at ambient seawater temperature (ca. 28°C) in a small aquarium filled with medium to coarse calcareous sand from the reef flat at Pago Bay in front of the laboratory (gravel-pebble fraction 3%, coarse-sand fraction 46%, medium-sand fraction 46%, fine-sand fraction 5%, by weight). At the beginning of a trial, the snail was placed on the surface of the sand. Burrowing time in minutes was measured from the onset of burrowing movements until the snail had buried itself completely. Most individuals were used only once, but a few were allowed to bury several times in succession. Following the trial, we measured animal mass (wet weight in grams) and four linear shell dimensions in millimeters:

shell length (distance from apex to anterior end), maximum shell width (taken to be perpendicular to length), aperture length (distance from anterior to posterior end of aperture), and aperture width (greatest distance from outer lip to left edge of smooth parietal area). Apertural dimensions were not measured in olivids because the left margin of the aperture is not well demarcated in these animals, in which the foot extends over the shell's exterior.

In order to compare burrowing performances among animals of different shapes and sizes, STANLEY (1970) devised the burrowing rate index (BRI), which he defined as the cube root of mass in grams divided by the time in minutes required for complete burial. SIGNOR (1982a) modified the index by replacing mass with volume in the numerator, because he believed that volume was more accurately measured. We chose to use Stanley's index not only because our data would then be directly comparable to his, but also because wet weight was quickly and accurately measured. Moreover, our results on terebrids closely parallel Signor's, so that we are confident that the patterns in our data are not artifacts of the particular index we used.

We tested the size-independence of the burrowing rate index in *Conus pulicarius*, the species for which the largest number and greatest size range of individuals were available. The least-squares fit of the data conforms to the equation

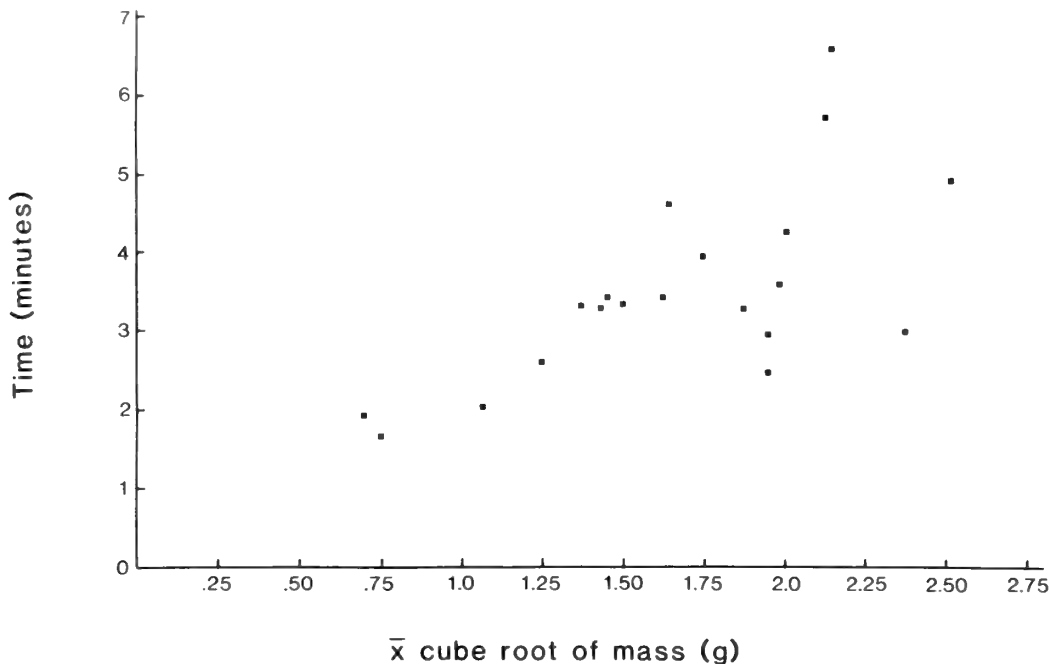


Figure 2

Plot of burrowing time (minutes) against cube root of mass (wet weight) for *Conus pulicarius*. As expected, the data reveal a straight-line relationship over most of the range in mass. Only the very large animals show a conspicuous scatter of points. Some of these large animals may remain partly exposed in the field, for the upper surface of the shell in these individuals may become pitted.

$$Y = 1.697X + 0.681 \quad (r^2 = +0.42, n = 20, P < 0.01),$$

where Y is burrowing time in minutes and X is the cube root of mass in grams (Figure 2). Almost all of the scatter of points was confined to large animals (mass 8 g and greater).

RESULTS

We investigated interspecific patterns of shell form and burrowing performance by analyzing the data in Table 1. The data are pictorially summarized in Figure 3. As expected, the 13 smooth-shelled species burrowed relatively faster than did the 20 spirally or axially sculptured species ($P < 0.01$ for both mean and maximum BRI, Mann-Whitney U-Test). Among high-spined species (ratio of aperture length to shell length less than 0.5), the three species with predominantly spiral sculpture all had a lower BRI than did the four with predominantly axial sculpture. No difference in burrowing performance was observed between the five spirally and six axially sculptured species in the low-spined group.

Species with a large foot were the fastest burrowers in both absolute and relative terms. The three fastest species (*Oliva miniacea*, *O. annulata*, and *Natica gualteriana*) are smooth-shelled, whereas the fourth fastest (*Nassarius*

granifer) has a pustulose sculpture. In *Oliva*, the foot extends over the outer shell surface during burrowing, so that rapid speed is achieved despite the narrowly elongate shell opening.

The slowest burrowers were either very high-spined (*Terebra funiculata*, *T. babylonica*, *Cerithium nesioticum*, *Otopleura nodicincta*) or narrow-apertured (*Conus tessulatus*, *Subcancilla verrucosa*), and all had a small shell opening. There was a highly significant correlation between relative aperture length (aperture length to shell length ratio) and BRI (Spearman Rank Correlation, +0.43 for mean BRI, +0.46 for maximum BRI; $P < 0.01$); that is, low-spined species are generally faster burrowers than are high-spined forms.

Species with a conical outline (*Imbricaria conularis*, *I. punctata*, and species of *Conus*) varied widely in burrowing performance, but none was fast. Among narrow-apertured species, there was not even a hint of a difference in burrowing performance between the eight conical species and the 10 species with a more cylindrical outline (*Vexillum*, *Oliva*, *Subcancilla*, *Graphicomassa*, and *Imbricaria olivaeformis*).

Within species, there was considerable variation in shell shape (shell length to shell width ratio) and in aperture shape (Table 1). We found no correlations between bur-

Table 1

Burrowing performance and shell form in gastropods from Guam. *Key*: Sc: sculpture—ax, axial; ra, ratcheted; sm, smooth; sp, spiral; tu, tuberculate. n: number of individuals tested. Sh.Sh.: shell shape—ratio of shell length to shell width. RAL: relative aperture length—ratio of aperture length to shell length. Ap.Sh.: aperture shape—ratio of aperture length to aperture width. Data are given with standard deviation whenever n is 4 or greater.

Species	Sc	n	Sh.Sh.	RAL	Ap.Sh.	Burrowing rate index	
						Mean	Max.
Family CERITHIIDAE							
<i>Cerithium nesioticum</i> Pilsbry & Vanatta, 1905	sp	1	2.86	0.26	1.73	0.17	0.17
<i>Rhinoclavis aspera</i> (Linnaeus, 1758)	ra	2	2.96	0.36	1.44	0.32	0.36
<i>R. articulata</i> (Adams & Reeve, 1850)	ra	1	2.88	0.33	1.09	0.25	0.25
<i>R. fasciata</i> (Bruguière, 1792)	ra	4	4.62 ± 0.08	0.27 ± 0.01	1.42 ± 0.08	0.32 ± 0.12	0.44
Family NATICIDAE							
<i>Natica gualteriana</i> (Récluz, 1844)	sm	1	1.38	0.72	1.22	1.38	1.38
Family COLUMBELLIDAE							
<i>Graphicomassa ligula</i> (Duclos, 1840)	sm	1	2.61	0.56	3.83	0.33	0.33
Family NASSARIIDAE							
<i>Nassarius granifer</i> (Kiener, 1834)	tu	3	1.56	0.90	1.38	0.83	1.03
Family COSTELLARIIDAE							
<i>Vexillum cadaverosum</i> (Reeve, 1844)	ax	3	2.12	0.56	4.02	0.18	0.25
<i>V. exasperatum</i> (Gmelin, 1791)	ax	11	2.48 ± 0.21	0.56 ± 0.03	3.65 ± 0.37	0.44 ± 0.10	0.61
<i>V. michaudi</i> (Crosse & Fischer, 1864)	ax	6	3.03 ± 0.24	0.55 ± 0.02	5.03 ± 0.33	0.24 ± 0.03	0.27
<i>V. semifasciatum</i> (Lamarck, 1811)	ax	2	2.39	0.58	3.94	0.25	0.38
Family OLIVIDAE							
<i>Oliva miniacea</i> Röding, 1798	sm	3	2.13	—	—	3.15	3.55
<i>O. annulata</i> Gmelin, 1791	sm	3	2.10	—	—	2.72	3.16
Family MITRIDAE							
<i>Ziba fulgetrum</i> (Reeve, 1844)	sp	1	2.71	0.68	5.75	0.45	0.45
<i>Subcancilla filaris</i> (Linnaeus, 1771)	sp	5	2.68 ± 0.40	0.60 ± 0.03	3.81 ± 0.40	0.37 ± 0.13	0.61
<i>S. verrucosa</i> (Reeve, 1845)	sp	1	2.88	0.58	5.00	0.37	0.37
<i>Imbricaria conularis</i> (Lamarck, 1811)	sm	7	2.26 ± 0.04	0.83 ± 0.02	6.22 ± 0.49	0.50 ± 0.10	0.65
<i>I. olivaeformis</i> (Swainson, 1821)	sm	10	2.48 ± 0.19	0.79 ± 0.05	6.09 ± 0.39	0.31 ± 0.13	0.53
<i>I. punctata</i> (Swainson, 1821)	sm	2	1.88	0.92	5.18	0.33	0.41
Family CONIDAE							
<i>Conus catus</i> Hwass, 1792	sp	1	1.54	0.88	5.28	0.54	0.54
<i>C. coronatus</i> Gmelin, 1791	sm	6	1.67 ± 0.07	0.88 ± 0.04	7.18 ± 0.61	0.27 ± 0.10	0.44
<i>C. eburneus</i> Hwass, 1792	sm	3	1.71	0.93	8.17	0.41	0.47
<i>C. pulicarius</i> Hwass, 1792	sm	20	1.72 ± 0.08	0.92 ± 0.02	7.57 ± 0.55	0.49 ± 0.12	0.79
<i>C. tessulatus</i> Born, 1778	sm	1	2.05	0.86	8.15	0.11	0.11
Family TEREBRIDAE							
<i>Hastula solida</i> (Deshayes, 1857)	sm	1	3.96	0.35	2.87	0.60	0.60
<i>Terebra affinis</i> Gray, 1834	ax	8	4.05 ± 0.29	0.31 ± 0.03	—	0.41 ± 0.09	0.60
<i>T. babylonica</i> Lamarck, 1822	sp	1	6.96	0.16	1.68	0.18	0.18
<i>T. felina</i> Dillwyn, 1817	sm	1	4.24	0.27	1.40	0.26	0.26
<i>T. funiculata</i> Hinds, 1844	sp	2	5.79	0.21	1.41	0.12	0.13
<i>T. maculata</i> (Linnaeus, 1758)	sm	4	3.57 ± 0.26	0.38 ± 0.07	—	0.51 ± 0.07	0.58
Family TURRIDAE							
<i>Eucithara stromboides</i> (Reeve, 1846)	ax	2	2.11	0.66	3.27	0.51	0.59
Family PYRAMIDELLIDAE							
<i>Otopleura nodicincta</i> (A. Adams, 1855)	ax	2	2.26	0.48	1.84	0.17	0.19
Family ACTEONIDAE							
<i>Pupa nivea</i> (Angas, 1860)	sp	3	2.16	0.74	2.87	0.23	0.29

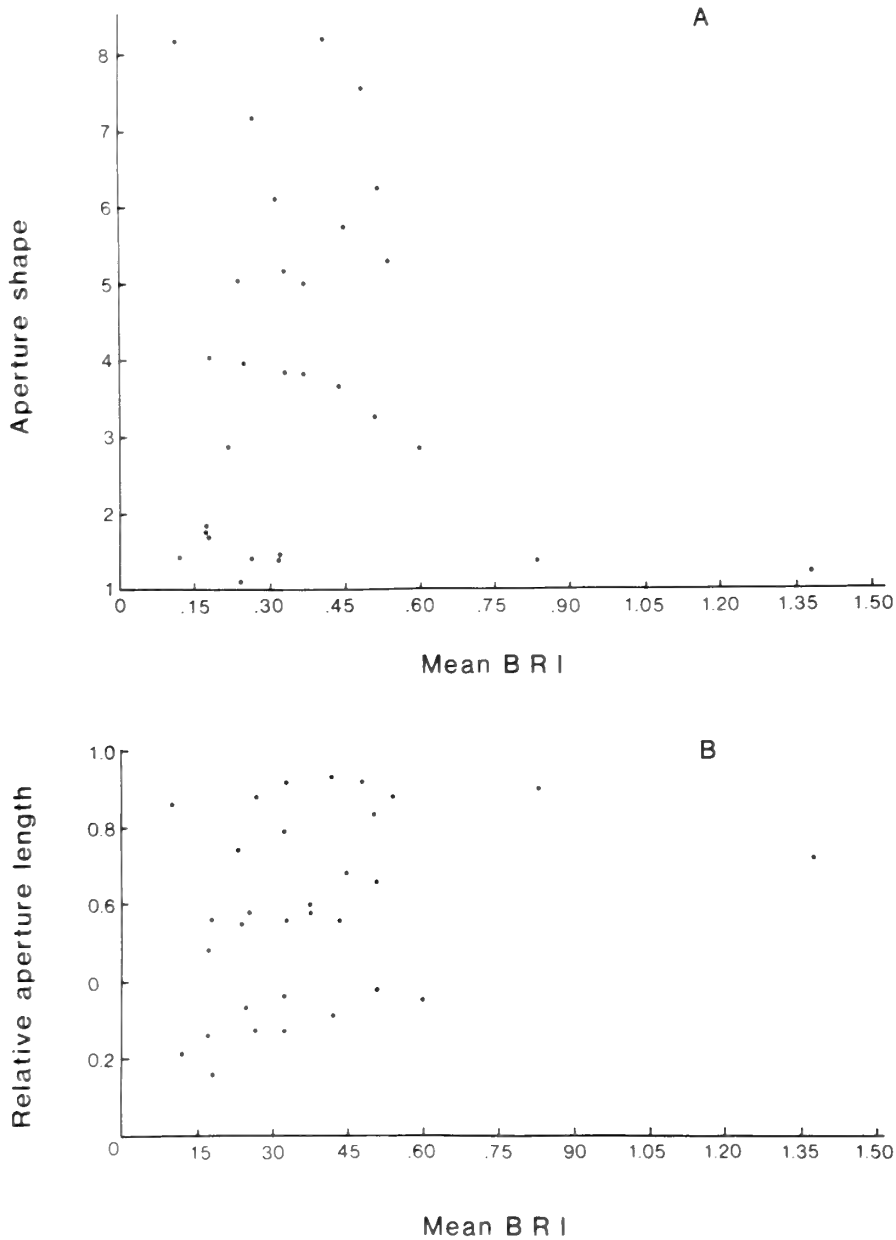


Figure 3

Plot of aperture shape (A) and relative aperture length (B) against mean burrowing rate index (BRI) for 33 species of gastropod. Aperture shape is defined as aperture length divided by aperture width. Relative apertural length is defined as aperture length divided by shell length. Data on which the figure is based are given in Table 1.

rowing performance and either shell shape or aperture shape in any of the species for which the number of individuals was eight or greater (*Vexillum exasperatum*, *Imbricaria olivaeformis*, *Conus pulicarius*, and *Terebra affinis*; $P > 0.20$ in all cases).

DISCUSSION

In his studies of burrowing in high-spired ("turritelliform") gastropods, SIGNOR (1982a, b, 1983) found that the burrowing rate index of terebrids with a squat shell

was higher than that in slender species. Our results corroborate his findings not only for terebrids, but for burrowing gastropods generally. Signor's suggestion that the faster burrowing results from greater power (that is, from the larger size of the foot) seems to be a reasonable explanation for this pattern.

Signor also found that strong sculpture was associated with a slender shape in terebrids, and that it generally implies a slow rate of burrowing. Again, our results are in accord with this finding. Among high-spined species, which drag the shell behind them as they burrow, axial sculpture oriented in the direction of movement is more conducive to burrowing than is spiral sculpture that is oriented at right angles to the direction of movement. The only form of sculpture that enhances burrowing is cuesta or ratchet sculpture, but even this feature is found only in relatively slowly burrowing gastropods such as species of *Rhinoclavis*, *Terebra*, and *Neocancilla*.

With the possible exception of ratchet sculpture, which among gastropods is found only in burrowers (SIGNOR, 1983), none of the shell features of rapidly burrowing gastropods is diagnostic of the burrowing habit. Cowries (family Cypraeidae), for example, have a large foot and a smooth, often highly streamlined shell, but they are incapable of burrowing. The conical shape is common among diverse burrowing gastropods (Marginellidae, Conidae, the cassid *Morum*, the mitrids *Imbricaria* and *Pterygia*, and most Conidae and some Turridae), but it also occurs widely among epifaunal crawlers (the strombid *Conomurex*, the columbellids *Parametaria* and *Minipyrene*, many species of Conidae, and the high intertidal pulmonate family Melampidae). It is possible that the conical form originated in burrowing forms and was subsequently adapted to an epifaunal existence, but even this cannot be proved.

The diversity of habits displayed by conical gastropods raises the important point that convergence in shell form does not guarantee similarity of function. This point is further underscored by the great difference in burrowing capacity of *Oliva*, a fast burrower, and the aptly named *Imbricaria olivaeformis* (Figure 1). Although the latter's shell shape and smooth shell exterior are closely similar to those of *Oliva* (Figure 1), the foot of *Imbricaria* is small and does not extend over the shell as it does in *Oliva*. The convergence in form between these two gastropod genera may be functionally significant (as an adaptation against shell-peeling calappid crabs, for example; see VERMEIJ, 1982), but it does not reflect convergence in locomotory function.

The burrowing gastropods that we studied broadly overlap in burrowing performance the pelecypods studied by STANLEY (1970). Some donacid and tellinid pelecypods have a higher burrowing rate index than do any of the gastropods we examined, but some south African and south Asian species of *Bullia* (Nassariidae), *Umbonium* (Umboniidae in the Trochacea), and *Oliva* are capable of extremely rapid burial and may be comparable in perfor-

mance to the fastest pelecypods (ANSELL & TREVALLION, 1969; MCLACHLAN & YOUNG, 1982). Our *Oliva*, *Nassarius*, and *Natica* have burrowing performances comparable to those of many carditid, venerid, maclrid, and tellinacean pelecypods (STANLEY, 1970). Pelecypods and gastropods with a burrowing rate index ranging from 1.0 to 5.0 show morphological specializations for burrowing that are absent in the more slowly burrowing species. In pelecypods, these specializations include a large foot, a wedge-shaped anterior end, smooth or asymmetrically sculptured surface, and a flattened or cylindrical cross-sectional shape.

We conclude from our survey that most burrowing gastropods in the shallow-water sandy habitats of Guam are slow and not externally specialized for burrowing. How robust is this conclusion for the species we studied, and how applicable is it to burrowing gastropods generally? Although many of the species we studied were represented by only one individual (Table 1), our data as well as those of SIGNOR (1982a, b, 1983) indicate that the burrowing rate index varies little within species. We therefore believe that additional data, though always welcome, would not substantially alter our conclusions. The infaunal gastropod assemblage in Guam is closely similar, both taxonomically and geometrically, to other Indo-west-Pacific infaunal assemblages from shallow-water sandy environments. Assemblages from the continental shores of New Guinea, Indonesia, and the Philippines as well as those of the tropical eastern Pacific have a proportionately larger representation of potentially fast-burrowing olivids and nassariids, but probable slow burrowers such as turrids are also well represented in these faunas. It will be interesting to compare the spectrum of burrowing performances of gastropods on various continental shores with those of gastropods from more oceanic settings such as Guam.

The fact that the narrow-apertured and high-spined species that predominate in tropical Pacific infaunal gastropod assemblages burrow at all raises the question of how gastropods benefit from burrowing. A definitive answer to this question cannot be given with the presently available evidence, but active flight from predators can be safely ruled out as an important factor for all but the fastest burrowers. In Guam and elsewhere, burrowing gastropods that prey on other gastropods are by far the fastest among the infaunal gastropods, in both a relative and an absolute sense. The two species of *Oliva* that we studied were the only gastropods capable of burrowing completely in less than 1 min. All other species, including much smaller ones, feed on animals other than gastropods and required intervals of 1 min to more than 10 min to achieve complete burial, depending on the species. Gastropod-eating burrowing gastropods could, therefore, easily overtake most prey that tried to escape by burrowing. Calappid crabs, which in Guam are among the most important predators of sand-dwelling gastropods (VERMEIJ, 1982), burrow more rapidly than do any of the gastropods

we studied. Like many other infaunal crabs (SAVAZZI, 1982), calappids are able to bury themselves in 5–10 sec. We suspect that burrowing may enable infaunal gastropods and comparably slow pelecypods to remain unobtrusive to visually hunting predators such as fishes and crabs. Once they are found, these prey rely chiefly on armor for their defense (VERMEIJ, 1982). Even for species that are potentially fast enough to burrow away from enemies, escape over the surface of the sediment may be more effective. Many rapidly burrowing gastropods (some olivids, naticids, and umboniids) and pelecypods (cardiids, mac-trids, solenids) typically jump or swim away from predators before reburrowing (STANLEY, 1970). It is possible that burrowing constituted an effective method of escape when it first evolved, but evolutionary strides in the major predators of gastropods have probably made burrowing by gastropods chiefly a way of preventing detection.

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Ultrastructure of the Gill Epithelia of the Dorid Nudibranchs *Archidoris pseudoargus* (von Rapp, 1827) and *Peltodoris atromaculata* Bergh, 1880 (Gastropoda: Opisthobranchia)

by

MECHTHILD JONAS

Zoologisches Institut der Universität Münster, Hüfferstrasse 1, D-4400 Münster, West Germany

Abstract. The epithelia of the tripinnate gills of two species of Eudoridoidea, *Archidoris pseudoargus* and *Peltodoris atromaculata*, were investigated with light microscopy and transmission electron microscopy. The epithelial cells rest on a thick basal lamina overlying a collagenous connective tissue and are the only barrier between the hemolymph and surrounding water; an endothelial lining is not present in the hemolymph spaces. The characteristic respiratory cells are similar in both species and have a prominent nucleus, numerous mitochondria, an extensive basal labyrinth, a microvillar border, and sometimes cilia. The cells can be extremely flattened. Nerve endings often occur in deep epithelial folds. In both species, gland cells (some mucous, some granular) and pigmented cells are distributed over the entire gill surface but are more numerous on the gill branches. The extensive basal labyrinth and microvillar border of the respiratory cells suggest that they may function in ion exchange as well as respiration.

INTRODUCTION

ALTHOUGH THE gills of dorid nudibranchs have been utilized for classification and figured in species descriptions, few investigations have included histological studies and no ultrastructural accounts are known. The histology of the dorid gill has been described in light microscopical investigations by HERDMAN (1890) for *Doris* (= *Acanthodoris pilosa*, RAO (1936) for *Kalinga ornata*, POTTS (1981) for *Archidoris pseudoargus* and *Onchidoris bilamellata*, and WÄGELE (1984) for *Phyllidia pulitzeri*. The ultrastructure of the gill epithelium has been described for a few species within the mollusks: e.g., for the anaspid *Aplysia californica* (PORVAZNIK *et al.*, 1979), the prosobranch *Patella vulgata* (NUWAYHID *et al.*, 1978), the bivalve *Anodonta* (NAKAO, 1975), and the cephalopod *Sepia officinalis* (SCHIPP *et al.*, 1979). Recently bivalve gill structure has been investigated for several species containing symbiotic bacteria (e.g., FISHER & HAND, 1984; GIERE, 1985).

The present work examines the ultrastructure of the gill epithelium of two dorid species, *Archidoris pseudoargus* (von Rapp, 1827) and *Peltodoris atromaculata* Bergh, 1880.

A previous paper (JONAS, 1985) describes the circulatory system of the gills of *P. atromaculata*. The gills of the two dorid species are very similar; they are tripinnate, encircle the anus in a horseshoe shape, and can contract as well as retract into a branchial pocket. This investigation describes the different types of cells in the epithelial layer of the gills of *A. pseudoargus* and *P. atromaculata*, and compares these gill epithelia with the epithelia of other molluscan gills.

MATERIALS AND METHODS

Eight specimens of *Archidoris pseudoargus* (length 50-100 mm) were collected intertidally in Roscoff (Brittany) and by divers in Banyuls sur Mer (southern France). Six specimens of *Peltodoris atromaculata* (length 20-80 mm) were collected by divers in Banyuls sur Mer and Naples (Italy). Material for light microscopy was fixed in Bouin's fluid and stained with Prenant trichrome, Giemsa, or alcian blue and periodic acid Schiff (PAS) (PEARSE, 1968; ROMEIS, 1968). For the ultrastructural research, gills were fixed in one of the following:

- (1) 2.5% glutaraldehyde in 0.2 M Soerensen phosphate buffer with 0.14 M NaCl for 0.5 h, followed by post-fixation in 2% osmium tetroxide in 1.25% NaHCO₃ (pH 7.4) for 1 h.
- (2) 2% osmium tetroxide and 0.5% K₂Cr₂O₇ in 70% seawater (pH 7.4) for 1 h.

After dehydration through acetone, the tissue samples were embedded in Durcupan ACM (Fluka). Silver thin sections were cut on a LKB microtome and a Reichert Ultracut then stained with lead citrate (REYNOLDS, 1963) and examined with a Siemens Elmiskop 101. Semi-thin sections were stained with toluidine blue-1% borax solution.

RESULTS

The gill complex consists of 8–9 tripinnate gills in *Archidoris pseudoargus* and 6–8 tripinnate gills in *Peltodoris atromaculata*. The main branch of each gill divides into two orders of lateral branches (Figure 1a) which bear gill leaflets or pinnules (Figures 1a, b). Each gill branch contains two main blood vessels: the afferent taking blood to the gill pinnules and the efferent taking blood from the pinnules (ELIOT, 1910; POTTS, 1981; JONAS, 1984, 1985).

Semi-thin sections of the gills of the two dorid species reveal the same epithelial structure. The branches and outer margin of the larger pinnules are covered by a simple columnar epithelial layer (height 10–50 μm) within which are dispersed numerous glandular cells (Figure 1a). The pinnules are covered by a cuboidal epithelium (height 4.5–8 μm) with very few glandular cells (Figure 1a). Beneath the epithelium lies a basal lamina followed by collagenous connective tissue that forms the only lining of the blood spaces. In the main gill branches the connective tissue contains numerous spicules that are not found in the smaller branches and the pinnules. The hemolymph lacuna of the pinnules is traversed by trabecular cells joining the two opposite epithelial layers of each pinnule (Figures 1a, c, d).

The electron microscopical investigation shows that three different types of epithelial cells cover the gills in both dorid species: respiratory, glandular, and pigmented cells.

Respiratory Cells

The respiratory cells are mainly distributed on the gill pinnules and only sparsely on the gill branches. The height of the cells varies depending upon location. The respiratory epithelium of the gill leaflets is flat and rests upon a thick, partly folded basal lamina which overlies a thin layer of collagenous connective tissue (Figure 2a). Nerve and muscle fibers are frequently found in the connective tissue layer. Above the folded parts of the basal lamina the epithelial cells often diminish in height to 0.5 μm in *P. atromaculata* and 1–1.2 μm in *A. pseudoargus* (Figure 2b). Usually, nerve fibers terminate in these folds.

The respiratory cells are linked together by junctional structures near the apical cell surface. The surface is covered with densely packed microvilli, and about half of these cells bear cilia of the usual 9+2 type (Figure 2a). The respiratory cells are characterized by a well developed basal labyrinth (Figure 2c). The oval or round nucleus (diameter about 3.5–5.5 μm) contains a prominent nucleolus and granular heterochromatin (Figure 2d). The outer membrane of the nucleus is covered with ribosomes and is connected with a well developed granular endoplasmic reticulum that sometimes contains an electron-dense, finely granulated material. A Golgi complex is usually found near the nucleus. Small vesicles that may be primary lysosomes are situated very near to the concave surface of the Golgi complex. Mitochondria are distributed throughout the cytoplasm and are particularly numerous in the apical cytoplasm of the ciliated cells. Other organelles such as free ribosomes, microtubules, vesicles, and cytoplasmic filaments are scattered in the cytoplasm. Single rosettes of glycogen or larger accumulations of glycogen often occur. Some respiratory cells contain very large lysosomes filled with complexes of variable electron density and membranous material. These vesicles often reach a diameter of 4–5 μm and may be secondary lysosomes. In all ciliated and nonciliated respiratory cells minute membrane-bound bodies, containing a dense homogeneous material, are found in the apical cytoplasm, near the surface membrane (Figure 2d). The vesicles are spherical or rod-shaped (diameter 0.04–0.07 μm ; length up to 0.5 μm) and are only observed after glutaraldehyde fixation (Figures 2e, f).

Glandular Cells

Glandular cells of varied appearance are observed in the gill epithelia, particularly on the gill branches and the outer margin of the larger pinnules. These cells are distinguishable into two groups, granular gland cells and mucous gland cells. Whether these are really different types or whether they represent different degrees of maturity of the secretion is difficult to determine.

Granular gland cells: These cells appear as three different morphological types. Type I, containing a giant vacuole, and type II, containing an ovoid "vacuole body," occur only in *Peltodoris atromaculata*. Type III cells, containing very fine granules, occur in both species.

Type I: Cells with giant vacuoles (Figure 3a). The goblet-shaped cells are typical for the epithelia on the gill branches of *Peltodoris atromaculata*. The apical surface membrane bears only a few microvilli and is partly covered with projections of adjacent cells. The single secretion vacuole occupies about two-thirds of the cell; the remaining one-third contains most of the cytoplasm and a few organelles such as mitochondria, endoplasmic reticulum, and an irregularly shaped nucleus adjacent to the vacuole.

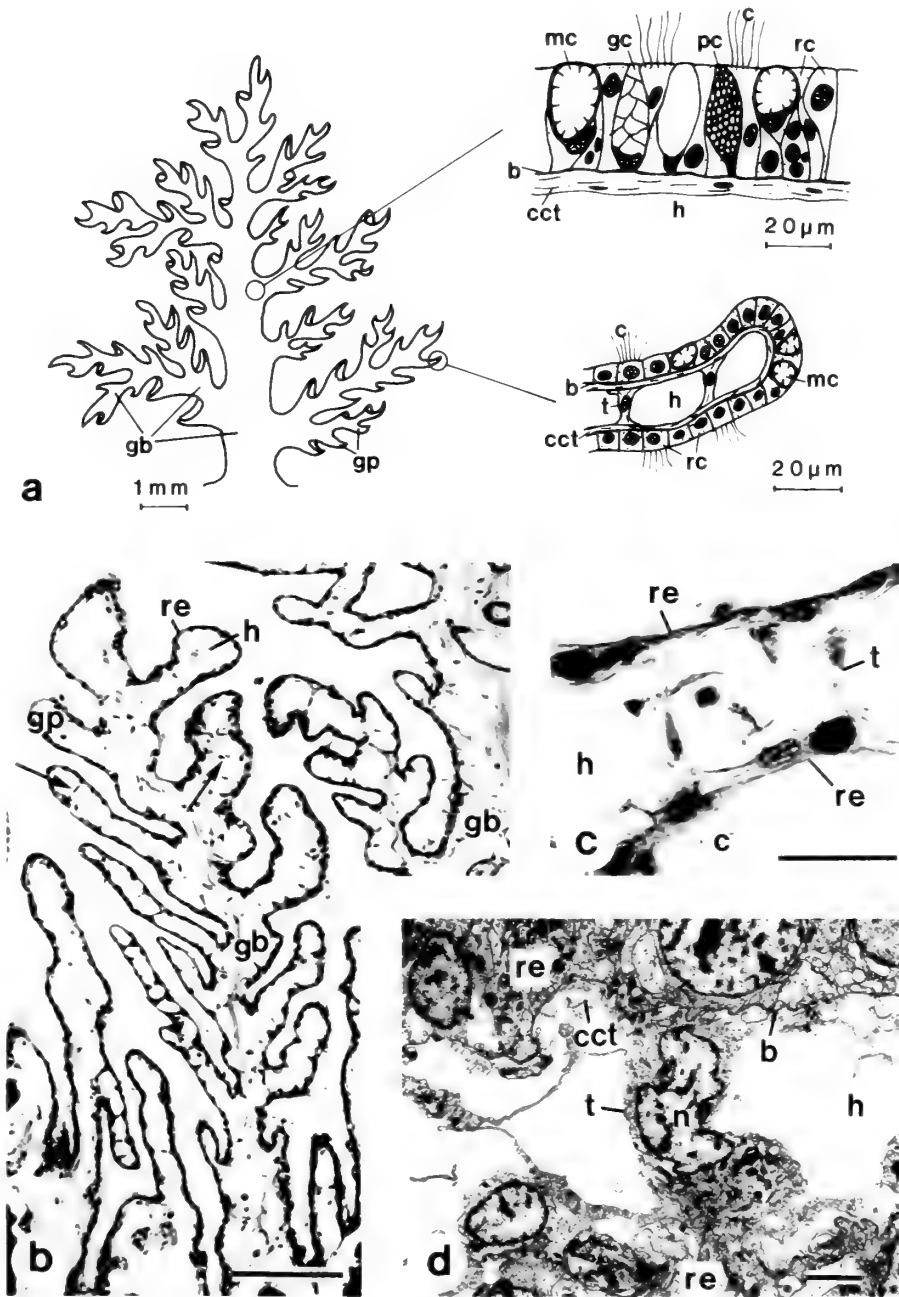
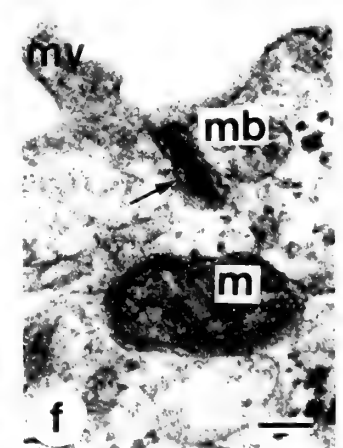
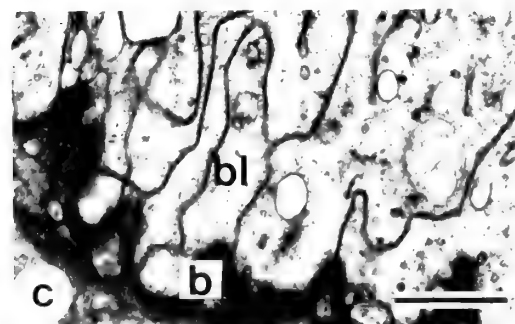
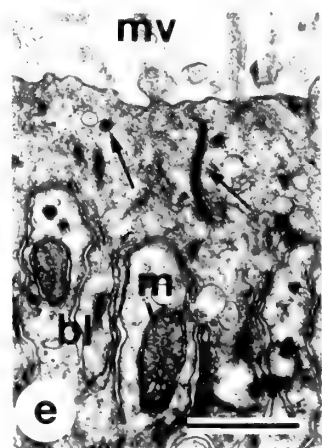
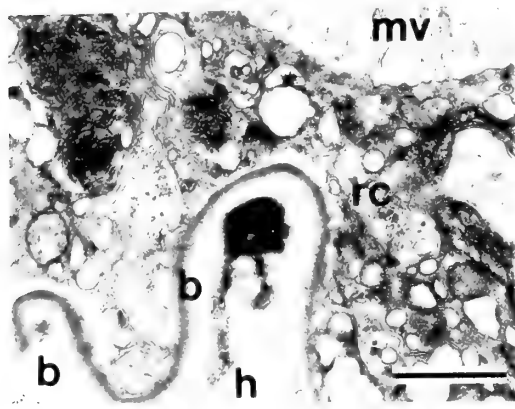
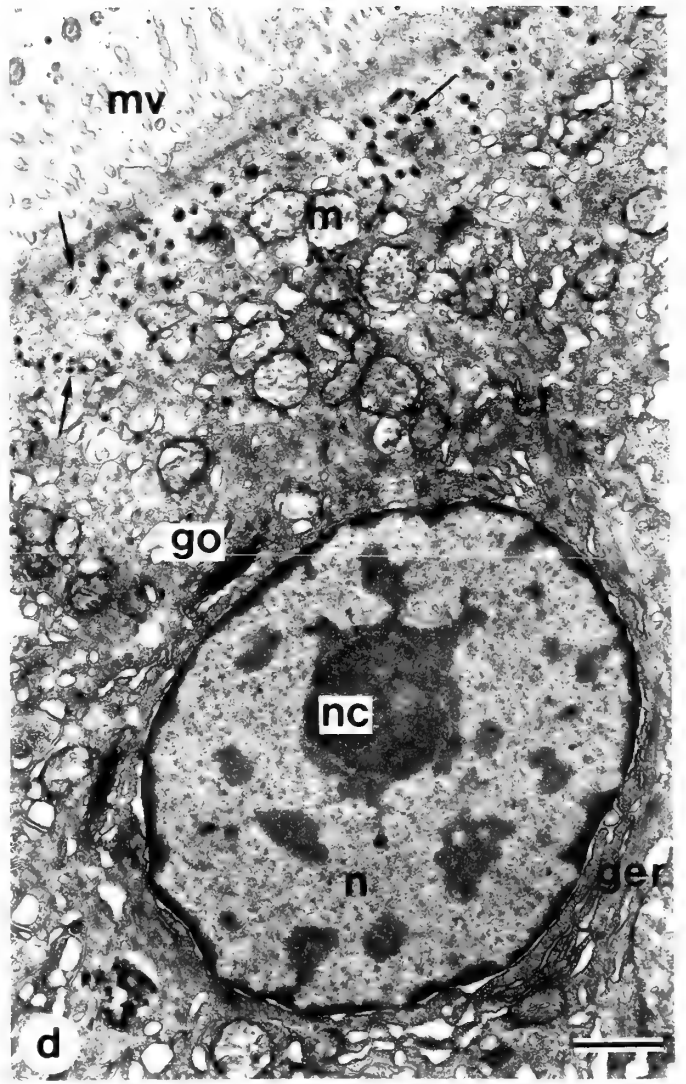
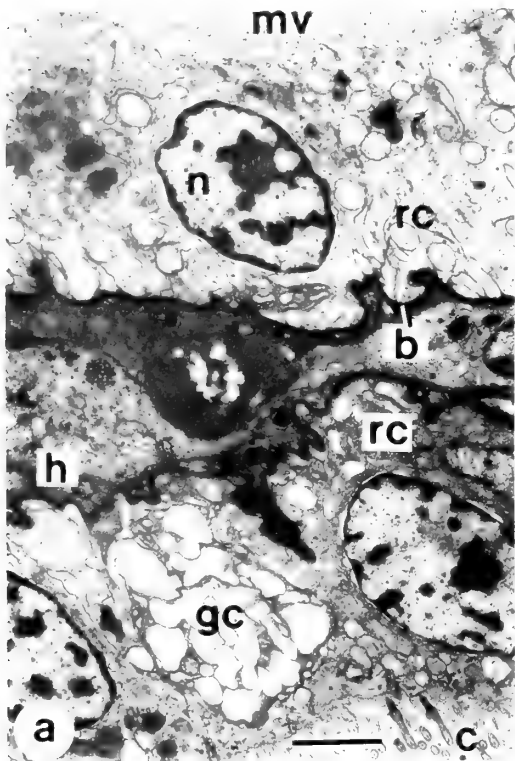


Figure 1

a. Generalized diagram of the tripinnate doris gill; left: external morphology; right: two different types of epithelia and their location on the gill (above: gill branch; below: gill pinnule). b. *Archidoris pseudoargus*. Light microscopical section of a gill branch showing pinnules with trabecular cells (arrow). Bouin, Giemsa; scale = 125 μm . c. *Archidoris pseudoargus*. Light microscopical section of a gill pinnule; trabecular cells traverse the hemolymph lacuna. Bouin, Prenant trichrome; scale = 20 μm . d. *Peltodoris atromaculata*. Fine structure of a trabecular cell joining the opposite epithelial layers of a pinnule (re). Glutaraldehyde/ OsO_4 ; scale = 2 μm . Key: b, basal lamina; c, cilia; cct, collagenous connective tissue; gb, gill branch; gc, granular gland cell; gp, gill pinnule; h, hemolymph lacuna; mc, mucous cell; n, nucleus; pc, pigmented cell; rc, respiratory cell; re, respiratory epithelium; t, trabecular cell.



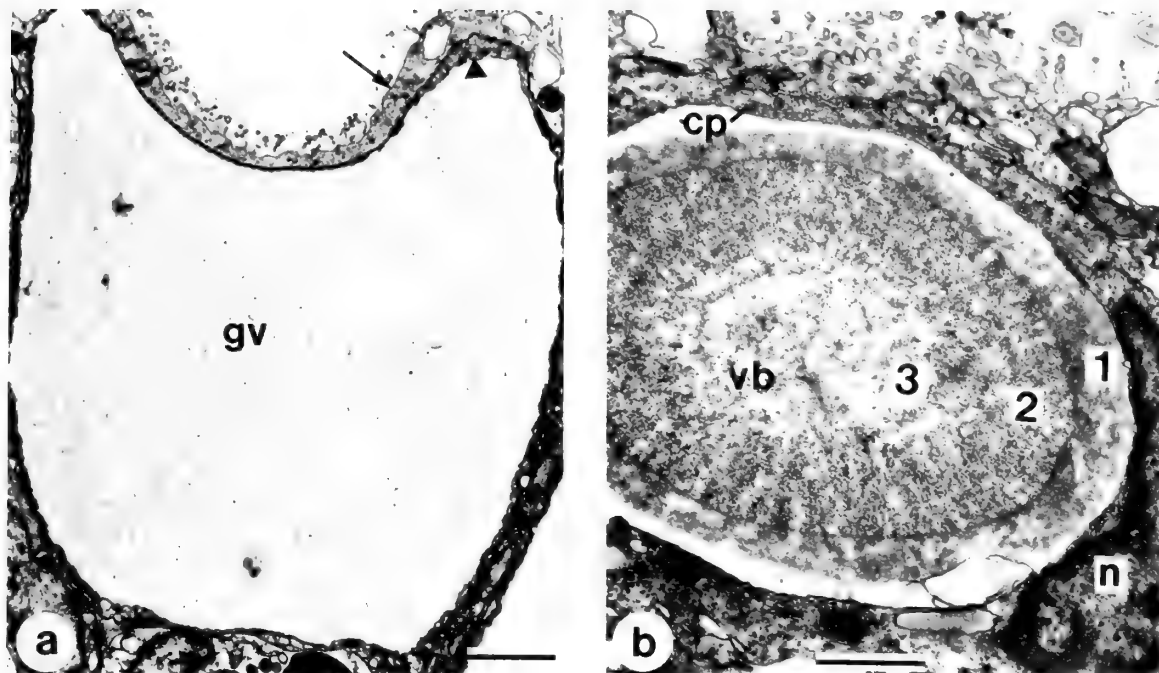


Figure 3

Glandular cells. *Peltodoris atromaculata*. a. Granular gland cell type I in the epithelium of a gill branch; arrow indicates cell processes of adjacent cells; arrowhead points to thin cytoplasmic layer of the glandular cell; scale = 2 μm . b. Glandular cell type II in the epithelium of a gill pinnule; the "vacuole body" shows three different concentric layers (1, 2, 3) of granular material; scale = 1 μm . All fixations: glutaraldehyde/OsO₄. Key: cp, cytoplasm; gv, giant vacuole; n, nucleus; vb, "vacuole body."

A thin cytoplasmic layer surrounding the secretion vacuole contains a flat Golgi complex. When cut in semi-thin sections and stained with toluidine blue, the very finely granulated secretion turns pale gray to violet. In transmission electron microscope (TEM) preparations it displays a low electron density and a loose structure. Some vacuoles seem to be "empty" but not collapsed.

Type II: Cells with a "vacuole body" (Figure 3b). These cells are very sparsely distributed in the gill epithelia of *Peltodoris atromaculata*. They are typically found between the epithelial cells of the pinnules. Most of the cell is

occupied by a large vacuole containing an ovoid body (length 3–10 μm ; diameter 1–5 μm) which consists of concentric layers of coarse-grained material. The cross-section of a "vacuole body" shows a thin margin (height 0.25–0.5 μm) followed by a broad middle zone (height 0.75–1.5 μm) and a central zone (diameter up to 1.5 μm) (Figure 3b: 1, 2, 3).

Type III: Cells with very fine granules (Figure 4b). These slender, bottle-shaped cells contain either a single large or several small vacuoles that are filled with a very finely granulated secretion of low electron density. The

Figure 2

Respiratory cells. *Archidoris pseudoargus*. a. Section of a gill pinnule; the pinnule is contracted; the hemolymph lacuna is narrow and shows trabecular cells; scale = 2 μm . b. Deeply folded basal lamina; extremely flattened cytoplasmic layer between hemolymph lacuna and epithelial surface; scale = 1 μm . c. Extensive basal labyrinth; scale = 1 μm . d. Respiratory cell of a gill pinnule; arrows indicate membrane-bound dense bodies; scale = 1 μm . e. Apical part of a respiratory cell, with extensive basal labyrinth and membrane-bound bodies (arrows); scale = 0.5 μm . f. Membrane-bound dense bodies (arrow) near the surface membrane of a respiratory cell; scale = 0.1 μm . All fixations: glutaraldehyde/OsO₄. Key: b, basal lamina; bl, basal labyrinth; c, cilia; cf, cytoplasmic filaments; gc, glandular cell; ger, granular endoplasmic reticulum; go, Golgi complex; h, hemolymph lacuna; m, mitochondrion; mb, membrane-bound body; mv, microvilli; n, nucleus; nc, nucleolus; rc, respiratory cell.

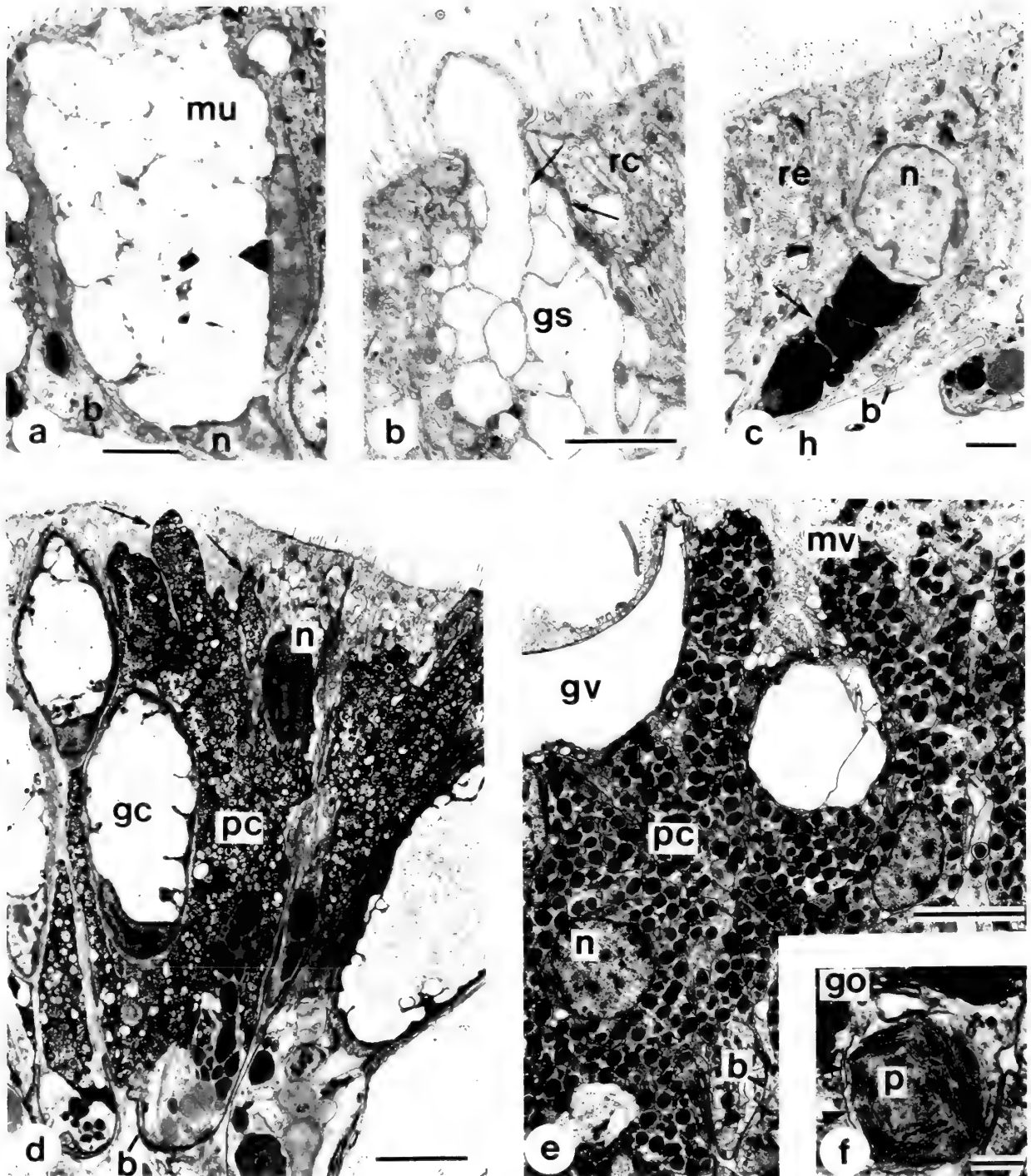


Figure 4

Glandular cells. a. *Pellodoris atromaculata*. Section of a gill branch showing mucous cell; scale = 2 μ m. b. *Archidoris pseudoargus*. Granular gland cell type III in the epithelium of a gill branch; arrows indicate thin cytoplasmic layers; scale = 2 μ m. Pigmented cells. c. *Archidoris pseudoargus*. Pigmented cell in the epithelium of a gill pinnule; arrow indicates a few basal granules; scale = 2 μ m. d. *Archidoris pseudoargus*. Pigmented cell with numerous pigment granules in the epithelium of a gill branch; the fingerlike apical projections extend to the epithelial surface (arrows); cells with netlike residues of a secretion (granular gland cell type III?) (gc); scale = 5 μ m. e. *Pellodoris atromaculata*. Pigmented cell with numerous pigment granules in the epithelium of a gill branch; glandular cell with a giant

nucleus is irregularly shaped and located basally or laterally. The cell surface lacks cilia or microvilli. The cytoplasm forms a thin layer around the secretion vacuoles and is concentrated at the base. It contains a few mitochondria, a moderately developed granular endoplasmic reticulum, free ribosomes, and isolated rosettes of glycogen. Although these cells resemble the mucous gland cells, histochemical light microscopical tests show a negative result using the PAS and the alcian blue reactions, indicating that the secretion is not a mucoprotein and is neither a neutral nor an acidic mucopolysaccharide.

Some glandular cells appear to be of the above type but contain a reticular secretion, probably the residue left after the extrusion of the fine granules. The cytoplasm of these cells is so dense that the nuclei are the only distinguishable organelles (Figure 4d).

Mucous gland cells: These gland cells (Figure 4a) occur in both *Archidoris pseudoargus* and *Peltodoris atromaculata* on the gill branches and less numerous on the gill pinnules. The goblet-shaped cells contain a large mucous vacuole, a basally located sickle-shaped nucleus, and lack cilia and microvilli. At the base of the cells the cytoplasm contains a few slender mitochondria, free ribosomes, a smooth endoplasmic reticulum, and some rosettes of glycogen. The Golgi complex is well developed and lies adjacent to the mucous vacuole of the cell.

Histochemical tests on light microscopical sections result in a positive staining with alcian blue (pH 2.5 and pH 1) of all mucous gland cells. After additional staining with PAS, a positive reaction could only be observed for half of the mucous gland cells. These results suggest that the secretion product is dominated by acidic mucopolysaccharides.

Pigmented Cells

Two different types of pigmented cells are recognizable, those with few pigment granules, which occur only in *Archidoris pseudoargus*, and those with numerous pigment granules, which are present in both species.

Pigmented cells with few pigment granules: These cells (Figure 4c) occur in the epithelia on the gill branches but more often on the pinnules of *Archidoris pseudoargus*. They differ in height depending on the epithelia where they are found. The cells contain few dense granules, which are always at the base. The central round nucleus lies above the granules. In some respects these cells are reminiscent of respiratory cells or they may represent a type of pigmented cell in *A. pseudoargus* that resembles the epithelial

pigment cell with basal granules reported for *Hermisenda crassicornis* (BÜRGIN, 1965).

Pigmented cells with numerous pigment granules:

These irregularly shaped cells have long, fingerlike apical projections that seem not to reach the surface of the epithelium (Figures 4d, e). The cells are reminiscent of the pigment cells of the dorsal epithelium of *Peltodoris atromaculata* (HAEFELFINGER, 1961). The projections contain densely packed pigment granules. Only a few organelles such as mitochondria, free ribosomes, and granular endoplasmic reticulum are scattered in the cytoplasm. In *Archidoris pseudoargus* (Figure 4d) the nucleus is of irregular shape and lies in the upper part of the cell. The membrane-bound pigment granules (diameter 0.2–0.5 μm) contain an homogeneous material that can be clearly distinguished after fixation with glutaraldehyde. In *P. atromaculata* (Figure 4e) the nucleus of the pigment cells is spherical or ovoid and lies basally or in the central part of the cell. The membrane-bound pigment granules (diameter 0.3–1 μm) contain groups of numerous very fine needles of variable length and 0.0075 μm diameter lying in an electron-dense matrix (Figure 4f). Some vesicles seem to contain only the dense matrix material. Unlike that of *A. pseudoargus*, the Golgi complex is well developed and scattered between the pigment granules. Near the concave surface of the Golgi complex lie small vesicles containing amorphous material of low electron density. There are numerous mitochondria and groups of glycogen rosettes.

Trabecular Cells

A very typical non-epithelial type of cell is the trabecular cell (Figure 1d). These cells can be found in the hemolymph lacunae of the gill pinnules but never in the vessels of the gill branches. Their elongate cell bodies traverse the hemolymph space, and they are attached by their broad bases to the collagenous connective tissue of the opposite epithelial layers of the pinnule. Long, slender processes often occur at the cell bases. The nucleus is usually oval, but can be round or of irregular shape. Mitochondria, granular endoplasmic reticulum, free ribosomes, vesicles, and myofilaments are distributed in the cytoplasm.

DISCUSSION

The histology and ultrastructure of the gill epithelia are similar in the two dorid species *Archidoris pseudoargus* and *Peltodoris atromaculata*, as was also reported for the cir-

←
vacuole (gv); scale = 5 μm . f. *Peltodoris atromaculata*. Detail: membrane-bound pigment granule (arrowhead); scale = 0.3 μm . All fixations: glutaraldehyde/OsO₄. Key: b, basal lamina; gc, glandular cell; go, Golgi complex; gs, granular secretion; gv, giant vacuole; h, hemolymph lacuna; p, pigment granule; pc, pigment cell; rc, respiratory cell; re, respiratory epithelium.

culatory system of the gills for both species (ELIOT, 1910; POTTS, 1981; JONAS, 1984, 1985). Two "types" of epithelia are observed, a high, glandular epithelium on the gill branches and a low epithelium with only a few gland cells on the gill pinnules. These pinnules, which consist of two thin epithelial layers separated by a hemolymph space, are strikingly similar to the gill leaflets of other opisthobranchs (FÖRSTER, 1934; HOFFMANN, 1940; THOMPSON & SLINN, 1959; MORTON, 1972; WÄGELE, 1984), of bivalves (RIDEWOOD, 1903; NAKAO, 1975), of the prosobranch *Patella vulgata* (NUWAYHID *et al.*, 1978), and of the cephalopod *Sepia officinalis* (SCHIPP *et al.*, 1979). Because it seems most likely that the major gas exchange in dorid gills takes place at the gill pinnules, I have called these epithelia respiratory epithelia and the epithelial cells respiratory cells. The following characteristics of the pinnule epithelia support their respiratory function: (1) The great number of pinnules results in an increase of the respiratory surface of the gill. (2) The dense microvillar border at the cell surface increases the respiratory surface of each single cell. (3) The well developed basal labyrinth increases the contact zone of the cell and the hemolymph. (4) The small height of the respiratory cells decreases above the deep folds of the basal lamina to only 1 or less than 1 μm , which facilitates gas exchange between hemolymph and water. (5) The water currents around the gill pinnules caused by the ciliated cells on the whole gill surface and directed contrary to the blood flow within the pinnules (POTTS, 1981) provide a permanent water exchange at the respiratory surfaces. The relative importance of gill respiration as a supplement to cutaneous respiration in adult dorids could be tested by experiments such as those performed by POTTS (1983), in which he measured the differences in oxygen uptake in dorids with extended and retracted gills.

In addition to respiration, an excretory function has been suggested for the gill leaflets of *Patella vulgata* (NUWAYHID *et al.*, 1978) and for the gills of *Sepia officinalis* (SCHIPP *et al.*, 1979). In *S. officinalis*, the enzyme pattern and cytomorphology of the inner branchial epithelium are similar to the transport active epithelia of the excretory organs (SCHIPP *et al.*, 1979). A well developed basal labyrinth is typical for the excretory cells of dibranchiate (SCHIPP & BOLETZKY, 1975) and tetrabranchiate cephalopods (SCHIPP *et al.*, 1985) as well as the pulmonate gastropod *Helix pomatia* (BOUILLON, 1960). Whether the extensive basal labyrinth in the respiratory cells of the dorid gills indicates a participation in excretory activities cannot be determined without experimental studies.

The gills, like the rest of the body surface in gastropods, are involved in osmotic and ionic regulation (BETHE, 1934; ROBERTSON, 1964). This function requires transport mechanisms for ion exchange in the participating epithelia. In addition to the elaborate basal labyrinth, fine structural features that indicate a transport active cell in the crustacean gill include a brush border, a high mitochon-

drial content, and numerous vesicles (MANTEL & FARMER, 1983). Although the present ultrastructural study provides no direct evidence that substances are transported through the gill epithelia of dorids or what these substances might be, the presence of features similar to those of the crustacean gill suggests that they are capable of active transport.

Of special interest is the presence of the membrane-bound bodies of unknown function near the apical surface of the respiratory cells. These structures have also been described for the gill of *Anodonta* (NAKAO, 1975) and the gill leaflets of *Patella vulgata* (NUWAYHID *et al.*, 1978). The membrane-bound bodies contain a homogeneous electron-dense material that seems to be fixed only with glutaraldehyde, a fixation that has been used here for the dorids studied as well as for *Anodonta* and *P. vulgata*. It is possible that the membrane-bound bodies play some role in transport activities.

No endothelial lining such as that described for the gill of *Sepia officinalis* (SCHIPP *et al.*, 1979) has been identified in this study of the dorid gill. Epithelial cells and basal laminae that overlie a collagenous connective tissue are the only barrier between outside and inside media. No sensory nerve cells could be found in the epithelia, but the nerve endings often lie in deep epithelial folds very near to the gill surface, and the reception of stimulation is presumably possible on the whole surface of the gill. The nerve endings in the gills of *Archidoris pseudoargus* and *Peltdoris atromaculata* never perforate the basal lamina, as has been described in *Anodonta* by NAKAO (1975).

The naked body of a nudibranch mollusk is covered with a great number of different gland cells that are involved in protection and defense (THOMPSON, 1960). The numerous mucous and granular gland cells of the gills probably serve these functions as well (POTTS, 1981), even if the gills, as in the Eudoridoidea, are retractable. The mucous secretion keeps the integument clean of sediment and prevents the settlement of other organisms (POTTS, 1981). Ciliated cells occurring in tufts all over the mantle and gill surface probably help to distribute the mucous discharge (KRESS, 1981; POTTS, 1981).

The granular, non-mucous gland cells in the dorsal epithelia of nudibranchs seem to be involved in the secretion of distasteful or even toxic substances (THOMPSON, 1960; JOHANNES, 1963; EDMUNDS, 1968). The distastefulness of dorid secretions is related to the chemical structure of compounds derived from their diet (CIMINO *et al.*, 1982). In contrast to the results of this study, in which numerous granular gland cells were observed, THOMPSON (1960) reported few non-mucous (granular?) gland cells in the gills of some dorid species, including *Archidoris pseudoargus*.

Only the gill epithelia of *Peltdoris atromaculata* contain a rare cell type, the "vacuole body" cell. The "vacuole body" consists of a relatively insoluble material that persists after various light and electron microscopical fixa-

tions, unlike the aragonitic spicules (HAEFELFINGER, 1960) that are almost completely dissolved during fixation. The "vacuole body" cells of *P. atromaculata* differ from those found in the midgut gland of Nudibranchia (SCHMEKEL & WECHSLER, 1968) and Saccoglossa (HÖFELMEIER, 1985) in that they are sparsely distributed and contain a single vacuole with one "vacuole body." In fine structure, the "vacuole bodies" resemble the excretion granules in the kidney of *Helix pomatia* (BOUILLON, 1960) and the spherites of the calcium cells in the midgut gland of *H. pomatia* (ABOLINS-KROGIS, 1965, 1970). Although the function of the "vacuole body" cells was not determined their exclusive occurrence and sparse distribution in *P. atromaculata* implies they are not involved in general gill functions.

Another vacuolized type of epidermal cell ("Spezial-vakuolenzelle") has been described in all groups of Nudibranchia (SCHMEKEL, 1982; SCHMEKEL & WECHSLER, 1967). Each of these cells contains numerous vacuoles, each with a "vacuole body," and thus is quite different from the "vacuole body" cells in the gill epithelia of *Pelto-doris atromaculata*. SCHMEKEL (1982) reported many vacuolized cells on the rhinophores and some on the notum in *Archidoris pseudoargus* and *P. atromaculata* but they are not present on the gills of either species.

Typical cell elements of the dorid gill pinnules are the trabecular cells that traverse the hemolymph space and join the opposite pinnule epithelia. Trabecular cells have been described for several mollusk gills, e.g., by PERRIER & FISCHER (1911), FÖRSTER (1934), RAO (1936), MORTON (1972), POTTS (1981), and WÄGELE (1984) for Opisthobranchia, by NUWAYHID *et al.* (1978) for the prosobranch *Patella vulgata*, by RIDEWOOD (1903) and NAKAO (1975) for Bivalvia, and by SCHIPP *et al.* (1979) for the cephalopod *Sepia officinalis*. In all these mollusk groups the trabecular cells seem to be of the same structure: elongate cell bodies attached to the collagenous connective tissue layer beyond the epithelial cells, with broad bases toward the basal lamina or long slender processes; the cytoplasm contains an oval or round nucleus and myofilaments. The trabecular cells are similar in appearance and position to the pillar cells of fish gills. NAKAO (1975) compared the fine structure of these two cell types and found fundamental morphological differences. He concluded that the trabecular cells of *Anodonta* are modified muscle cells of the vessel wall and are not analogous to the pillar cells of fish gills.

Further research on the ultrastructure of opisthobranch gills, other than nudibranchs, will allow more equivalent comparisons of the respiratory organs of this group.

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Ultrastructural Analysis of Spermiogenesis and Sperm Morphology in *Chorus giganteus* (Lesson, 1829) (Prosobranchia: Muricidae)

by

ROBERTO JARAMILLO, ORLANDO GARRIDO, AND BORIS JORQUERA

Instituto de Embriología, Facultad de Ciencias, Universidad Austral de Chile,
Casilla 567, Valdivia, Chile

Abstract. Spermatid differentiation and the morphology of mature spermatozoa in the gastropod *Chorus giganteus* (Lesson, 1829) were investigated. Five phases of spermiogenesis are proposed based on the polarization of organelles, nuclear elongation, and chromatin condensation. The ultrastructure of the spermatozoa of *Chorus giganteus* is compared to those of other Muricidae. Possible phylogenetic and functional relationships among prosobranch spermatozoa are discussed.

INTRODUCTION

STUDIES DEALING with spermatogenesis in mollusks have shown close relationships between sperm morphology and certain aspects of reproductive strategy. In particular, sperm dimorphism appears correlated with the presence of nutritive eggs in prosobranchs (PORTMAN, 1931a; TUZET, 1930; NISHIWAKI, 1964; TOCHIMOTO, 1967). In the species studied, both normal (or typical) spermatozoa and abnormal (or atypical) spermatozoa have been recognized. The latter can be oligopyrene (*i.e.*, with a small quantity of chromatin) or apyrene (*i.e.*, with no chromatin) (PLATNER, 1889; AUERBACH, 1896; MEVES, 1903). These atypical spermatozoa could play a role in the feeding of normal embryos by giving rise to abortive embryos. However, all prosobranchs that utilize nutritive eggs do not exhibit sperm dimorphism, nor do all those prosobranchs that exhibit sperm dimorphism utilize nutritive eggs (O. HYMAN, 1925; L. HYMAN, 1967; ANKEL, 1930; PORTMAN, 1927, 1931b).

A second correlation has been established between the morphology of typical spermatozoa and the nature of the medium in which fertilization occurs (TUZET, 1950; FRANZÉN, 1955, 1956, 1970; FAWCETT, 1970). FRANZÉN (1955), after studying 15 species of gastropods, has classified spermatozoa into two types. Type I, or primitive spermatozoa, belong to species with external fertilization; these have a cone-shaped head and a short middle piece containing mitochondria at the base of the nucleus. Type II, or modified spermatozoa, are found in species with

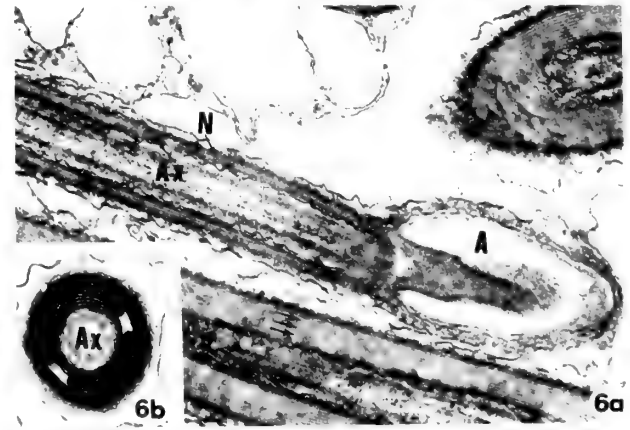
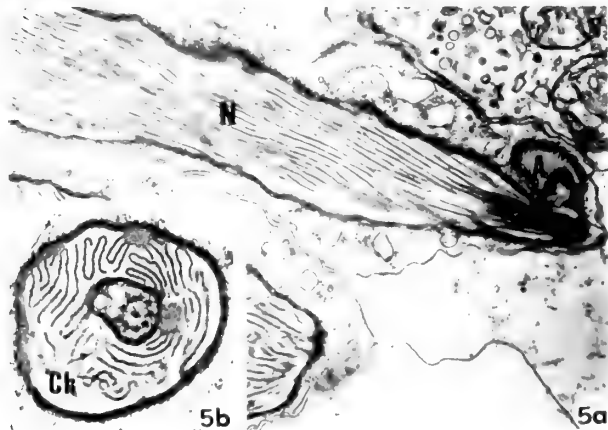
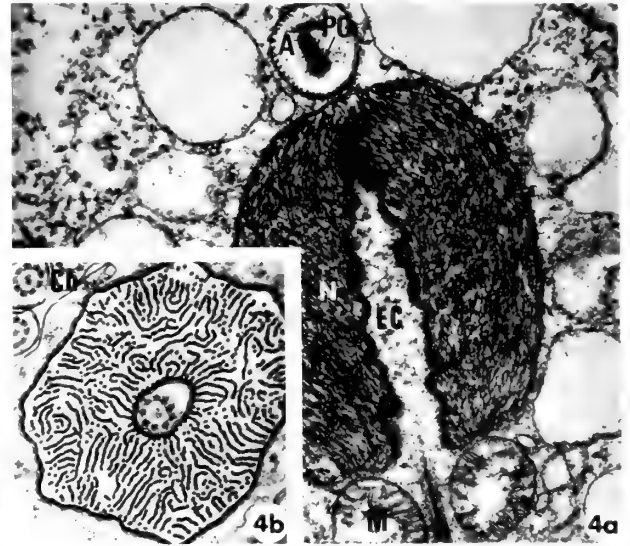
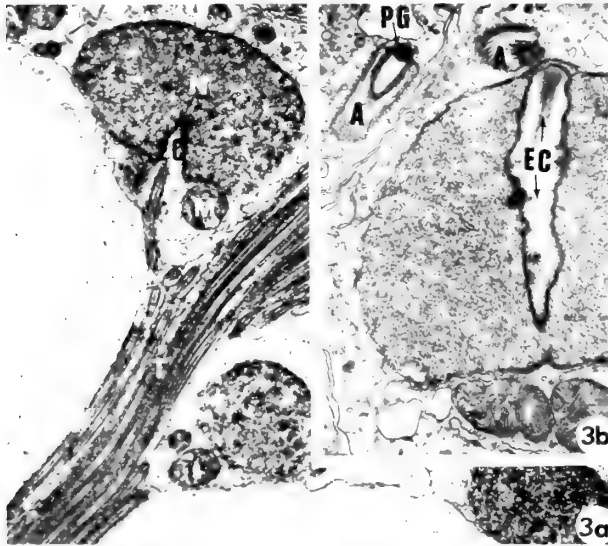
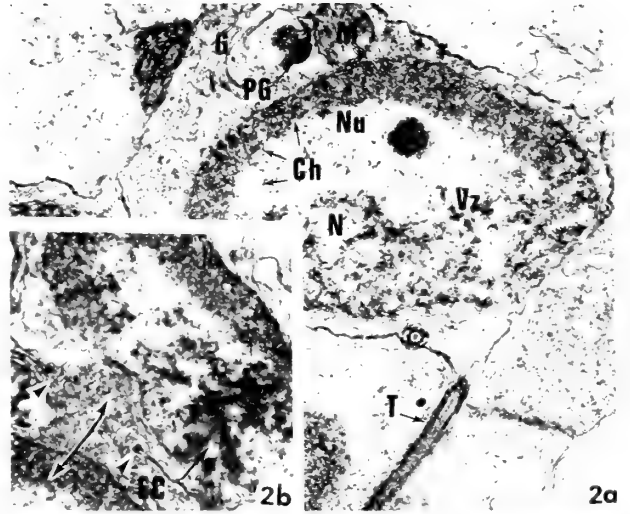
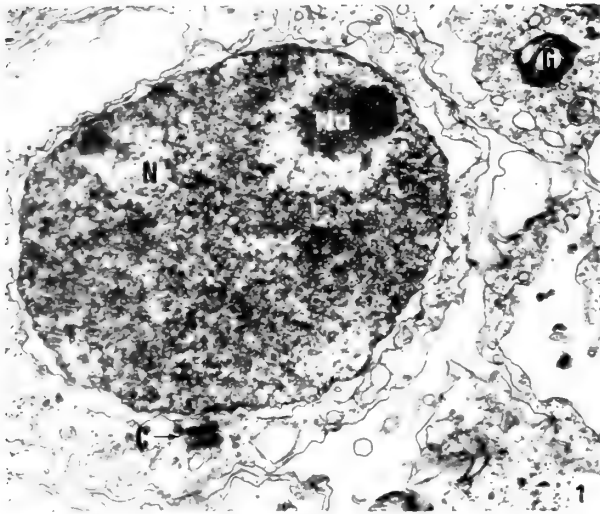
internal fertilization; they display a threadlike head, an elongate middle piece, and mitochondria arranged around the axial filament. NISHIWAKI (1964) reported that some Japanese prosobranchs also have typical and atypical spermatozoa, which he classified as typical spermatozoa of types I and II in keeping with Franzén's original scheme. Members of the Neogastropoda have internal fertilization (HYMAN, 1967; FRETTER & GRAHAM, 1962) and most neogastropod spermatozoa are considered as a modified type.

Ultrastructural analyses of spermiogenesis and mature spermatozoa have been reported for the muricid prosobranchs *Nucella lapillus* (WALKER & MACGREGOR, 1968; WALKER, 1970) and *Concholepas concholepas* (HUAQUÍN & BUSTOS-OBREGÓN, 1981) and the buccinid prosobranch *Colus stimpsoni* (WEST, 1978). In histological studies of *Nucella lapillus* (PORTMAN, 1931a) and *Chorus giganteus* (AMÍN *et al.*, 1984), some aspects of spermatogenesis were included.

However, there are no ultrastructural analyses of spermiogenesis and mature spermatozoa in *Chorus*. This paper identifies the type of spermatozoa in *Chorus giganteus* and correlates the type with functional and phylogenetic aspects of the animal's reproductive strategy.

MATERIALS AND METHODS

Mature specimens of *Chorus giganteus* were collected by diving at Puerto Claro, Valdivia (39°53'S, 73°22'W) in different seasons of the year.



Pieces of testis and seminal vesicles (AMÍN *et al.*, 1984) were fixed for 2 h in a three-fold aldehyde mixture containing 2.5% glutaraldehyde, 10% para-formaldehyde, and 2% acrolein, buffered to pH 7.2 with 0.2 M phosphate (RODRÍGUEZ, 1969). After washing with the same phosphate buffer, tissues were postfixed for 2 h in buffered 1% OsO₄ and embedded in an epon-araldite mixture (RICHARDSON *et al.*, 1960). Ultrathin sections were stained either (1) with uranyl acetate and lead citrate (GLAUERT, 1965) or (2) according to the method of THIERY & RAMBOURG (1974) for the demonstration of polysaccharides. In the last method, sections were treated with 1% periodic acid solution, rinsed in three successive changes of distilled water, and refloated on the surface of 1% thiosemicarbazide in 10% acetic acid; sections were then rinsed thoroughly in distilled water, refloated in 1% aqueous silver proteinate solution, rinsed in distilled water, and mounted on copper grids. Smears of mature spermatozoa, obtained by puncturing the seminal vesicles, were fixed as described above and prepared for light microscopy (LM) and scanning electron microscopy (SEM). For LM, smears were stained with hematoxylin-eosin and, for SEM, they were dehydrated in acetone, critical point dried, and coated with gold.

Observations were done with a Philips 300 (TEM) and Hitachi H-700 (TEM and SEM).

RESULTS

Ultrastructural Changes during Spermiogenesis

Spermiogenesis in sections of *Chorus giganteus* testis was studied ultrastructurally, and the process divided into 5 phases.

Phase 1 involves polarization of the centriole. Initial spermatids were small, rounded cells, 8 µm in diameter, grouped into clusters of approximately 8 cells linked by cytoplasmic bridges. Each had a spherical nucleus, 3 to 4 µm in diameter; chromatin was homogeneously distributed and a vacuolization zone surrounded an excentric nucleolus. A typical Golgi apparatus was formed by 7–8

curved saccules facing the nucleus. Small vesicles associated with the tips of the saccules accumulated on the concave side of the complex. A single centriole occupied a position opposite to that of the nucleolus, thus establishing the cell's polar axis. Adjacent to the centriole the nuclear membrane presented a thickening of nuclear material. Some mitochondria also were seen (Figure 1).

Phase 2 is the polarization of the Golgi apparatus. During this phase the nucleus became ovoid, with the major axis perpendicular to the cell's polar axis. A semilunar-shaped zone of condensed chromatin appeared in the apical nuclear pole and the vacuolization zone around the nucleolus became larger than in phase 1 (Figure 2a).

The Golgi complex migrated to the apical cytoplasm, near the position of the nucleolus. During this migration the small vesicles associated with the concave side of the Golgi saccules produced an electron-dense proacrosomal granule (Figure 2a). The remaining cytoplasm contained scattered mitochondria. An invagination at the nuclear basal pole progressively elongated and became the endonuclear channel. This channel was delimited by a thickening on the inner side of the nuclear membrane. The centriole was located inside the channel and gave rise to an axoneme of 9+2 microtubules, which upon elongation forms the tail. Individual spermatids still remained joined by cytoplasmic bridges (Figure 2b).

Phase 3 is the polarization of mitochondria. In the cytoplasm, mitochondria were grouped in the vicinity of the nuclear base forming a single mitochondrial annulus corresponding to the developing middle piece. The tail continued its elongation and endonuclear channel formation ended (Figures 3a, b).

Condensed chromatin was homogeneously distributed throughout the nucleus, and a nucleolus was no longer seen. Over the proacrosomal granule, the Golgi apparatus formed the early double membrane acrosomal vesicle. At the inner surface of the outer acrosomal membrane appeared a dense crest, giving the membrane a helicoidal appearance (Figure 3b). The major axis of the vesicle was perpendicular to the cell's polar axis.

Explanation of Figures 1 to 6

Figure 1. Spermatid, phase 1. N, nucleus; Nu, nucleolus; G, Golgi apparatus; C, centriole. ×16,000.

Figure 2. Spermatid, phase 2. 2a. N, nucleus; Nu, nucleolus; G, Golgi apparatus; PG, proacrosomal granule; M, mitochondria; T, tail; Ch, chromatin; Vz, vacuolization zone. ×12,000. 2b. Arrows show a cytoplasmic bridge; EC, endonuclear channel. ×18,000.

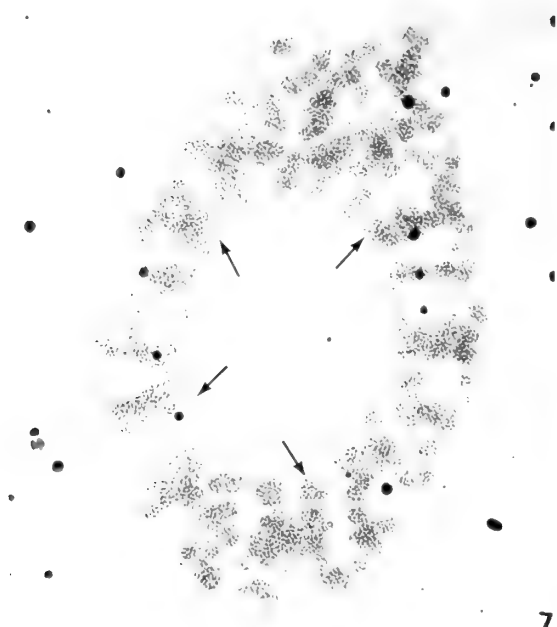
Figure 3. Spermatid, phase 3. 3a. N, nucleus; M, mitochondria; EC, endonuclear channel; T, tail. ×10,000. 3b. A, acrosome; PG, proacrosomal granule; EC, endonuclear channel. ×12,000.

Figure 4. Spermatid, phase 4. 4a. N, nucleus; A, acrosome; PG,

proacrosomal granule; M, mitochondria; EC, endonuclear channel. ×16,000. 4b. Cross section of spermatid. Ch, chromatin radially arranged. ×18,000.

Figure 5. Spermatid, in early phase 5. 5a. A, acrosome; N, nucleus. ×18,000. 5b. Cross section of the head of a spermatid with initial rearrangement of chromatin (ch). ×34,000.

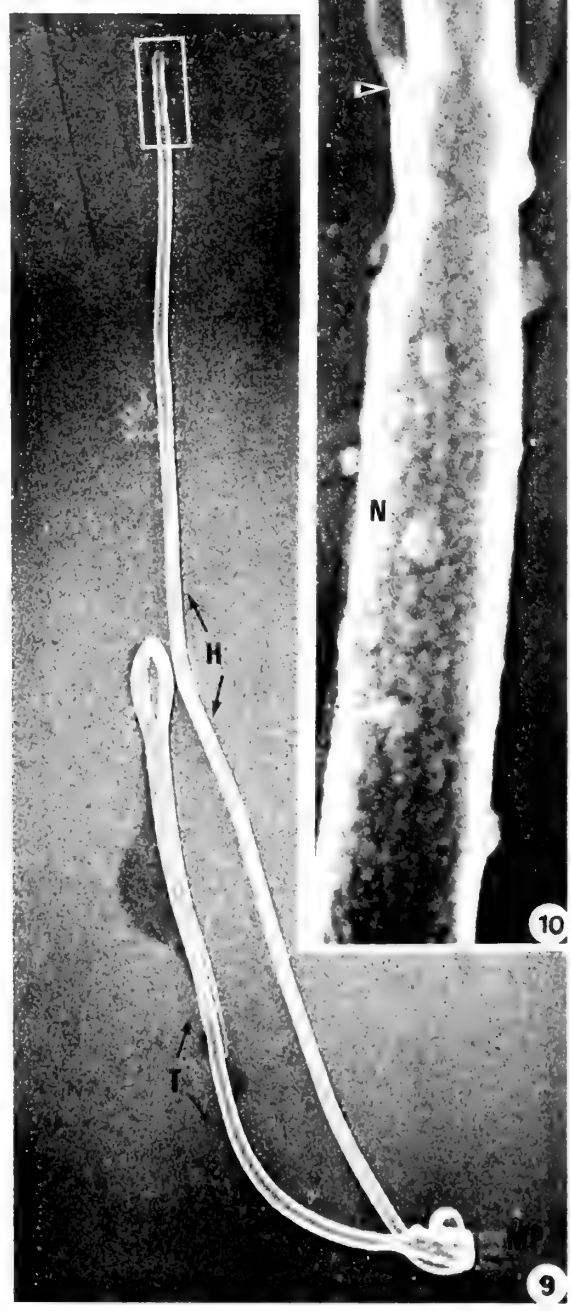
Figure 6. Spermatid, in late phase 5. 6a. A, acrosome; Ax, axoneme; N, nucleus; arrows show the lamellar distribution of the chromatin around the nucleus. ×29,000. 6b. Cross section of the head of a spermatid with concentric lamellae of chromatin. Ax, axoneme. ×30,000.



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Phase 4 is nuclear elongation. The nucleus elongated along the cell's polar axis to establish a 2:1 length-diameter ratio (Figure 4a). Chromatin appeared, forming irregularly arranged longitudinal filaments that later fused in a lamellar fashion radial to the endonuclear channel (Figure 4b). The middle piece showed no modifications, but tail elongation continued. Between the cells cytoplasmic bridges were not observed.

Phase 5 is termed the lamellar chromatin phase. During this time the nucleus, now approximately 0.6 μm in diameter in its middle region, continued its elongation. The chromatin lamellae lost their radial appearance and became rearranged to form 6 to 12 profiles of dense lamellae concentric to the endonuclear channel (Figures 5a, b, 6a, b).

By this time, the acrosome had turned 90° so that its major axis became parallel to the cell's polar axis (Figure 6a). In the middle piece, new mitochondrial annulae were added until a mitochondrial layer 6 to 8 μm deep was reached. The differentiated principal piece contained a granular material that was arranged into nine rosettes spatially related to the nine pairs of microtubules of the axoneme. These rosettes reacted positively to Thiery's test for polysaccharides (Figure 7).

Mature Spermatozoon

At the light microscopic level, the spermatozoa of *Chorus giganteus* appeared as simple filiform structures averaging 100 μm in length. The head, which had a densely stained, cylindrical and pointed nucleus, corresponded to 50% of total sperm length (Figure 8). These proportions agree with measurements reported by AMÍN *et al.* (1984).

With SEM, the different segments of the spermatozoon could not be distinguished and the diameter appeared rather uniform along its length. In the apical region of the head, an acrosome was evident (Figures 9, 10).

In TEM observations, all mature spermatozoa of *Chorus giganteus* were morphologically identical. The head, about 50 μm in length, was 0.4 μm in diameter at the anterior end and 0.7 μm at the posterior end. At the top of the head, a cylindrical-conic acrosome, about 1.2 μm in length, was observed. Between the outer and the inner acrosomal membrane a homogeneous granular material was present. Adjacent to the outer acrosomal membrane this material was condensed, forming crests of helicoidal appearance. The inner acrosomal membrane defined a

conical subacrosomic space containing dense material, apparently a remnant of the proacrosomic granule (Figures 11, 12).

The nucleus, about 50 μm in length, was perforated by an endonuclear channel that ended blindly at its anterior end. The endonuclear channel was uniformly 0.2 μm in diameter. In mature spermatozoa, the chromatin, previously seen as concentric lamellae, appeared as a compact mass of high electron density. The axial filament, which originated from the centriole situated in the apex of the endonuclear channel, had the typical 9+2 configuration (Figures 12-14).

The middle piece, 6-8 μm in length and 0.7 μm in diameter, was characterized by a mitochondrial sheath tightly packed around the axoneme. The mitochondrial complex was surrounded by a common membrane produced by the breakdown and subsequent fusion of the outer mitochondrial membranes. At the distal end of the middle piece, the annulus, or Jensen's ring, was observed (Figures 14-16).

The principal piece, at about 42 μm in length, was the longest medial part of the flagellum and tapered from 0.5 μm in diameter to about 0.3 μm at the beginning of the end piece. The glycogen particles that surround the axoneme were present all along the principal piece, but decreased in number distally (Figures 15, 16).

The end piece, about 2 μm in length and 0.25 μm in diameter, was the short posterior part of the flagellum. It was formed by the axoneme and the surrounding plasma membrane (Figures 17, 18).

DISCUSSION

Our findings provide new evidence regarding some relationships among sperm morphology, the nature of the medium in which fertilization occurs, and the presence of nutritive eggs.

Spermiogenesis in *Chorus giganteus* shows characteristics similar to those described for *Nucella lapillus*, *Colus stimpsoni*, and *Concholepas concholepas* (WALKER & MACGREGOR, 1968; WALKER, 1970; WEST, 1978; HUAQUÍN & BUSTOS-OBREGÓN, 1981). In all of these species, including *Chorus giganteus*, the morphogenetic changes of the differentiating spermatids are, principally, aggregation and condensation of chromatin, acrosome formation, changes in mitochondrial distribution, formation of an endonuclear channel, and elongation of the axial

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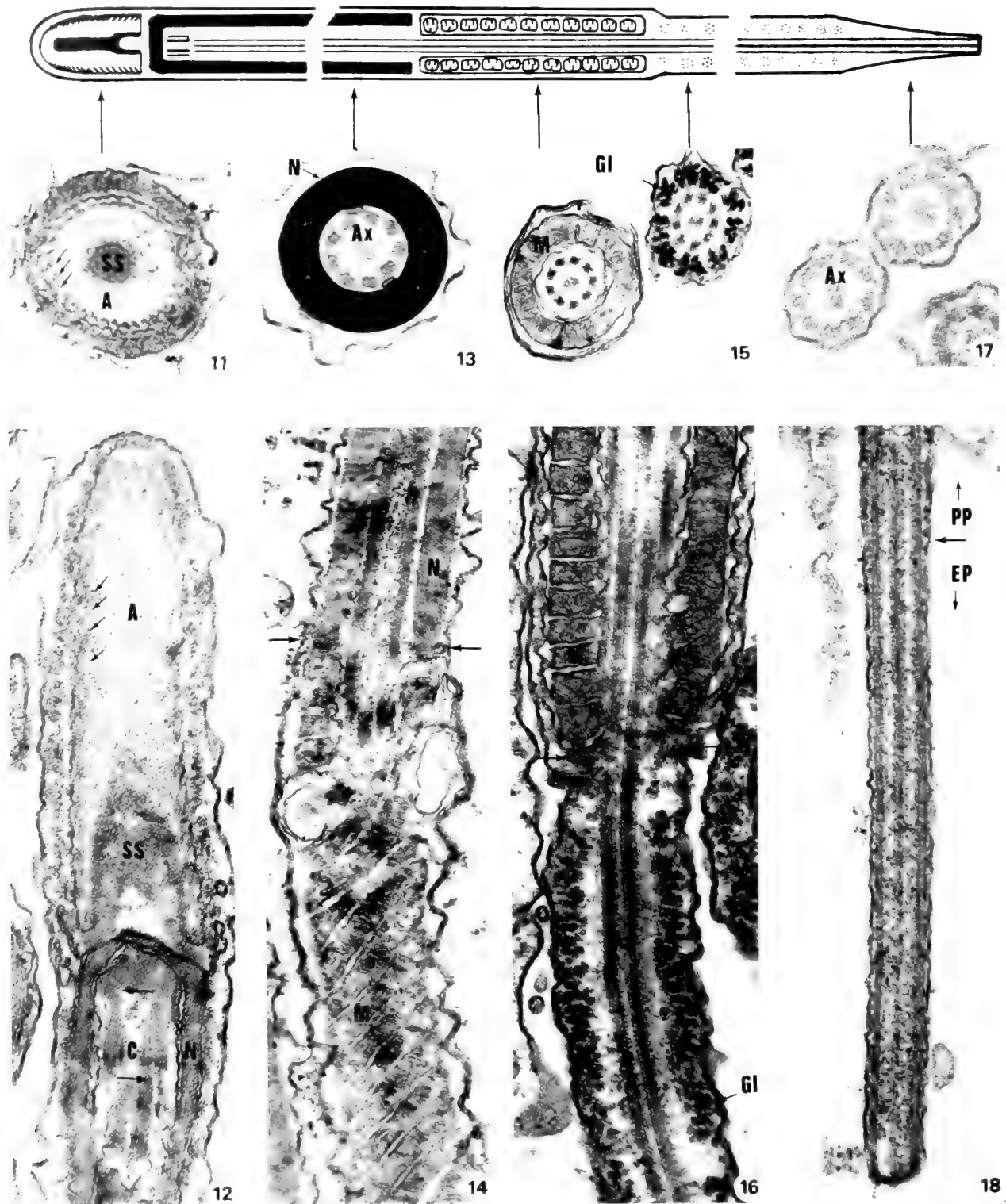
Explanation of Figures 7 to 10

Figure 7. Cross section of the principal piece of a late spermatid, stained by Thiery's method. Arrows indicate glycogen particles. $\times 110,000$.

Figure 8. Smear of mature spermatozoa, observed with light microscope. $\times 800$.

Figure 9. SEM micrograph of the whole sperm. H, head; MP, middle piece; T, tail. $\times 2200$.

Figure 10. SEM micrograph of the head. A, acrosome; N, nucleus. $\times 28,000$.



filament. However, some particular differences can be mentioned. In the early spermatid development of *Chorus giganteus*, chromatin is irregularly distributed throughout the nucleus, with a vacuolized zone around the nucleolus. In *Colus stimpsoni*, there is a similar distribution of chromatin, leaving a large zone of clear nucleoplasm near the nuclear envelope that contains a single dense "granule" (WEST, 1978). This vacuolized zone is called the polar nucleoplasm. The polar nucleoplasm moves to the anterior pole, forming a polar nucleoplasmic cone toward which the anterior end of the endonuclear channel projects. We suggest that the "dense large granule" described for *Colus stimpsoni* has a similar nucleolar morphology.

In *Chorus giganteus* the granules of chromatin fuse, eventually forming filaments and, then, lamellae concentrically arranged around the flagellum. At the end of spermiogenesis the lamellar arrangement is lost and the nucleus develops a tubular shape with a dense and homogeneous appearance. In *Nucella lapillus*, observations of the breakdown of the mature sperm's nucleus reflect the condensation pattern of chromatin described by WALKER (1970) as a "lamellar" type. This "lamellar" arrangement of the chromatin could be a common feature with *Chorus giganteus*.

In the apical end of the early acrosome of *Colus stimpsoni*, a ring of electron-dense material and a dense layer below the base are formed. During further maturation the ring disappears and the basal layer forms a subacrosomal plate between the acrosome and the nucleus. This plate is perforated by a single hole which is penetrated by a portion of the centriole (WEST, 1978). The electron-dense ring and the subacrosomal plate have not been seen in the maturing acrosome of *Chorus giganteus*, *Nucella lapillus*, or *Concholepas concholepas*.

Although there are differences in spermiogenesis, the morphology of the mature spermatozoa in *Chorus giganteus* is similar to that described in *Nucella lapillus* (WALKER & MACGREGOR, 1968; WALKER, 1970; RETZIUS, 1906), *Colus stimpsoni* (WEST, 1978), and *Concholepas concholepas* (HUAQUÍN & BUSTOS-OBREGÓN, 1981). All of these species exhibit the presence of type II (modified) sper-

matozoa, but not atypical sperm. Typical type II spermatozoa in the above-mentioned species having internal fertilization (AMÍN *et al.*, 1984; GUZMÁN *et al.*, 1972; WEST, 1979; GALLARDO, 1979; GALLARDO & PERRON, 1982) support the possibility that sperm morphology and mode of fertilization may be interrelated phenomena.

This correlation is supported by the presence and disposition of structures that may be involved in the transport and maintenance of spermatozoa within the female genital tract. In *Chorus giganteus*, the female genital system conforms to the general pattern found in other neogastropods, with a few exceptions (unpublished data). The bursa copulatrix receives sperm at copulation and passes them on to the seminal receptacle or directly transfers them along the ventral channel of the pallial oviduct. It appears that fertilization occurs in the albumin gland at the posterior end of the pallial oviduct (HOUSTON, 1976). At this level the eggs are surrounded by two special envelopes, the vitelline membrane and the chorion, and presumably additionally by a thin cover of albumin.

In the mature sperm of *Chorus giganteus*, the continuation of the flagellum into the endonuclear channel allows for undulating movements throughout the head length. This activity certainly depends on the numerous mitochondria present in the middle piece. LONGO & ANDERSON (1970) have postulated that glycogen particles that surround the axoneme in the main piece represent the storage of endogenous substrate to be used by the mitochondria for ATP formation. This provides an energy source either for sperm movement along the female genital tract or for sperm maintenance in the seminal receptacle.

The granular material of crested appearance that is adjacent to the inner surface of the outer acrosomic membrane could play a role during fertilization in *Chorus giganteus*. In lampreys, subacrosomal material forms a long helical fiber that is extruded to form the core of a true acrosomal tubule during the acrosome reaction (NICANDER & SJÖDEN, 1968). This acrosomal tubule makes the first contact with the egg surface, as in many invertebrates (COLWIN & COLWIN, 1967). The crest of helical appearance in the acrosome of *Chorus giganteus*

Explanation of Figures 11 to 18

Figure 11. Cross section of the acrosome (A). Arrows indicate dense crests of the acrosome; SS, subacrosomal space. $\times 103,000$.

Figure 12. Longitudinal section of the acrosomal and nuclear regions. A, acrosome; C, centriole; N, nucleus; SS, subacrosomal space; arrows indicate dense crests of acrosome. $\times 62,000$.

Figure 13. Cross section of the nucleus (N). Ax, axoneme. $\times 62,000$.

Figure 14. Longitudinal section of the boundary region (arrows) between the nucleus (N) and middle piece. M, mitochondria. $\times 53,000$.

Figure 15. Cross section of the middle piece and principal piece. Gl, glycogen particles; M, mitochondria. $\times 45,000$.

Figure 16. Longitudinal section of the middle piece and principal piece. Ax, axoneme; Gl, glycogen particles; M, mitochondria; arrows show Jensen's ring in the boundary between the middle piece and the principal piece. $\times 56,000$.

Figure 17. Cross section of the end piece. Ax, axoneme. $\times 96,000$.

Figure 18. Longitudinal section of the limit (arrow) between principal piece (PP) and end piece (EP). $\times 50,000$.

could represent a similar adaptation to promote the penetration of the spermatozoon through the egg investments.

The absence of sperm dimorphism and the presence of nutritive eggs in *Chorus giganteus* (GALLARDO, 1980), *Colus stimpsoni* (WEST, 1981), *Nucella lapillus* (WALKER, 1970), and *Natica catena* (ANKEL, 1930) disagree with the proposition that the atypical spermatozoa play a role in the determination of nutritive eggs. Alternative explanations could be those proposed by PORTMAN (1931a), according to whom there is a "dimorphism of physiological nature" based on differences in nuclear condensation during spermatogenesis in *Thais lapillus*, or by RAVEN (1970) who implicated follicle cells in influencing ooplasmic localization in *Lymnaea stagnalis*.

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The Reproductive Cycles of the Intertidal Bivalves *Crassostrea cucullata* (Born, 1778) and *Perna perna* (Linnaeus, 1758) from the Transkei Coast, Southern Africa

by

THERESA LASIAK

Department of Zoology, University of Transkei, Private Bag X5092,
Umtata, Transkei, Southern Africa

Abstract. Histological analysis was used to determine the reproductive cycles of the rock oyster *Crassostrea cucullata* and the brown mussel *Perna perna* from the Transkei coast, Southern Africa. Gametogenesis in *C. cucullata* took place between August and January, and spawning occurred in late summer (February to March), after which time, the animals became inactive and of indeterminate sex until the cycle recommenced. The observed cycle is compared with that described in tropical and temperate regions. *Perna perna* has an extended breeding season characterized by low levels of asynchronous, intermittent spawning between February and September. It is suggested that such a reproductive cycle may be an adaptive strategy to ensure survival of some larvae in their unpredictable "upwelling" environment.

INTRODUCTION

NUMEROUS STUDIES have been carried out on the reproductive cycles and spawning of bivalves (see ANDREWS, 1979, and SASTRY, 1979, for reviews). However, relatively little is known of the reproductive cycles of South African bivalves. The only notable studies are those of DE VILLIERS (1973) on *Donax serra* and GRIFFITHS (1977) on *Aulacomya ater* and *Choromytilus meridionalis*. This paper describes the reproductive cycles of two intertidal bivalves, abundant on the Transkei coast: the rock oyster *Crassostrea cucullata* and the brown mussel *Perna perna*.

The rock oyster *Crassostrea cucullata* forms conspicuous bands on rocks in the upper balanoid zone. It is Indo-Pacific in origin, ranging from East Africa to the Pacific islands (BRALEY, 1982). The reproductive biology of *C. cucullata* has not been studied previously in Southern Africa. However, elsewhere this species has received considerable attention because of its cultivation potential. Information on the reproduction of *C. cucullata* is available from Australia (ROUGHLEY, 1933), Guam (BRALEY, 1982), Pakistan (ASIF, 1980), India (NAGABHUSHANAM & BIDARKAR, 1977), Singapore (LING, 1970), and East Africa (VAN SOMEREN & WHITEHEAD, 1961).

Perna perna is widely distributed in tropical and subtropical regions of the Indo-Atlantic (SIDALL, 1980). On the east coast of Africa it has been recorded from central Mozambique around to False Bay in the Cape (KILBURN & RIPPEY, 1982). It is usually associated with wave-exposed situations, often forming dense aggregations on rocky shores from the lower balanoid zone down to 5 m below chart datum (BERRY, 1978). A brief description of the spawning periods of *P. perna* on the subtropical Natal coast, just north of Transkei, is given by BERRY (1978). Information is also available on the reproduction of *P. perna* from the Congo (CAYRE, 1981) and Venezuela (VELEZ & MARTINEZ, 1967; CARVAJAL, 1969; VELEZ, 1971).

MATERIALS AND METHODS

At monthly intervals, between August 1982 and September 1983, specimens of *Crassostrea cucullata* and *Perna perna* were collected from the shore at Hluleka (31°49'S, 29°19'E). All collections were made at spring low tide and random samples of 20 to 30 individuals were taken. Gonadal tissue from the mid-region of the mantle lobe was removed and fixed in either Bouin's or 10% formol-saline

Table 1

Distribution of gonad stages in samples of *Crassostrea cucullata* from Hluleka, Transkei (n = sample size; GI = gonad index; d₁ to d₅, r, and s are developmental stages).

Date	n	Number of individuals at each stage															GI
		Male							Female								
		d ₁	d ₂	d ₃	d ₄	d ₅	r	sp	d ₁	d ₂	d ₃	d ₄	d ₅	r	sp	in	
Aug 1982	21	3		1	1			1	1						3	11	0.71
Sept	26		1	7	4				1	9	3					1	2.58
Oct	26		1	5	4					1	10	4				1	3.12
Nov	26		1	2	8					1	6	8					3.54
Dec	30	2	1	4	10	3	1	1				3	5				3.73
Jan 1983	25				4	9						2	8	1		1	4.48
Feb	24				1	4	9						1	8	1		3.38
Mar	24					1	15							6	2		2.29
Apr	23					1	3	9							5	5	1.22
May	23						2	10	1						1	9	0.74
June	24						1	16							2	5	0.79
July	18	1			1		2	3	3			1	1		2	4	1.56
Aug	23	1	8	1	1			2	4	1	4					1	1.91
Sept	19		1	3	4					1	4	6					3.42

prior to routine preparation for histological studies. The embedded material was sectioned at 7 μ m, and then stained with Delafield's haematoxylin and eosin.

The sectioned material was examined microscopically and subjectively allocated a maturity index based on the differing proportions of the various gametogenic cells present. The classification scheme adopted here is a modification of that used by SEED (1969). Four main stages in the annual cycle can be recognized: inactive (in), developing (d), spawning (r), and spent (sp). The "developing" stage is further divided into five sub-stages—d₁, d₂, d₃, d₄, and d₅—which reflect the progression of gametogenesis. For each monthly sample the mean gonad index (GI) was determined by multiplying the number of individuals at each stage by a factor representing the arbitrary rating of the stage. The sum of these products was then divided by the total number of individuals in the sample. The gametogenic stages were assigned ratings as follows: stage d₁ = 1, d₂ = 2, d₃ = 3, d₄ = 4, d₅ = 5, r = 3, sp = 1, and in = 0.

RESULTS

Crassostrea cucullata

Only three instances of hermaphroditism were noted among the 333 oysters sectioned. Two of these revealed occasional oocytes among the spermatogenic cells at the edge of the follicles. Both male and female gametes were evident in the other hermaphrodite; the oocytes were attached to the follicle wall and spermatozoa were restricted to the lumen. The oysters examined were within the 20 to 80 mm size range. No differences were found in the size distributions of males and females. The only deviations from a 1:1 sex ratio were those associated with the

occurrence of oysters of indeterminate sex in May and June 1983.

Increases in the gonad index from August 1982 to January 1983 and from June 1983 to the cessation of sampling in September 1983 marked periods of gametogenic development. Spawning appeared to take place between February and May 1983, as indicated by the declining gonad index (Table 1). Throughout most of the reproductive cycle, the development of male *Crassostrea cucullata* paralleled that of females. Inactive oysters of indeterminate sex were prevalent in August 1982 and from April to July 1983. The occurrence of individuals at various developmental stages each month indicated a lack of gametogenic synchrony. Spawning oysters (stage r) constituted over 40% of the population between February and March. Animals in this state were recorded up to July. There was no evidence of redevelopment during the spawning period.

Perna perna

The sexes are separate, and no hermaphrodites were found. At maturity, females could be distinguished by the orange coloration of the mantle tissue, compared to the white mantles of males. At the beginning of the reproductive cycle, such visual observations were often misleading. Resting animals, in which connective tissue filled the mantle, were easily confused with mature males. Of the 307 mussels sectioned, 142 were male, 133 female, and 32 of indeterminate sex. There were no significant departures from the expected 1:1 sex ratio ($P < 0.05$). Mussels examined were between 20 and 70 mm total length. Parasitic infestation by digenean trematode larvae was prevalent, sometimes resulting in parasitic castration.

Table 2

Distribution of gonad stages in samples of *Perna perna* from Hluleka, Transkei (n = sample size; GI = gonad index; d₁ to d₅, r, and s are developmental stages).

Date	n	Number of individuals at each stage																GI
		Male							Female									
		d ₁	d ₂	d ₃	d ₄	d ₅	r	sp	d ₁	d ₂	d ₃	d ₄	d ₅	r	sp	in		
Aug 1982	22			3	3	4	2				1	3	1	4	1			3.64
Sept	19					2	9		3						2	3		1.05
Oct	22	2	2	4		3			2	1	2				1	5		1.55
Nov	26	2		2	4		1		2	2	3					10		1.73
Dec	27	2	2	4	1					6	5				2	5		1.89
Jan 1983	19			2	5	1			1	2	2		1			5		2.47
Feb	28		2	2	7	2	1		1	1	2	5	4	1				3.68
Mar	20		2	6	2					3	4	3						3.00
Apr	26				7	1	4				1	4	5	4				3.50
May	22				1	7	3					1	7	3				4.36
June	21				2		8				2			8		1		2.95
July	20				2	6	4						7	1				4.40
Aug	13				1	1	1					1	7	1		1		4.15
Sept	22	1	1	4	2		2			2	1	2	1	2	2	2		2.59

There was a gradual increase in the gonad index between September 1982 and February 1983, indicating gametogenic development (Table 2). The presence of animals at several developmental stages in the monthly samples indicated asynchronous development. The development of male *Perna perna* generally paralleled that of the females. Decreased gonad index values in March, June, and September may be indicative of spawning activity. However, reference to data on the distribution of gonad stages indicated that only developing individuals at stages d₂, d₃, and d₄ were present in the March sample. It is therefore suggested that the decline in gonad index at this time does not reflect spawning but is rather associated with the regeneration of sexual products following a partial spawning in February. Between April and July over 20% of the mussels examined were in spawning condition, characterized by partially empty gonadal follicles. In some cases further gametogenesis was evident, which lends support to the suggestion that *P. perna* is a partial spawner. Spent mussels, with residual gametes present in the follicles, were relatively scarce. Mussels of indeterminate sex, apparently in a resting state, constituted more than 20% of the population between October and January.

DISCUSSION

Studies on the reproductive cycle of *Crassostrea cucullata* have been completed at seven locations (Table 3). Continuous reproductive activity is reported in the tropical populations (AWATI & RAI, 1931; LING, 1970; NAGABHUSHANAM & BIDARKAR, 1977; ASIF, 1980; BRALEY, 1982). Despite some asynchrony, temperate populations of *C. cucullata* and its recognized subspecies (ROUGHLEY, 1933; DINAMANI, 1974; Lasiak, this study) have a single

annual reproductive cycle. This follows the general trend shown by other oysters of the genus *Crassostrea* in temperate latitudes; spawning takes place in summer and animals enter a regressed or inactive phase during the colder months (LOOSANOFF, 1942; KENNEDY & BATTLE, 1964; GALTISOFF, 1964; BERG, 1969).

Differences in the periods of gametogenesis and breeding activity have been recorded in geographically separated populations of various bivalve species (SASTRY, 1979). The reproductive cycles of latitudinally separated populations of *Crassostrea cucullata* follow the temperature-latitude zoogeographic principle outlined by THORSON (1946). That is, tropical and subtropical species are expected to spawn earlier and over a more extended period than their counterparts at the poleward limits of their distribution. SASTRY (1970) proposed that variations of this kind represent adaptive responses to geographic differences in temperature and food production. Although the gonadal cycle of *C. cucullata* in temperate waters appears to be linked to seasonal temperature patterns, temperature does not regulate gametogenesis in tropical populations. Several workers (LING, 1970; NAGABHUSHANAM & BIDARKAR, 1977; STEPHEN & SHETTY, 1981) have shown that reduction in salinity, associated with heavy monsoon rains, acts as a trigger initiating spawning in some populations of *C. cucullata*. However, BRALEY (1982) was unable to correlate spawning activity of *C. cucullata* from Guam with environmental perturbations in water temperature, salinity, turbidity, or climate. The continuous spawning activity of the latter population may result from a lack of exogenous cues for spawning, as suggested by GIESE & PEARSE (1974).

The reproductive cycle of the brown mussel *Perna per-*

Table 3
Geographic location and reproductive cycle of *Crassostrea cucullata*.

Location	Latitude	Reproductive cycle	Source
Singapore	2°S	Continuous, three peaks after monsoons	LING (1970)
Guam	13°S	Gametogenic cycle 3–4 months long. Spawning continuous, three major peaks, Nov–Dec, Mar–April, and late June	BRALEY (1982)
Ratnagiri, India	17°S	Gametogenesis from February onward; all ripe by July but no spawning until after monsoon. Spawning from late September to January	NAGABHUSHANAM & BIRDARKAR (1977)
Bombay, India	19°S	Continuous, except for monsoon periods	AWATI & RAI (1931)
Karachi, Pakistan	25°S	Continuous with three peaks, Jan, May, and Oct–Nov	ASIF (1980)
Hluleka, Transkei	32°S	Gametogenesis begins in July–Aug and reaches maximum development in November. Major spawning Feb–Mar	Lasiak, this study
Sydney, Australia	34°S	Summer spawning extending to April–May	ROUGHLEY (1933)

na does not conform to the sequence expected for tropical species near the poleward limits of their distribution. Fluctuations in the gonad index indicate that *P. perna* on the Transkei coast has an extended breeding season characterized by low levels of spawning activity from February to September. Two well-defined spawning peaks in winter (May to August) and spring (September to October) have been described in *P. perna* from the Natal coast (BERRY, 1978). However, Berry also noted that spawning activity tended to take place over an extended period, with 25% of the population breeding for three to six months of the year. Asynchronous, intermittent spawning has also been reported in two mussels, *Aulacomya ater* and *Choromytilus meridionalis*, on the west coast of Southern Africa (GRIFFITHS, 1977). A protracted breeding season has also been recorded for *P. perna* from Venezuela (VELEZ & MARTINEZ, 1967; CARVAJAL, 1969; VELEZ, 1971) (Table 4).

Spawning and larval settlement of *Perna perna* have been linked to periods of lower surface water temperature, intense winds, and maximum upwelling (VELEZ & MARTINEZ, 1967; CARVAJAL, 1969; ACUNA, 1977; CAYRE, 1981). No information is available on temporal fluctua-

tions in environmental parameters or food availability off the Transkei coast during the course of this study. However, incursions of cold water, associated with upwelling, are known to occur in this area, particularly in the winter (MACNAE, 1962). Although it is difficult to demonstrate a causal relationship between temperature and reproductive activity, it is probable that either a threshold temperature or a rate of change in temperature influences gametogenesis and acts as a cue for spawning (SASTRY, 1979). VELEZ & EPIFANIO (1981) have shown that gametogenesis in *P. perna* is inhibited by high temperatures. Both CARVAJAL (1969) and LUNETTA (1969) found spawning of *P. perna* to occur when sea temperature dropped from 28 to 22°C. Upward temperature shocks have also been used to induce spawning in this mussel (SIDALL, 1980).

BAYNE (1976) has discussed the need to coordinate the time of spawning so that larvae and adults have access to abundant food supplies. Such a strategy should maximize the probability of successful recruitment. GRIFFITHS (1977) has proposed that, in upwelling areas, spawning in response to the rate of change in temperature ensures that larvae will be produced at a time when phytoplankton

Table 4
Geographic location and reproductive cycle of *Perna perna*.

Location	Latitude	Reproductive cycle	Source
Sucre, Venezuela	10°S	Continuous, peak activity January to April	VELEZ & MARTINEZ (1967)
		Three peaks in condition index indicating spawning from October to January, February to April, and from July to August	VELEZ (1971)
		Three periods of intense spawning activity: September to December, February, and April to June	CARVAJAL (1969)
Congo	4°S	Two spawning seasons: June to September and December	CAYRE (1981)
Natal, South Africa	30°S	Two spawning peaks: first, always the greatest, between May and August, with second peak in spring, September to October	BERRY (1978)
Hluleka, Transkei	32°S	Protracted spawning with major peak April to July	Lasiak, this study

availability is enhanced. Asynchronous intermittent spawning may be an adaptation to life in the unpredictable environment characteristic of upwelling areas. As NEWELL *et al.* (1982) have pointed out, continuous dribble spawning ensures that in the face of some catastrophic event, which could kill or prevent settlement of larvae, only a small proportion of potential recruits would be lost. More frequent sampling coupled with continuous environmental monitoring is needed to clarify the apparent relationship between temperature change and spawning activity in the mussel *Perna perna*.

ACKNOWLEDGMENTS

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Seasonal Occurrence of *Anodonta cataracta* Say, 1817, Glochidia on Three-spined Sticklebacks, *Gasterosteus aculeatus* Linnaeus

by

WILLIAM THRELFALL

Department of Biology, Memorial University of Newfoundland,
St. John's, Newfoundland, Canada A1B 3X9

Abstract: Glochidia of *Anodonta cataracta* were recovered from three-spined sticklebacks, *Gasterosteus aculeatus*, caught in Ocean Pond, Newfoundland, Canada. A marked seasonal cycle of prevalence and intensity of infestation was noted, with both parameters being highest in the winter. No differences were noted between infestation and weight and sex of the host. The majority of glochidia were located on the gills and fins.

INTRODUCTION

THE SPECIES and distribution of filter-feeding unionid clams in Newfoundland, Canada, are poorly known. Indeed the molluscan fauna of the Province, other than commercially important marine species, has received little attention during recent years. The major works on this region are those of VANATTA (1925, 1927, 1930), BROOKS & BROOKS (1940) and LA ROCQUE (1953, 1961). CLARKE & RICK (1964) discussed the status of *Anodonta brooksiana* van der Schalie, 1938, and placed it in synonymy with the polymorphic species *Anodonta cataracta* Say, 1817. The life cycle of the unionid clams usually involves a free-living adult form, with a short-lived parasitic larval (glochidial) phase (COKER *et al.*, 1922). KAT (1984) recently reviewed parasitism within the Unionacea (Bivalvia). During a study of the metazoan parasites of three-spined sticklebacks (*Gasterosteus aculeatus* Linnaeus, 1758) in Newfoundland, glochidia were frequently found. This note reports the occurrence and intensity of infestation with glochidia on *G. aculeatus*.

MATERIALS AND METHODS

A total of 615 three-spined sticklebacks was caught at two sample sites in Newfoundland, Canada (Ocean Pond [OP]—47°25'N, 53°27'W—428 fish; Great Pond [GP]—47°40'N, 52°46'W—187 fish), using minnow traps and dip nets. The sampling periods, during which attempts were made to catch 20 fish per month, extended from November 1970 to December 1972 (OP) and October 1971 to December 1972 (GP). Occasional samples were

also taken in late summer, fall, and winter of 1974, 1976, 1978, 1980, and 1982. Winter weather conditions (temperatures to -20°C, combined with 60-80 km/h winds, ice cover up to 60 cm, and unplowed roads) made acquisition of the desired sample size difficult on occasion. Fish were transported back to the laboratory alive, and necropsied within 48 h using conventional techniques (FERNANDO *et al.*, 1972). Fish were weighed to the nearest g and measured to the nearest mm prior to necropsy. Glochidia found were treated as outlined in FERNANDO *et al.* (1972). Parasitological terminology is that recommended by MARGOLIS *et al.* (1982).

Sample Sites

As glochidia were recovered only from fish taken in Ocean Pond, only this sample site will be described. The morphometry of Ocean Pond and its physicochemical characteristics were well described by SEABROOK (1962) and JAMESON (1974). It is a large shallow lake, with a mean length of 5.50 km and mean width of 0.55 km. The total area is approximately 328 ha, with a maximum depth of 9.75 m and a mean of 4.54 m. The lake has a much-indented shoreline and contains 30 islands. The north end of the lake, where sampling occurred, has a bottom covered with large boulders and up to 2.44 m of gray mud.

RESULTS AND DISCUSSION

Data will be analyzed and discussed with regard to prevalence and intensity of infestation, relationship of infestation to fish size (weight and length), and distribution of

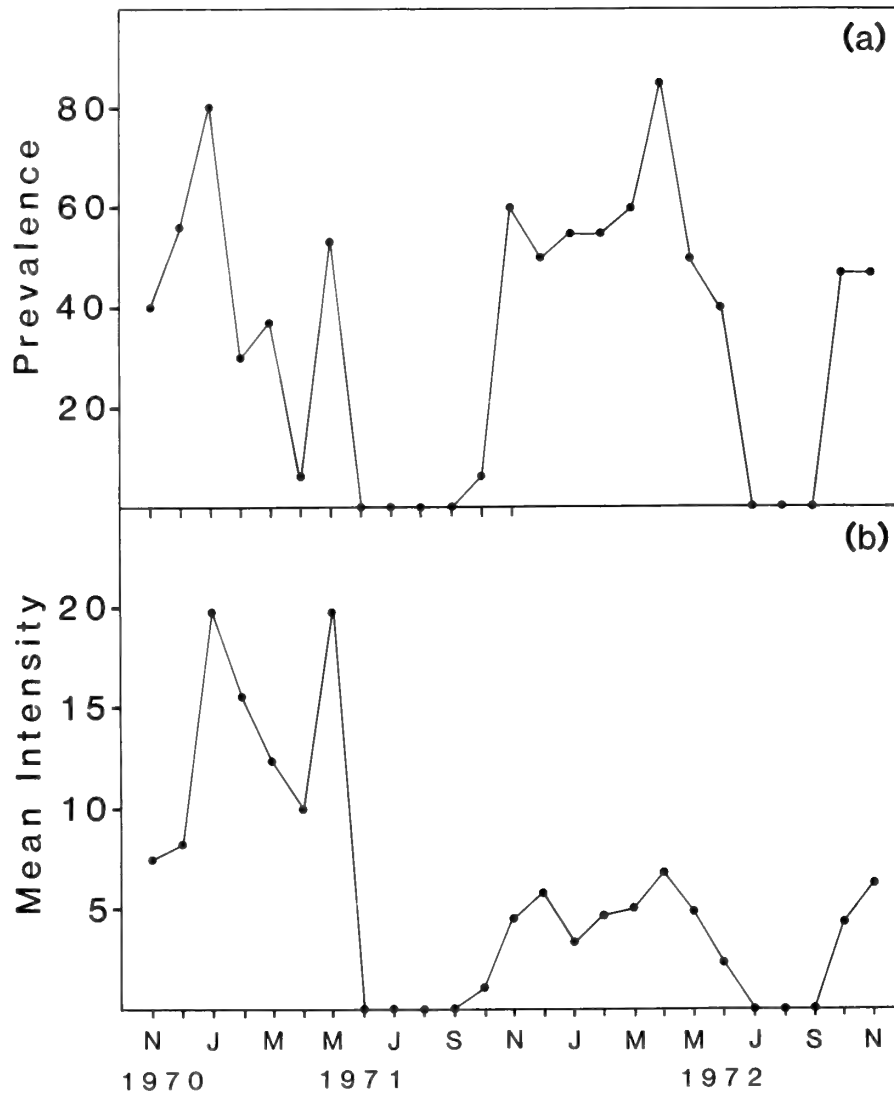


Figure 1

a. Monthly prevalence of glochidia on *Gasterosteus aculeatus*. b. Mean number of parasites per infested host (intensity) for each monthly sample.

the glochidia on the host body. DARTNALL & WALKEY (1979) used a similar scheme in their report on the distribution of *Anodonta cygnea* on *Gasterosteus aculeatus* in England. The present parasites were identified as *A. cataracta* on the basis of glochidial morphology and measurements that approximated those given by WILES (1975). This identification was confirmed by examination of shells of adults collected from the pond. (No glochidia or adults were recovered from Great Pond.) A total of 148 fish (35%) was infested with glochidia (mean number per infested fish 7.5 ± 7.5 , range 1-40). Monthly variation in prevalence is shown in Figure 1(a), with a marked sea-

sonal cycle being evident. No glochidia were found in the periods June-September 1971 and July-September 1972. The number of infested fish then rose to a peak in January 1971 and April 1972 respectively. The number of fish infested with glochidia in April 1971 was much lower than in April 1972 for uncertain reasons. Since 1972 no glochidia have ever been found on a fish in the July-September period and prevalence has been within 5% of the figures given for 1972 for fish collected in other months and years. The mean intensity of infection (Figure 1[b]) was higher in the period December 1970-May 1971 than it was at any other time during the survey period. The

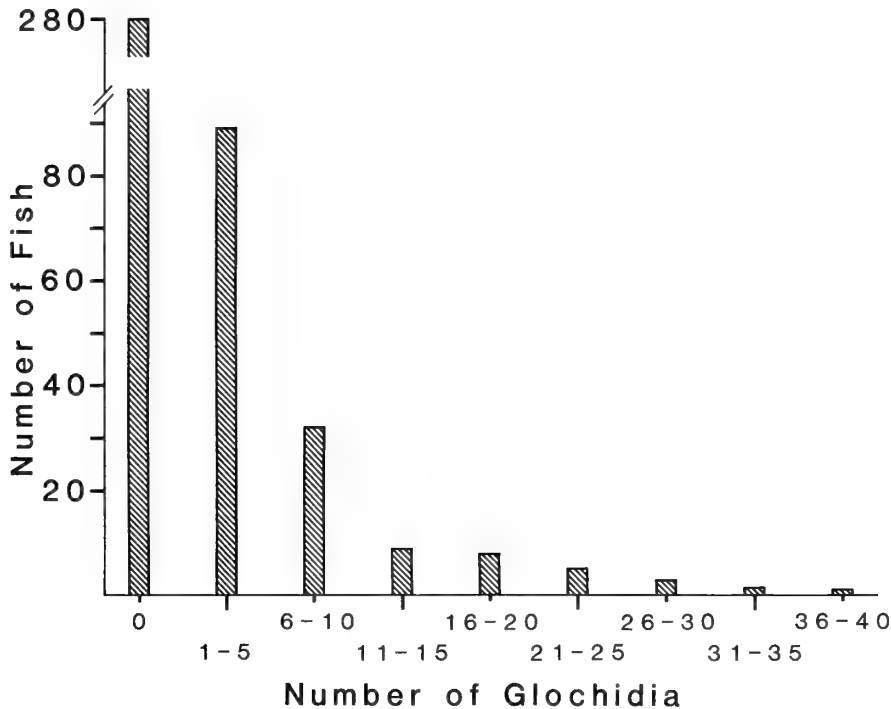


Figure 2

Frequency distribution showing the burdens of glochidia on *Gasterosteus aculeatus*.

mean intensity since 1972 has approximated that noted during 1972. Unlike the findings of DARTNALL & WALKEY (1979) no significant differences were noted in the prevalence and intensity of infection in relation to length of the host. Moreover, no differences were noted when weight and sex of the host were considered (85 females [37.8%], 58 males [29.4%] infected; mean number glochidia/infected female 8.8, male 5.7).

The distribution of glochidial burdens within the fish population was overdispersed (Figure 2). The majority of hosts (280, 65%) were uninfested, and a few members of the host population (18, 4%) were host to a large proportion of the total parasite population (448 glochidia; 43% of total number of glochidia recovered). Such a distribution is typical of many parasites (ANDERSON, 1978).

Glochidia were found most frequently on the gills (71% of cases where exact location was recorded), with 21% being found on the fins. Four percent were located in the mouth and 4% on the opercula. This situation is unlike that noted by DARTNALL & WALKEY (1979) and by DUDGEON & MORTON (1984), who found the fins to be most heavily infested, but similar to that reported by WILES (1975), who found only gills infested. Of the glochidia on the fins, some 80% were taken from the pectorals. In only two cases were glochidia found on the fins in the absence of glochidia on the gills. The fins were usually

not infested unless large numbers (>30) of glochidia were found on the fish. A single glochidium was found in the stomach of one fish. No evidence of previous infestation was noted on the body of uninfested fish, and no pathological conditions were observed in infested fish. Each glochidium was enclosed in a cyst of host origin which was composed of host epidermal cells and other neighboring cells that had moved into the region.

This parasite has previously been recovered in Canada from *Catostomus commersoni* by WILES (1975). In the present study a marked host-specificity was noted with only one glochidium being located on 31 specimens of *Salmo salar* (landlocked) and one on 31 *Salvelinus fontinalis* taken from Ocean Pond in September–November 1972. None was recovered from 10 specimens of *Pungitius pungitius* taken in December 1970–May 1971.

Data collected in this study confirm WILES' (1975) suggestion that *Anodonta cataracta* is a winter breeder in the Atlantic region of Canada. It is also of interest to note that DARTNALL & WALKEY (1979) found glochidia on fish only when the temperature was below 12°C.

The glochidial population in Ocean Pond has remained relatively stable over the past decade, with regular cycles in prevalence and numbers of glochidia being noted. However, further monitoring would be worthwhile as summer residences are being built along the shoreline. The con-

struction and use of these structures may well alter the physicochemical parameters of the lake waters, causing changes in the populations of *Anodonta*.

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Particle-Size Selectivity in the Freshwater Bivalve *Elliptio complanata* (Lightfoot)¹

by

COLIN G. PATERSON

Department of Biology, Mount Allison University,
Sackville, New Brunswick, Canada E0A 3C0

Abstract. The freshwater bivalve *Elliptio complanata* shows an increase in apparent filtration rate with decreasing particle-size class down to particles between 3.17 and 4.00 μm in diameter, after which filtration rate declines.

INTRODUCTION

FRESHWATER BIVALVE mollusks obtain required energy by filtering sestonic particles from the water column. Workers such as HAUKIOJA & HAKALA (1978) have assumed that differences in growth rates observed among populations of a species reflect differences in the availability of usable sestonic material. PATERSON & CAMERON (1985) partially explained differences in growth rate between two populations of *Anodonta cataracta* on the basis of differences in the abundance of sestonic particles and on differences in the filtration rate of the two populations. HORNBACK *et al.* (1984), in a study of filtration dynamics of *Sphaerium striatinum* for particles of 2.02 μm diameter, concluded that the extent of filtration was insufficient to supply individuals with their energy requirements.

One difficulty with attempting to elucidate the ecology of freshwater bivalves based on some measurement of seston abundance or filtration activity is that for marine suspension-feeding bivalves it has been shown that variations in filtration rate are brought about by such factors as particle size (VAHL, 1973; BAYNE *et al.*, 1977) and abundance (RICE & SMITH, 1958; ALI, 1970; TENORE & DUNSTAN, 1973; FOSTER-SMITH, 1975; WIDDOWS *et al.*, 1979). In addition, various marine species show selectivity for particle size in that the filtration rate calculated as the amount of water pumped per unit time varies with the size of particles used in making the determination. These marine species had maximum filtration rates for particles between about 6 and 10 μm in diameter.

PATERSON (1984) found that the freshwater unionid *Elliptio complanata* (Lightfoot) showed responses similar to those observed in marine species in that filtration rate increased with increasing particle abundance to a maximum and then progressively declined. Filtration rates calculated for varying size classes of particles showed progressive increase as particle size decreased down to a size class of particles of diameters between 4.0 and 5.04 μm , the smallest size class for which filtration rate was measured.

This paper extends the work of PATERSON (1984) to examine possible particle-size selectivity by *Elliptio com-*

Table 1

Particle-size distribution as monitored by the Coulter Counter using a 70- μm aperture.

Channel	Mean geometric volume (μm^3)	Minimum volume (μm^3)	Minimum diameter (μm)
3	1.481	1.047	1.26
4	2.962	2.094	1.59
5	5.924	4.189	2.00
6	11.85	8.378	2.52
7	23.70	16.76	3.17
8	47.39	33.51	4.00
9	94.78	67.02	5.04
10	189.6	134.0	6.35
11	379.1	268.1	8.00
12	758.3	536.2	10.08
13	1516	1072	12.7
14	3033	2145	16.0
15	6006	4289	20.2
16	12,130	8579	25.4

¹ The technical assistance of L. Cormier is acknowledged. This research was supported by NSERC Grant A-6299 and the Donner Canadian Foundation.

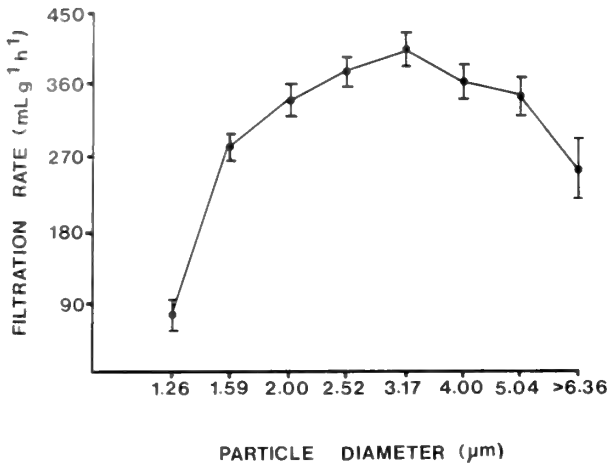


Figure 1

Filtration rate ($\text{mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) of *Elliptio complanata* as determined for different size classes of particles. The particle diameters indicate the smallest diameter found in each particle-size class. Vertical lines represent one standard error about the mean.

planata for particles with diameters less than $4\ \mu\text{m}$, as such particles might make substantial contributions to the energy requirements of the species if effectively filtered from the water column.

MATERIALS AND METHODS

Specimens of *Elliptio complanata* were collected by dragging in Morice Lake, a relatively old (ca. 1765) poly-mictic, mesotrophic reservoir located approximately 3 km north of Sackville, New Brunswick, Canada. Experiments were conducted in six plastic containers measuring 27.5×23.5 cm and having a depth of 14 cm. Containers were equipped with outlet valves 8.5 cm from the bottom. Six liters of freshly pumped lake water were added to each container. Five specimens of *E. complanata* with a maximum length of 6–7 cm were gently scrubbed and placed into each of four containers. The remaining containers served as controls.

At the initiation of the experiment, 50-mL water samples were removed through the outlet of each container and diluted 1:1 with an electrolyte solution; then, 0.25-

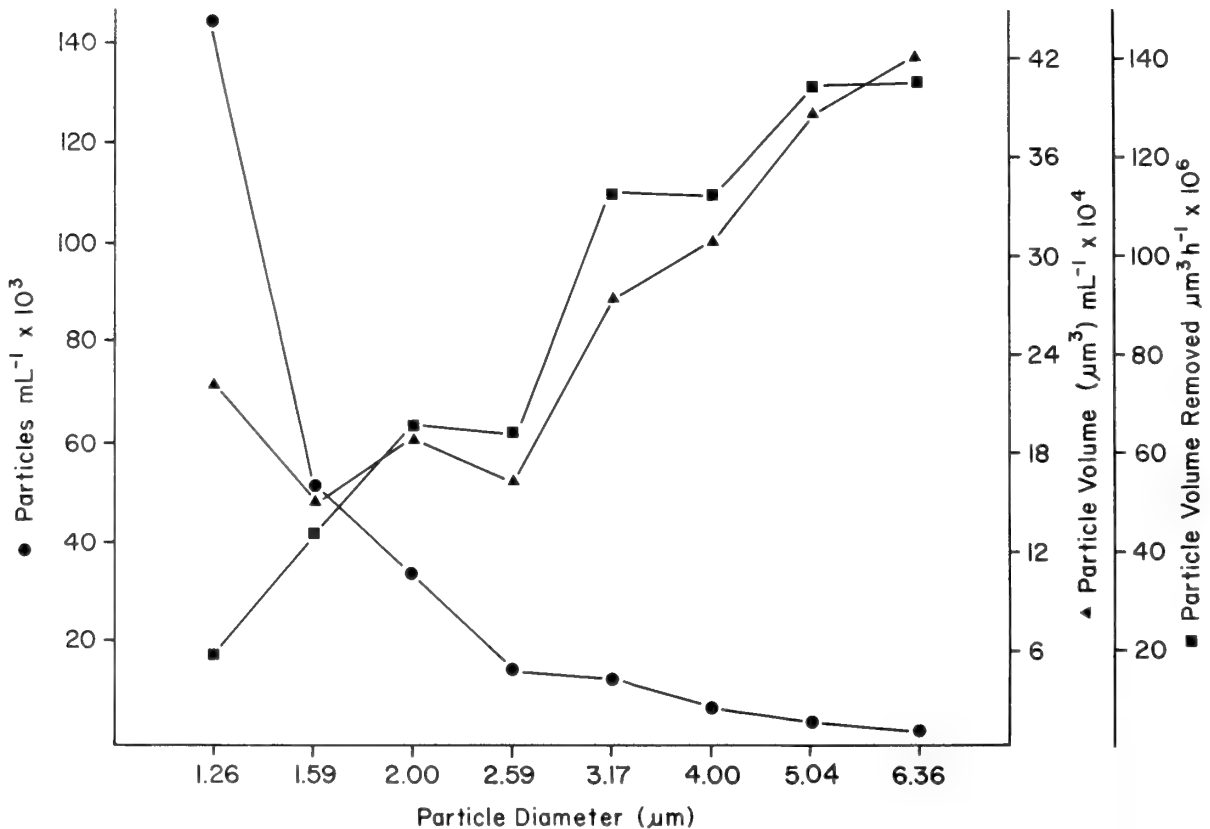


Figure 2

The relationship between the abundance (●) and volume (▲) of particles in the water of Morice Lake, New Brunswick, and the rate of particle volume removal (■) by *Elliptio complanata*.

mL samples were passed through a 70 μm aperture of a model TAIH Coulter Counter equipped with a Population Mode. In all cases, triplicate particle counts were taken and averaged. This procedure was then repeated after 2 h. When a particle passes through the aperture, it is counted as well as being assigned to one of 15 channels (channel 3 through channel 16) based on particle size. The mean geometric volume, minimum volume, and minimum diameter of the particles measured by each channel when a 70 μm aperture is used are given in Table 1. Because particle counts in channels 10 to 16 were too low to accurately determine filtration rate, these particle counts were pooled. The background count due to the electrolyte solution was determined and suitable corrections made. Each experiment consisted of measuring changes in particle abundance in four test containers each containing five *Elliptio complanata* and two control containers. This experimental procedure was repeated nine times during the summer months at experimental temperatures that ranged from 19.0 to 21.0°C.

At the end of an experiment, the length of each bivalve in a container was determined to the nearest 0.5 mm using calipers and filtration rate ($\text{mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) determined as in PATERSON (1984).

RESULTS AND DISCUSSION

Average filtration rate ($\text{mL}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) varied significantly (ANOVA $F = 5.46$; $df\ 7,64$; $P < 0.001$) over the range of particle sizes, with a maximum rate observed for channel 7 which contains particles with diameters between 3.17 and 4.00 μm (Figure 1). These data extend the findings of PATERSON (1984) to show that, in *Elliptio complanata*, filtration rate increases with decreasing particle size down to a minimum diameter of about 3.17 μm after which filtration rate progressively declines with further decreases in particle size.

The filtration rate calculated for any particle size is a measure of the amount of water that would need to be pumped across the gills if particle removal were 100% efficient. The results presented in Figure 1 indicate that efficiency of particle removal is greatest for particles in the size class 3.17–4.00 μm . This then raises the question of the potential significance of this peak value for removal efficiency when *Elliptio complanata* is filtering a natural array of particles in lake water. When the particle volume per milliliter for each channel is multiplied by the filtration rate observed for the particles in that channel, the

total volume of particles removed per hour increases with increased size (Figure 2). To *Elliptio complanata* filtering Morice Lake water, there is no readily apparent advantage to having a maximum efficiency of removal for particles in the 3.17–4.00 μm size class. However, the Coulter Counter does not distinguish between organic and inorganic particles. In addition, no information is available on possible relationships among efficiency of removal, ingestion, and energy assimilation for different sized particles.

It is apparent, however, that any attempts to relate such factors as growth rate or abundance to sestonic abundance, or to measure potential energy intake, must be undertaken within a framework that takes into account both particle abundance and particle size.

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Records and New Host of Pea Crabs (Decapoda: Pinnotheridae) for Baja California, Mexico

by

ERNESTO CAMPOS-GONZÁLEZ

Escuela de Ciencias Biológicas, Universidad Autónoma de Baja California,
Apartado Postal 2300, Ensenada, B.C., Mexico

Abstract. *Tivela stultorum* is a new definitive host of *Pinnixa littoralis*, and for first time *P. littoralis* and *Fabia subquadrata* are recorded in Baja California, Mexico.

INTRODUCTION

THE PINNOTHERIDAE are symbiotic crustaceans that live with ascidians, annelids, crustaceans, echinurans, echinoderms, and mollusks (SCHMITT *et al.*, 1973). At present, eight pinnotherid species are recorded from the temperate zone of the west coast of Baja California from the U.S.-Mexican border to Punta Eugenia (SCHMITT *et al.*, 1973; GARTH & ABBOTT, 1980). The present note adds two species and a new host for one of them.

DESCRIPTION

Pinnixa littoralis Holmes, 1894

Previously known distribution: "Prince William Sound (Alaska) to San Diego," California, U.S.A. (GARTH & ABBOTT, 1980).

Recorded host: GARTH & ABBOTT (1980) list 18 hosts for this species, but only *Tresus capax* (Gould, 1850), *T. nuttalli* (Conrad, 1837), and *Saxidomus nuttalli* Conrad, 1837, are recorded as definitive hosts (i.e., hosts for the adult crab).

New definitive host and new record: 4 females (3 ovigerous) and 3 males were found in the mantle cavity of the Pismo clam, *Tivela stultorum* (Mawe, 1823), collected from the sandy beach of Bahía Santa María, about 10 km south Bahía San Quintín, Baja California, Mexico (30°23'N, 115°54'W), in August 1984, by S. I. Salazar-V. and G. Gandica.

Measurements (mm): Carapace width (length) of females—13.76 (8.0), 14.06 (8.38), 15.16 (9.8); of males—

8.34 (4.56), 7.66 (4.52). No measurements were made on one male and one female.

Remarks: According to the observations of Mr. Gandica (clam salesman in Ensenada, Baja California), *Pinnixa littoralis* is rare in *Tivela stultorum*. To obtain one or two specimens he has to dissect several hundred clams. All of the collected pea crabs occurred as a male-female pair, except for one solitary female. Other pea crabs recorded from the Pismo clam are *Fabia concharum* (Rathbun, 1893) and *F. subquadrata* Dana, 1851 (SCHMITT *et al.*, 1973).

Fabia subquadrata Dana, 1851

Previously known distribution: "Akutan Pass (Aleutian Islands, Alaska) to La Jolla (San Diego Co.)," California, U.S.A. (GARTH & ABBOTT, 1980).

Material examined: Punta San Miguel, Bahía Todos Santos (BTS), Ensenada, B.C. (31°16'N, 116°45'W), intertidal, commensal in *Mytilus californianus* Conrad, 1837, January 1984, by S. I. Salazar-V., 2 females (ovigerous); Punta Morro, BTS, Ensenada, B.C. (31°54'N, 116°36'W), intertidal, commensal in *M. californianus*, 11 March 1985, by Patricia Alemán-D., 2 females (ovigerous); Ejido Eréndira, Ensenada, B.C. (31°54'N, 116°38'W), intertidal, commensal in *M. californianus*, November 1981, by Rosana Suárez, 4 females (3 ovigerous).

Measurements (mm): Carapace width (length) of females—10.2 (9.44), 12.54 (10.4), 12.72 (10), 11.18 (8.72), 9.56 (8.44), 13 (10), 13.04 (10.9), 11.5 (11.3).

Remarks: Previously, GARCÍA-PÁMANES *et al.* (1982) re-

corded *Fabia subquadrata* from Eréndira, B.C. However, the material that supported this record has been lost. My record confirms the presence of this species on the west coast of Baja California.

The characteristics that differentiate *Fabia subquadrata* from *F. concharum* are present in the material that I examined (see diagnosis of female in RATHBUN, 1918, and DAVIDSON, 1968). The only character that did not agree with the diagnosis of RATHBUN (1918) was the relative length of the propodus and dactyl of the outer maxilliped. Rathbun noted that the dactyl reaches the end of the penultimate segment in *F. subquadrata*, but in the material that I examined the last segment did not extend completely to the end of the propodus (see DAVIDSON, 1968:fig. 1A). Even so, dactyl length serves to separate this species from *F. concharum*, whose dactyl is conspicuously smaller.

ACKNOWLEDGMENTS

The author is most grateful to G. Gandica and S. I. Salazar-V., who collected the specimens of *Pinnixa littoralis*, to Dr. John S. Garth (University of Southern California) for his continuous support, and Ruben Ríos-G. (Centro de Investigación Científica y Educación Superior de En-

senada) for the criticism of the manuscript. The material is included in the collection of Invertebrates, Escuela de Ciencias Biológicas, Universidad Autónoma de Baja California (Ensenada, B.C.).

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NOTES, INFORMATION & NEWS

A Range Extension of *Phidiana stearnsi*
(Cockerell, 1901) (Gastropoda: Nudibranchia)

by

Linda Nelson

P.O. Box 55E, Santa Cruz Municipal Wharf,
Santa Cruz, California 95060, U.S.A.

On 23 January 1985, a single specimen of *Phidiana stearnsi* (Cockerell, 1901) was collected by the author from an approximately 60-yr-old piling near the end of the Santa Cruz Municipal Wharf. This much rotted piling had just been pulled up by crane onto the decking of the wharf. The 30-mm-long specimen agrees with the description in McDONALD (1984:204) with the following exceptions: (1) it lacks the irregular, longitudinal band of brilliant vermilion to scarlet-orange on either side of the head, from the base of the oral tentacles to the base of the rhinophores, (2) it lacks the irregular blotches of scarlet-orange to vermilion on either side of the dorsum, between groups of cerata, and (3) it lacks minute cream-to-white flecks between and posterior of the bases of the rhinophores. The general ground color is very light cream-white.

The previously recorded range of *Phidiana stearnsi* was from Santa Barbara, Santa Barbara Co., California, to La Jolla, San Diego Co., California (McDONALD, 1984: 204). This note extends the known range approximately 318 km (198 mi) northward.

In addition, two specimens of the mussel blenny *Hypsoblenius jenkinsi* Jordan & Evermann were collected from the same piling. The previously reported range of this fish was from Coal Oil Point, Santa Barbara Co., California, to Puerta Marquis, Mexico (MILLER & LEA, 1972:172; ESCHMEYER & HERALD, 1983:247). The known range of this species is likewise extended approximately 318 km (198 mi) northward.

The nudibranch identification was confirmed by Gary McDonald, of Long Marine Laboratory, and the fish identification was confirmed by Robert N. Lea, of the Monterey Office of the California Department of Fish and Game. The specimens are currently at the above institutions respectively.

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International Commission on
Zoological Nomenclature

The following Opinions of potential interest to our readers have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature*, volume 43, part 1, on 9 April 1986:

Opinion No. 1370 (p. 17). *Neadmete okutanii* Petit, 1974, designated as type species of *Neadmete* Habe, 1961 (Mollusca, Gastropoda).

Opinion No. 1372 (p. 21). *Donax hanleyanus* Philippi, 1847 (Mollusca, Bivalvia): conserved.

Opinion No. 1375 (p. 27). *Glossodoris* Ehrenberg, 1831, *Hypselodoris* Stimpson, 1855, and *Chromodoris* Alder & Hancock, 1855 (Mollusca, Gastropoda): conserved.

Opinion No. 1376 (p. 30). *Cuspidaria (Rhinoclama) adamasi* Morgan & Heppell, 1981, designated as type species of *Rhinoclama* Dall & Smith, 1866 (Mollusca, Bivalvia).

In addition, the Commission has given notice of the possible use of its plenary powers in the following case:

Case No. 872. *Clausilia* Draparnaud, 1805 (Mollusca, Gastropoda): proposed correction of Opinion No. 119.

The following applications have been received by the Commission and have been published in volume 43, part 2, of the *Bulletin of Zoological Nomenclature* on 9 July 1986. Comment or advice on them is welcomed and should be sent % The British Museum (Natural History), London, England.

Case No. 2507. *Risomurex* Olsson & McGinty, 1958 (Mollusca, Gastropoda): proposed designation of type species.

Case No. 1212. SINUITIDAE Dall, 1913, MACLURITIDAE Fischer, 1885, and EUOMPHALIDAE de Koninck, 1881 (Gastropoda, Archaeogastropoda): proposed conservation by suppression of PROTOWARTHIDAE Ulrich & Schofield, 1897, MACLURAEIDEA Gill, 1817, and SCHIZOSTOMATIDAE Eichwald, 1817.

Case No. 2408. *Laplysia viridis* Montagu, 1804 (Mollusca, Gastropoda): conservation proposée par la suppression de *Laplysia viridis* Bosc, 1801.

American Society of Zoologists
1986 Meeting

The American Society of Zoologists will hold its annual meeting in Nashville, Tennessee, from 27 to 30 December. Meeting in conjunction with the ASZ will be the

American Microscopical Society, Animal Behavior Society, The Crustacean Society, International Association of Astacology, and Society of Systematic Zoology. Several symposia of likely interest to our readers have been planned, including ones on energetics and animal behavior, phylogenetic development of self-non-self recognition, nervous system regeneration in the invertebrates, habitat selection and evolution, and history of marine biology and marine biological institutions. For more information contact: Mary Adams-Wiley, Executive Officer, American Society of Zoologists, Box 2739, California Lutheran University, Thousand Oaks, California 91360. Telephone: (805) 492-3585.

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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

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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.

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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.

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a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *Veliger* 4:132-134.

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Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

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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.

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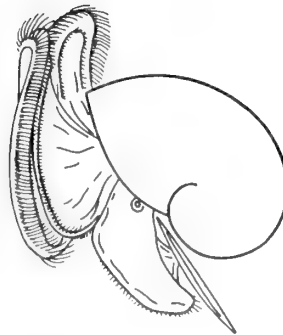
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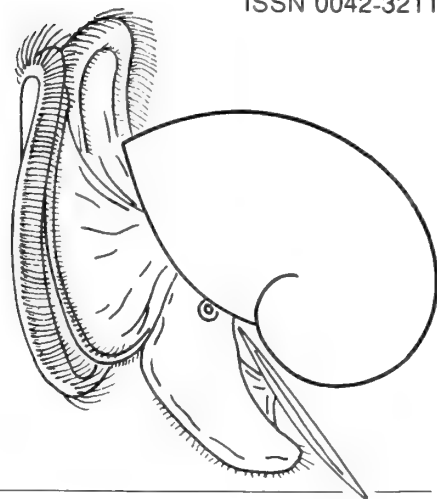
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THE VELIGER

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The Radula and Ascus of *Elysia chlorotica* Gould (Opisthobranchia: Ascoglossa)

by

BRUCE G. RAYMOND¹ AND J. SHERMAN BLEAKNEY

Department of Biology, Acadia University, Wolfville, Nova Scotia, Canada B0P 1X0

Abstract. The radulas from 230 *Elysia chlorotica* of body lengths 2–45 mm were examined. The ratio of the length of the tooth base to the length of the cusp was constant at 0.33. The number of teeth in the ascending and descending limbs of the radular ribbon was similar with means of 7.8 and 8.4. The ascus sac contained 6–76 discarded teeth. A literature report of 6 ascending limb teeth, 11 descending limb teeth, and 4 ascus teeth in a 20-mm specimen is inconsistent with the number of teeth observed in 20-mm specimens in this study, which had no less than 36 discarded teeth. The relationship of total number of teeth with body length varied (inexplicably) among years.

INTRODUCTION

THE ASCOGLOSSAN GASTROPODS are, with rare oophagous exceptions, specialists in algal sap-sucking (CLARK & BUSACCA, 1978) utilizing a single row of radular teeth to draw out the cell sap. The intertidal ascoglossan *Elysia chlorotica* Gould, 1870, which occurs from the Minas Basin (BAILEY & BLEAKNEY, 1967) to Florida (MARCUS, 1980), begins feeding upon the alga *Vaucheria* immediately after metamorphosis (WEST *et al.*, 1984) and soon becomes a vivid green due to the algal chloroplasts, which it retains in its tissues in a functional state (GRAVES *et al.*, 1979). It must, therefore, develop a functional tooth at a body length of less than 1 mm.

The *Elysia chlorotica* population in the marshes of the Minas Basin, Nova Scotia, often produces individuals 35–45 mm in length (BLEAKNEY & MEYER, 1979) which is larger than other accounts of lengths of 20–30 mm (ABBOTT, 1974; GOSNER, 1978). MARCUS (1972) reported *Elysia chlorotica* to possess 6 teeth in the ascending limb (where they are formed), 11 teeth in the descending limb, and 4 discarded teeth in the ascus sac. As ascoglossans continually produce teeth and store all discarded teeth in the ascus sac, we began this study to determine whether the size of the buccal mass and radula, and the number of radular teeth, would increase with increasing body length and if the ascus progressively enlarged to accom-

modate the many more discarded teeth of larger individuals.

MATERIALS AND METHODS

Specimens of *Elysia chlorotica* have been collected from local salt marshes since 1965 and some of this material through to 1983 was used in this study. Material for the statistical analyses was collected in 1981 except for comparisons of tooth cusp versus tooth base, tooth length versus body length, and teeth number versus body length, which utilized 1981 and 1983 specimens. The 1981 sample comprised 85 specimens. An additional 145 specimens from 1966, 1970, 1973, 1981, 1982, and 1983 were also examined.

Specimens were measured while crawling at full extension in seawater, then relaxed in 1% urethane and preserved by transferring to Boardman's Solution for 15 min and finally storing in 70% ethanol. The radular material was prepared by either removing the entire head of small specimens or dissecting out the buccal mass (Figure 1) of larger animals. The radular material of the 1981 specimens was mounted in Berlese's Fluid (GASCOIGNE, 1975) and the teeth measured after the tissue cleared. As it was difficult to flatten the ascus and spread out the jumble of teeth, the Berlese's Fluid was removed by soaking in water overnight and then a tissue solubilizer, 0.5 N quaternary ammonium hydroxide (BLEAKNEY, 1982), was added to dissolve the tissues. The entire examining process was shortened to 20–30 min for specimens of other years by simply using the solubilizer as the clearing agent and the dissociation agent. Specimens were placed in depression

¹ Present address: Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1.

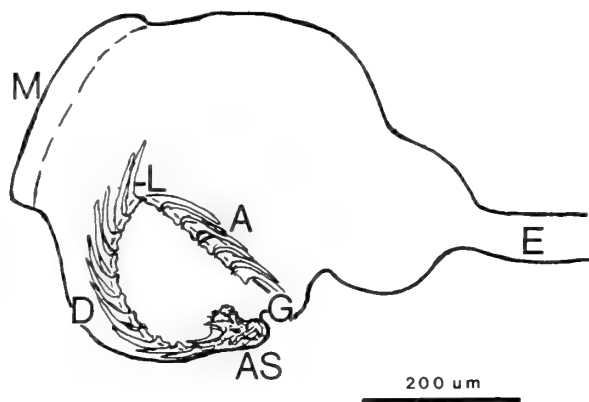


Figure 1

Buccal mass of *Elysia chlorotica* showing relative positions of ascending limb (A), ascus sac (AS), descending limb (D), esophagus (E), ghost tooth (G), leading tooth (L), and mouth (M).

slides and flooded with the solubilizer. The tissues cleared in approximately 4 min at which time the teeth in the ascending and the descending limbs were measured and counted. After an additional 10 min, the tissue was sufficiently digested to press beneath a coverslip and then the ascus contents were examined.

Two technique problems arose. First, many of the specimens over 15 mm body length had a red pigmented deposit in the ascus which adhered to and obscured the teeth. The tissue solubilizer had little effect, but the standard histological destaining solution of 1% acid-alcohol cleared the material overnight. Inexplicably, this was only noticed in individuals from the November 1965, August 1966, September–November 1981, and April–May 1983 samples.

Second, in specimens from the September 1981, April–May 1982, and October–November 1982 samples, the proximal part of the tooth shaft, where it attached to the larger rectangular tooth base, was tinted with a reddish pigment; invariably the tissue solubilizer digested this section of the tooth, immediately separating the shaft and base (Figure 2). Teeth in the ascending limb were unpigmented and unaffected. Accurate tooth counts for the descending limb and the ascus sac were obtained utilizing the solid rectangular tooth bases, as these are optically the

most conspicuous portion of the tooth. These differences in solubility of the tissues and the pigment deposits were not related to body size nor season. Only teeth with red-tinted bases separated into two pieces, even after they had been in preservatives for over a year. Specimens from other years lacked the red pigment.

Radulas were prepared for scanning electron microscope (SEM) examination by dissolving the soft tissues with the solubilizer, then rinsing the solubilizer off with a drop of toluene. A drop of 95% ethanol was added and allowed to evaporate, which caused the radular ribbon to curl, thus exposing the tooth cusps. The radula was then pressed lightly into the smooth but tacky surface of a drop of black dissecting tray wax on an aluminum SEM stub. The final mount was coated with gold and palladium and examined using a JEOL JSM-255 scanning electron microscope.

RESULTS

Tooth length increased rapidly relative to body length for specimens of 5–20 mm length, then showed little increase for larger specimens even to body lengths of 40–45 mm: tooth length = $65.2 \log(\text{body length}) + 15.8$, $r = 0.903$, $P < 0.001$ (Figure 3). For most specimens, the newly generated teeth were the largest, and in the smallest individuals there was a graded series of these teeth along the radular ribbon (Figure 4). For specimens >10–15 mm body length, the teeth of the ascending radular limb were all about maximum size and there was only a slight or nil gradation evident (Figure 2). The magnitude of the initial gradation was conveniently recorded in the teeth of the ascus sac (see Figures 4, 5). However, unknown factors can affect this process of tooth generation, as we have found examples of a single tooth in a series with a base that was only one-half to two-thirds that of adjacent teeth. We also have found series of three to four new teeth being produced in decreasing sizes as in Figure 6 where the smallest tooth base was only 42% that of the largest tooth.

For teeth with cusp lengths of 40–120 μm , the relationship of base length to cusp length was linear: base = $0.33 \text{ cusp} - 0.76$, $P < 0.001$ (Figure 7). The regression line in Figure 7 may not be accurate for teeth with cusp lengths <25–30 μm , as the smallest teeth in the ascus generally were observed to have a cusp only as long as

Explanation of Figures 2 and 4 to 6

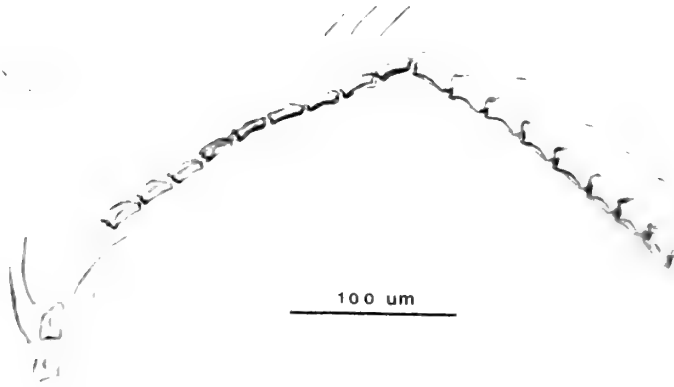
Figure 2. Radula of *Elysia chlorotica* showing the differential effect of the tissue solubilizer on the bases of teeth from the ascending limb (at the right) and the descending limb (to the left). Ghost tooth is at extreme right and the two teeth at the lower left are in the transit tube to the ascus sac.

Figure 4. Part of a graded series of 31 teeth from the ascus sac of an *Elysia chlorotica* 4 mm in length.

Figure 5. Distribution of 64 teeth from an *Elysia chlorotica* 4 mm in length: ascending limb, $n = 8$; descending limb, $n = 8$; in transit tube, $n = 6$; in ascus sac, $n = 42$.

Figure 6. Ascending limb of a radula from an *Elysia chlorotica* (2 mm in length) with a large ghost tooth (at left) following an unusual series of four recently produced teeth that progressively decreased in size.

2



100 um

4

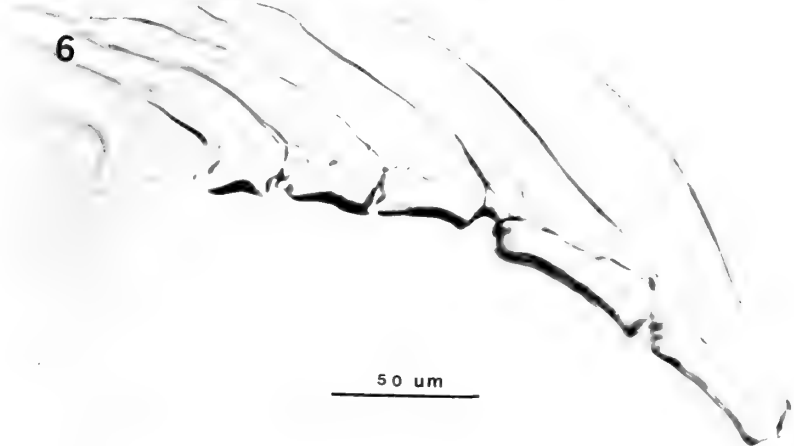


5



100 um

6



50 um

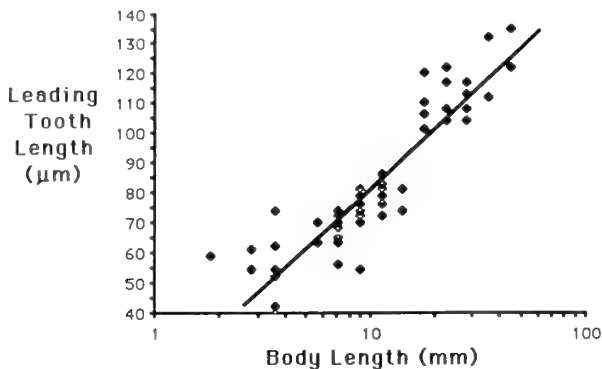


Figure 3

Leading tooth length versus body length of *Elysia chlorotica* collected from September 1981 to January 1982.

their 8- μm base whereas the regression line would indicate a cusp of approximately 24 μm for a tooth with an 8- μm base. Thus, a different development pattern was evident for these small, first-formed teeth.

The number of teeth in the ascending and descending limbs remained constant with no significant differences relative to body length (F -test, $P > 0.05$). In specimens from 2 to 46-mm body length, the ascending limb had 5–12 teeth (mean 7.8) and the descending limb had 5–13 teeth (mean 8.4). Additional teeth in the descending limb were often due to the radular ribbon remaining intact and extending into the tubular conduit between the descending limb and the ascus chamber (Figure 1).

The number of teeth stored within the ascus ranged from 6 to 76, with larger specimens having higher numbers. We have not examined any individuals less than 2 mm body length, but seven specimens (2–3 mm body length) averaged 23 teeth in the ascus sac and none had fewer than six. The highest tooth count was 76 in an ascus from a specimen 20 mm in body length, but there were

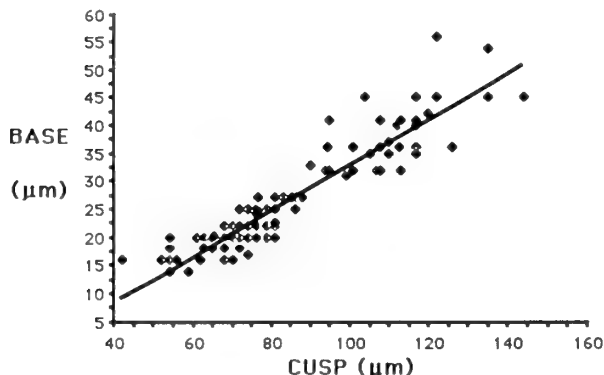


Figure 7

Tooth cusp length versus base length of various sizes of teeth from *Elysia chlorotica*.

seven larger animals (23–35 mm body length) in that same collection of 14 July 1983 that had ascus sacs so large and complex that they could not be dissected intact from the general connective tissue and thus these counts were lost. If an ascus sac or ascus complex were ruptured during dissection, several to many of the teeth would slip out and drift away under the coverslip, nullifying the possibility of a valid count. Those seven specimens may have had counts of 80–90 teeth within the ascus complex.

The ascus of *Elysia chlorotica* usually was a simple sac but was sometimes bilobed or even trilobed. The lobes, which were globose or elongate, were either clustered together at their bases or at the end of a narrow neck, or strung out under the esophagus in the form of a chain of two or three cylindrical chambers. The ascus often projected to either side of the buccal mass and sometimes was as long as the buccal mass and extended posteriorly under the esophagus. A tubular passageway extending from the descending limb to the ascus sac often contained several teeth that were detached from the radular ribbon and not yet compacted into the ascus chamber (two in Figure 2 and six in Figure 5). Teeth within the ascus were generally a jumbled mass of individual teeth, but occasionally there were linear series of 2–6 teeth arranged as they were on the radular ribbon. A coil of the first 8–10 teeth was found in the ascus sac on several occasions.

The total number of teeth, which is a function of the storage of discarded teeth within the ascus, varied tremendously and ranged from 6 to 76 teeth in our sample of 168 animals over the period 1966–1983. In large samples, the number of teeth increased with body length (Figure 8). In 1983, the number of teeth was higher in specimens collected during the summer months; ANCOVA, $F = 110.5$, $P = 0.001$ (Figure 9).

A single row of fine denticles, first photographed by BLEAKNEY (1982), extended from the tip of the cusp to

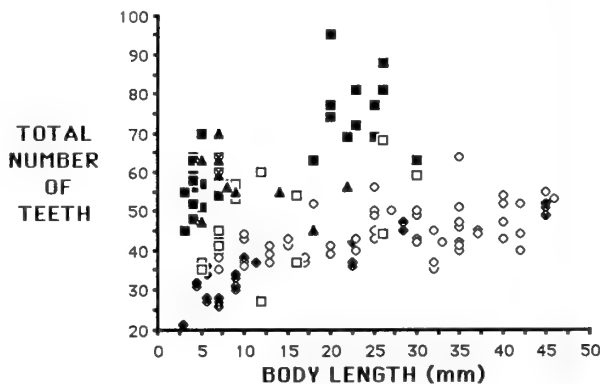


Figure 8

Total number of teeth versus body length of *Elysia chlorotica* from different samples. (▲—June, July 1970; ◆—September 1981; ◇—October, November 1982; ■—June, July 1983; □—October, November 1983)

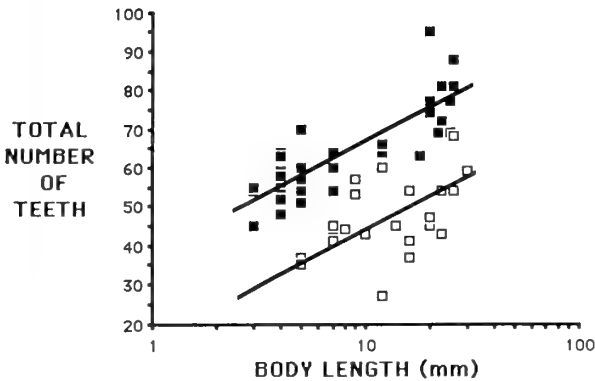


Figure 9

Total number of teeth versus body length of *Elysia chlorotica* from different seasons in 1983. (■—summer; □—fall)

the base on all teeth examined. The row of denticles was medial along the cusp, then curved to the right and terminated on the right shoulder of the basal plate, which was also the right side of the animal.

DISCUSSION

Most of the teeth of *Elysia chlorotica* have a similar morphology that is independent of the size of the tooth. Each tooth has a single row of minute denticles, which presumably assist in slicing open algae during feeding (BLEAKNEY, 1982). The ratio of base length to cusp length is constant at 0.33 (smallest measured had a cusp of 20 μm) except the first formed teeth, which have cusps that are not much larger than their base.

The numbers of teeth in the ascending and descending limbs are similar, with means of 7.8 and 8.4. There is no significant correlation between numbers of teeth in either limb with body length. The asci contained 6–76 teeth, but this may not be the full range as recently metamorphosed juveniles would not be expected to have teeth in the ascus, and the teeth of specimens with more than 70–80 teeth in the ascus could not be accurately counted. MARCUS' report (1972) of four teeth in the ascus of a 20-mm long *Elysia chlorotica* is not consistent with the present study because none of our 18–22-mm specimens had less than 36 teeth in the ascus.

The ascoglossan ascus is an enigmatic structure: why should a mollusk retain all its discarded teeth intact within a sac that has no obvious function? In *Elysia chlorotica* the teeth are evidently not broken down and recycled because a graded series of teeth is always present and the tissue solubilizer has no more effect on the old small teeth than on the new large ones. As more teeth are produced, the storage problem increases as is evident by configurations of the ascus in our samples. Although the ascus is usually considered as a simple sac projecting caudad from beneath the muscular buccal mass (GASCOIGNE & SARTORY, 1974),

the ascus of *E. chlorotica* may also be bilobed or even trilobed.

In large samples, total number of teeth increased rapidly with body length among animals with body lengths up to approximately 10 mm, then slowed dramatically even though individuals reached 45 mm in length. Nevertheless, the description and analysis of the ascus tooth counts became more inexplicable sample by sample. Among different samples, similar-size animals can have dissimilar numbers of teeth; for example, ascus counts of 5-mm specimens ranged from 6 to 71 teeth.

The data from 1983 show two clusters of results (Figure 9). The highest counts were in June and July when tooth number was almost doubled for all size classes (Figures 8, 9). (The data from other years were inadequate to determine whether this was an annual occurrence. As well, insufficient knowledge of the natural growth of *Elysia chlorotica* prevented analysis of tooth number versus age.) The decrease in October and November of 1983 for specimens of similar size is unexpected because smaller individuals of that high-count population of July should have had even higher counts by autumn. These results may have been caused by an increase in body length without a corresponding increase in tooth number. Alternatively, if they voided some teeth and the ascus is not a total accumulation, the ascus would not contain the graded set of tooth sizes that was observed in all specimens. If the summer population died out, any new generation would have had to grow to 30–40 mm by mid-October. This is inconsistent with laboratory studies at 18–19°C where *E. chlorotica* was less than 10 mm in length at 73 days post-metamorphosis (WEST *et al.*, 1984).

Our analysis of the ascus contents became more inexplicable sample by sample and certainly contradicted our intuitive assumptions. We have recounted this experience so that other malacologists may be wary of ascoglossans bearing statistical gifts in the guise of a radular data bank.

ACKNOWLEDGMENTS

The authors thank Marlene Henry for her skillful operation of the scanning electron microscope. This study was financed, in part, by a NSERC operating grant A2009 awarded to J.S.B.

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The Effect of Human Predation on the Size Distribution of *Siphonaria gigas* (Mollusca: Pulmonata) on the Pacific Coast of Costa Rica

by

SONIA ORTEGA

Department of Biology, University of South Carolina, Columbia, South Carolina 29208, U.S.A.

Abstract. At a site accessible to fishermen, the mean and maximum sizes of *Siphonaria gigas* were smaller than at a National Park where limpets have remained undisturbed for at least 7 years. Measurements of empty shells and home scars of limpets that had been consumed by fishermen demonstrated a selection for larger limpets. At the site accessible to fishermen, the population of *S. gigas* has been kept at a reduced mean size. It has persisted because of the equilibrium between human predation and recruitment.

INTRODUCTION

MAN HAS COLLECTED shellfish for food since prehistoric times along rocky shores (SHIAPPACASSE & NIEMEYER, 1964; MONTANE, 1964; SPEED, 1969; PARKINGTON, 1977; DILLEHAY, 1984). Shell middens in South Africa date back 30,000 years (SPEED, 1969). In recent years the study of the disturbance by man on intertidal communities has become of primary importance especially in the Southern Hemisphere where human predation is intense (BRANCH, 1975; CASTILLA, 1981; MORENO *et al.*, 1984, 1986; CASTILLA & DURAN, 1985; SIEGFRIED *et al.*, in press; HOCKEY & BOSMAN, 1986; OLIVA & CASTILLA, in press). After the exclusion of man from biological reserves in Chile, the size distribution of some heavily harvested species changed drastically (MORENO *et al.*, 1986). Some of these species played a key role in the organization of intertidal communities (MORENO *et al.*, 1984; CASTILLA & DURÁN, 1985).

In this paper I document the effect of human consumption on the size distribution of the pulmonate limpet *Siphonaria gigas* Sowerby, 1825, on the Pacific coast of Costa Rica. *Siphonaria gigas* is one of the most abundant limpets along the Pacific coast of Central America (GARRITY & LEVINGS, 1983; LEVINGS & GARRITY, 1984; LUBCHENCO *et al.*, 1984; ORTEGA, 1985). It is predominantly found on exposed shores and returns to a home scar after each foraging excursion (GARRITY & LEVINGS, 1983). Although *S. gigas* can attain sizes of up to 80 mm in length in Panama (LEVINGS & GARRITY, 1984), the mean size in Costa Rica

is usually smaller (ORTEGA, 1985, and this paper). I present evidence that suggests that humans, as size-selective predators, have reduced the mean size of *S. gigas* in areas accessible to them, whereas in areas protected from harvesting the mean size of *S. gigas* is larger.

STUDY SITES

This work was conducted at two sites along the Pacific coast of Costa Rica. The first site is the same as described in ORTEGA (1985), a rocky headland called Punta Mala (=Punta Judas) (9°31'N, 84°32'W). At this site, fishermen often visit the intertidal zone to fish and collect intertidal organisms for food. My observations were made on the extreme westerly point of Punta Mala (herein referred to as Punta Mala West). The second site, the southern point of a rocky shore at Manuel Antonio National Park, is located approximately 40 km south of Punta Mala. Collection of flora and fauna has been prohibited inside the park for 7 years. Both sites are exposed to moderate amounts of wave shock.

MATERIALS AND METHODS

To determine the mean size of resident populations of *Siphonaria gigas*, 9 and 10 permanent quadrats (0.25 m²) were established in the mid-high intertidal zone (1.60–2.00 m above MLW) of Punta Mala West and Manuel Antonio National Park, respectively, in July 1984. Limpets were individually numbered with plastic tags glued to the shells with underwater polyoxy (Pettit Co., Spring

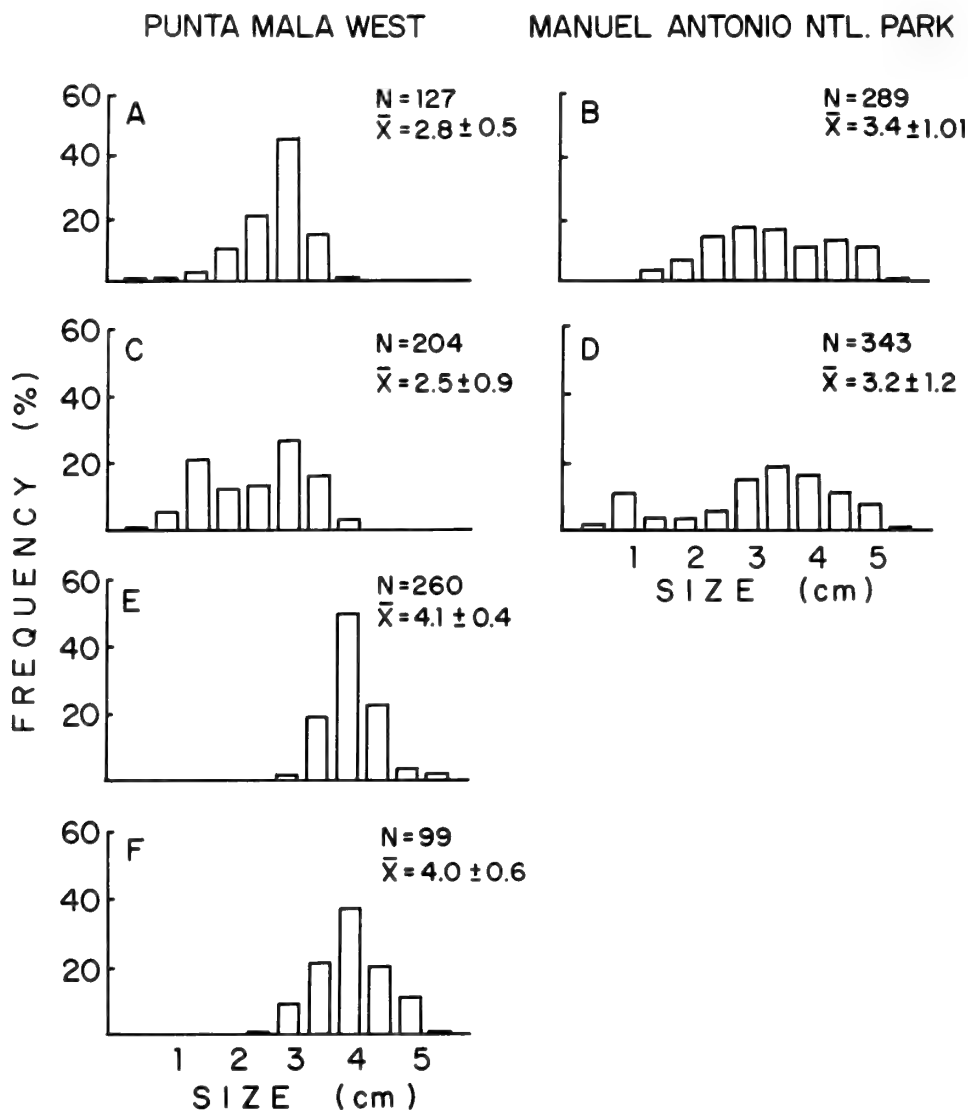


Figure 1

Size-frequency distribution of *Siphonaria gigas* at Punta Mala West (left column) and Manuel Antonio National Park (right column). A-D, resident populations; E, shell collection; F, shell midden. A and B July 1984; C-F November 1984.

Valley, CA). Shell length was measured to the nearest 0.1 mm with dividers (*e.g.*, SUTHERLAND, 1970) in July and November 1984.

To determine whether the difference in mean size of *Siphonaria gigas* between the two sites was due to a difference in growth rate, approximately 50 limpets (<2 cm in shell length) were individually numbered and the shell length measured at each site in November 1984. These limpets were measured again in February 1985. Only individuals labeled at both sampling dates were considered in the statistical analysis.

In November 1984 extremely low spring tides provided

access to some isolated rock outcrops near Punta Mala West. Fishermen were observed collecting *Siphonaria gigas* at that time. On the following day, bits of limpet tissue were still present on some scars previously occupied by limpets. Because the shell margin of the limpet usually fits the rock exactly, the lengths of home scars were assumed to be equivalent to the lengths of limpets that had been collected. Empty scars as well as uncollected individuals were photographed at that time with a Nikonos camera using a 16 × 25-cm focal framer. Thirty six pictures were taken haphazardly for a total of 123 scars and 150 limpets. Lengths of empty scars and limpets were

Table 1

Mean size and length increase \pm standard deviation (size ranges) of marked *Siphonaria gigas* at Punta Mala West (PMW) and Manuel Antonio National Park (MANP). Only numbered individuals (N) at both sampling times were included.

	n	November 1984	February 1985	Increase in length
PMW	33	1.6 \pm 0.1 (1.3-2.0)	2.0 \pm 0.2 (1.6-2.4)	0.4 \pm 0.1 (0.2-0.6)
MANP	6	1.5 \pm 0.2 (1.3-1.9)	1.9 \pm 0.2 (1.6-2.1)	0.4 \pm 0.1 (0.3-0.6)

measured from the photographs by projecting the negatives onto a computerized digitizing pad (Summagraphics bit pad, SUTHERLAND & ORTEGA, 1986).

Finally, shell lengths of *Siphonaria gigas* that had been collected by fishermen in November 1984 from the rock outcrop and from another site near Punta Mala West were measured. Shell lengths of *S. gigas* were measured from shells collected from a midden found near the house of a fisherman.

For simplicity, shell lengths were divided into size classes of 0.5 cm. Due to the heterogeneity of variances between samples, differences in mean size between sites were analyzed with a Kruskal-Wallis test (SOKAL & ROHLF, 1981).

RESULTS

The mean densities (number/m² \pm SD) of *Siphonaria gigas* in the permanent quadrats at Punta Mala West were 56.4 \pm 26.1 and 88.0 \pm 60.0 for July and November 1984. At Manuel Antonio National Park mean densities for the same dates were 116.0 \pm 33.6 and 110.8 \pm 35.2 respectively.

The mean size of *Siphonaria gigas* at Punta Mala West in July 1984 was significantly smaller than at Manuel Antonio National Park (Figures 1A, B; Kruskal-Wallis test, $P < 0.05$, d.f. 1, $H = 36.61$). At Punta Mala West the maximum size of *S. gigas* was 4.1 cm whereas at Manuel Antonio National Park the maximum size was 5.5 cm. In November 1984 the mean size of *S. gigas* was again significantly larger at Manuel Antonio National Park (Figures 1C, D; Kruskal-Wallis test, $P < 0.05$, d.f. 1, $H = 70.62$). Maximum size of *S. gigas* was 4.2 at Punta Mala West and 5.5 at Manuel Antonio National Park. Smaller individuals (<1.5 cm) were more numerous in November than in July at both sites, suggesting that some recruitment had occurred during the period between samples.

Increases in length of juvenile limpets did not differ significantly between the two sites from November 1984 to February 1985 (Table 1; $P > 0.05$, d.f. 1,37, $F = 0.0030$) which suggests that the differences in mean and

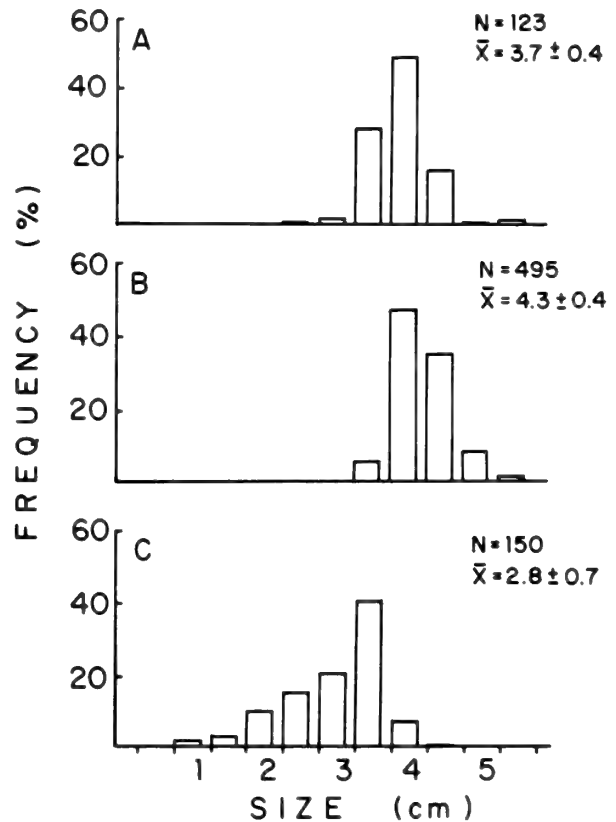


Figure 2

Size-frequency distribution of empty scar lengths (A), shell collection (B) and resident population (C) of *Siphonaria gigas* on an isolated rock at Punta Mala West in November 1984.

maximum sizes of limpets between sites were not due to differences in growth rate.

Measurements of shell collections from Punta Mala West indicated that the size range of limpets collected by fishermen was between 2.7 and 5.6 cm (Figures 1E, F, 2B). Large size classes were mostly absent in the resident population (Figures 1A, C). The size range of empty limpet scars was between 2.4 and 5.5 cm, which approximately coincided with the size range of the limpets collected by people from the same site (3.4 and 5.6; Figures 2A, B). The maximum size of the remaining population was 4.2 cm (Figure 2C) which was clearly smaller than the maximum size of empty scars and the shell collection. The larger size classes that were missing in the resident population were present in the size distribution of the empty scars, shell collections, and shell midden, which indicates a selection for larger limpets by human predators.

DISCUSSION

This paper demonstrates that human predation may play an important role in regulating the size structure of the

population of *Siphonaria gigas* on Punta Mala West. The mean size of *S. gigas* was smaller in the area visited by fishermen than in the National Park where collection was prohibited (Figure 1). Fishermen removed the larger sizes (Figures 1E, F, 2A, B) indicating that man is a size-selective predator (BRANCH, 1975; MORENO *et al.*, 1984, 1986; HOCKEY & BOSMAN, 1986). Selection for larger sizes has also been demonstrated for fish and thaid gastropods preying upon populations of *S. alternata* (COOK, 1980; MENGE, 1973).

Homing behavior in limpets has been shown to be a defense against fish predation (GARRITY & LEVINGS, 1983; FRANK, 1981). In Costa Rica, man, not fish, appears to be the main predator of limpets (ORTEGA, 1986). Neither a large size nor home scar provides a refuge from humans. Other limpets found at Punta Mala West, such as *Siphonaria maura* (Sowerby) and *Fissurella virescens* (Sowerby), are not eaten by man, the former because of its smaller size and the latter because of the widespread belief among local people that its unusual taste may be caused by a toxic substance. Many *Siphonaria* species are unpalatable or even toxic (BRANCH, 1981; BENNETT *et al.*, 1983; HOCKEY, 1983; BRANCH & CHERRY, 1985). BRANCH & CHERRY (1985) demonstrated that *S. capensis* produces a milky mucus when irritated. This limpet is avoided by fish, birds, and seastars that commonly feed on other limpets. BIGALKE (1973) reported that indigenous people on the southern African coast harvest patellid limpets but not siphonariids in spite of their abundance and accessibility. *Siphonaria gigas* is the only *Siphonaria* species in which polypropionates (presumed to be antipredatory chemicals) have not been detected (Faulkner, personal communication). Clearly *S. gigas* has no antipredatory defenses against humans.

Along the Pacific coast of Costa Rica *Siphonaria gigas* reaches larger sizes in areas inaccessible to fishermen than in areas disturbed by them. Intense predation might drive a species to local extinction. This appears to have occurred at Punta Mala West for the coiled gastropod *Nerita scabricosta*. *Siphonaria gigas* has persisted at Punta Mala West because intense recruitment (Ortega, unpublished data) has balanced predation by man.

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Spawning and Hatching of *Cypraecassis testiculus* Linnaeus, 1758 (Tonnacea: Cassidae)

by

ROGER N. HUGHES AND HELEN P. I. HUGHES

School of Animal Biology, University College of North Wales, Bangor, Gwynedd, LL57 2UW, U.K.

Abstract. *Cypraecassis testiculus* spawn in the shallow water of reef flats of Barbados during the spring. Egg capsules are deposited in double, arc-shaped rows on the undersides of stones. Each cylindrical capsule contains some 1500 eggs of about 150 μm in diameter when newly laid. A female produces about 800 capsules and so has a fecundity of about 1.2 million eggs per spawning. The eggs lie as a single layer between the capsular wall and a central jelly matrix. During early development, veligers appear to consume this central "albumen." Prior to emergence, veligers jettison the pair of dark red larval kidneys. Veligers emerge from the capsule after 13-17 days, depending on temperature, and enter a planktrophic phase of unknown duration, but during which the protoconch grows 1-2 additional whorls.

INTRODUCTION

Cypraecassis testiculus, family Cassidae, superfamily Tonnacea, inhabits rocky reef-flats throughout the Caribbean Sea, where it feeds on echinoids (HUGHES & HUGHES, 1981). In common with other cassids, *C. testiculus* deposits egg capsules on hard substrata. The numerous eggs in each capsule develop over a period of about 2.5 weeks into planktonic veligers. Capsular morphology and hatching time have been documented by BANDEL (1976) who did not, however, describe the stages of embryological development. Here we present data on the deposition of egg masses, embryological development, and the embryonic consumption of capsular "albumen." Although the mode of development and nutrition of embryos are known for some cassids (D'ASARO, 1969; FIORONI, 1966), they have been described in detail only for *Galeodea* (=Cassidaria), which is atypical of the family in having relatively few eggs per capsule, embryonic cannibalism, and direct development (FIORONI, 1966; HUGHES, 1986). The genera *Cassis* and *Phalium* (ABBOTT, 1968; D'ASARO, 1969) produce numerous eggs per capsule, similar to *Cypraecassis*, and development is probably always indirect.

MATERIALS AND METHODS

Two mating pairs of *Cypraecassis testiculus* were collected while snorkelling at night off St. Lawrence, Barbados. Extensive searching in this and similar habitats around

the island failed to reveal further specimens although two egg masses were found, suggesting that the captured snails had visited the habitat temporarily to spawn. Non-spawning individuals perhaps live farther seaward in the wave-washed zone where their echinoid prey are most abundant. In one pair, the male was 4.3 cm in shell length and the female 5.9 cm, whereas in the other the male was 5.3 cm and the female 6.5 cm. The specimens were kept in a water table containing a 4-cm layer of sand and 18-cm depth of running seawater at 29°C. Since collection, each female had eaten several urchins (*Diadema antillarum* [Philippi] and *Echinometra lucunter* [Linnaeus]) over a period of four days before spawning. Several egg capsules were scraped off the aquarium wall each day and examined beneath a Wild dissecting microscope.

RESULTS

Spawning was initiated by the larger female between 2400 and 2430 h. She deposited capsules on the concrete wall of the aquarium (Figure 1) and one hour later consumed a *Diadema antillarum* before burrowing into the sand. On the next evening she emerged from the sand at 0200 h, deposited egg capsules until dawn (0500 h), and then burrowed into the sand. Spawning and feeding were entirely nocturnal for both females. Capsules were deposited in curved, double rows of 10-17 capsules per arc (Figure 1), secured to the substratum by a jellylike cement forming a

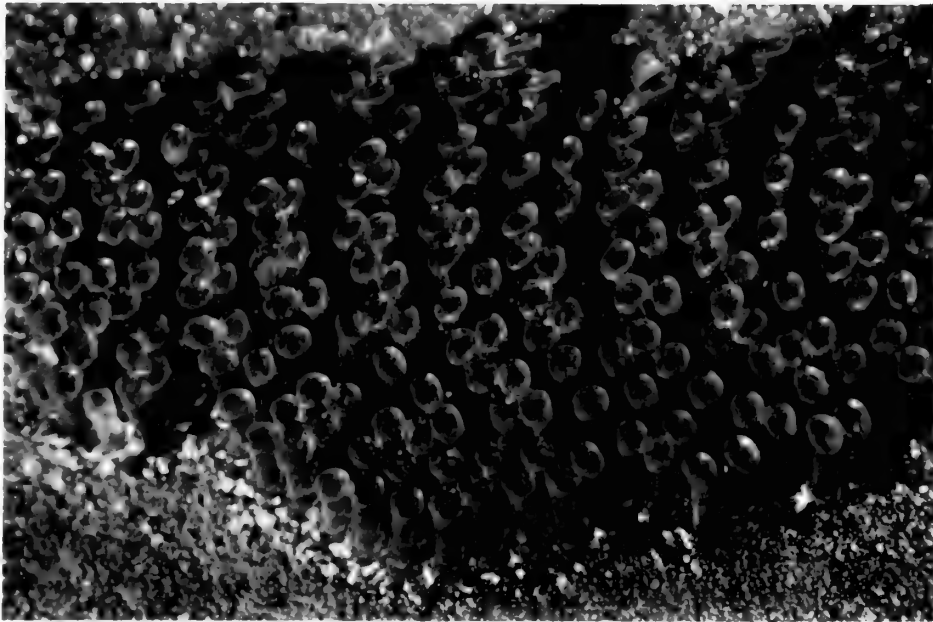


Figure 1

The egg mass of *Cypræacassis testiculus* showing arrangement of the capsules in double arc-shaped rows. Each capsule is about 8 mm tall and 2 mm in diameter. The pigmented eggs impart a deep reddish-purple color to the newly laid egg mass.

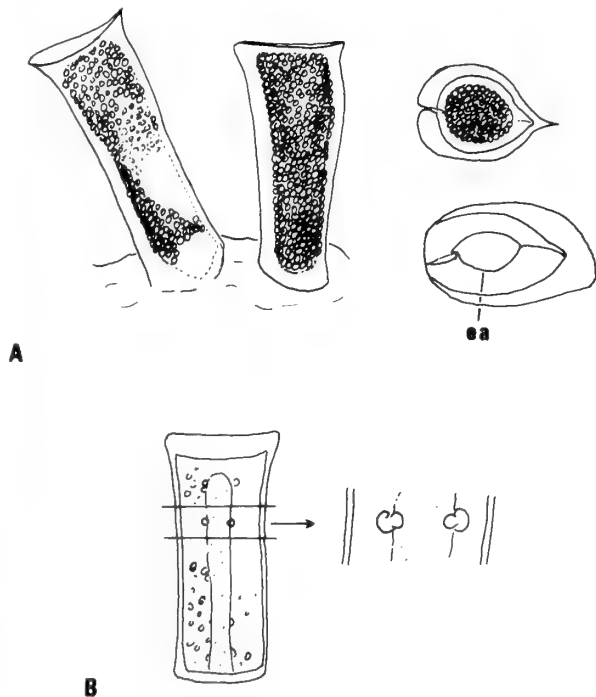


Figure 2

A. The eggs are arranged in a single layer between the capsular wall and a central jelly matrix. The capsular wall is about 900 μm thick. The apical plate of the capsule is elliptical and drawn

common basal sheet for the egg mass. Each capsule was cylindrical with a slightly flared distal rim surrounding the apical plate containing the aperture through which the larvae eventually escaped (Figure 2A). One side of the rim was drawn into a lateral keel, and faint ridges ran along the length of the capsular wall. The eggs formed a single layer, apparently held against the capsular wall by a clear gel (albumen) that filled the lumen.

Development to hatching (Figure 3) took 13-14 days. The deep reddish-purple eggs developed into similarly colored embryos that on the fifth day began to revolve slowly within the spherical egg membrane. By the seventh day, the embryos became more irregular in shape and the egg membrane developed protrusions. By the eighth day, the larvae began to develop the protoconch and the reddish-purple pigmentation became concentrated into two bilateral and one posterior patch. Beating of velar cilia became evident at this stage. By the tenth day, veliger larvae emerged from the egg membranes and were moving freely about the narrow space between the capsular wall and the inner jelly matrix. Macroscopically, the larvae had changed from the initial deep reddish-purple color to

←
out into a lateral keel (right hand figures) and is about 2.9 mm in longest diameter. ea, escapement aperture. B. Veligers tend to grasp the central jelly matrix with their velar lobes, as if feeding on it.

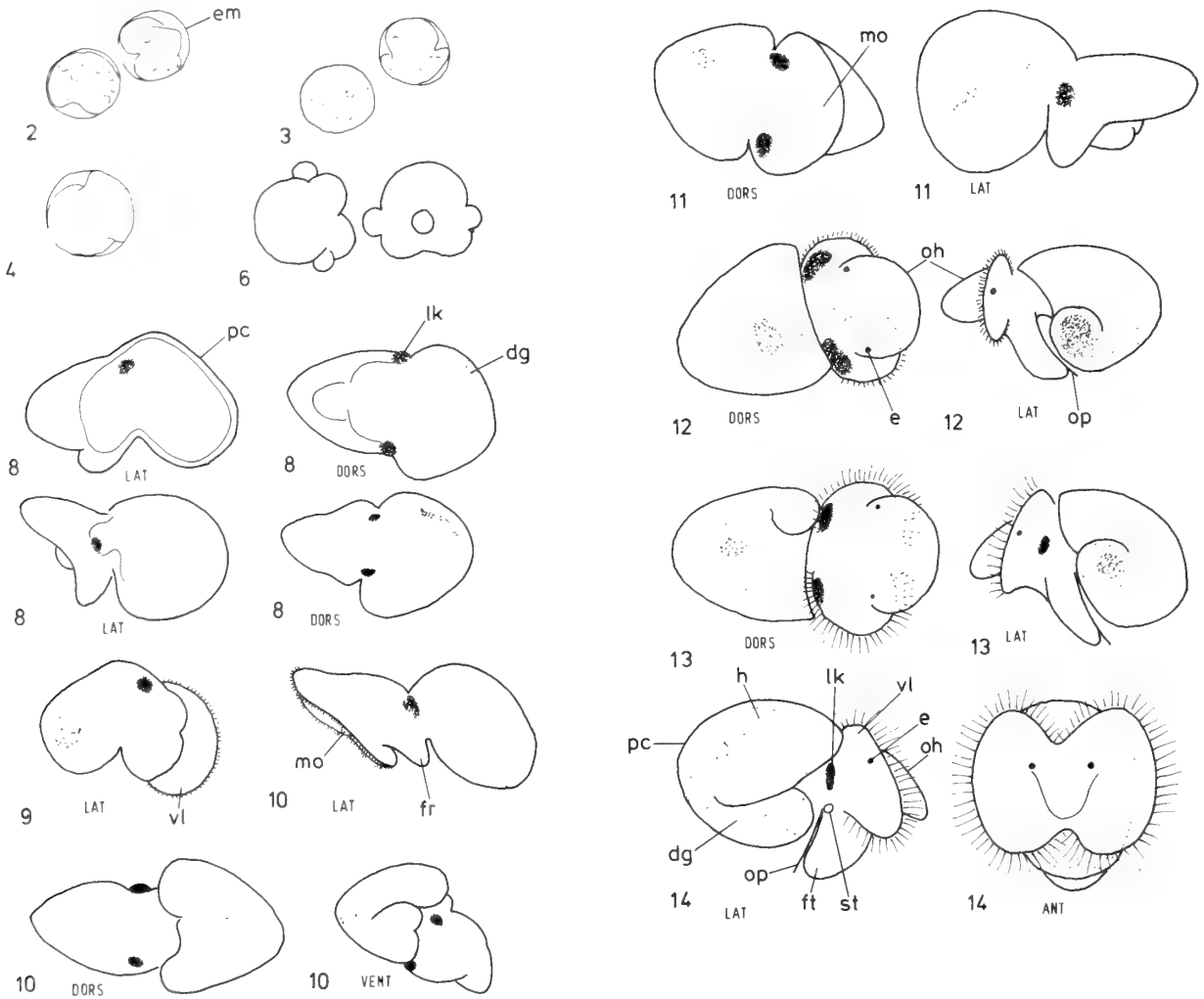


Figure 3

Stages (not all drawn to same scale) in the embryological development of *Cypraecassis testiculus*. Numbers refer to days since oviposition. Approximate sizes of embryos along their major axes are: day 4 = 200 μm , day 9 = 340 μm , day 11 = 400 μm , day 13 = 400 μm . Key: dg, digestive gland; e, eye; em, egg membrane; fr, foot rudiment; ft, foot; h, heart; lk, larval kidney; mo, mouth; oh, oral hood; pc, protoconch; st, statocyst; vl, velar lobe.

a creamy pinkish-brown. By the eleventh day, the protoconch and velum were more fully developed, and some veligers began to grasp the jelly matrix with their velar lobes and appeared to be feeding on it (Figure 2B). This "albumen" matrix shrank considerably during days 10–11, leaving a much wider space between itself and the capsular wall. By the twelfth day, black eye spots and the operculum were visible and the ciliary rim of the velar lobes had become reddish-pink. In many larvae the lateral reddish-brown pigment aggregations had become pinched off into external lobes (larval kidneys) and in some cases these had become detached from the body. By the thirteenth day, many detached pigment aggregations were ad-

hering to the jelly matrix. The colorless heart, the tan-brown visceral mass, and the pair of statocysts in the foot were well developed, and some larvae began to escape from the egg capsules. Most larvae emerged from the capsules within the next 2 days.

DISCUSSION

The deposition of egg capsules in double, arc-shaped rows occurs also in other tonnaceans, notably *Tonna* sp. (KNUDSON, 1950; OSTERGAARD, 1950). The general structure of the capsules is similar to that found in other cassids (ABBOTT, 1968; D'ASARO, 1969; HUGHES, 1986) and the arrangement of eggs in a single peripheral layer facilitates

Table 1

Reproductive data for two *Cypraeacassis testiculus*.

	Date and number of capsules deposited				Total
	4/15/ 80	4/16/ 80	4/17/ 80	4/18/ 80	
A Spawning schedules					
Large female (6.8 cm)	11	300	400	100	811
Smaller female (5.9 cm)		200	350	250	800
B Measurement of eggs and larvae					
Mean number of eggs per capsule	= 1529, SE = 26, n = 6				
Mean number of eggs per female	= 1.23×10^6 , n = 2				
Mean diameter of eggs at day 1	= 149 μ m, SE = 3, n = 28				
Mean height of protoconch at hatching	= 0.2 mm, SE = 0.01, n = 25				
Number of whorls at hatching	= 1.5				
Mean height of protoconch at apex of adult shell (i.e., at settlement)	= 2.5 mm, SE = 0.2, n = 15				
Number of whorls at settlement	= 3 to 4				

gaseous exchange, as it does in other prosobranchs producing egg capsules (STRATHMANN & CHAFFEE, 1984).

Jettison of the pigmented larval kidneys prior to emergence from the capsule may be a means of disposing of waste products. It has also been recorded in *Crepidula fornicata* (Linnaeus, 1758) (CONKLIN, 1897) but its significance and generality remain to be verified (Rivest, personal communication). Although the larval kidneys excrete granules in *Thais haemastoma floridana* (CONRAD, 1837), they are themselves absorbed by the veligers prior to hatching (D'ASARO, 1966). Other aspects of embryological development in *Cypraeacassis testiculus* are typical of related prosobranchs. Cannibalism among sibling veligers was not observed and, since the eggs are not heavily endowed with yolk, planktotrophic development appears likely. Indeed, planktotrophy would be essential to sustain migrants during their transatlantic journey to western Africa (SCHELTEMA, 1978), where a race of *C. testiculus* is also found (ABBOTT, 1968). A prolonged planktonic phase is indicated by the ten-fold increase in height of the protoconch between hatching and initial growth of the teloconch at settlement (Table 1). Larvae of *Cypraeacassis testiculus* probably share the planktotrophic habit with *Cassid* spp. (D'ASARO, 1969) but not with the cassid *Galeodea echinophora* (Linnaeus, 1758) in which abortive embryos

are cannibalized, allowing development to proceed to the crawling stage prior to emergence from the capsule (HUGHES, 1986). Planktotrophic development in *C. testiculus* is commensurate with a high fecundity, about 1.2 million eggs per female per spawning (Table 1) compared with a fecundity of about 2000 eggs per female per spawning in *G. echinophora*. Whether spawning occurs more than once a year remains unknown.

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Gametogenesis and Spawning in a Population of *Macoma balthica* (Pelecypoda: Tellinidae) from Long Island Sound

by

DIANE J. BROUSSEAU

Department of Biology, Fairfield University, Fairfield, Connecticut 06430, U.S.A.

Abstract. A population of *Macoma balthica* in Long Island Sound, Stonington, Connecticut was studied for 24 months during a 4-yr period to determine the sequence of gametogenic development of gonadal tissue and the frequency and duration of the spawning cycle under natural conditions. This population was observed to spawn annually in March–April. Sexes were distinguishable in all size classes studied, except those individuals in an “inactive” condition. A low incidence of simultaneous hermaphroditism suggests that *M. balthica* is a stable gonochoric species. There was no evidence of protandry. Females predominated in the population in the ratio of 9:11. Photomicrographs of the gametogenic cycle of both male and female clams are included.

INTRODUCTION

THE CIRCUMARCTIC BIVALVE *Macoma balthica* (Linnaeus, 1758) is widely distributed, common to littoral and shallow sublittoral habitats in boreal and temperate waters of both Europe and North America. Most studies of *M. balthica* reproduction have been done on European (CADDY, 1967; LAMMENS, 1967; VON OERTZEN, 1972) and Canadian (SULLIVAN, 1948; LAVOIE, 1970) populations. Other studies of North American populations were carried out in Buzzards Bay (GILBERT, 1978), Chesapeake Bay (SHAW, 1965), and San Francisco Bay (NICHOLS & THOMPSON, 1982).

Macoma balthica is dioecious; the sexes can be conclusively distinguished only after examination of the gonads. *Macoma balthica* apparently has a single annual spawning season in all populations studied except in the Chesapeake Bay population, where a biannual cycle of larval settlement was reported (SHAW, 1965).

In an attempt to define more clearly the latitudinal patterns of reproduction in this species, a population of *Macoma balthica* from Stonington, Connecticut, was studied to determine (1) the age of maturation and occurrence of gametogenic development and (2) the frequency of spawning. This paper presents the results of that 4-yr study of the breeding habits of this species in Long Island Sound.

MATERIALS AND METHODS

Specimens of *Macoma balthica* were collected from an intertidal sandflat located at Barn Island in Stonington, Connecticut (41°20'N, 71°53'W). Monthly collections were made from April to August 1982, November to April 1982–1983, June to March 1983–1984, and February to April 1985. Sample sizes varied from 12 to 112 clams, which were 10.1 to 27.3 mm in shell length. A total of 740 clams were examined and used in the analysis of the reproductive cycle.

The clams were counted and individual maximum lengths (± 0.1 mm) were measured. The visceral mass was removed and fixed in 10% buffered formalin. The tissues were then prepared for histological examination (BROUSSEAU, 1978). A microscopic examination was made to assign each individual to the appropriate category of gonadal condition. There was evidence of seasonal changes in gonadal color as reported by LAMMENS (1967) and CADDY (1967). When ripe, ovaries appear gray to gray-orange in color and the testes are white. Mean oocyte diameter was estimated for a sample of 20 females reported in a “ripe” gonadal condition.

The reproductive condition of the clams was measured by stereology, a procedure adapted by BAYNE *et al.* (1978), NEWELL *et al.* (1982), and BROUSSEAU (1983) for mussels. This method is based on a procedure referred to as point-

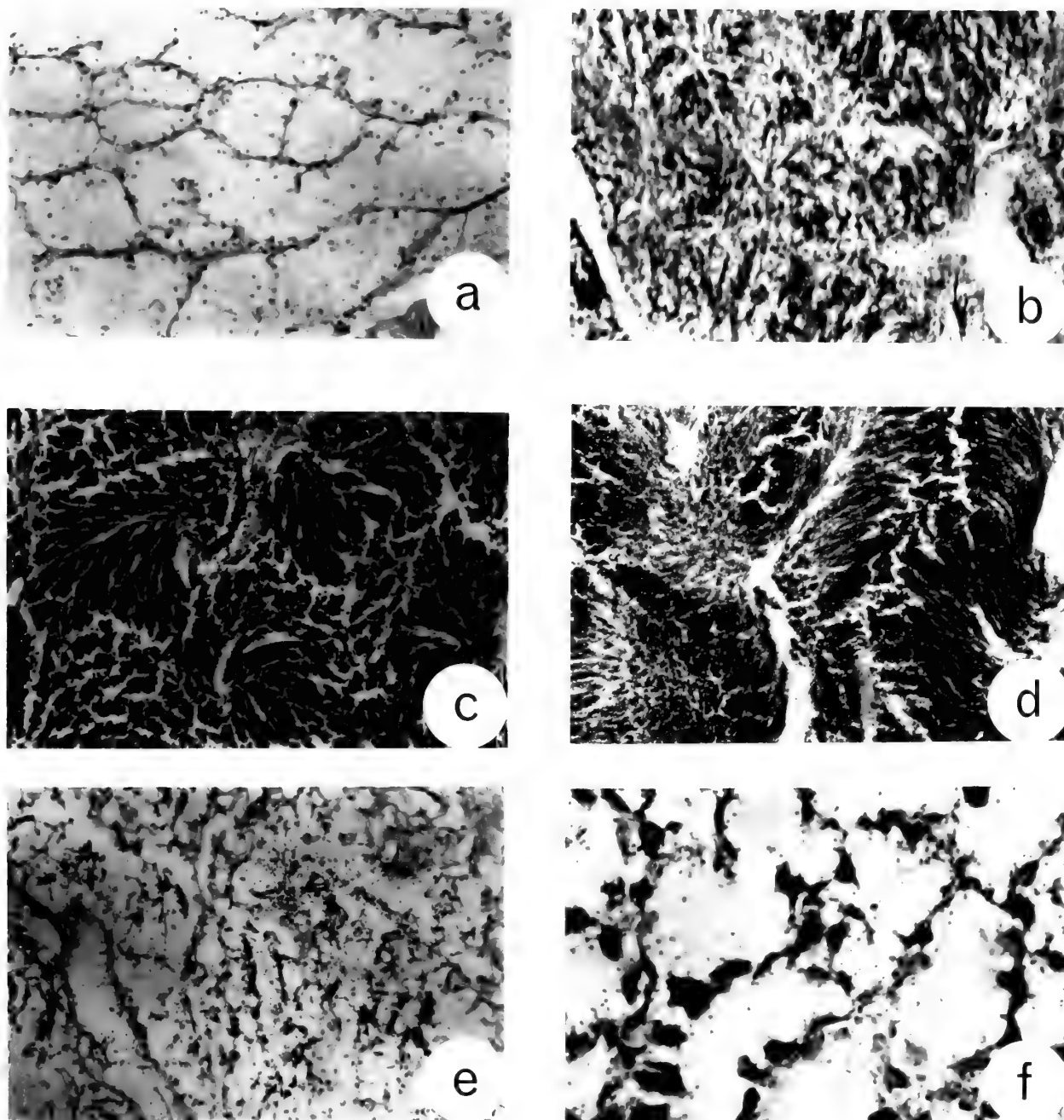


Figure 1

Photomicrographs of gonadal stages of male and female *Macoma balthica* at 125 \times magnification. a, indifferent male or female, 27 May 1982. b, developing male, 6 November 1983. c, ripe male, 26 April 1982. d, spawning male, 15 April 1983. e, spent male, 26 April 1982. f, developing female, 4 December 1983.

counting volumetry, which is accomplished by superimposing a regular point lattice on the tissue section and counting the points that lie on transections of the sex cells (WEIBEL *et al.*, 1966). The proportion of gonadal tissue consisting of follicles containing developing or ripe ga-

metes is reported as the "gamete volume fraction" (GVF). For any individual clam, the GVF can vary between zero, for a reproductively inactive clam, and one, for a clam showing maximal reproductive development. The monthly mean GVF represents the mean of 10 estimates of the

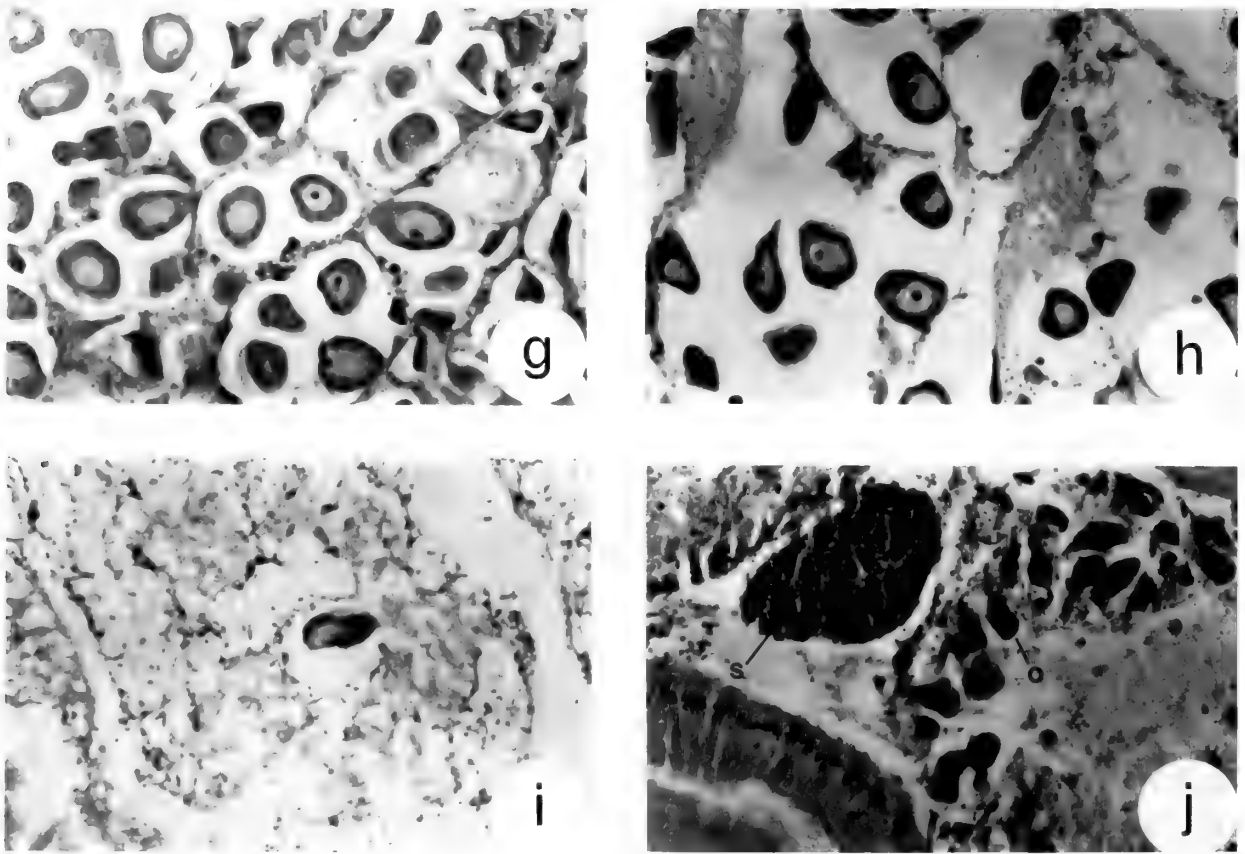


Figure 1 (continued)

g, ripe female, 15 April 1983. h, spawning female, 26 April 1982. i, spent female, 27 May 1982. j, hermaphrodite, 15 February 1984.

GVF from each clam sampled. The number of clams included in the estimate varied from 9 to 109. These proportions were then arcsine transformed and the variance for each monthly GVF was calculated.

RESULTS

Categories of Gonad Condition

The following descriptions of the male and female developmental stages represent and attempt to divide the reproductive process (either spermatogenesis or oogenesis) into distinct phases. The criteria used are based solely on morphological observations. Categories comparable to those already in use for other species (ROPEs & STICKNEY, 1965; BROUSSEAU, 1978, for *Mya arenaria*; PORTER, 1964; KECK *et al.*, 1975, for *Mercenaria mercenaria*; BROUSSEAU, 1981, for *Petricola pholadiformis*; BROUSSEAU, 1982, for *Geukensia demissa*) have also been used in the study where appropriate.

Developmental Stages of the Male

Indifferent stage: The interfollicular space dominates and consists almost entirely of large vacuolated nutritive cells with a few spermatogonia scattered along the periphery or near the central axis. There were no pycnotic cells nor multinucleated non-pycnotic cysts apparent in the follicles (Figure 1a).

Developing stage: The spermatogenic cells begin to proliferate around the follicle walls and between the follicular cells within the developing follicle. Maturation of spermatozoa is most rapid in the center of the follicle. Gradually the follicle breaks down and spermatozoa developing in the middle of the follicle are joined by those arising from the periphery (Figure 1b).

Ripe stage: The mass of mature spermatozoa increases in volume and the individual cells arrange themselves in bands, with tails pointing toward the center of the lumen (Figure 1c).

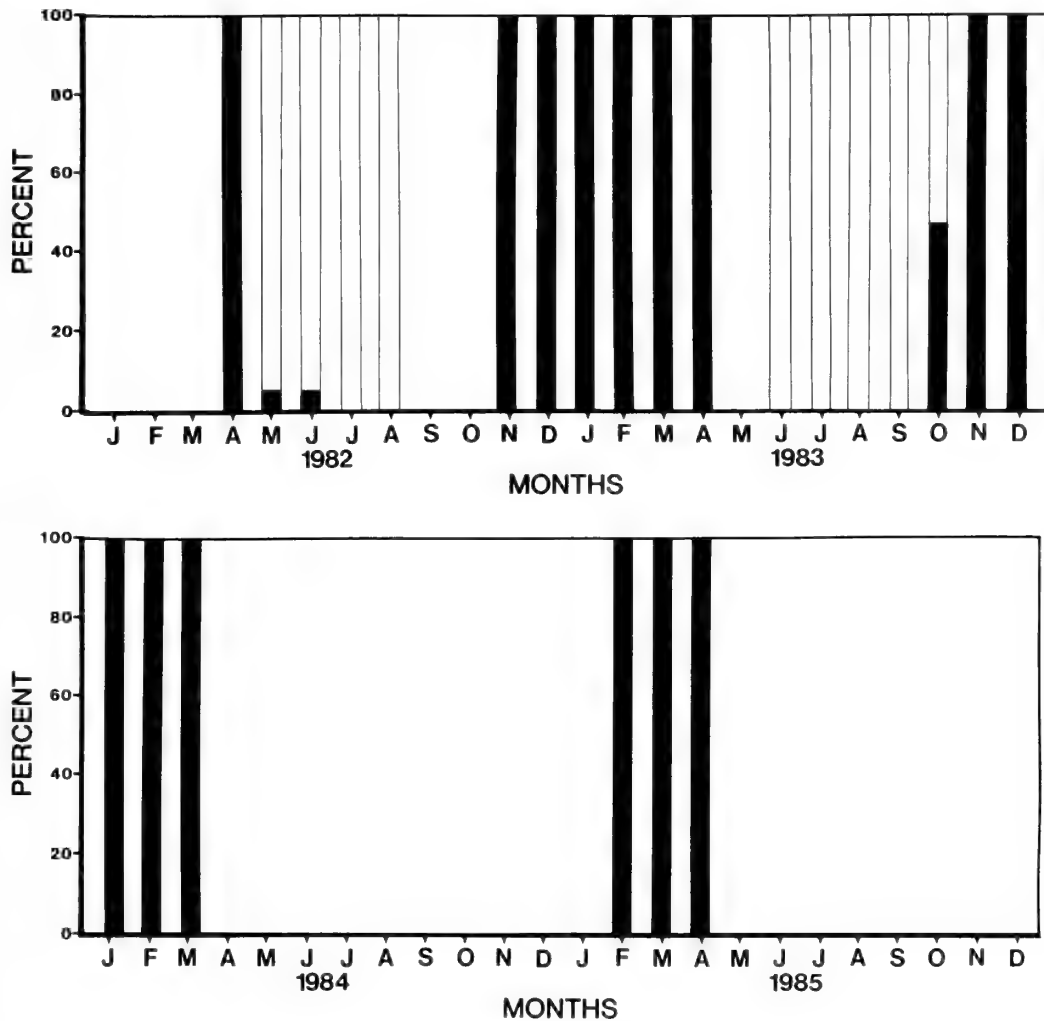


Figure 2

Percentage of *Macoma balthica* population with active or inactive gonads during 1982–1985. Open portions of each represent inactive gonads (indifferent or spent); solid portions represent active gonads (developing, ripe gametes or partially spawned). Observations on both males and females are combined.

Partially spawned stage: A marked decrease occurs in the number of spermatozoa filling the lumen with most follicles emptying or empty (Figure 1d).

Spent stage: In totally spawned males a few residual sperm are visible but the majority of follicles are empty. Spermatozoocytes are rare (Figure 1e).

Developmental Stages of the Female

Indifferent stage: The interfollicular space dominates and consists almost entirely of large vacuolated cells. The follicles are empty except for occasional residual free oocytes (Figure 1a).

Developing stage: Oocytes become more noticeable along the follicle walls, increasing in size and number. The developmental phase is a continuous process, involving a proliferation and maturation of the oocytes, with an accompanying reduction in interfollicular connective tissue. The developing oocytes, which begin as hemispherical or cylindrical cells attached to the wall of the follicle, become enlarged spherical cells 30 to 40 μm in diameter as maturity approaches (Figure 1f).

Ripe stage: Ripe females are characterized by large, round oocytes, 65 to 70 μm in diameter, some of which are attached to the follicular wall by slender stalks. Others are free oocytes in the lumen of the follicle. A prominent ec-

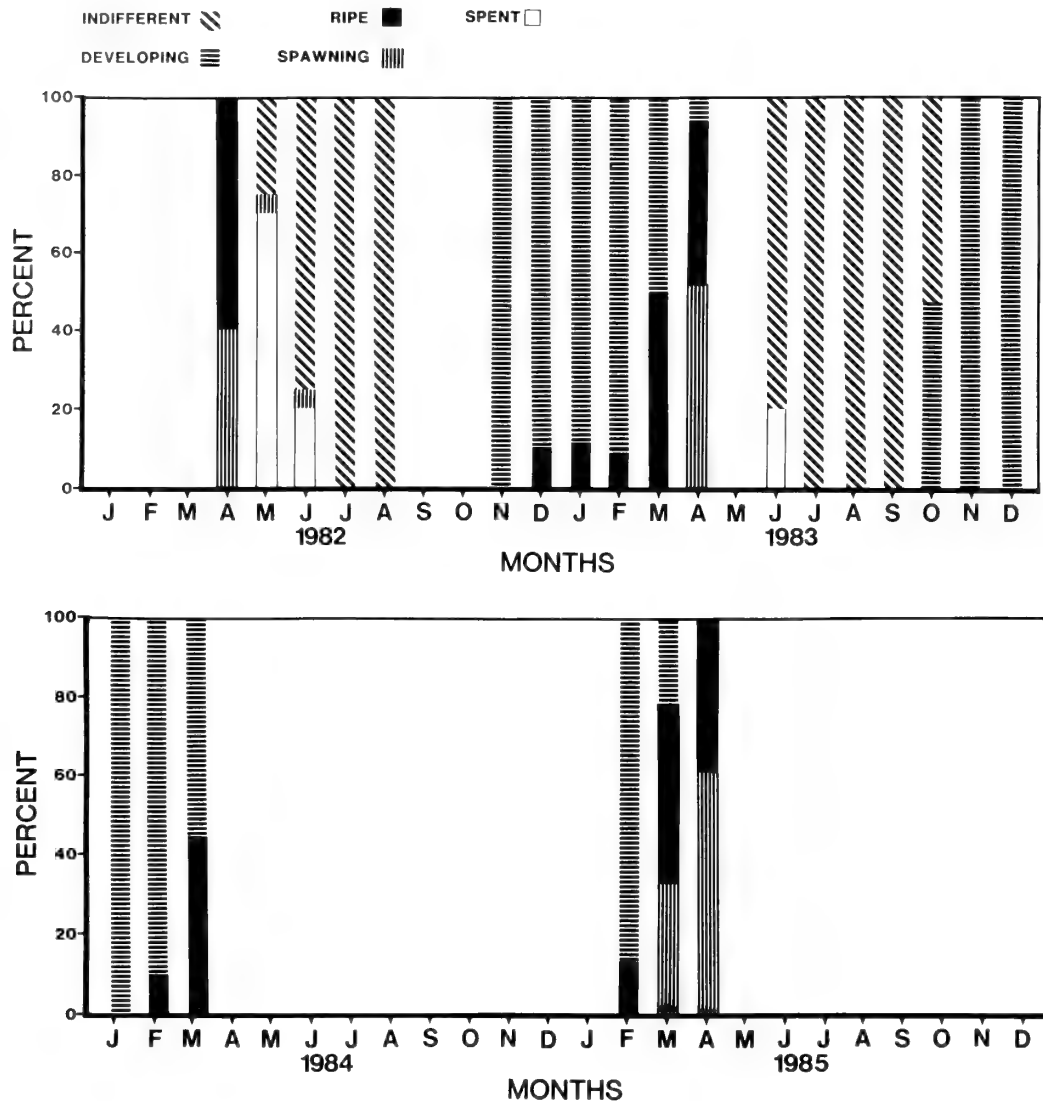


Figure 3

Percentages of *Macoma balthica* with gonads in each developmental phase during 1982-1985. Values for males and females are combined.

centrically placed nucleolus is visible within the nucleus (Figure 1g).

The number of ripe oocytes decreases in the lumen, and some follicles completely lack gametes (Figure 1h).

Spent stage: Clams that have recently undergone oogenesis can be recognized by the presence of a few unspawned oocytes in the lumen. These may be in various degrees of cytolysis. Resumption of oogenic activity may be evident in some individuals (Figure 1i).

Reproductive Cycle

Reproductively active individuals (developing, ripe, and spawning) were encountered throughout the 4-yr study

period, except in June through September. The largest numbers of active individuals occurred in November through April (Figure 2). Gametogenesis began in October each year in both sexes, but fully ripe individuals did not appear until December in 1982 and February in 1984 and 1985 (Figure 3). Spawning individuals were first observed in April of 1982 and 1983 and in March of 1985. Discharge of eggs was completed by early summer. By mid-May over 90% of the clams had completely spawned or had returned to the indifferent condition.

The GVF values for male and female *Macoma balthica* from this population are shown in Figure 4. The pattern of GVF values and the maximum GVF attained were similar during each year of the study. The post-spawning

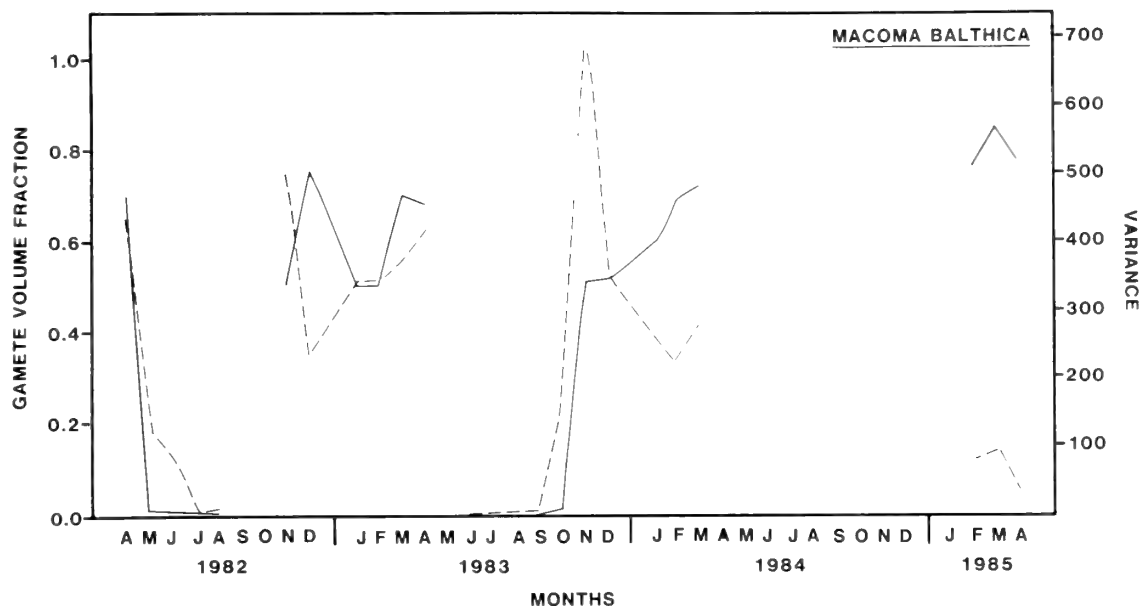


Figure 4

Mean gamete volume fractions (solid line) and variance (dotted line) for *Macoma balthica*. Values for males and females are combined.

minimum GVF values occurred in June through September. Increasing GVF values in November were due to the onset of gametogenesis. Peak GVF values of 0.85 were observed in March 1985.

Variance in GVF during each sampling period provides a measure of the intrapopulation synchrony of the reproductive cycle. The larger the variance, the greater the variability in the gametogenic condition of individuals during that sampling period. In general, the clams were least closely synchronized (*i.e.*, had the highest variance) during the fall and winter months, indicating that the clams were ripening at different rates. This increased

variance continued through the spawning period, suggesting that spawning occurred at different times during a 2-month period.

In the Stonington population, the proportion of females in all size classes ($n = 589$) differed significantly from one-half (Table 1). Male and female gonads were distinguishable in all size classes studied (> 11.0 mm). Although no protandry was observed, there was evidence of simultaneous hermaphroditism in two individuals (Figure 1j). Hermaphrodites were collected in February and March and appeared to be undergoing normal gametogenic development.

DISCUSSION

At Barn Island, the population of *Macoma balthica* shows a single annual spawning period which occurs during the spring. This pattern coincides with those reported for *M. balthica* throughout most of its geographic range (see GILBERT, 1978 for a review). Of the three studies in which multiple spawnings were reported, however, only that by SHAW (1965) points to the occurrence of more than one major gametogenic cycle during the year. The work by BATTLE (1932) and CADDY (1967) suggests that one or more pulses of gamete release may occur during spawning in this species.

As a rule, North Atlantic species of bivalves spawn during the warmer months of the year (SASTRY, 1979) and ripening of gametes begins in the spring. One unusual feature of the reproductive cycle of *Macoma balthica* is that gonadal development occurs only during the winter months.

Table 1

Proportion of females in each size class studied in the population of *Macoma balthica* from Stonington, Connecticut. The number of individuals per sample is given in parentheses. Year classes were determined using external growth annuli (Brousseau, unpublished). * $P < 0.05$.

Size class (mm)	Year class	Proportion females	Confidence limits (95%)
11.0-14.9	2	0.533 (15)	0.266-0.787
15.0-17.9	3	0.510 (96)	0.406-0.613
18.0-19.9	4	0.625 (152)	0.539-0.696*
20.0-21.9	5	0.534 (161)	0.451-0.608
22.0-22.9	6	0.515 (68)	0.388-0.631
23.0	6	0.536 (97)	0.426-0.632
Total		0.552 (589)	0.509-0.590*

This is probably due in part to the feeding behavior of *M. balthica*. Unlike most other species of bivalves, which feed on plankton, *M. balthica* is primarily a deposit feeder. Hence, its food source is available throughout the year.

Macoma balthica is dioecious; the sexes are distinguishable either by examining the sex products, or from inspection of gravid individuals. Ovaries are orange when gravid, whereas testes are cream colored. Although few species of bivalves can be sexed in this manner, there are some exceptions, the most notable being the blue mussel *Mytilus edulis* (CAMPBELL, 1969). The low incidence of hermaphroditism exhibited by *Macoma balthica* suggests stable gonochorism, a condition characterized by the presence of some hermaphrodites in a normally gonochoristic species.

Information on sex ratios in this species shows little agreement among populations. The proportion of females in the population studied here is slightly greater than one-half (Table 1). In a population in the Thames River, England, males predominated in a ratio of 9:7 (CADDY, 1967). Caddy attributed this to a preponderance of 2-yr old males undergoing protandric development (a primary male phase). On the other hand, a population in Falmouth, Massachusetts (GILBERT, 1978) was reported to have a 50:50 sex ratio. The large differences in sex ratios among populations of *M. balthica* suggest either that patterns of sexual differentiation vary from population to population or that more information is needed before generalizations can be made.

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Observations on the Opisthobranch Mollusks of Punta Gorda, California, with Notes on the Distribution and Biology of *Crimora coneja*

by

JEFFREY H. R. GODDARD

Oregon Institute of Marine Biology, University of Oregon, Charleston, Oregon 97420, U.S.A.

Abstract. Thirty-eight species of opisthobranchs were observed intertidally at Punta Gorda on the southern coast of Humboldt County, California. *Acanthodoris hudsoni*, *A. lutea*, *Cuthona fulgens*, *Diaphana californica*, and *Eubranchus olivaceus* are new county records, and the range of *Acanthodoris lutea* is extended northward. *Crimora coneja*, absent from the study area in June 1983, was the most abundant opisthobranch one year later. Compared to their abundance on other parts of the California and Oregon coast, sponges and their nudibranch predators were uncommon. High levels of sediments in the near-shore waters of the King Range area may be limiting the abundance of sponges and, thus, eudoridacean nudibranchs.

Crimora coneja is usually found on the undersides of boulders, where it preys on at least one species of encrusting bryozoan. Although known from San Diego and Humboldt counties, and known to produce planktotrophic larvae, this conspicuous dorid nudibranch has not been found, despite extensive observations, in the rest of California. This absence may be real, possibly reflecting a lack of suitable prey, but is more likely an artifact of observations biased toward open, intertidal habitats. *Crimora coneja* and *Laila cockerelli* possess a number of ecological and morphological similarities and may (along with *Triopha catalinae*) form a mimicry complex.

INTRODUCTION

THE OPISTHOBRANCH FAUNA of Humboldt County, California, has recently been extensively described by JAECKLE (1984). He reported 68 species, presenting notes on the biology of many. However, of the 23 collection sites listed by Jaeckle, only 4, yielding 10 species, were located on the southern half of the Humboldt County coast. This is the Cape Mendocino-King Range area, one of the most rugged and isolated parts of the California coast. This paper reports on intertidal observations, made in June 1983, May 1984, and May 1985, of the opisthobranch fauna of Punta Gorda, a major promontory on the King Range coast.

Crimora coneja is a striking but rarely observed dorid nudibranch with a perplexingly disjunct geographical distribution—only one specimen has been reported previously between Cape Arago, Oregon, and San Diego, California (GODDARD, 1984:148, 157). Large numbers of *Crimora coneja* were observed, apparently for the first time, during the present study. If anything, these observations

only further obscure the explanation of why this species has not been found along more of the California coast. A review of what is known about the distribution and biology of *Crimora coneja* is presented at the end of this paper, along with some hypotheses concerning its distribution, in the hope of stimulating further observation and research on this little known but intriguing species.

STUDY AREA

The King Range coast is characterized by mountainous terrain, deep nearshore waters (four submarine canyons virtually touch the shore), narrow, steep beaches punctuated by rock stacks and small rock shelves, and extreme exposure to ocean swells. Northwest winds during the spring and summer produce some of the strongest upwelling on the Pacific coast of North America and keep sea-surface temperatures relatively low (BAKUN *et al.*, 1974). The steep slopes and sedimentary origins of the King Range, combined with moderate seismic activity, high rainfall, and loss of vegetation to grazing by domestic an-

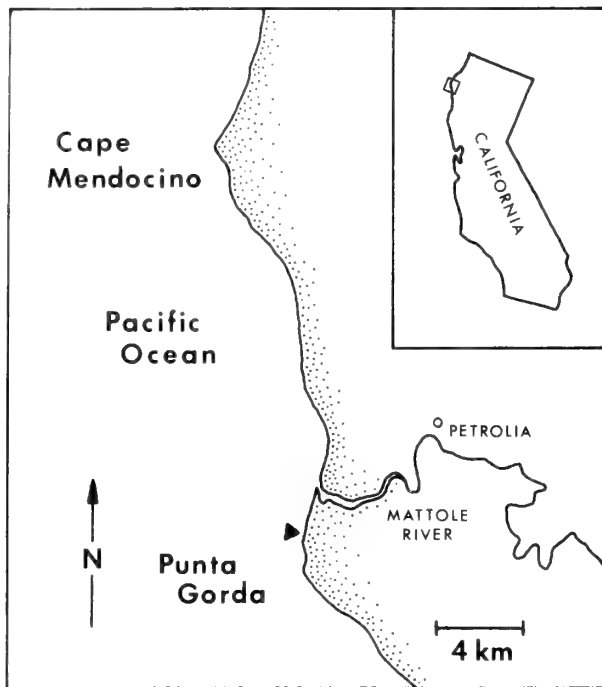


Figure 1

Map of Punta Gorda (40°15'40"N, 124°21'47"W) and Cape Mendocino, California, showing location of study site (black triangle).

imals and logging, result in an unusually high transport of sediments into the coastal waters (JONES & STOKES ASSOCIATES, INC., 1981; personal observations). This transport, combined with the suspension of the finer sediments by high surf and upwelling, results in turbid near-shore waters. A thin layer of sediment often covers everything in tidepools undisturbed by surge at low tide. As will be discussed later, the turbidity of the nearshore waters may be affecting the abundance of sponges and, thus, eudoridacean nudibranchs.

The study area consists of three relatively small rock shelves located 1–2 km south of the Mattole River estuary and 1–2 km north of the tip of Punta Gorda (Figure 1). This is site 22 on JAECKLE's (1984) map. The area is accessible via Lighthouse Road, an unpaved road ending at the beach on the south side of the Mattole River estuary.

Composed of dense sandstone, the shelves constituting the study area are riddled with surge channels and deep tidepools and are separated from one another by short, steep beaches. The shelves are fully exposed to ocean swells, and during periods of high surf the low intertidal zone is inaccessible, even during the lowest tides. The frequent high winds and turbid waters can significantly impair one's view into the tidepools here. Turnable boulders are present in some of the tidepools and surge channels.

The organisms on the rock shelves are generally typical for open-coast rocky shores of the north Pacific as described by RICKETTS *et al.* (1985) and KOZLOFF (1983). However, sponges are relatively uncommon, and, with the exceptions of *Eurystomella bilabiata* (Hincks, 1884) and *Hincksina minuscula* (Hincks, 1882), encrusting cheilostome bryozoans appear to be uncommon.

RESULTS

Thirty-eight species of opisthobranchs were found during the present study (Table 1). Twenty-nine of these are new records for the King Range area, and *Acanthodoris hudsoni*, *A. lutea*, *Cuthona fulgens*, *Diaphana californica*, and *Eubranchius olivaceus* are new records for Humboldt County. The only previous record of *Crimora coneja* in Humboldt County is McDONALD's (1983:163) vague report of one specimen "identified from a photograph, collected near Humboldt Bay, Humboldt County." The present observations confirm the presence of *Crimora coneja* in the county. *Aplysiopsis smithi* was observed in September 1976 and August 1979 feeding on *Cladophora* sp. in high intertidal pools at the tip of Punta Gorda (personal observations). *Doriopsilla albopunctata* (Cooper, 1863) is the only species reported from the King Range by JAECKLE (1984) not found in the present study.

Notes on the biology of a few species (arranged alphabetically) follow.

Acanthodoris hudsoni

Eight specimens, 4–30 mm long, were found in May 1984. One of these was crawling upside down on the surface film of a calm tidepool. Specimens observed in 1985 were not measured. Two individuals were collected in June 1983 and brought back to the laboratory to obtain egg masses for observations of larval development. HURST (1967) described the white egg masses, gave egg capsule dimensions, and reported one egg per capsule and a 16-day embryonic period at 8–11°C. She did not state the egg or veliger sizes and mentioned (pp. 276–277) that the veligers she observed may have had abnormally shaped shells. I observed veliger development in two egg masses. In one, the mean uncleaved egg diameter was 66.8 μm (SD = 1.8 μm , n = 10); after an 11-day embryonic period at 14–16°C, the veligers hatched possessing clear type-1 shells with a mean length of 127.0 μm (SD = 3.3 μm , n = 10). Eggs from the second egg mass had a mean diameter of 66.4 μm (SD = 1.9 μm , n = 10) and developed into hatching veligers with a mean shell length of 126.7 μm (SD = 3.1 μm , n = 10) in 9 days at 14–16°C. Veligers from both egg masses lacked eyespots and propodium, and were clearly planktotrophic. Their shells were normal in appearance.

Acanthodoris lutea

Two individuals, 20 and 24 mm long, were observed in May 1985 mating near three *Acanthodoris lutea* egg masses

Table 1
Opisthobranchs observed at Punta Gorda, 1983–1985.

Species	Number found		
	1983*	1984	1985
<i>Acanthodoris hudsoni</i> MacFarland, 1905	x	8	14
<i>Acanthodoris lutea</i> MacFarland, 1925			2
<i>Acanthodoris nanaimoensis</i> O'Donoghue, 1921			2
<i>Aeolidia papillosa</i> (Linnaeus, 1761)		4	1
<i>Ancula pacifica</i> MacFarland, 1905	3		
<i>Anisodoris nobilis</i> (MacFarland, 1905)			2
<i>Aplysiopsis smithi</i> (Marcus, 1961)†			
<i>Archidoris montereyensis</i> (Cooper, 1863)	1		
<i>Cadlina modesta</i> MacFarland, 1966	1		
<i>Catriona columbiana</i> (O'Donoghue, 1922)			2
<i>Crimora coneja</i> Marcus, 1961	0	66	2
<i>Cuthona abronia</i> (MacFarland, 1966)	x		
<i>Cuthona albocrusta</i> (MacFarland, 1966)	x	11	4
<i>Cuthona divae</i> (Marcus, 1961)	x	6	2
<i>Cuthona flavovulva</i> (MacFarland, 1966)	x		1
<i>Cuthona fulgens</i> (MacFarland, 1966)	x		
<i>Cuthona lagunae</i> (O'Donoghue, 1926)	2	2	
<i>Dendronotus frondosus</i> (Ascanius, 1774)	x	1	4
<i>Dendronotus subramosus</i> MacFarland, 1966		2	2
<i>Diaphana californica</i> Dall, 1919		1	
<i>Dialula sandiegensis</i> (Cooper, 1863)		1	2
<i>Dirona albolineata</i> Cockerell & Eliot, 1905			2
<i>Dirona picta</i> MacFarland in Cockerell & Eliot, 1905		2	1
<i>Discodoris heathi</i> MacFarland, 1905			1
<i>Doto amyra</i> Marcus, 1961	x	7	2
<i>Doto kya</i> Marcus, 1961	x		5
<i>Eubranchius olivaceus</i> (O'Donoghue, 1922)			1
<i>Eubranchius rustyus</i> (Marcus, 1961)			4
<i>Flabellina trilineata</i> (O'Donoghue, 1921)	x	26	12
<i>Hallaxa chani</i> Gosliner & Williams, 1975			5
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	x	11	2
<i>Hopkinsia rosacea</i> MacFarland, 1905	0	1	1
<i>Janolus fuscus</i> O'Donoghue, 1924		1	3
<i>Placida dendritica</i> (Alder & Hancock, 1843)		3	
<i>Rostanga pulchra</i> MacFarland, 1905	x	12	22
<i>Triopha catalinae</i> (Cooper, 1863)	x	20	28
<i>Triopha maculata</i> MacFarland, 1905	x	3	24
<i>Tritonia festiva</i> (Stearns, 1873)	x	6	4
Totals		194	157

* Between 20 and 25 species were found in 1983, but, owing to the loss of the field notes, only part of the 1983 data (that saved in laboratory notes, preserved specimens, and photographs) can be presented. x indicates occurrence (in unknown numbers) of a species in 1983. 0 indicates a species definitely

in a pool in a small cave. The egg masses are white, wavy ribbons laid on edge in a loose spiral of 1–2 turns and are similar in appearance to those described by HURST (1967) for *A. hudsoni*.

The sighting of the above two specimens extends the range of *Acanthodoris lutea* from Dillon Beach, Marin County, California (STEINBERG, 1963; BEEMAN & WILLIAMS, 1980; McDONALD & NYBAKKEN, 1980). BEHRENS (1980) erroneously reported Vancouver Island as the northernmost limit of this species (D. Behrens, personal communication).

Acanthodoris nanaimoensis

Two specimens, 40 and 5 mm long, were found in 1985. The latter was on the fleshy ctenostome bryozoan *Alcyonidium* sp. Other species of *Acanthodoris* are known to feed on ctenostomes and compound ascidians (THOMPSON, 1964; McDONALD & NYBAKKEN, 1978; personal observations).

Crimora coneja

No specimens of *Crimora coneja* were observed in June 1983, but, as seen in Table 1, *C. coneja* was the most abundant opisthobranch in May 1984, constituting 34% of the total number of individuals found. The difference in abundance between the 2 years is probably real, as I had 2 days of ideal conditions for observation in June 1983 and was able to search carefully a wide variety of habitats. In 1984 a few individuals of *Crimora coneja* were observed crawling on algae in tidepools and on the surface film of calm pools, but most were found under boulders on the encrusting bryozoan *Hincksina minuscula*, the only known prey of *C. coneja* (GODDARD, 1984). Individuals ranged in length from 5 to 23 mm, and many egg masses were observed, also under boulders. Eighteen specimens were found on the underside of a single, medium-sized boulder. The population of *C. coneja* had decreased greatly by May 1985, when only two specimens were observed. Five specimens of *C. coneja* collected in May 1984 from this locality have been deposited in the invertebrate collection of the California Academy of Sciences (voucher number 056221).

Cuthona divae

This aeolid appears to prey mainly, if not exclusively, on hydroids of the genus *Hydractinia* (McDONALD & NYBAKKEN, 1978; GODDARD, 1984; JAECKLE, 1984) and is cryptic on them (personal observations). However, based on the distributional observations of ROBILLIARD (1971: 164), it is possible that *Cuthona divae* preys on other hy-

← not observed in 1983 (indicated primarily for comparison with the following years).

† Found in September 1976 and August 1979 (see text).

droid genera, including *Tubularia*. Further observations are needed to confirm this.

Patches of *Hydractinia* sp. were observed during the present study on the walls of surge channels and underneath ledges. Individuals of *Cuthona divae* were among the polyps of a number of these colonies, and egg masses of *C. divae* were observed on the exposed basal stolonial mat of previously grazed portions of the colonies. Specimens of *C. divae* were also found on algae in pools.

Cuthona lagunae

Two large specimens were found in June 1983 on the hydroid *Sertularella turgida* (Trask, 1857). Feeding on this hydroid was not confirmed. Two more specimens were observed at the surface of a calm pool in May 1984.

Dirona picta

Two *Dirona picta*, both about 30 mm long, were observed in May 1984. One was on the arborescent anascan bryozoan *Scrupocellaria californica* Trask, 1857. The color pattern of the cerata (patches of olive green against a background of semi-translucent tan with minute white flecks) and their warty texture made this *D. picta* quite cryptic on the light-brown colored, highly branched bryozoan. Examination of gut contents revealed that it had been feeding on *S. californica*. This is a new food record for *D. picta*.

MCDONALD & NYBAKKEN (1978) reported finding *Dirona picta* on "*Thaumatoporella* sp." I am unable to find this genus in the bryozoan literature and thus assume they meant *Thalamoporella* sp.

Doto amyra

MCDONALD (1983:184-185) remarked that "the species of the Genus *Doto* found along the California coast are presently quite confused" and that "a detailed study . . . is needed to clearly define and differentiate the species . . ." In order to facilitate field identification, such a re-evaluation of the Pacific coast species of *Doto* should include an examination of the variation in morphology and color pattern found in each species. Knowledge of the habitats and prey of the various species may further help to differentiate them in the field and should also be pursued.

In May 1984 I observed seven specimens of *Doto* that most closely resembled the *D. amyra* of MCDONALD & NYBAKKEN (1980) and GODDARD (1984). The five to eight pairs of cerata possessed short to medium length tubercles and had cream to orange to light-brown colored cores. Gonads were cream to orange colored. Some specimens had a subcutaneous black pigment on the body and head, but not on the cerata (unlike *D. kya*). With the exception of one specimen, which lacked black pigment and was found on hydroid-covered *Cystoseira*, all specimens were observed on algae in pools. Five of these specimens, and

one specimen found in June 1983, have been deposited in the invertebrate collection of the California Academy of Sciences (voucher numbers 056207, 056209 through 056212).

Doto kya

Five specimens were observed in 1985 among the basal stolons of the hydroid *Plumularia* sp. which was growing on the stipes of the brown alga *Laminaria* sp.

Eubranchus olivaceus

One 7-mm long specimen of this distinctive species was found in 1985. Its coloration matched that of specimens collected at Cape Arago, Oregon (GODDARD, 1984; personal observations) and also matched the specimens pictured in photograph 88 of MCDONALD & NYBAKKEN (1980) and photograph 119 of BEHRENS (1980) (the latter mistakenly identified as *Eubranchus rustyus*). The radular formula of the King Range specimen is 38(0.1.1.1.0).

Eubranchus rustyus

A cluster of five individuals and their egg masses were found on the branches of the hydroid *Plumularia* sp., which was growing on a stipe of *Laminaria* sp.

Hermisenda crassicornis

Two color varieties were observed: one with a bluish-white stripe up each ceras, and one lacking the stripes (see BEHRENS, 1980:93, lower and upper photographs respectively). The former variety appears to be more common in the northern part of the range of *Hermisenda crassicornis* (GODDARD, 1984; personal observations).

Hopkinsia rosacea

Two individuals were sighted: a 10-mm specimen in 1984, and a 12-mm specimen in 1985. Both were on *Eurystomella bilabiata*. Only one specimen of *Hopkinsia rosacea* has previously been reported from the county (JAECKLE, 1984).

Janolus fuscus

Only four specimens of *Janolus fuscus* were found during the present study. However, this species was abundant in the same locality in September 1976 (personal observations). Mid-summer through early fall appears to be the season of peak abundance for this species on the outer coast of northern California and Oregon (see GODDARD, 1984:152).

Triopha catalinae

Specimens observed in both 1984 and 1985 ranged in size from 5 to 80 mm. One 6-mm specimen was on a colony of the arborescent anascan bryozoan *Scrupocellaria*

californica, among the branches of which was entangled the vine-like cyclostome bryozoan *Filicrisia* sp. Both of these have been reported by NYBAKKEN & EASTMAN (1977) to be prey of mature *Triopha catalinae*. Two individuals, 10 and 17 mm long, were found on *Dendrobeatia lichenoides* (Robertson, 1900), a foliaceous anascan bryozoan reported by HARVELL (1984) to be eaten by *T. catalinae*. Patches of empty zoecia lacking frontal membranes were present on the outer (younger) half of the *D. lichenoides* colonies and were probably the result of predation by *T. catalinae*. HARVELL (1984) observed that nudibranch predators of *D. lichenoides* prefer younger portions of a colony.

Tritonia festiva

Two of the 10 *Tritonia festiva* found in this study were observed next to *Clavularia* sp., a known prey of *T. festiva* and also the only octocoral observed in the study area.

DISCUSSION

Sponge-feeding dorid nudibranchs were uncommon during the present study. Considering the data for 1984 and 1985 (as mentioned in a footnote to Table 1, the 1983 data are incomplete), a total of 45 individuals belonging to five species of sponge-feeding dorids were observed. Thirty-four (75%) of these were *Rostanga pulchra*, a small species that feeds on a variety of tough, orange-to-red colored, encrusting sponges (MCDONALD & NYBAKKEN, 1978; GODDARD, 1984). The remaining 11 individuals consisted of five normal-size *Hallaxa chani*, which is a specialist on the slime sponge *Halisarca* sp. (GODDARD, 1984), two 35-mm long *Anisodoris nobilis*, three *Diaulula sandiegensis*, 20, 22, and 35 mm long, and one 20-mm long specimen of *Discodoris heathi*. None of the latter three species were found on sponges. Thus, 17% (5 of 30) of the nudibranch species found in 1984 and 1985 were sponge-feeding dorids. This compares to 27% (14 of 51) for the outer coast of northern Humboldt County (JAECKLE, 1984), 29% (12 of 42) for Cape Arago, Oregon (GODDARD, 1984), and 27% (27 of 100) for California as a whole (MCDONALD & NYBAKKEN, 1980). Moreover, with the exceptions of *Hallaxa chani* and *R. pulchra*, sponge-feeding dorids from the King Range were smaller and less abundant than their counterparts in the latter two areas (personal observations).

As previously mentioned, sponges of all kinds (not just those preyed upon by nudibranchs) were uncommon in the study area. This probably accounts for the paucity of sponge-feeding dorids. The scarcity of sponges, in turn, may well be related to the high turbidity of the nearshore waters. High levels of suspended sediments can inhibit the growth of sponges by clogging their inhalant canals (or forcing constriction of their ostia) and thus reducing their water pumping and feeding activities (REISWIG, 1971; BERGQUIST, 1978; WILKINSON & VACELET, 1979).

On the Distribution and Biology of *Crimora coneja*

To date *Crimora coneja* has been reported from only three specific localities on the Pacific coast of North America: Point Loma, San Diego County, California, where it has been reported as uncommon or rare (LANCE, 1961: 64; MCDONALD, 1983) but where it has been known to occur consistently year after year (J. Lance, personal communication); the north side of Punta Gorda, Humboldt County, California, where its numbers have fluctuated dramatically over the past 3 years (present study); and Cape Arago, Oregon, where it has occurred consistently but in low numbers for at least the past 5 years (GODDARD, 1984, and unpublished data). All of these records are intertidal.

In part, the known distribution of *Crimora coneja* reflects geographically limited observations. With the exceptions of Humboldt County and Cape Arago, the nudibranch fauna of the outer coast of northern California, Oregon, and Washington is poorly known. *Crimora coneja* could occur throughout that region. However, extensive observations have made it unlikely that *C. coneja* occurs intertidally in central and most of southern California (COSTELLO, 1938; LANCE, 1961, 1966; MARCUS, 1961; STEINBERG, 1963; MACFARLAND, 1966; SPHON & LANCE, 1968; LEE & BROPHY, 1969; ROLLER & LONG, 1969; ROLLER, 1970; GOSLINER & WILLIAMS, 1970, 1973; BERTSCH *et al.*, 1972; NYBAKKEN, 1974, 1978; Goddard, unpublished data [monthly observations, 1975-1978, at Scott Creek, Santa Cruz County]; BEHRENS, 1980, personal communication; MCDONALD, 1983). Similarly, recently increased observations have not revealed *C. coneja* in British Columbia or Alaska (see MILLEN, 1983; LEE & FOSTER, 1985; and literature cited therein) or in Mexico (personal communications from H. Bertsch, T. Gosliner, and J. Lance).

The apparent absence of *Crimora coneja* from central and most of southern California is perplexing, especially considering the numbers of *C. coneja* observed in 1984 during the present study, the consistency of its occurrence intertidally at both Cape Arago and Point Loma, and the relative uniformity of hydrographic conditions and biota along the California coast, especially north of Point Conception (STEINBECK & RICKETTS, 1941:293-302; RICKETTS *et al.*, 1985). Moreover, *C. coneja* is known to produce planktotrophic veliger larvae which, judging from their morphology and small size at hatching (GODDARD, 1984, and unpublished observations), probably have a long obligatory planktonic stage (HADFIELD & SWITZER-DUNLAP, 1984). Depending on larval behavior, this almost certainly ensures wide dispersal (HADFIELD & SWITZER-DUNLAP, 1984). No other nudibranch known from both the San Diego area and north of northern California exhibits a disjunct distribution comparable to that possessed by *Crimora coneja* (see references cited above on northeast Pacific opisthobranchs).

In most of the studies of California opisthobranchs cited

above, observations have been largely confined to the intertidal zone. *Crimora coneja* may well be primarily sublittoral, with rare intertidal outbreaks. In Europe *C. papillata* Alder & Hancock, 1862, is known only from the sublittoral and, like *Crimora coneja* in the northeast Pacific, was until recently considered one of the rarest north Atlantic nudibranchs. Since 1972, large numbers of *C. papillata* have been found in "restricted sublittoral areas (down to 30 m)" (THOMPSON & BROWN, 1984:64).

The habitat requirements of *Crimora coneja* appear to be quite specific, stemming primarily from those of its bryozoan prey, *Hincksina minuscula*, and may have resulted in *C. coneja* being overlooked in some areas. *Crimora coneja* is almost always found on the undersides of boulders (GODDARD, 1984; J. Lance, personal communication; present study), where it preys on *H. minuscula* (GODDARD, 1984; present study). Preliminary observations suggest that *H. minuscula* can persist only in physically disturbed or spatially confined cryptic habitats (e.g., tight spaces under boulders or in cracks). This thinly encrusting bryozoan, which is readily overgrown by sponges, tunicates, and other encrusting bryozoans (personal observations at Cape Arago), appears susceptible to competitive exclusion in more open habitats (including relatively open cryptic habitats). Interestingly, *C. coneja* attains lengths of at least 23 mm but also possesses an extremely delicate, flaccid body (personal observations). This combination of size and flaccidity could be adaptive in allowing movement through tight spaces as well as the increased feeding rates associated with larger size. Although a delicate body might be more susceptible to damage by predators, contact with a variety of predators would be reduced in spatially confined cryptic habitats. The flat egg mass of *C. coneja* (GODDARD, 1984:148) may also be an adaptation to tight spaces. Other members of the Triophidae on this coast lay their egg masses in the typical dorid form of a ribbon laid on edge in a coil (BEEMAN & WILLIAMS, 1980; personal observations).

The parallels between *Crimora coneja* and *Laila cockerelli* MacFarland, 1905, a specialist on the thinly encrusting *Hincksina velata* (Hincks, 1881) (MCDONALD & NYBAKKEN, 1978; GODDARD, 1984) are intriguing. *Laila cockerelli* is similar in size to *C. coneja*, has a flattened body with long, delicate papillae that insert on the sides of the dorsum, and also lays its egg ribbon flat (GODDARD, 1984). The two are even similarly colored, raising the possibility of Müllerian or Batesian mimicry (*Triopha catalinae* may also be involved with this). Although *C. coneja* possesses brown-to-black-tipped papillae (in addition to the orange-tipped papillae), red appears black at depth, as noted by H. Bertsch (personal communication). However, unlike *C. coneja*, *L. cockerelli* has been observed (usually in low to moderate numbers) at numerous localities between Vancouver Island and Cabo San Lucas (see references in MCDONALD, 1983:192).

Like many other nudibranchs that usually occur on

sessile prey in cryptic habitats, *Crimora coneja* is occasionally observed in open habitats, on algae or bare rock, where it is presumably in transit, searching for new patches of food, mates, or a suitable place to deposit eggs (personal observations). Thus, even if the cryptic habitat of *C. coneja* has been overlooked in previous studies (a slim possibility raised earlier), it seems unlikely that *C. coneja* would have been missed altogether in so much of California. Assuming that *C. coneja* has not generally been overlooked, then the most plausible explanation for its absence from central and most of southern California is a lack of suitable prey in that region. It is not known how far south *Hincksina minuscula* ranges (to my knowledge, Punta Gorda is the known southern limit), what *C. coneja* feeds on at Point Loma, or if *C. coneja* preys on other species of bryozoans. It is conceivable (although it seems unlikely) that prey suitable for *C. coneja* are missing from much of California (which would leave us with the more difficult problem of explaining their absence). More observations, especially of the undersides of littoral and sublittoral boulders, are clearly needed before the disjunct distribution of *C. coneja* can be adequately explained.

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Redescription of *Assimineea infima* Berry, 1947, from Death Valley, California

by

ROBERT HERSHLER

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

Abstract. A morphological description, including aspects of the shell and soft-part anatomy, is provided for *Assimineea infima* Berry, 1947, from Death Valley, California. Habitat descriptions are given for Badwater Spring, the type locality, as well as for three new localities for the species. *Assimineea infima* typically occurs either under a salt-crust roof fringing the water's edge or on moistened riparian vegetation. Snails are often found fully submerged, and only occur in the vicinity of spring sources. A review of morphological data suggests that *A. infima* may be closely related to *A. californica* (Tryon, 1865), a Pacific coastal species.

INTRODUCTION

THE GENUS *Assimineea* Fleming, 1828 (Prosobranchia: Rissoacea), comprises 50-60 nominal species, with most restricted to tropical or subtropical regions. Members of the genus are amphibious, living in moistened areas near the edge of marine or permanent nonmarine water bodies (ABBOTT, 1958). The group presents an interesting ecological radiation of probable marine ancestry (ABBOTT, 1958; FRETTER & GRAHAM, 1962); yet the lack of a modern systematic analysis of the genus (few species have received anatomical study) precludes a meaningful analysis of the radiation.

Assimineea is represented in North America by several coastal species, one of which, *A. californica* (Tryon, 1865), has received detailed morphological study (FOWLER, 1977, 1980). In addition, there is an inland deployment of *Assimineea* among spring-fed habitats in the arid southwest U.S. (BERRY, 1947; MORRISON, 1956; TAYLOR, 1966, 1983; LANDYE, 1973; FULLINGTON, 1978). The inland fauna has received scant attention, with systematic study restricted to the brief description of *A. infima* Berry, 1947, from Badwater Spring in Death Valley.

It has long been known that additional *Assimineea* populations occur in the Death Valley region (MORRISON, 1956; LANDYE, 1973). As part of a recent survey of rissocean snails in the Death Valley region (HERSHLER, 1985), the author collected *A. infima* from Badwater Spring and three other localities in Death Valley (Figure 1). Based on study of this material, a morphological redescription of *A. infima* is provided herein that includes details of shell

morphology as well as anatomy. Detailed habitat descriptions are provided as is a morphological comparison between *A. infima* and *A. californica*.

MATERIALS AND METHODS

Assimineea infima was collected by hand at the four Death Valley localities during February and November 1985. These collections are now housed in the National Museum of Natural History (USNM catalogue numbers are given below). Snails from Badwater Spring were used for study of internal anatomy. Shell measurements and dissections were done at 50× using a Wild M-5 dissecting microscope equipped with an ocular micrometer. Shells, opercula, radulae, and critically point dried whole specimens were photographed using a Hitachi S-570 scanning electron microscope.

TAXONOMY

Family ASSIMINEIDAE

Genus *Assimineea* Fleming, 1828

Type species (by original designation): *Assimineea grayana* Fleming, 1828.

Assimineea infima Berry, 1947

(Figures 1-12)

Material examined: California, Inyo County: Badwater Spring, Bennetts Well quadrangle (1952), 1:62,500, T.

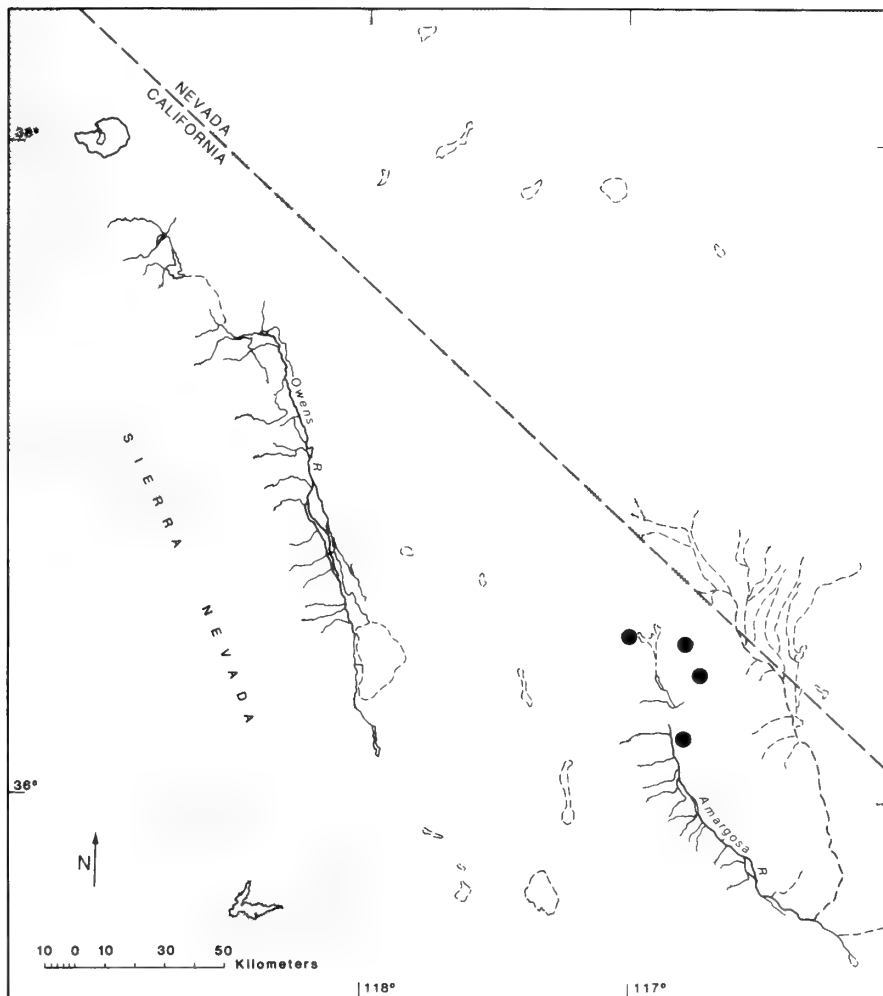


Figure 1

Map of the Death Valley drainage system, showing localities for *Assimineia infima*. The localities are (from north to south) Cottonball Marsh (west side of Death Valley), Nevares Springs (east side), Travertine Springs, and Badwater Spring. Stippled areas indicate the location of mountain ranges.

20S, R. 20E, 1.7 km SW of NE corner of quadrangle, USNM 591286 (paratypes), USNM 859018–859020 (all from North pool); Travertine Springs, Furnace Creek (1952), T. 27W, R. 1E, $\frac{1}{4}$ NW $\frac{1}{4}$ NW, Section 25, USNM 859021, USNM 859022; Nevares Springs, Chloride Cliff (1952), T. 28N, R. 1E, $\frac{1}{4}$ NE $\frac{1}{4}$ SW, Section 36, USNM 859023–859025; Salt Springs (feeding Cottonball Marsh), Chloride Cliff (1952), T. 17S, R. 45E, 0.7 km NE of SW corner of quadrangle, USNM 859026; Cottonball Marsh, Chloride Cliff (1951), T. 27S, R. 45E, 2.3 km NE of SW corner of quadrangle, USNM 859027, USNM 859028.

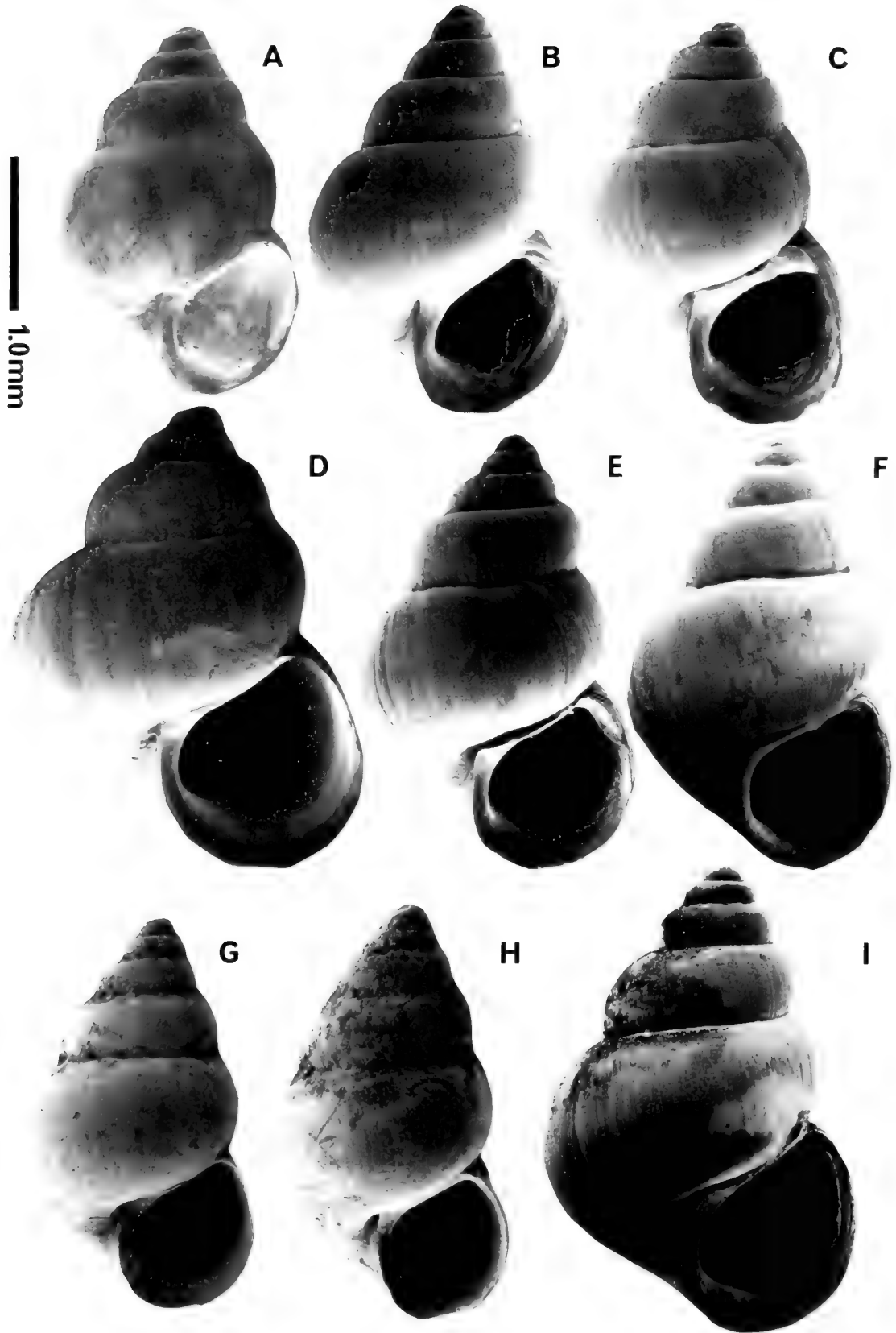
Diagnosis

A small-sized (shell height, 2.5–3.5 mm) species, distinguished from North American coastal *Assimineia* by its

Table 1

Summary of shell parameters for 14 mature adults from Badwater Spring.

Parameter	Mean	SD	Range
Shell height (mm)	2.81	0.22	2.62–3.25
Shell width (mm)	1.95	0.19	1.74–2.48
Aperture height (mm)	1.28	0.12	1.11–1.52
Aperture width (mm)	1.12	0.11	0.99–1.45
Body whorl height (mm)	2.02	0.16	1.74–2.41
Body whorl width (mm)	1.73	0.16	1.52–2.17
Number of whorls	4.73	0.17	4.5–5.0



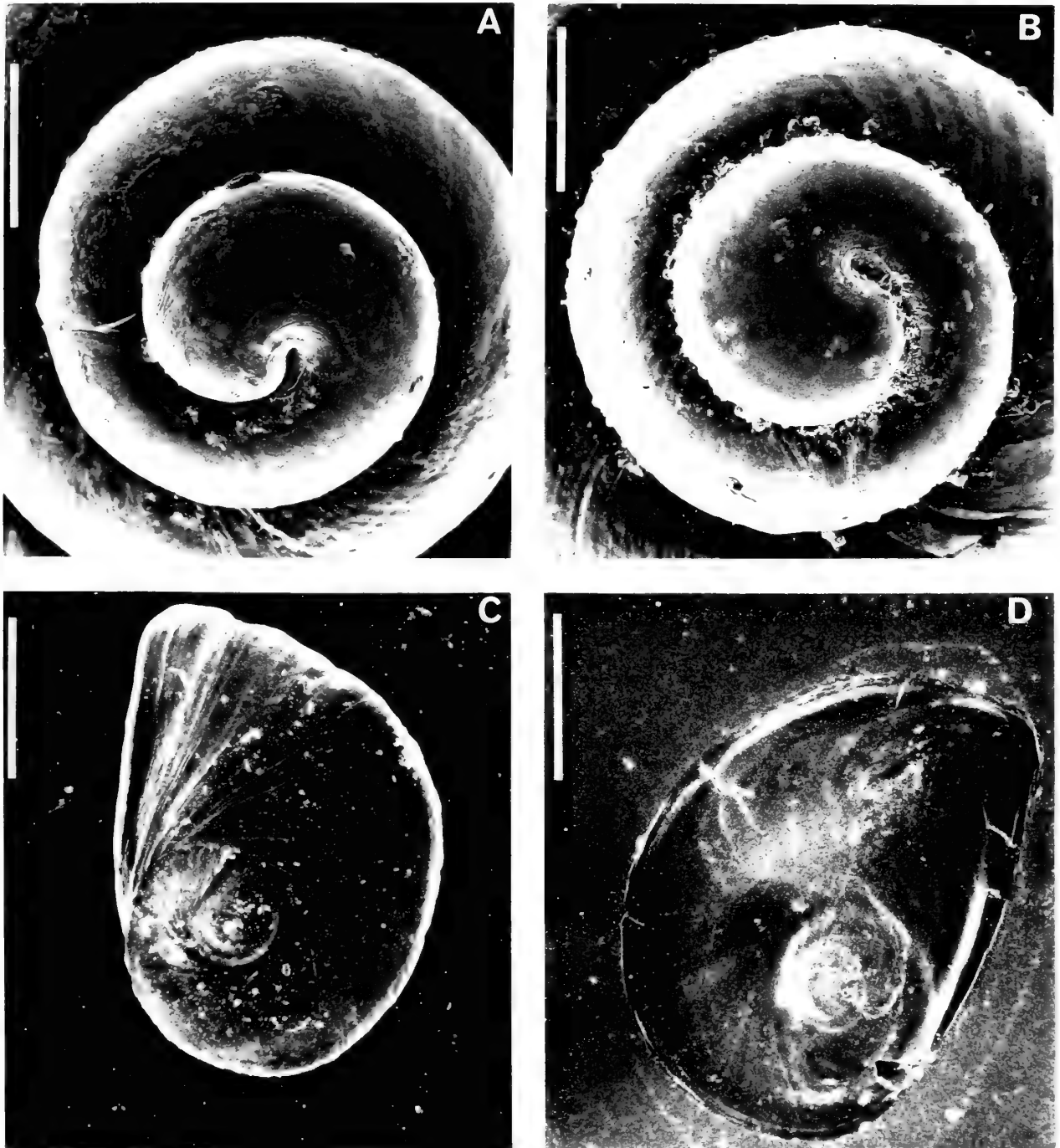


Figure 3

Photographs (SEM) of the protoconch (A, B; scale = 150 μm) and operculum (C, dorsal aspect; D, ventral; scale = 330 μm) of *Assimineea infima*.

Figure 2

Photographs (SEM) of *Assimineea infima* from Badwater Spring (A-F), Travertine Springs (G), Nevares Springs (H), and Cottonball Marsh (I).

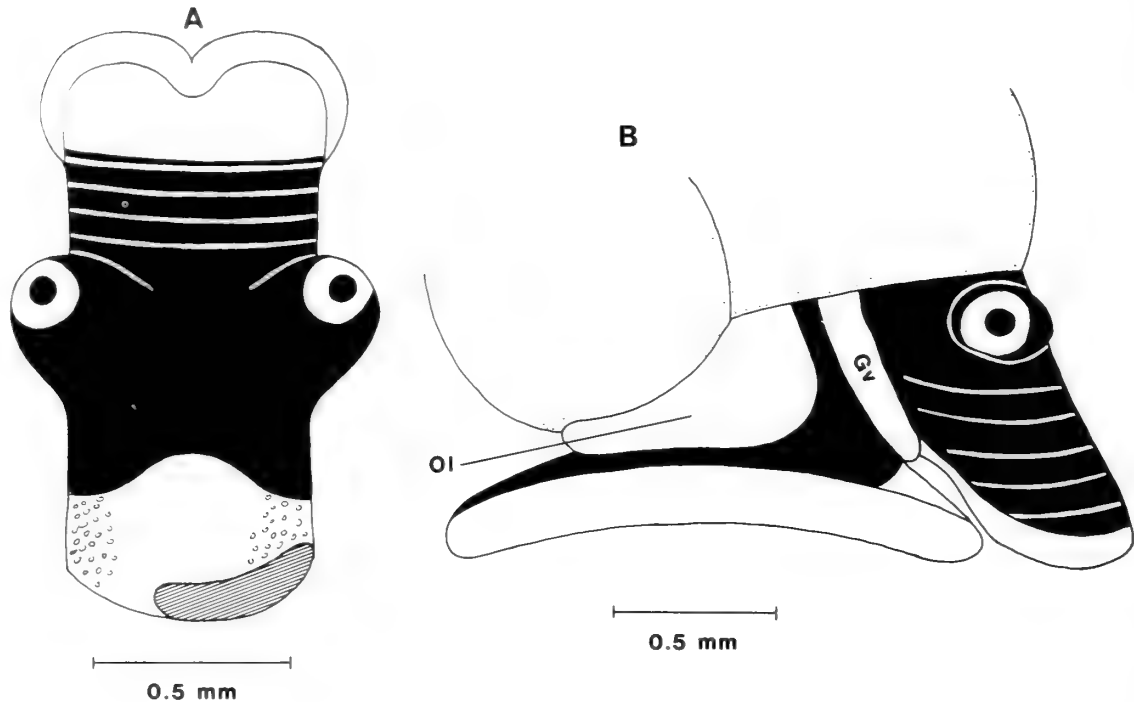


Figure 4

Head (A) and right lateral view of head-foot (B) of crawling, submerged *Assiminea infima*. Darkly pigmented regions are shaded black. The small circles posterior to the tentacles represent glandular clusters. Gv, ciliated groove; Ol, operculigerous lobe.

broadly conical shell with moderate to highly convex whorls (Figure 2). Other distinguishing features include the presence of a single, enlarged ctenidial filament anterior to the more typical, stubby filaments (Figure 6A), a thickened pallial swelling anterior to the rectum (Figure 6A), and the looping condition of the anterior vas deferens (Figure 11B).

Description

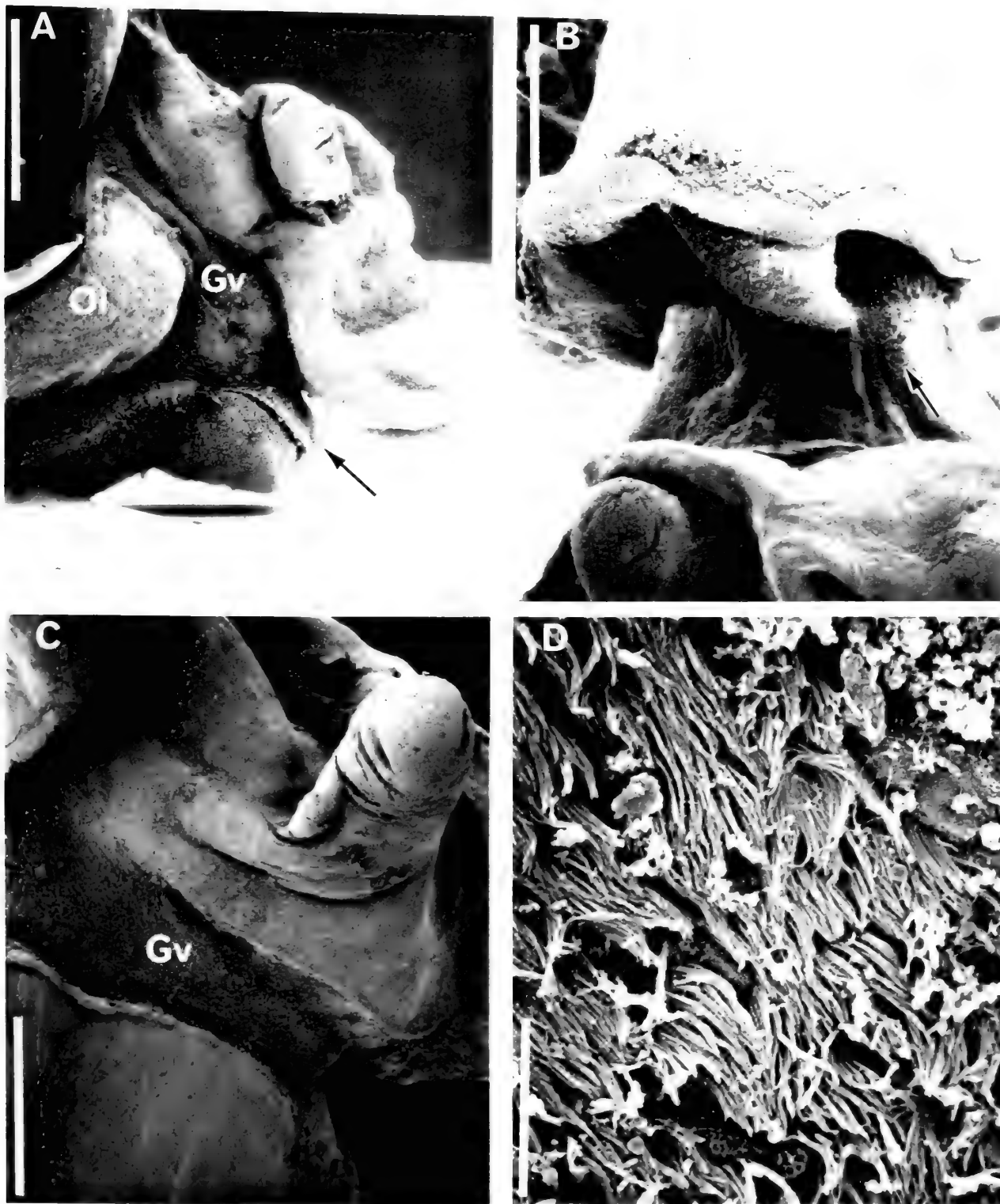
Shell: Measurements of shell parameters for 14 specimens from Badwater Spring (the only locality from which a large sample was obtained) (Figure 2) are summarized in Table 1. Adult shells have 4.0–5.0 whorls and shell height varies from 2.5 mm (Nevares Springs) to 3.5 mm (Cottonball Marsh). Females are typically slightly larger than males. Shells are fairly thin and translucent, with only a slight thickening at the aperture. Shell color is very light to dark amber. Shells from Badwater Spring and Cotton-

ball Marsh are relatively wider with more convex whorls than those from Travertine and Nevares springs (Figure 2). The aperture is longer than wide, rounded below, and angled above. The inner lip is fully formed only in the largest specimens, and in these it often forms a broadened callus (Figure 2). Separation of the inner lip from the body whorl is rare. The umbilicus is often restricted due to peristome overlap and appears chinklike. The protoconch, with 1.25 whorls, is smooth or with a few faint spiral lines (Figures 3A, B). Teleoconch sculpture consists of strong collabral growth lines. The paucispiral operculum (Figures 3C, D) is thin, amber-colored, and without unusual features.

Head-foot: The broadly bilobed snout (Figures 4, 5A) is dorsoventrally flattened, longer than wide, and creased along most of its length. The distal end of the snout flares outward to form broad, fleshy oral lappets. The tentacles are short, thickened, rounded at the tips, and without cilia.

Figure 5

Photographs (SEM) of critical point dried specimens of *Assiminea infima*. A. Right lateral aspect of head-foot (specimen partly collapsed), with the arrow indicating the dorsoanterior flap of the foot (scale = 380 μ m). Note



the stubby tentacles and bulging operculigerous lobe. B. Dorsal aspect of the neck, showing (arrow) the anterior portion of the ciliated patch on the pallial cavity floor (scale = 250 μ m). C. Right lateral aspect of the head-foot, showing the typically wide ciliated groove (scale = 250 μ m). D. Close-up of the ciliation in the groove (scale = 12 μ m). Gv, ciliated groove; Ol, operculigerous lobe; Pn, penis.

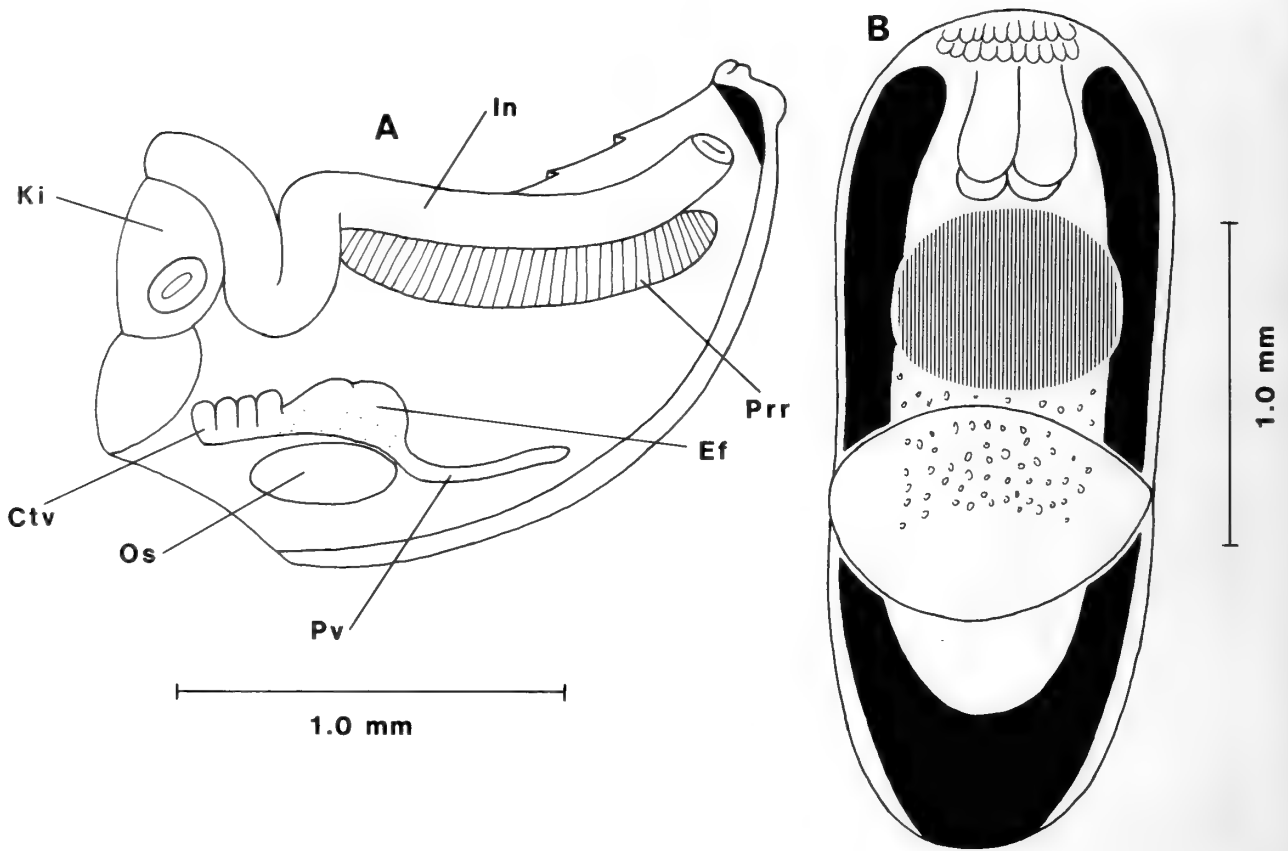
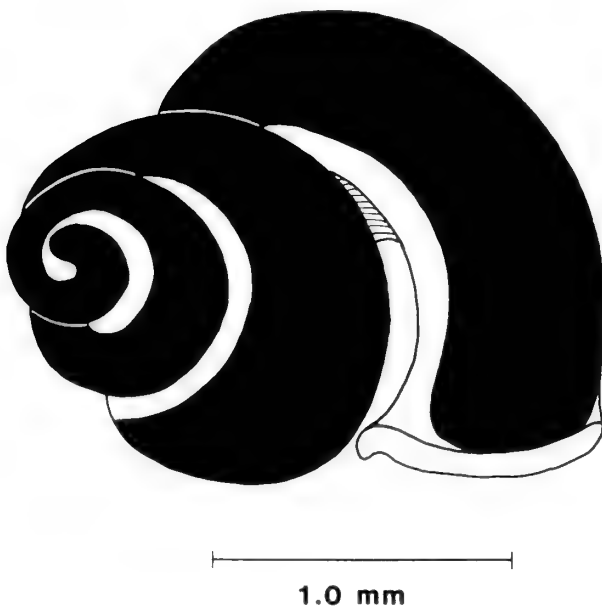


Figure 6

Pallial cavity and foot of *Assimineia infima*. A. Roof of the pallial cavity. Note the pigmented swelling anterior to the rectum. B. Dorsal aspect of the foot, showing the darkly pigmented region (black) and attachment area (lined screen) of the body. The pedal glands (at anterior end of foot), operculum, and glandular clusters (small circles) are also indicated. Ctv, ctenidial vestige; Ef, enlarged "filament"; In, intestine; Ki, kidney; Os, osphradium; Prr, ridged pallial roof; Pv, pallial vein.



The eyespots are near the distal ends of the tentacles (Figure 4A). A ciliated groove (Figures 4B, 5-Gv) extends along each side of the head-foot, originating where the snout joins the anterior foot and ending on the side of the "neck" (Figure 5B). The right lateral (or omniphoric) groove, along which fecal pellets frequently pass, is much wider than the left groove. The grooves are well inset and surrounded by angular, unciliated ridges. The operculigerous lobe (Figure 4-Ol) is quite swollen and fleshy, bulging outward from the surrounding portion of the head-foot (Figure 5A). The broad, thickened foot is rounded anteriorly and posteriorly (Figures 4, 5A). The center of the anterior pedal crease (Figure 5A) has a large pore through which pedal glands discharge. No suprapedal fold

Figure 7

Dorso-right lateral aspect of body (minus head) of *Assimineia infima*. Darkly pigmented areas are shaded black.

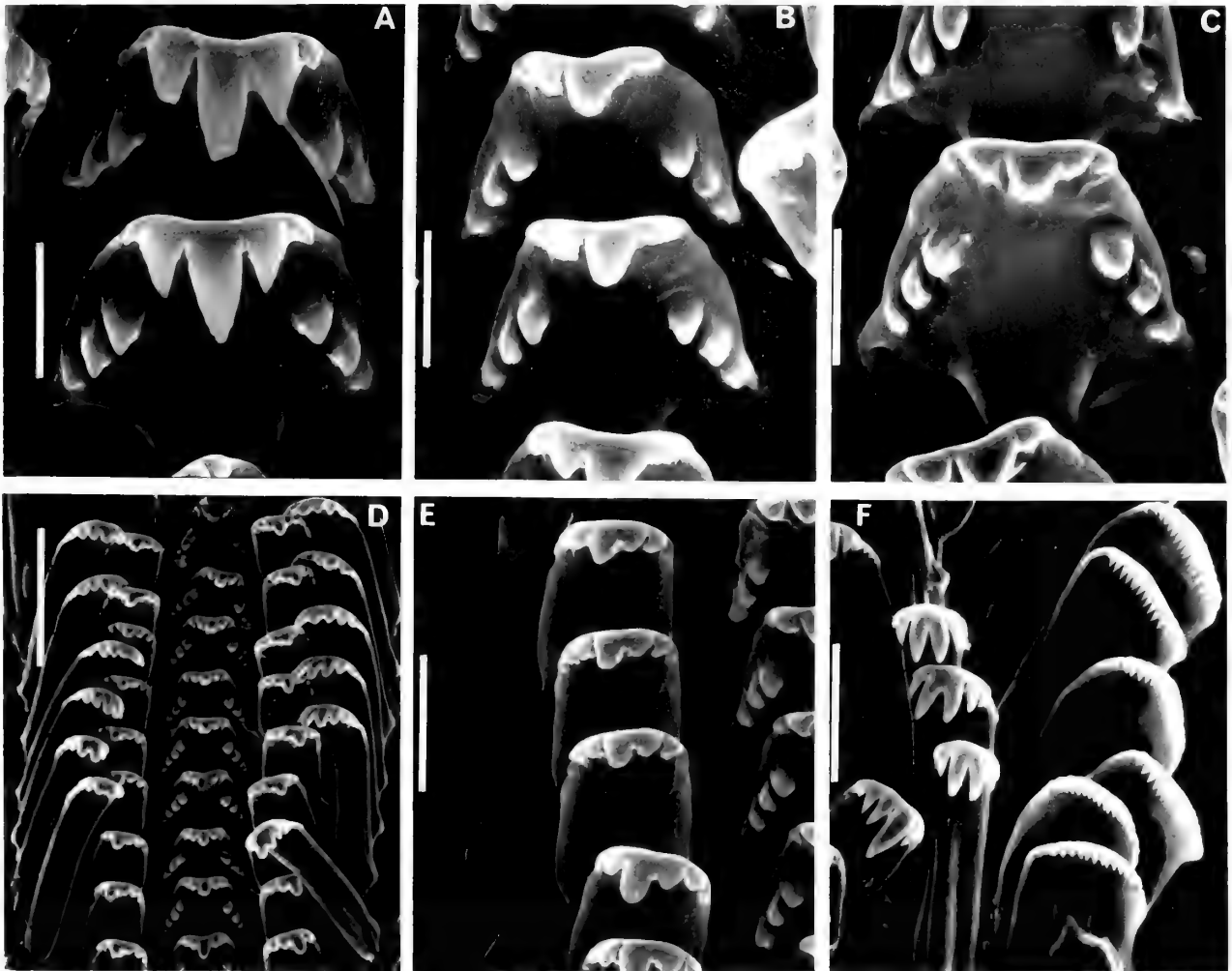


Figure 8

Photographs (SEM) of the radula of *Assimineea infima*. A-C. Centrals (scales = 8.6 μm , 10.0 μm , 8.6 μm). D. Section of radular ribbon (scale = 38 μm). E. Laterals (scale = 15 μm). F. Inner (to left) and outer (right) marginals (scale = 23.1 μm).

(*sensu* DAVIS, 1967) is evident, although the pedal crease extends slightly back along the foot (Figure 5A). A small dorsal flap is offset from the remainder of the foot by this crease and a shallow trough (Figures 4B, 5A). The pedal glands (Figure 6B) include both a large number of gray, small-sized glands as well as two pairs (one dorsal to the other) of much larger, white glands. The sole of the foot is densely ciliated.

The snails are active, especially when submerged. It is not known whether the snails tolerate prolonged submersion. Progression is steplike with the anterior quarter of the foot (the portion encompassing the dorsal anterior flap) lifting off the substratum, stretching and then adhering, with the posterior of the foot then following.

Pigmentation: For the Badwater Spring population, dark melanic pigment covers much of the head (posterior to the

oral lappets), although circular unpigmented areas surround the eyespots (Figure 4). Occasionally the oral lappets are also pigmented. The deep creases in the snout are also unpigmented or have only a light dusting of melanin. White granules are clustered behind the tentacles. Most of the side of the head-foot is darkly pigmented, although pigment is absent from the ciliated grooves and sides of the foot (Figure 4B). The operculigerous lobe, which contains glandular clusters, is unpigmented or has a gray-colored appearance. The entirety of the dorsal body surface is darkly pigmented (Figure 7). A similar pigmentation pattern for the head-foot and body occurs in snails from Cottonball Marsh, whereas specimens from Travertine and Nevares springs generally lack pigment in the head-foot and have dorsal melanic body pigment only on the gonad.

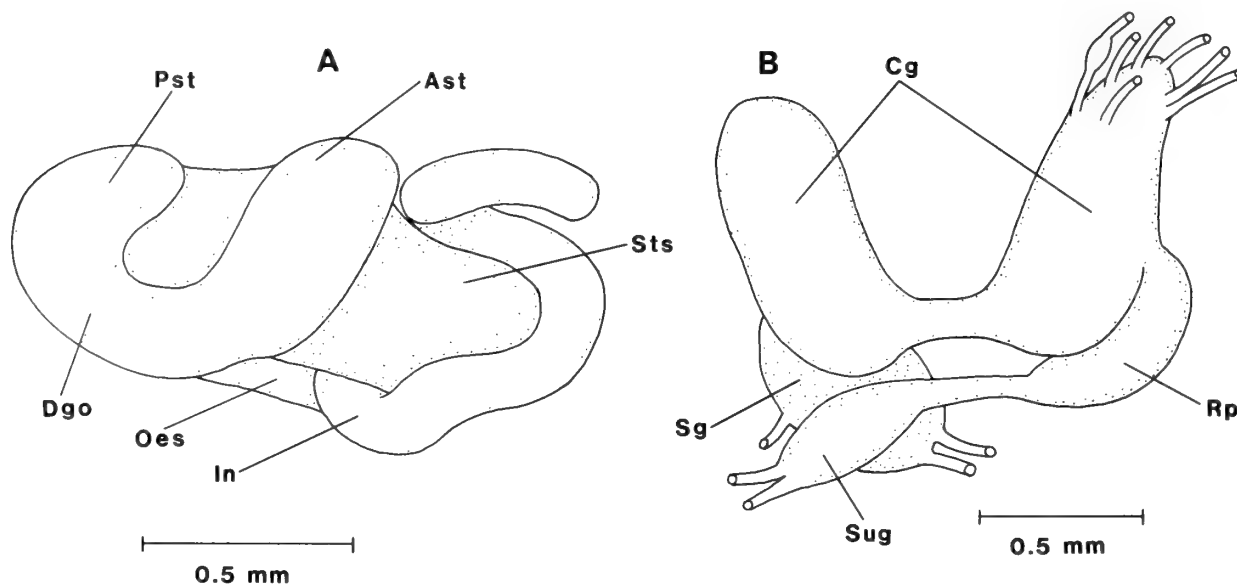


Figure 9

Stomach (A) and dorsal nervous system (B) of *Assimineea infima*. The positions of nerves are only indicated on the right cerebral ganglion. Note the enlarged ganglion (Sg) representing the fusion of the left pleural and suboesophageal ganglia. Ast, anterior stomach chamber; Cg, cerebral ganglion; Dgo, opening of the digestive gland into the stomach; In, intestine; Oes, oesophagus; Pst, posterior stomach chamber; Rp, right pleural ganglion; Sg, fused left pleural and suboesophageal ganglia; Sts, style sac; Sug, supraoesophageal ganglion.

Pallial cavity: The pallial cavity roof is shown in Figure 6A. The reduced ctenidium (Ctv) has three or four small, stubby filaments as well as a single broad, elongate "filament" (Ef) (anterior to the above), all of which are generously ciliated. It was not determined whether the latter has skeletal rods, which would indicate homology with true ctenidial filaments. The pallial vein (Pv) extends anterior to the filaments and ends near the mantle collar. The large osphradium (Os) is centered along the length of the ctenidial axis-pallial vein. The intestine (In) has a tight, U-shaped loop just anterior to the posterior end of the pallial cavity. Anterior to the loop, the intestine is fringed to the left (beneath in Figure 6A) by a well-delimited narrow, ridged area of the pallial roof (Prr), which is probably a hypobranchial gland. This region was seen (in section) to consist of tall, gobletlike cells. The mantle collar is smooth, except at the extreme right (above in Figure 6A), where a bulging swollen area (pigmented in the Badwater Spring population) occurs. The left side of the pallial cavity floor has dense, elongate cilia (Figure 5B) that are not continuous with the ciliary tract in the left lateral groove of the head-foot.

Digestive system: The radula is shown in Figure 8. The typical radular formula is as follows: central, 2-1-2/3-3; lateral, 2(3)-1-3; inner marginal, 9-10; outer marginal, 15-17. The width of the central tooth is about $2.19 \mu\text{m}$. Cusp wear was apparent in all radulae examined, with

cusps blunted or broken on the anterior portion of the ribbon. The basal process is well developed on the central tooth (Figure 8C). Note that the inner and outer marginals are quite dissimilar in tooth and cusp morphology (Figure 8F). The stomach and style sac are roughly equal

Table 2

Six morphological differences between *Assimineea infima* and *A. californica* (data from FOWLER, 1977).

<i>Assimineea infima</i>	<i>Assimineea californica</i>
1. Shell broadly conical, with moderate-highly convex whorls	More elongate-conic, whorls only slightly convex
2. Ctenidium with series of small, stubby filaments as well as a single, enlarged filament	Enlarged filament absent
3. Mantle collar with thickened swelling by the anus	Mantle collar smooth
4. Hypobranchial gland restricted to narrow region along left side of intestine	Gland covers most of pallial roof
5. Anterior vas deferens coils on right side of prostate	Anterior vas deferens without coils
6. Albumen and capsule glands nearly equal in length	Albumen gland relatively small

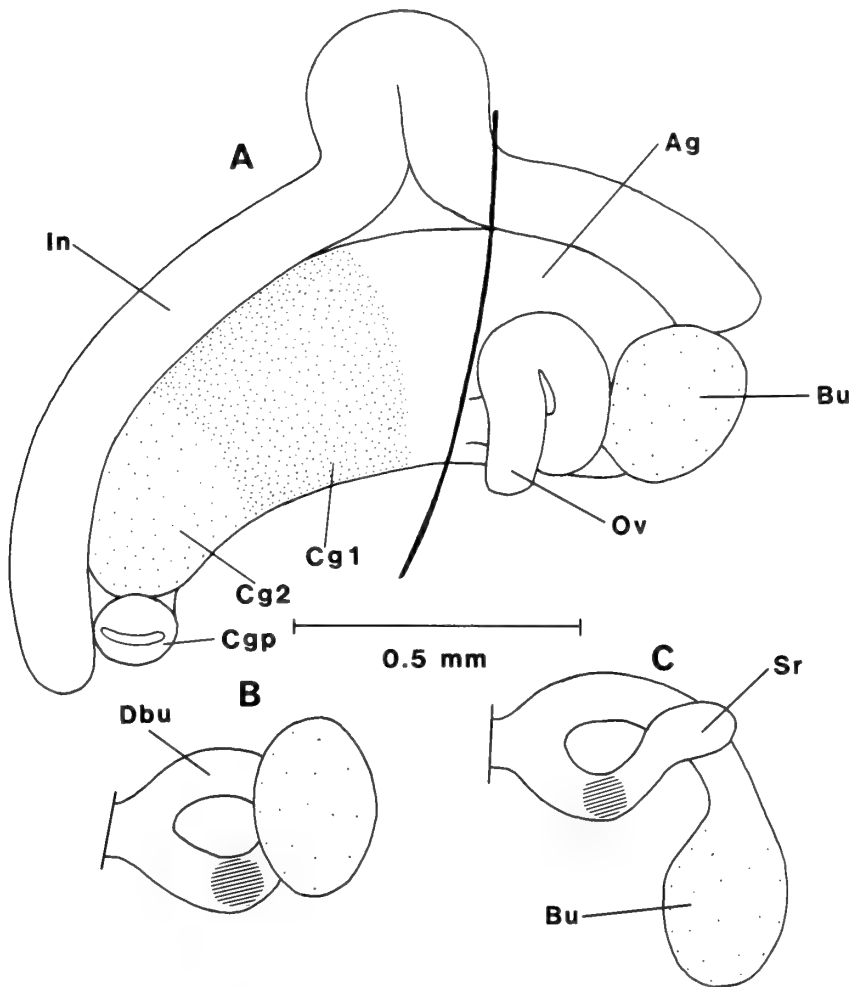


Figure 10

Right lateral aspect of pallial oviduct (A) and bursa copulatrix complex (B, C) of *Assiminea infima*. The oviduct coil was removed in B and C. Note the tripartite capsule gland. The thickened curving line in A (crossing the pallial oviduct) indicates the posterior end of the pallial cavity. The screened (lined) region in B and C indicates the junction with oviduct. In C, the bursa has been rotated to the left (toward the reader) to reveal the seminal receptacle. Ag, albumen gland; Bu, bursa copulatrix; Cgp, muscularized, anterior capsule gland section; Cg1, posterior capsule gland section; Cg2, middle capsule gland section; Dbu, duct of bursa; In, intestine; Ov, oviduct; Sr, seminal receptacle.

in length (Figure 9A). The posterior end of the stomach is well rounded and without a caecal chamber.

Nervous system: Study was restricted to the dorsal ganglion complex (Figure 9B). The cerebral ganglia (Cg) are connected by a short commissure. The right pleural (Rp) and supraoesophageal (Sug) ganglia are similarly connected by a short commissure; the RPG ratio (see DAVIS *et al.*, 1976) is 0.19. The left pleural ganglion and suboesophageal ganglion are fused, forming a single large ganglion (Sg).

Female reproductive system: The simple, lobate, white ovary occupies a single whorl posterior to the stomach. The pallial oviduct (Figure 10A) consists of the clear albumen gland (Ag) and three distinct capsule gland regions: a large, white-colored posterior section (Cg1), a smaller, clear, middle section (Cg2), and an anterior, muscular, papilla-like section (Cgp) with a slitlike terminal opening. The proximal end of the papilla is coiled onto the right side of the clear capsule-gland section into which it opens. The large bursa copulatrix (Bu) is positioned at the posterior end of the albumen gland (left side), while

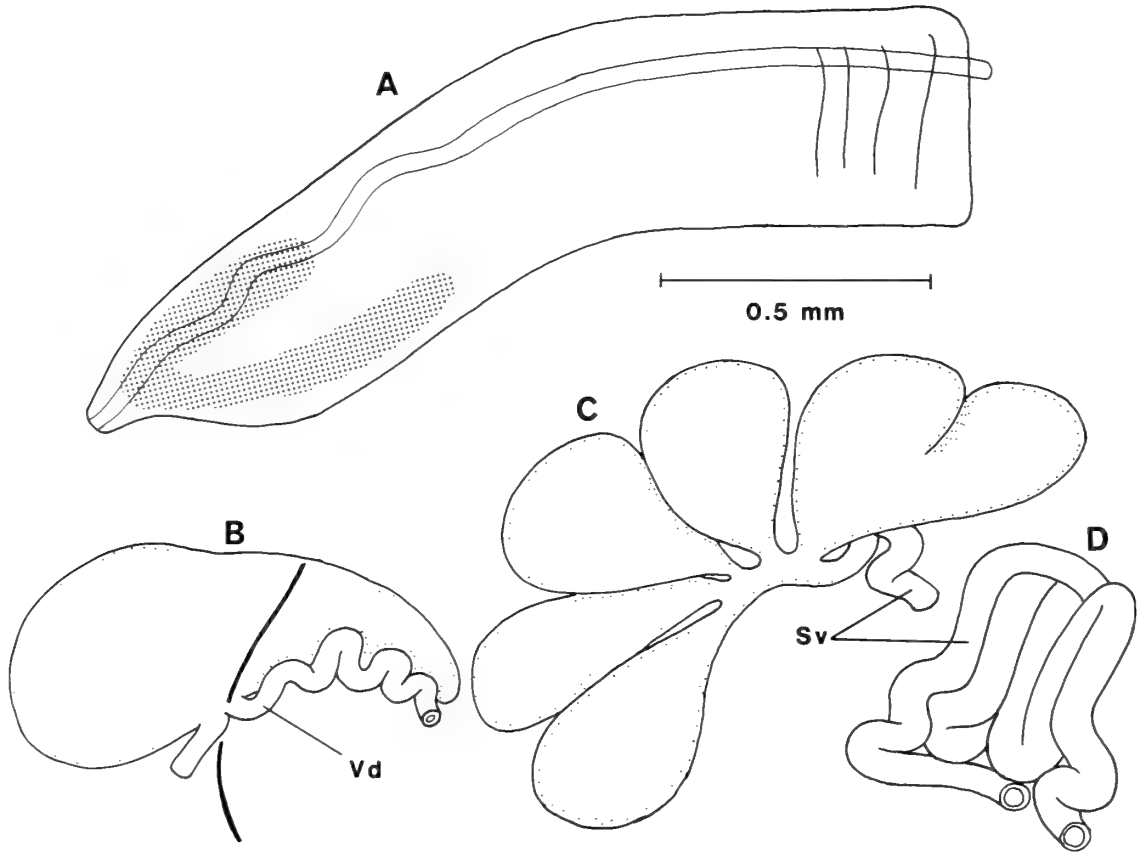


Figure 11

Male reproductive system of *Assiminea infima*. A. Dorsal aspect of penis. The stippled area indicates the densely glandular region. B. Right lateral aspect of prostate. The thickened curving line crossing the prostate indicates the end of the pallial cavity. C. Right lateral aspect of the testis, with the entirety of the seminal vesicle portrayed to the right. Sv, seminal vesicle; Vd, vas deferens.

the seminal receptacle (Sr) is pressed against the right side of the bursa (not visible in Figure 10A, but see Figure 10C). The oviduct (Ov) loops once on the left side of the albumen gland before receiving the duct of the seminal receptacle (Figures 10B, C). The oviduct and elongate bursal duct (Dbu) then join before entering the anterior end of the albumen gland (Figure 10C). Sperm enter the bursa via the pallial oviduct.

Male reproductive system: The testis, consisting of a few large lobes posterior to the stomach, is shown in Figure 11C. The seminal vesicle (Sv) consists of a small number of tall loops that are largely hidden by the testis. The prostate (Figure 11B) is elongate and enlarged, with half its length pallial. The anterior vas deferens (Vd, Figure 11B) exits near the mid-point of the prostate and continues as a loosely coiled, non-muscular tube before entering the "neck." The vas deferens also occasionally coils in the

base of the penis. The penis (Figure 11A), which coils counterclockwise on the "neck," is relatively large, simple, and bladelike, with a narrow tip. The penis tip has a terminal, eversible papilla. Small annulations (not shown in Figure 11A) extend along much of the inner curvature. The well-defined, dense cluster of glands (stippled area) occurs in the anterior one-third of the penis. The gray glandular clusters consist of groups of both large and quite small spherical bodies. The epithelia of the penis are glandular and unciliated throughout.

Habitat

Badwater: Small seeps at Badwater discharge into two shallow (less than 5 cm) pools, 70 m apart (Figures 12, 13A), occupying an estimated 2023 m² (HUNT *et al.*, 1966). The salt-crust-covered sump that Badwater occupies is moist throughout, with the water table lying at or just beneath ground level. Spring sources are particularly no-



Figure 12

Aerial photograph of Badwater, showing the two large, permanent pools (top of photo, south pool; bottom, north). The width of the highway is about 7 m. Note the two whitened outflow channels from the south pool and the pickleweed bushes fringing the northeast portions of the pools. Photograph by P. Rowlands (Jan. 1986).

ticeable at the northeastern corner of the south pool (Figure 13B). During most of the year Badwater has no outflow. HUNT *et al.* (1966) estimated total discharge as 0.63 L/sec; water temperature at one of the spring sources was 17.0°C. Badwater is virtually saline, with total dissolved solids averaging about 23,000 ppm (HUNT *et al.*, 1966). Aquatic vegetation consists of dense stands of ditch-grass (*Ruppia* sp.), which are most common in the north pool. Pickleweed (*Allensolfia occidentalis*) fringes parts of both pools. The perimeter of the north pool is largely fringed by a salt-crust roof overhanging (sometimes just touching) the water's edge by 5–10 cm (Figure 13C). The south pool perimeter has been trampled down over the years by

tourist activity and a salt-crust roof is currently restricted to the southeastern portion of the pool and seep inflows to the pool. *Assimineea infima* is most common on the undersides of the salt-crust roof (Figure 13D), where the snails are moistened and sometimes submerged. Snails were removed and counted from a few measured pieces of salt crust fringing the north pool (23 February 1985), yielding densities ranging up to 6748/m². Snails also occur under emergent offshore salt-crust pieces, on submerged drift-grass, and on moistened pickleweed roots in shaded situations. As much as 70–80% of the total Badwater population dwells in the north pool, with the density highest on the northern side of the pool where algal growth is low

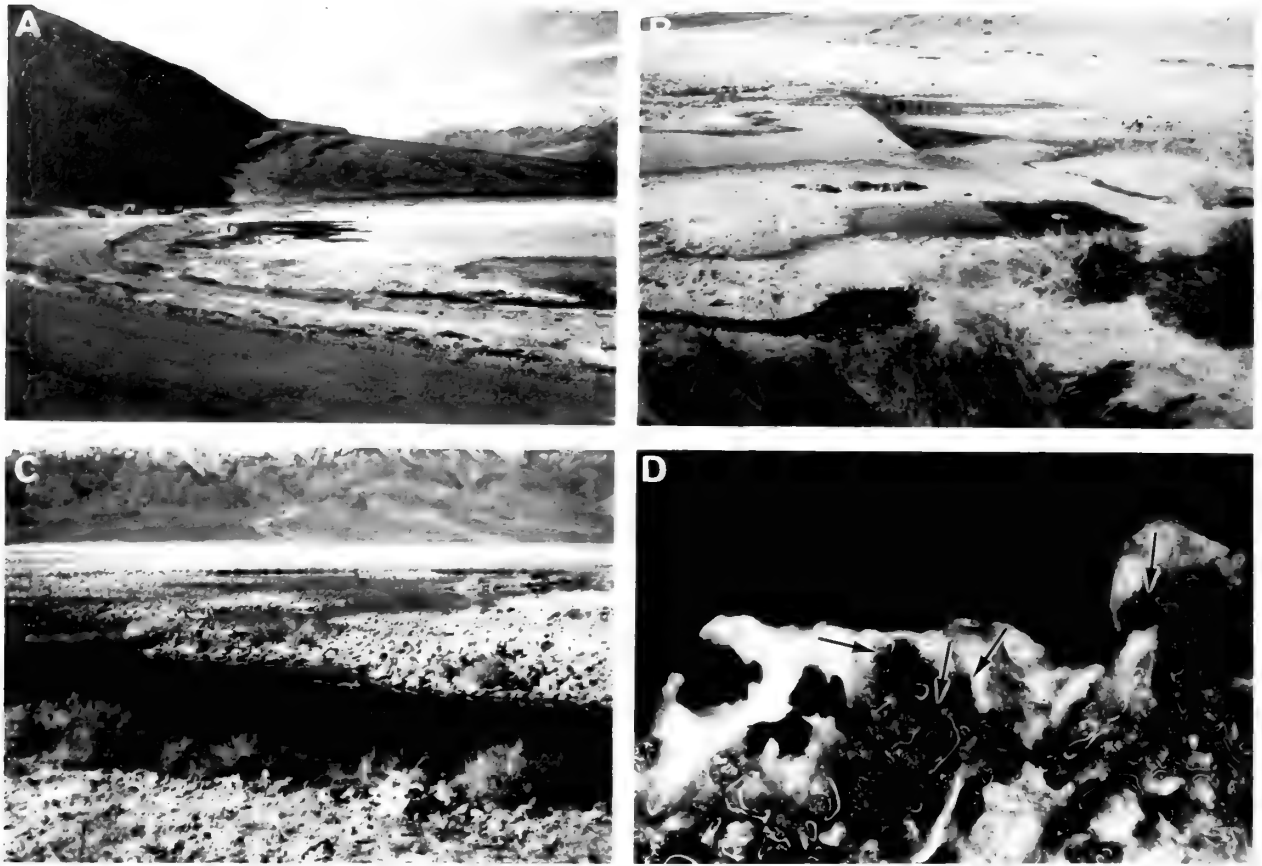


Figure 13

Badwater Spring. A. North (right) and south (left) pools (16 Feb. 1985). B. Seeps (3 cm across) feeding the south pool (23 Feb. 1985). C. North pool, with fringing salt crust and occasional pickleweed (16 Feb. 1985). D. Underside of salt-crust roof at north pool (piece measuring about 13 cm across), showing *Assimineia infima* (indicated by arrows). Photograph (Jan. 1986) by P. Rowlands.

and spring inflow probably occurs. Additional details of *A. infima* ecology at Badwater can be found in BERRY (1947) and TAYLOR (1981).

Travertine Springs: Travertine Springs emerge from low travertine mounds as a series of thermal (30–32°C) rheocrenes draining into Furnace Creek Wash. The springs are fairly small, with outflows typically 0.5 m across and 1–5 cm deep. The spring water is much softer than that at Badwater, with total dissolved solids of 640 ppm (HUNT *et al.*, 1966). Dense sedge growth fringes the outflows (Figure 14B), shading much of their length. One of the larger springheads has been partly capped and the lower reaches of the streams now collect into diversion works. *Assimineia infima* is uncommon at Travertine Springs, with occasional individuals found in moistened masses of living and dead sedges along the stream outflows. This habitat is quite limited at Travertine Springs as the extent of sloping banks, which provide a moistened riparian environment, is minimal.

Neavares Springs: Neavares Springs emerge from a large travertine mound as thermal (30–35°C) rheocrenes, coalescing to form a single stream flowing along a wash (Figure 14C). The shallow (less than 6 cm) spring outflows occupy either narrow (about 0.5 m) incised channels or fan out as broad (3 m) streams. Riparian sedges are common along the streams on the mound, but are absent from the well-scoured wash. The largest spring has been capped, and at least one springhead was dug out in the past in an effort to increase discharge. *Assimineia infima* is moderately common in dense, moistened riparian vegetation lining the sides of upper spring outflows; no specimens were found along the stream in the wash.

Cottonball Marsh: Cottonball Marsh occupies a large (about 2.56 km²) area on the west side of Death Valley. Salt Springs emerge west of the marsh and flow into large pools, which drain into the marsh farther out on the salt pan. Additional springs emerge on the salt pan in the middle of Cottonball Marsh (Figure 14A). HUNT *et al.*

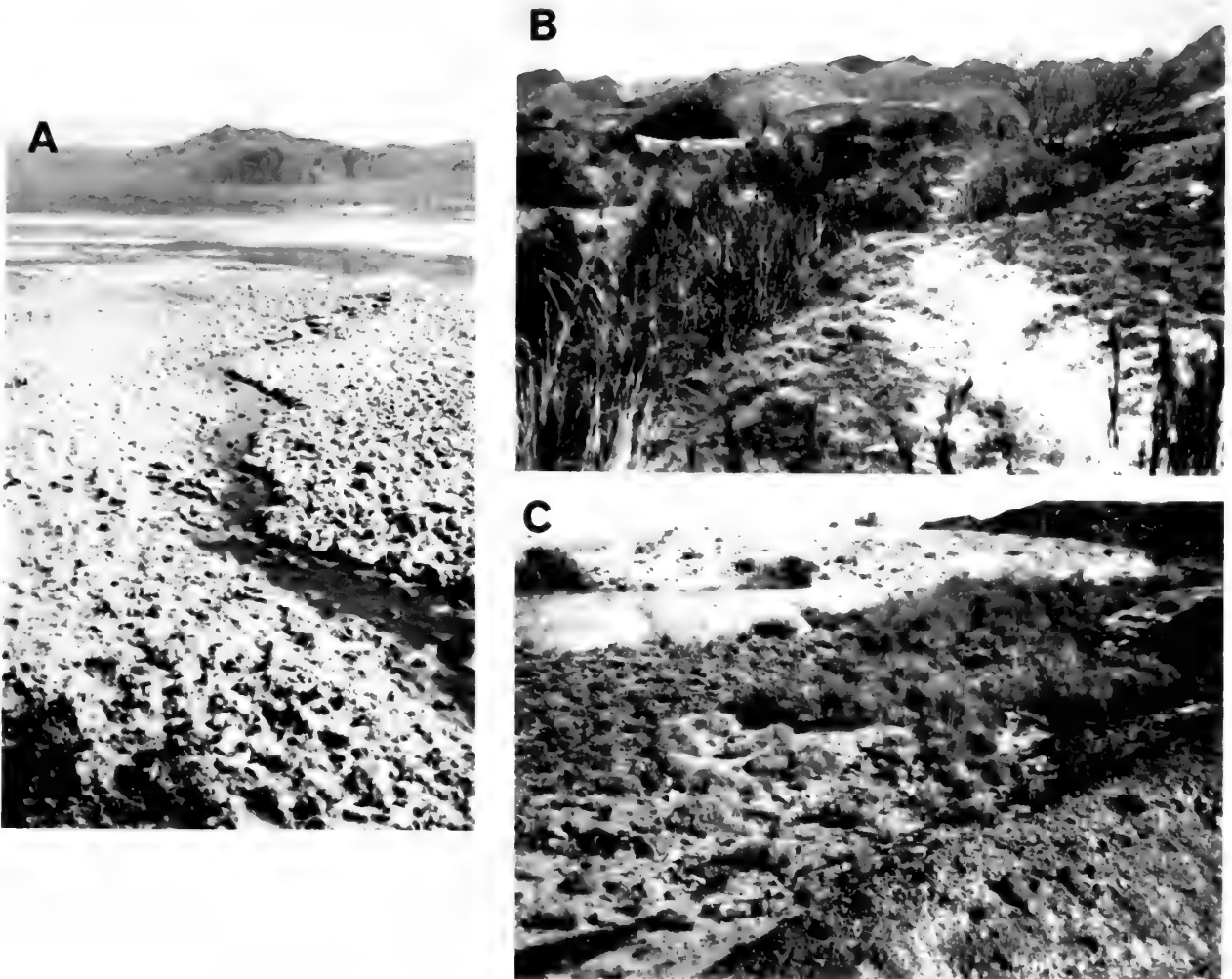


Figure 14

Assimineia infima localities. A. Spring brook (0.5 m across) flowing eastward (away from viewer) in Cottonball Marsh (22 Feb. 1985). B. Outflow of Travertine Springs, with dense riparian cover (2 Feb. 1985). C. Nevares Springs (1 Feb. 1985). Springs emerge on large travertine mound in background.

(1966) estimated the total discharge of the marsh to be 44 L/sec. Spring inflows to the marsh are thermal (31°C) and the marsh is saline, with total dissolved solids ranging from 14,000 to 160,000 ppm (HUNT *et al.*, 1966; LABOUNTY & DEACON, 1972). Water depth varies from less than 1 cm to nearly 1 m in the deep pools. As at Badwater, a salt crust covers much of the marsh and forms a fringing roof at the water's edge in many places. Saltgrass (*Distichlis* sp.) and pickleweed are common only at Salt Springs; the remainder of the marsh is almost entirely devoid of vegetation. Cottonball Marsh is in a remote portion of Death Valley rarely visited by people and remains in pristine condition. At Salt Springs *Assimineia infima* is common on the bases of moistened riparian vegetation and on the undersides of the salt-crust roof. Snails were not found

between Salt Springs and the point where additional springs emerge, about 1.6 km out onto the salt pan. At those latter springs, *A. infima* is very common under the salt-crust roof (moistened or submerged) fringing stream outflows, especially on algal-covered salt-crust pieces.

DISCUSSION

FOWLER's (1977, 1980) detailed study of *Assimineia californica* provides sufficient data for a morphological comparison with *A. infima*. Such a comparison is of interest as *A. californica*, found in the upper intertidal along the Pacific coast from Puget Sound to the Gulf of California (TAYLOR, 1981), is the geographically closest coastal representative of the genus to Death Valley, located 280 km

inland. The two species can be placed in ABBOTT's (1958) *A. nitida* complex, a worldwide group of small, translucent- and brown-shelled taxa. The two taxa are further united by joint possession of an unusual character-state, fusion of the left pleural and suboesophageal ganglia. Such a character-state is neither seen in Atlantic coast *A. succinea* Pfeiffer, 1840 (MARCUS & MARCUS, 1965:figure 34) nor is its presence mentioned in discussions of the nervous system of *Assiminea* found in ABBOTT (1958:223) and FRETTER & GRAHAM (1962:313). A number of morphological differences do separate these two species (Table 2), the most significant of which involve the pallial-cavity complex. The hypobranchial gland of *A. infima* is quite reduced in areal extent relative to that of *A. californica*, whereas the latter lacks the pallial swelling near the anus (FOWLER, 1977; Hershler, personal observation). Despite these differences it appears likely that the two species are closely related.

The systematics of *Assiminea* in the Death Valley region is by no means resolved in this paper. Snails from additional localities in Death Valley and nearby areas do differ from *A. infima* somewhat in terms of size and shell features. The rarity of *Assiminea* at most of these localities has thus far precluded the collection of samples large enough to allow the detailed morphometric study necessary to resolve the systematic status of these populations.

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Redescription of *Bela ampla* Smith, 1884 (Gastropoda: Turridae)

by

ØYSTEIN STOKLAND

Rogaland Research Institute, Department of Water Research,
Box 2503, 4001 Stavanger, Norway

Abstract. In the course of systematic work on the turrid group *Bela* auct., comprising the genera *Bela* and *Lora*, I examined the holotype of *Bela ampla* Smith, 1884. The only record in the literature of the species is the original description, which is without any illustration and is phrased mostly in comparative terms. A redescription of this species is provided.

INTRODUCTION

THE TURRID GASTROPOD GROUP *Bela* auct. includes a large number of species of similar appearance, many of which have great intraspecific variation. This has led to taxonomic chaos. As such the group *Bela* auct. comprises species in the genera *Bela* and *Lora*, misnamed by several authors, including G. O. SARS (1878) and DALL (1919).

In the course of a systematic study of the group in the northeast Atlantic, types of all species described from the Arctic and Atlantic oceans have been borrowed. In addition, all systematic descriptions of members of the group published earlier than 1884 have been studied and the types borrowed. During the work, descriptions of all Pacific species have also been considered, and material from Scandinavian museums has been studied.

As the species *Bela ampla* Smith, 1884, has been overlooked since the time of its description, and because the original description of this species is without an illustration and is mostly phrased in comparative terms, there is a clear need for redescription. This redescription is based on the holotype of *Bela ampla* (Figure 1) which was borrowed from the British Museum (Natural History), reg. no. 198230.

DESCRIPTION AND REMARKS

Description

Compared with related species the shell is large, 17 mm in height, ovoid, and with a relatively low, eroded spire. The body whorl is large, ventricose, and somewhat eroded with a very weakly angled shoulder and straight sides. The color is pale yellowish gray.

Sculpture on body whorl consists of faint, straight,

somewhat distant irregular folds that are somewhat oblique to the suture and reach about half-way down to the canal. The folds have a low angular profile and reach the columella above the aperture. On the penultimate whorl the axial elements are strong, straight, angular ribs at right angles to the suture, rather close and regular, and extending to the suture. The concentric sculpture consists of broad transverse ribs with narrow incised lines. On the body whorl the transverse ribs vary in width, and the incised lines are somewhat irregular. On the penultimate whorl, the concentric sculpture is more regular.

The aperture is elongate-oval, with a thin, evenly curved outer lip. The lip joins the body whorl at a right angle, without any anal sinus. The columella is curved in the middle and rather straight posteriorly and near the canal. The canal is short and broad, with a slight angle where it meets the outer lip.

Remarks

The most pronounced character of *Bela ampla* is the large body whorl. Within *Bela* auct., this character is typical of a relatively well-defined group to which BARTSCH (1941:4) gave generic status and named *Obestoma*. Another common character of these species is the eroded apex in adult specimens.

The lack of an anal sinus also links the species to *Obestoma*, or even to *Propebela* Iredale, 1918. The latter genus, however, generally has angled shoulders, a relatively small body whorl, and prominent axial ribs. Large shells like *Bela ampla* are also more common in *Obestoma* than in other groups of *Bela* auct. Therefore, taking everything into consideration, it seems justifiable to include the species in *Obestoma* Bartsch, 1941.

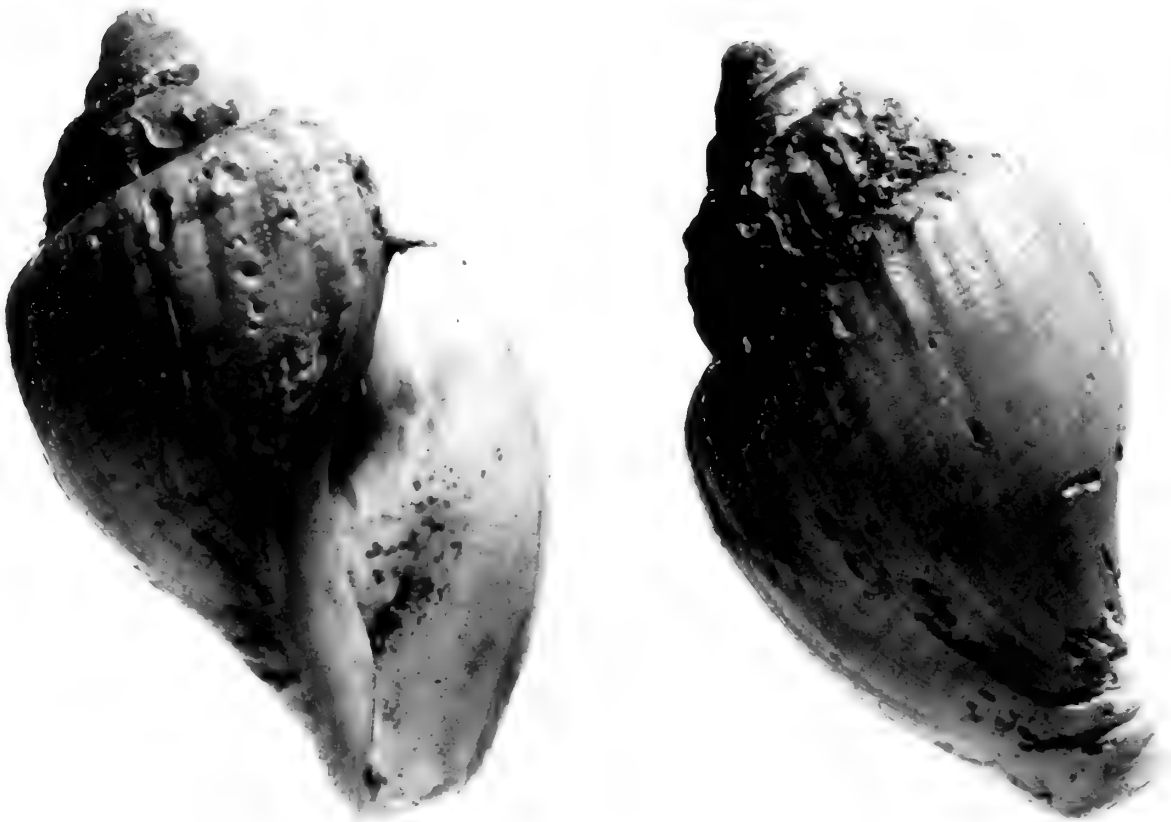


Figure 1

Bela ampla Smith, 1884, holotype. $\times 8$.

The sculpture, which is a rather important character within *Bela* auct., has a rather unusual appearance in *Bela ampla*. Compared with other species of *Obestoma*, it has much in common with *O. gigantea* (Mørch ex Leche, 1878) (= *Pleurotoma violacea* var. *gigantea* Mørch ex Leche, 1878). In this species however, the axial and concentric elements of the sculpture are more similar to one another, thereby giving the sculpture a more regularly reticular appearance. This regularity is even more marked in the two Arctic-Pacific species *O. tenuilirata* (Dall, 1871) and *O. murchisoniana* (Dall, 1885). The two circumarctic species *O. schantarica* (Middendorff, 1849) and *O. simplex* (Middendorff, 1849) have both distinctly narrower concentric elements and less prominent axial elements, if any, on the body whorl.

The fact that the axial ribs are stronger on the penultimate whorl than on the body whorl indicates that young individuals probably have a rather different appearance from that of adults. In this respect the species is similar to *Obestoma schantarica* (Middendorff, 1849), and proba-

bly also to *O. gigantea* (Mørch ex Leche, 1878) in which the body whorl in adults is weakly sculptured and young individuals have prominent axial ribs.

Type Locality

The habitat for *Bela ampla* was given by SMITH (1884) as the Arctic Ocean. This locality is also given in another handwriting on the original label: "Bering Straits?—coll. by Capt. Maclure?" This note was probably added later (K. Way, personal communication). The label also indicates that the holotype was purchased from Damon. The indication of the Bering Straits, or at least the Pacific side of the Arctic, is probably correct as *Bela ampla* is not recorded from the relatively well investigated Atlantic Ocean.

ACKNOWLEDGMENTS

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holotype of *Bela ampla* Smith, 1884. Further, I am indebted to Dr. Jon-Arne Snøli, Biological Station, University of Trondheim, Dr. Anders Warèn, Swedish State Museum, Stockholm, and Mr. George Crawford, Grendon, Northampton for advice and critical remarks. Mr. Crawford has kindly corrected my English text.

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Description of a New Pleurobranch (Opisthobranchia: Notaspidea) from Antarctic Waters, with a Review of Notaspideans from Southern Polar Seas

by

RICHARD C. WILLAN

Department of Zoology, University of Queensland, St. Lucia,
Brisbane, Queensland 4067, Australia

AND

HANS BERTSCH¹

Department of Biological Sciences, National University,
San Diego, California, U.S.A.

Abstract. This paper describes the first side-gilled sea slug from Antarctica—*Bathyberthella antarctica*, spec. nov. It is unusually large for a member of its group and distinguished externally by its remarkably large foot and dark gray, blotched markings. Anatomically it compares closely to the abyssal *B. zelandiae* Willan, the only other species of the previously monotypic genus. The chief differences relate to body size, proportions of the foot, shell, and reproductive system. *Bathyberthella antarctica* has secondarily lost its penial gland. Three other species of the Pleurobranchidae, all belonging to the genus *Berthella*, occur in Subantarctic waters: *B. patagonica* (Orbigny), *B. platei* (Bergh), and *B. medietas* Burn.

INTRODUCTION

WITHIN THE OPISTHOBRANCH order Notaspidea, the greatest diversity of genera and species occurs in tropical seas and very few taxa exist in polar waters—indeed the genera *Tylodina*, *Tylodinella*, *Umbraculum*, *Pleurobranchus*, *Berthellina*, *Pleurehdera*, *Euselenops*, *Pleurobranchaea*, and *Pleurobranchella* are completely absent. Hitherto only three species of *Berthella* (*B. patagonica*, *B. platei*, and *B. medietas*) have been reported authentically from Subantarctic waters. Two species of *Pleurobranchaea* (one

unidentified and *P. maculata*) have distributions whose southern limits impinge upon Subantarctic waters. This present work adds one additional genus, *Bathyberthella*, to the list of southern polar taxa, and the new species, *B. antarctica*, has the most southerly distribution of any recorded notaspidean species. Actually it is the only species of the order that could be termed truly Antarctic. Because of this species' novel locality and phylogenetic importance, we wish to describe it in a separate paper and, in doing so, review the known notaspideans from adjacent Subantarctic waters.

Fifteen specimens of this new notaspidean were located among a collection of opisthobranchs procured under the auspices of the United States Antarctic Research Program (USARP). The entire marine faunal collection, which was

¹ Mailing address: 6056 Beeman Avenue, No. Hollywood, CA 91606, U.S.A.

dredged by the Antarctic Research vessels *Hero*, *Islas Orcada*, and *Eltanin* between the years 1962 and 1983, has been curated by the Smithsonian Oceanographic Sorting Center of the United States National Museum. The 456 specimens constituting the opisthobranch collection represent six major taxonomic groups: cephalaspideans, notaspideans, gnathodorids, cryptobranch dorids, dendro-notaceans, and aeolids (BERTSCH, 1985).

TAXONOMY

Genus *Bathyberthella* Willan

Type species, by original designation, *Bathyberthella zelandiae* Willan, 1983.

Bathyberthella antarctica Willan & Bertsch, spec. nov.

Figures 1a, 2–17

Description: Only preserved specimens were available for study. They ranged between 65 and 93 mm so, assuming a reduction in size of about one-quarter due to contraction on death, we believe the maximum extended crawling length for an adult would be approximately 120 mm. The mantle is ovate or elliptical in shape and slightly convex dorsally; the anterior margin is truncate and straight across; the two sides are parallel; the posterior margin is broadly rounded. The mantle is free from the underlying foot all round and much smaller than the foot, particularly posteriorly. This important character is illustrated diagrammatically in Figure 2. The mantle's surface is smooth, somewhat puckered and wrinkled posteriorly and laterally (possibly through contraction on death), but not pustulose. The foot is very large, thick, and spongy, and from above its edges are visible all round in all our specimens. Like the mantle, the upper surface of the foot is puckered and wrinkled posterior to the mantle, but it is not in the least pustulose. The sole of the foot has a very large, circular, thickened pedal gland posteriorly; its borders are not sharply marked off from the surrounding tissue on the tail's ventral surface. The front edge of the foot bears an extensive, semicircular mucous-gland groove dorsally. The point of fusion of the moderately short, widely diverging rhinophores is visible in front of the mantle in some of our specimens, but this is probably not the situation in life. The trapezoidal oral veil is as broad as the mantle; its anterior margin, which is almost straight across, is neither notched nor papillate; the longitudinally grooved sides extend, as tentacular extensions, a short distance anterolaterally. The gill is prominent, although its rear end does not extend to level with the hind end of the mantle. Its rachis is relatively narrow and entirely smooth, there being 17–21 (mean = 19.9) pinnae on (the upper side of) the rachis. The gill is free for about one-half its length, and the anus opens on the upper side of the gill at the hind end of the basement membrane.

The body is uniformly creamish gray in color with the

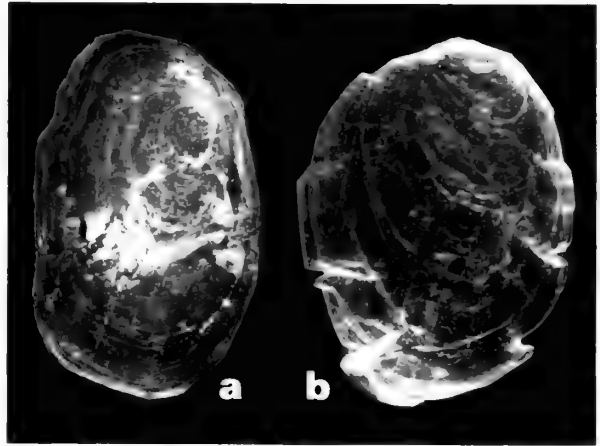


Figure 1

External view of shells of paratypes of *Bathyberthella* species. a, *B. antarctica*; length 63 mm × width 39 mm. Specimen from 360 to 480 m, west of South Sandwich Islands, Scotia Sea, Antarctica, 30 May 1975. Preserved length 70 mm; b, *B. zelandiae*; length 23 mm × width 18 mm. Specimen from 1676 m, northern side of Bounty Trough, New Zealand, 26 Oct. 1979. Preserved length 30 mm.

upper surface of the foot being paler than the mantle. The mantle itself is covered with extensive areas of dark pigment that are distinguishable as irregular blotches centrally and become confluent marginally. This darker pigment is not easily rubbed off. No specific markings are recognizable on the sides of the body, rhinophores, oral veil, or gill.

A shell (Figure 1a) was present beneath the mantle in all the specimens examined. It is large (e.g., 63 × 39 mm in a specimen of 70 mm preserved length). The shell roofs the entire visceral cavity. There are no muscles attached to it and neither is it connected to the body wall or underlying integument. The shell is cuticular, thin, and fragile, and little more than a flexible membrane. It is easily deformed in any direction. All the shells possessed some vestigial calcification, merely a patch of thin white flakes, near the center a little to the right of the midline. The shape is oval to elongate with the greatest width nearer the anterior end than at the center; the anterior margin and posterior flange are both broadly rounded; and the lateral margins are slightly wavy and diverging. The protoconch is situated toward the posterior left corner, but not at the margin (i.e., it is subterminal) and there is an extensive posterior flange to the right of, and behind, it. The shell itself is virtually flat with concentric growth lines constituting the only sculpture. It shows localized crumpling caused by compression of the overlying mantle during fixation. It is shining, hyaline centrally, and faintly golden toward the margins.

The heart, which lies transversely, is located beneath

Table 1
Radular data for *Bathyerthella antarctica*.

Specimen no.	No. rows	Formula	Preserved length (mm)
1	86	250.0.250	71
2	71	207.0.207	70

the shell's anterior margin a short distance behind the base of the rhinophores. The spherical, thick-walled ventricle is in the midline, and the conical, thin-walled auricle is situated immediately to its right.

The proboscis was everted in several specimens and this cylindrical, muscular introvert was moderately long, being about equal to the pharyngeal bulb in length. The pharyngeal bulb (Figure 3) has a sharp, oblique ridge on either side, and the single, tubular, dorsal accessory gland enters in the midline anteriorly at the front of the pharyngeal bulb. This gland is remarkably long (measuring about 250 mm when fully unravelled), with thinner walls and a greater diameter (approximately 1 mm) than the salivary glands. It is packed initially on the floor of the visceral cavity beneath the digestive gland on the right side, and then is further stacked at the top left corner. At no point along its length does it branch. The two extrinsic pharyngeal-bulb retractor muscles originate as one from the roof of the visceral cavity in the midline at the center of the body.

Radulae from two specimens were examined. Their formulae, together with the preserved length of each animal, are given in Table 1.

All the teeth are rather large and of simple form. Each consists of an erect, tall, parallel-sided blade that tapers gradually to a slightly recurved, sharp-pointed apex. The inner laterals (Figures 4a, b, 10) are relatively short (with a mean vertical height of 228.6 μm) and relatively broad; often the middle region of the outer face of the blade has one or two undulations (Figure 4b); the base is enlarged and triangular. The middle and outer laterals (Figures 4c, d, 11, 13, 14) are proportionately longer and narrower (with a mean vertical height of 292.9 μm). The outermost lateral teeth (Figures 4e, 12) are smallest, broader, and more curved than the inner or middle laterals, and none of the outermost laterals is reduced or peglike.

The two jaws (Figure 5) that line the pharyngeal bulb are large, elongate, and rather thin. The maximum length of a jaw, when flattened on a slide, is 14 mm and this corresponds to a width (measured between the parallel sides of the jaw, not at the anterior margin) of 6 mm. Each jaw is parallel-sided, with the anterior end much expanded and truncate where it curves back to join the labial cuticle. The jaws are composed of numerous, crowded mandibular elements that are irregularly grouped into wide, longitudinal rows with bare strips between them.

The mandibular elements themselves (Figures 6, 15-17) are narrow and elongate, and there is no indication of lateral processes on the sides of any of them (*i.e.*, the elements are not cruciform). At the surface of the jaw, the elements bear 1, 2, or 3 (rarely 4 or 5), sharp, conical cusps; all are well cuticularized. Rarely, subdenticles (*i.e.*, subsidiary points) are present on the sides of a few of the cusps (Figure 17). Generally, one stronger cusp is situated in advance of the others, but rarely all are in a line and each is of equal strength to all the others. These cusps project on the jaw's surface in wavy, frequently discontinuous, transversely oblique rows, and they are sometimes disorganized. The number of cusps on any one particular element seems to have no relationship with the numbers possessed by the element next to it.

The genital organs emerge, in preserved specimens, from a relatively large swelling and from this projects a high, raised ring of skin that forms a continuous circle around the everted genitalia.

The reproductive system of a mature individual occupies the bulk of the space within the visceral cavity. The ovotestis, which lies above and obscures the digestive gland, takes up the whole rear half of the visceral cavity. The anterior genital complex occupies the right front section. Three organs of the anterior genital complex are immediately visible from above: a bulky mucous gland at the back, a muscular vagina sandwiched in the middle, and the prostate gland at the front. The hermaphrodite duct passes, as a tubular ampulla, between the ovotestis and anterior genital complex dorsally close to the right body wall. The ampulla maintains its diameter throughout its considerable length and only constricts where it enters the anterior genital complex from the left side immediately behind the bursa copulatrix. The hermaphrodite duct runs, as a slender tube, through the middle of the genital complex; it gives off a short side branch (the proximal vas deferens), and then swells slightly before entering the nidamental glands.

The proximal vas deferens enlarges almost immediately to an enormous prostatic section (Figure 7). This section is uniformly glandular throughout its entire length, folded back upon itself, compressed, and closely applied to the ventral (*i.e.*, inner) surface of the bursa copulatrix. Ultimately, it narrows to a tightly coiled distal vas deferens which, without any appreciable change in diameter or presence of penial gland, eventually passes into the penis within a globular and muscular penial sheath. The penis is conical, elongate, and smooth, and it narrows evenly to an acutely pointed tip. Its interior possesses the vas deferens and numerous retractor muscles (Figure 8).

Immediately behind the penis is the vagina. This muscular canal, which tapers gradually along its length, leads straight to a large, spherical bursa copulatrix. Another duct of a slightly smaller diameter (the uterine duct) leads away from the base of the bursa, and a short distance along its length (approximately 8 mm) is a separate canal

to the receptaculum seminis. This is a small, fingerlike organ of uniform diameter that lies beside the bursa and next to the nidamental glands; it never reaches the surface of the genital mass. After that, the uterine duct continues via a great many sinuous loops (that are narrower than the section between the bursa and receptaculum) to enter the nidamental glandular complex at almost exactly the same point the hermaphrodite duct terminates.

The nidamental glands are enormous in a sexually mature animal. Two regions are discernible; a thin-walled, hollow mucous gland, whose walls are regularly pleated, that occupies the entire posterior face and a more solid area (consisting of possibly more than one gland) of closely packed, solid tubules. This is probably the albumen gland. These glands are not shown in Figure 9 because their gelatinous nature rendered the drawing of an exact outline impossible. Figure 9 represents a diagrammatic view of the structure of the reproductive organs in which omission of the nidamental glands could give the unintentional impression of a diallic condition. This is not the arrangement, as there are three quite separate canals (*i.e.*, vas deferens, oviduct, and uterine duct) within the pallial gonoduct.

Material examined: Holotype: 85 mm long (*i.e.*, length from anterior edge of oral veil to tip of tail) \times 54 mm wide (*i.e.*, maximum mantle width); 360–486 m depth, 56°40.6'S, 27°00.8'W, west of South Sandwich Islands, Scotia Sea, R/V *Islas Orcada* (cruise 575; station no. 62), 30 May 1975. United States National Museum of Natural History, Reg. No. USNM 859009.

Paratypes: Specimens collected with the holotype at station no. 62, undissected specimens dispersed as follows: 2 specimens, 93 mm long \times 59 mm wide and 78 mm long \times 50 mm wide, United States National Museum of Natural History, Reg. No. USNM 859010; 2 specimens, 74 mm long \times 47 mm wide and 54 mm long \times 32 mm wide, Los Angeles County Museum of Natural History, Reg. No. 2120.

Two specimens, 128–165 m depth, 63°50'S, 62°35'W, west of Graham Land, Antarctica, South Pacific Ocean, R/V *Eltanin* (cruise 6; station no. 439), 9 January 1963, both undissected, dispersed as follows: 1 specimen, 88 mm long \times 52 mm wide, California Academy of Sciences, Reg. No. CASIZ 057393; 1 specimen, 78 mm long \times 55 mm wide, Australian Museum, Sydney, Reg. No. C145497.

Remarks: Several of the characters of *Bathyberthella antarctica* merit comment. First of all is the size attained by adults. Although we have not seen a live specimen, we estimate the extended length of an adult would be approximately 120 mm. This size makes *B. antarctica* much larger than its single congener, *B. zelandiae* Willan, or any member of the three most closely related pleurobranch genera, *Berthella*, *Berthellina*, and *Pleurehdera*. In fact, it means *B. antarctica* falls within the size range of

species of *Pleurobranchus* (which attain between 60 and 300 mm crawling length as adults) and thus rekindles the old question of the natural subgroups of pleurobranchine pleurobranchs. (The debate, and resulting conflicting classifications of ODHNER [1926] and BURN [1962] were summarized by WILLAN [1983].) However, the large size of *B. antarctica* poses no real challenge to the now accepted scheme of Burn, because it is the only character *B. antarctica* shares with *Pleurobranchus* species. None of the other apomorphies of *Pleurobranchus* (*i.e.*, tuberculate mantle, mid-anterior mantle cleft, or flaps surrounding the genital aperture) is possessed by *Bathyberthella antarctica*. Therefore, this new species actually reinforces Burn's scheme, later supported by WILLAN (1983), that the Pleurobranchinae is divided naturally into two subgroups. Each should be ranked as a tribe. One tribe, Berthellini Burn, 1962, consists of "smaller" species with a non-tuberculate, non-emarginate mantle, and (usually) smooth gill rachis, and the other, Pleurobranchini Menke, 1828, consists of "larger" species with tuberculate, emarginate mantle, and pustulose gill rachis. Further evidence in support of these groupings has recently come from investigations of sperm ultrastructure (HEALY & WILLAN, 1984). *Bathyberthella antarctica* is the largest member of the former tribe. It exhibits gigantism, a common phenomenon among Antarctic biota (CALMAN & GORDON, 1933; PECKHAM, 1964; HARTMAN, 1966; WOHLSCHLAG, 1968; KOLTUN, 1970).

In pleurobranchs, the relative proportions of the mantle and foot change depending on the state of activity of the specimen. When one is crawling actively, the tail of the foot usually extends behind the mantle and at rest the foot tucks up beneath the mantle. The very large foot of *Bathyberthella antarctica* is surely an exception and, in life, it must extend beyond the mantle at all times. In one of our preserved specimens, the foot exceeded the mantle by 20 mm posteriorly. Possibly the substratum on which *B. antarctica* lives has necessitated this enlargement. Could it be that the foot now prevents this relatively large pleurobranch from floundering when it is crawling over fine muds?

One of the specimens collected in 1963 (C145497) has several forked pinnae on the upper side of the rachis near the end of the gill. The bifurcation commences high up near the point of origin from the rachis. We have never observed any bifurcation of pinnae like this previously in the Notaspidea. We are confident this configuration is the result of a mutation of the particular individual and not an aberration resulting from a previous injury or artifact of collection.

As is typical for the genus, *Bathyberthella antarctica* has a large number of teeth within radular rows but there is little differentiation (of size or shape) of teeth within the row.

The reproductive system is peculiar for the enormous development and bulk of the ovotestis, occupying as it does

Table 2
Comparison of character states between the two species of *Bathyberthella*.

Character	<i>B. antarctica</i> , spec. nov.	<i>B. zelandiae</i>
Maximum size (extended crawling length)	120 mm	40 mm
Color of mantle in life	Creamish gray with extensive areas of dark pigment, as blotches, centrally and more or less continuous marginally	Uniform translucent cream marked with small, vague white flecks and speckles; yellow spots occasionally present
Position of protoconch on shell	Subterminal (Figure 1a)	Terminal (Figure 1b)
Mean number of rows of teeth for adult	78.5	62.2
Mean number of teeth per row for adult	228.5	217
Penial gland	Absent	Present
Retractor muscle attached to vagina	Absent	Present

the entire back half of the visceral cavity. This increased gonad area could indicate extremely high fecundity. In addition to the magnitude of the ovotestis, the nidamental glands are also disproportionately large. The most important specific character as regards the reproductive system is the absence of a penial (sometimes referred to as accessory prostate) gland. This gland is present in *Bathyberthella zelandiae* and every species belonging to the three most closely related genera (*Berthella*, *Berthellina*, and *Pleurehdera*) that has been examined anatomically. We conclude the absence of the penial gland in *B. antarctica* is the result of loss. One can speculate that a section of the considerably enlarged prostate gland has taken over the function of the penial gland.

The discovery of a second species of a previously monotypic genus is always a special event for a systematist because of the foresight involved in erecting such a new taxon in the first place. Thus, the discovery of *Bathyberthella antarctica* is both gratifying and remarkable, and made all the more so by the significant place presently occupied by *Bathyberthella* within the family Pleurobranchidae (WILLAN, 1983). Willan initially suggested that this genus possessed characters linking the two subfamilies (Pleurobranchinae and Pleurobranchaeinae) of the Pleurobranchidae, but it is now apparent that *Bathyberthella* belongs in the Pleurobranchinae. However, we maintain strongly that the two higher taxa are subfamilies and not families as some taxonomists continue to do (e.g., EV. MARCUS & GOSLINER, 1984). Characters apparently possessed jointly by *Bathyberthella* and members of the Pleurobranchaeinae (specifically regarding the mandibular elements on the jaws) must now be reinterpreted in some way other than owing to retention of the plesiomorphic condition.

Bathyberthella antarctica and *B. zelandiae* both possess (1) a smooth mantle and gill rachis, (2) a very large, flexible, cuticular shell, (3) numerous, narrow, erect, smooth radular teeth, (4) oval or elliptical mandibular elements that lack lateral processes and have an irregu-

larly denticulate anterior margin, (5) a triaulic reproductive system with vas deferens extensively dilated into a prostate gland, (6) a smooth penis, (7) a globular penial sheath, and (8) two allosperm receptacles. The particular character states for the shell, radula, and mandibular elements are synapomorphies that together justify the continued recognition of *Bathyberthella* as a valid genus.

On the other hand, the two species possess several dissimilar characters that irrefutably separate them. Those characters existing in clearly different states are summarized in Table 2. Chief among them are the last two that involve the reproductive system, the more notable being the lack of a penial gland in *Bathyberthella antarctica*. In that species, the prostate gland is relatively more extensive, the uterine duct is longer, and the receptaculum seminis does not come directly off the base of the bursa copulatrix but instead it begins a short distance (approximately 8 mm) down the bursal stalk. Apart from those to do with the reproductive system, two other characters are evident, both involving relative proportions of the body. One concerns the mantle and foot; in *B. antarctica* the mantle is much smaller than the foot all round, whereas in *B. zelandiae* the mantle is only a little shorter than the foot at the rear. The other character is the length of the extended proboscis; this structure is shorter in *B. antarctica*, being able to evert for about 10 mm in an adult, whereas in *B. zelandiae* it can be protruded for a distance equal to half the body length.

REVIEW

For over a century and a half, international expeditions have been sampling southern polar (i.e., Antarctic and Subantarctic) oceans and so the benthic fauna is reasonably well known today. The mollusks have arguably received the most attention and, among them, the opisthobranchs have been amply covered. Usually opisthobranchs are neglected on non-specific sampling voyages because of difficulties inherent in preserving them. An extensive lit-

erature search has been made to review what is known about Antarctic and Subantarctic notaspidean opisthobranchs and the results are presented here.

We preface this review by explaining that we follow DELL's (1962) subdivision of southern polar waters into three more or less concentric zones (High Antarctic, Antarctic, and Subantarctic) and five biogeographic regions (Continental Antarctic, Magellanic, Tristan da Cunha, Kerguelenian, and South Georgian District). Dell argues strongly and cogently against the need for, or validity of, marine faunal provinces (*e.g.*, DELL, 1962, 1972). We find much to support in his plea for distributional data instead of more marine provinces.

Knowledge of the southern polar opisthobranch fauna has been gained from the following expeditions and investigators (*i.e.*, only those researchers who actually reported on opisthobranchs): A. d'Orbigny's explorations in southern America, for which he documented the opisthobranchs himself (ORBIGNY, 1835-1846); the *Challenger* expedition (1873-1876) documented by WATSON (1886); L. Plate's expedition to South America documented by BERGH (1898); The Belgian Antarctic Expedition (1897-1899) documented by PELSENEER (1903); a Falkland Islands collection documented by ELIOT (1907a); the Swedish South Polar Expedition (1901-1904) documented by STREBEL (1908) and ODHNER (1926); the German South Polar Expedition (1901-1903) documented by THIELE (1912); the Scottish National Antarctic Expedition (1901-1904) documented by ELIOT (1905, 1907b); the French Antarctic Expeditions (1903-1905 and 1908-1910) both documented by VAYSSIÈRE (1906, 1917 respectively); the British Antarctic (*Terra Nova*) Expedition (1910-1913) documented by EALES (1923) and ODHNER (1934); the Australasian Antarctic Expedition (1911-1914) documented by HEDLEY (1916); Mortensen's Pacific Expedition (1914-1916) documented by ODHNER (1924); the Norwegian Antarctic Expeditions (1927, 1928 *et seq.*) documented by ODHNER (1944); the Discovery Investigations (1925-1939) documented by POWELL (1951); the British-Australian-New Zealand Antarctic Research Expedition (1929-1931) documented by POWELL (1957, 1958) with summaries and extensions to Subantarctic islands by POWELL (1955, 1960, 1965); the Lund University Chile Expedition (1957) documented by ER. MARCUS (1959); the 12th (1961-1963) and 15th (1964-1965) French Antarctic Expeditions documented by VICENTE & ARNAUD (1974); a Davis Sea collection documented by MINICHEV (1972).

The combined total of notaspideans from all of these investigations on opisthobranchs is a mere two species, both belonging to the genus *Berthella*. Each will be dealt with separately below. Two species of *Pleurobranchaea* from opposite extremes of the southern Pacific have distributions that could possibly impinge, at their southern limits, upon Subantarctic waters. *Pleurobranchaea maculata* (Quoy & Gaimard) is known from the southern New

Zealand mainland and southern Tasmania so, like *Berthella medietas* mentioned below, *P. maculata* may well occur at the Subantarctic islands to the south of New Zealand or Australia. Specimens of another species of *Pleurobranchaea* have been taken on two occasions near the Juan Fernandez Islands off the central Chilean coast (BERGH, 1898; ODHNER, 1922). This species may possibly have a Magellanic distribution with its range extending, in Subantarctic waters, down the west coast of South America. However, because of the uncertainty of existing records (all being based on juvenile specimens) and the impreciseness of BERGH's (1898) account, no one can be sure of the identity of this particular southeastern Pacific *Pleurobranchaea* species. BERGH (1898) called it *P. maculata* (Quoy & Gaimard) probably because that name was the only one established for any Pacific species (then known) belonging to *Pleurobranchaea*. VAYSSIÈRE (1901: 51) and EV. MARCUS & GOSLINER (1984) refuted Bergh's identification. Clearly no advance can be made until a thorough redescription of adults of this species is published.

Berthella patagonica (Orbigny, 1840)

Synonymy

Pleurobranchus patagonicus ORBIGNY, 1840 (date from RUSSELL, 1971): 203-205, pl. 17, figs. 4, 5; PILSBRY, 1896:200, 201, pl. 74, figs. 92, 93; BERGH, 1898:496-499, pl. 28, fig. 26, pl. 29, figs. 10-16.

Bouvieria patagonia (Orbigny): VAYSSIÈRE, 1898:289-291; CARCELLES & WILLIAMSON, 1951:312; ODHNER, 1926: 22.

Berthella patagonia (Orbigny): EV. MARCUS, 1984:50, figs. 2, 3.

The type locality for this pleurobranch is Ensenada de Ros on the southeastern coast of Argentina (41°S; *i.e.*, in the Magellanic Region). ORBIGNY's (1840) original description merely sketched the external features of this species, and it is apparent from his text (in particular the reference to the moundlike genital swelling and chalky nature of the shell) as well as from the illustration (especially the everted penis) that the account was prepared from preserved material. VAYSSIÈRE (1898) added nothing more when he wrote his comprehensive monograph on the Pleurobranchidae, but he did transfer the species to his new genus *Bouvieria*. BERGH (1898) had access to four specimens from Quiriquina in southern Chile and his account supplied many essential anatomical details. Because this species has apparently not been collected or reported on subsequently, our knowledge of its anatomy rests solely on the words of Bergh. This species undoubtedly belongs in the genus *Berthella* Blainville because of its small size, smooth and non-emarginate mantle, relatively large and rectangular shell, simple and curved radular teeth, and cruciform mandibular elements with denticulate blades. The color in life is, according to Orbigny, yellowish am-

ber: or translucent white with delicate yellowish tinges according to Bergh (*i.e.*, as reported in Plate's field notes). Unfortunately the two descriptions provide few significant characters that we can use to distinguish *Berthella patagonica* unambiguously from the thirteen other similar-looking, small pleurobranch species that occur elsewhere in the world, *i.e.*, *Berthella plumula* (Montagu), *B. aurantiaca* (Risso), *B. stellata* (Risso), *B. sideralis* (Lovén), *B. agassizii* (MacFarland), *B. strongi* (MacFarland), *B. tupala* Er. Marcus, *B. tamiu* Ev. Marcus, *B. americana* (Verrill), *B. platei* (Bergh), *B. pellucida* (Pease), *B. serenitas* (Burn), and *B. medietas* Burn.

Because *Berthella patagonica* was collected intertidally by Orbigny and Plate, it should be recollected without great difficulty. Hopefully a critical comparison will then be undertaken.

Berthella platei (Bergh, 1898)

Synonymy

- Pleurobranchus platei* BERGH, 1898:494-496, pl. 11, figs. 28-38; VAYSSIÈRE, 1901:77.
Bouvieria platei (Bergh): ODHNER, 1926:22, 24, pl. 1, figs. 6, 7; CARCELLES & WILLIAMSON, 1951:312.
Berthella platei (Bergh): ER. MARCUS, 1959:24-27, figs. 34-38.

The holotype was dredged in 18-34 m near Calbuco in southern Chile. ODHNER (1926) recorded a second specimen taken in 137-150 m on the Burdwood Bank west of Tierra del Fuego. Later ER. MARCUS (1959) provided further comparative data on 12 individuals that had been collected between 70 and 300 m off southern Chile. *Berthella platei* thus occurs in Subantarctic waters within the Magellanic Region.

The accounts of Bergh, Odhner, and Er. Marcus have provided a firm set of diagnostic characters by which *Berthella platei* can be defined. *Berthella platei* is, in life, pale and translucent pink with reddish-brown tinges on the mantle margin, oral veil, and rhinophores. Its large, circular, calcareous shell entirely roofs the visceral cavity. Its radula consists of simple, curved teeth and the cruciform mandibular elements possess three or four (either strong or weak) denticles on both sides of the blade. (Note, however, that BERTSCH [1975] AND WILLAN [1984] have shown that great intraspecific variability can exist in pleurobranchs' mandibular elements.) *Berthella platei* is unusual in that its anus opens above the anterior third of the gill basement membrane, the state also found in *B. medietas*. This character alone should provide a ready distinction between Magellanic pleurobranchs, even if only preserved specimens are available.

Berthella medietas Burn, 1962

Synonymy

- Pleurobranchus aurantiacus* Risso: BERGH, 1900:210-211, pl. 20, figs. 34-38 (non *Pleurobranchus aurantiacus* Risso, 1818).

Bouvieria (Pleurobranchus) aurantiaca (Risso): ODHNER, 1924: 51; POWELL, 1939:217, no. 1232 (non *Pleurobranchus aurantiacus* Risso, 1818).

Bouvieria aurantiaca (Risso): POWELL, 1955:118 (non *Pleurobranchus aurantiacus* Risso, 1818).

Pleurobranchus punctatus Quoy & Gaimard: BURN, 1957: 15 (non *Pleurobranchus punctatus* Quoy & Gaimard, 1832).

Berthella medietas BURN, 1962:135-137, 142, 146, pl. 1, fig. 3, pl. 2, figs. 7, 8, text figs. 1C, 2C (erroneously spelled *mediatas* on p. 142); MACPHERSON & GABRIEL, 1962: 252; BURN, 1966:271, no. 26 (erroneously spelled *mediatas*); 1969:80, no. 15 (erroneously spelled *mediata*); WILLAN, 1983:243-248, figs. 8, 32-44; 1984:43; WILLAN & MORTON, 1984:57; BURN in Phillips, 1984:71 (all erroneously spelled *mediatas*).

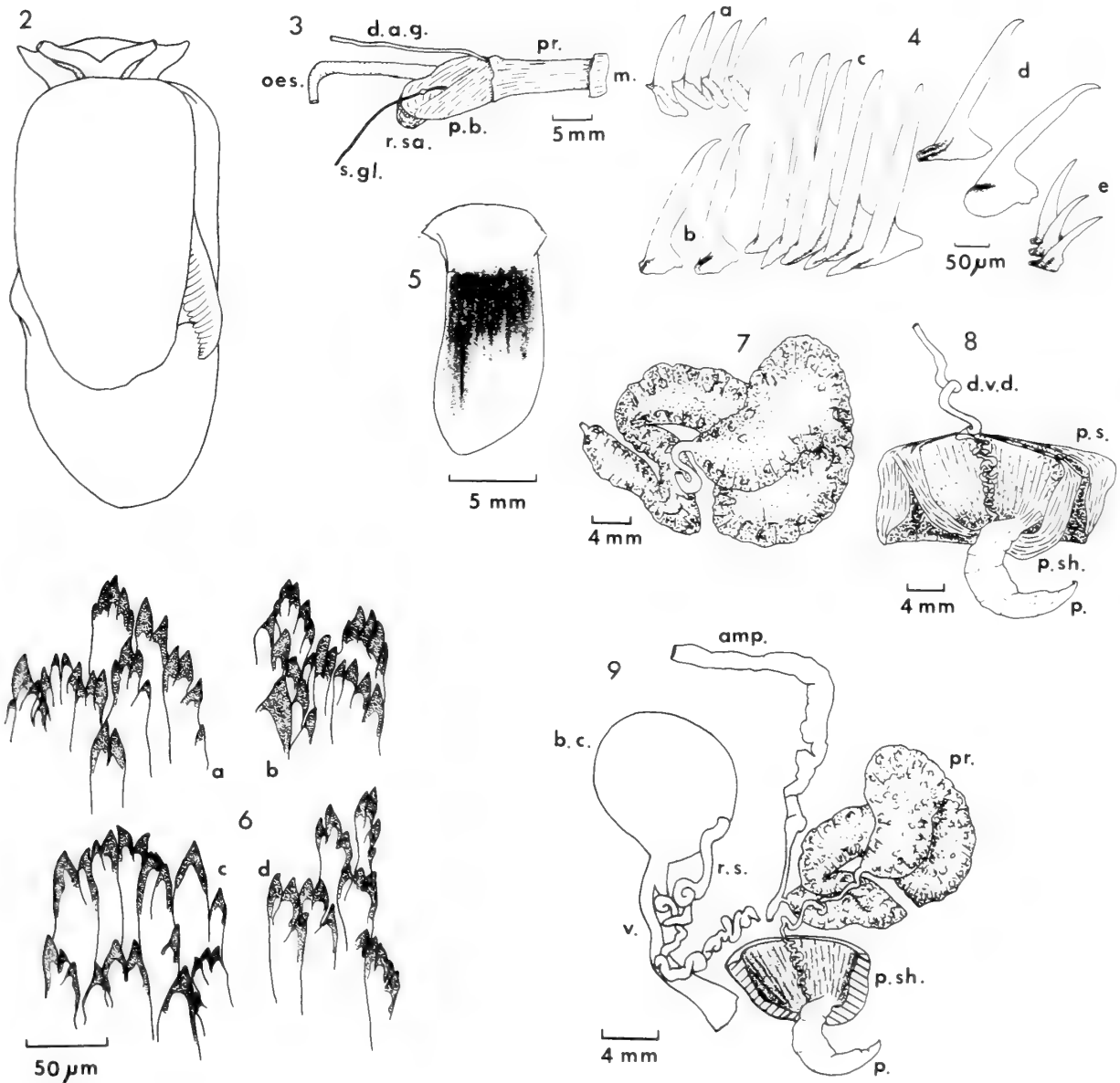
Burn (*in litt.*, 28 September 1985) states that a hitherto unnoticed error occurs in the spelling of the specific name for this species at the head of the original description (BURN, 1962:142, line 7). The correct spelling is *medietas*—Latin, feminine, meaning "the middle, midst, that which is in the middle." "The specific name is given because of the median position of the anus along the gill membrane" is the explanation for the specific name originally given by BURN (1962:143). Elsewhere in Burn's paper, the specific name occurs five times (pp. 135-137, 146) and is spelled correctly each time. Under the I.C.Z.N. (1985 edition), Article 32 (c) (ii), the specific name must be corrected to *medietas*.

Berthella medietas was first described from the central Victorian coastline of Australia (BURN, 1962) which is well north of the Subantarctic zone, and BURN in Phillips (1984) subsequently recorded it from South Australia and Tasmania. In the meantime, WILLAN (1983) recognized it from both main islands of New Zealand as well as Stewart Island and the Chathams. Furthermore, Willan identified ODHNER's (1924) species from Masked Island, Auckland Islands, which Odhner had wrongly called "*Bouvieria aurantiaca* (Risso)," as belonging to this species. At 50°30'S, the Auckland Islands lie on the northern boundary of the Subantarctic zone, so this species is admissible in this present review.

The distinctive characters of *Berthella medietas* are its pale, brownish-orange mantle which has a highly glandular (*i.e.*, porous) texture, deeply sinuous anterior margin to the oral veil, anus opening above the anterior third of the gill's basement membrane, large and rectangular shell with a flange on the columellar side, simple and hook-shaped teeth that show differentiation in size and curvature across rows, cruciform mandibular elements with (usually) strong denticles on the blades, possession of a penial gland, vas deferens lacking an enlarged prostatic section, and two allosperm receptacles of which the receptaculum seminis is distinctly club-shaped.

ACKNOWLEDGMENTS

We thank Dr. Gordon Hendlar (currently of the Los Angeles County Museum of Natural History) and Mrs. Bet-



Explanation of Figures 2 to 9

Figures 2 to 9. Anatomy of *Bathyberthella antarctica*.

Figure 2. Dorsal view of adult depicting supposed appearance in life.

Figure 3. Right profile of foregut (extrinsic muscles not shown). Abbreviations: d.a.g., dorsal accessory gland; m., mouth; oes., oesophagus; p.b., pharyngeal bulb; pr., proboscis; r.sa., radular sac; s.gl., salivary gland.

Figure 4. Radular teeth: a, group of four inner (tooth on right is innermost) laterals from row three; b, isolated inner laterals; c, group of five middle laterals from center of radular row; d, isolated outer laterals; e, group of three outermost laterals.

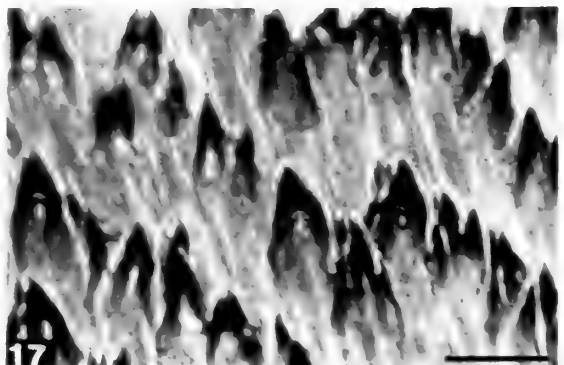
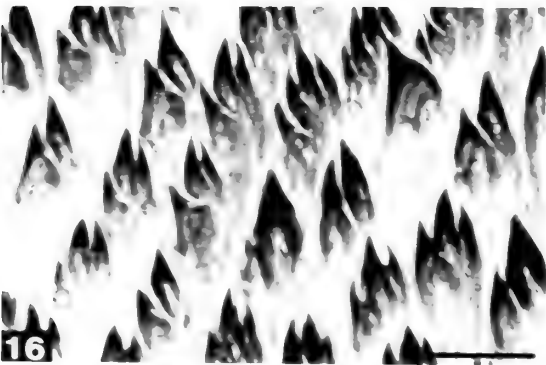
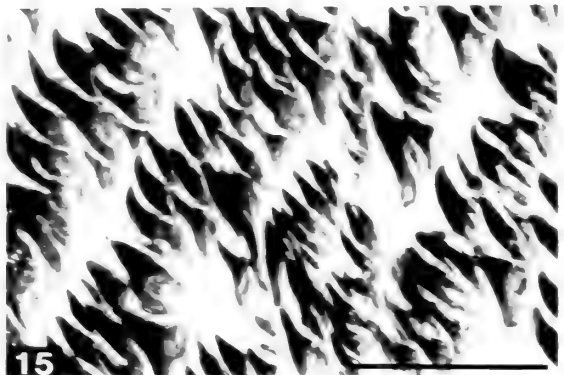
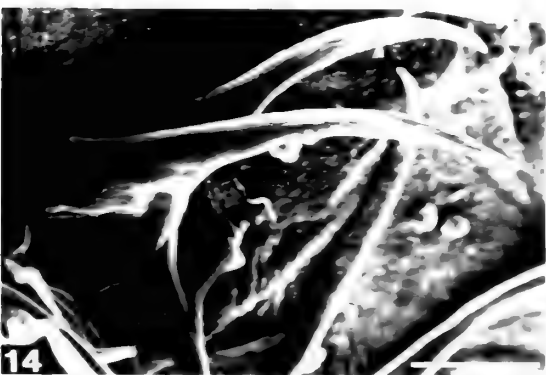
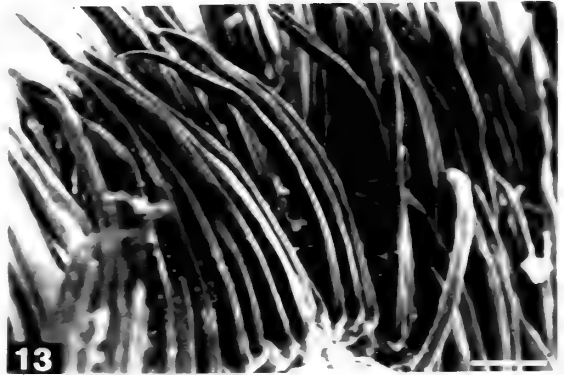
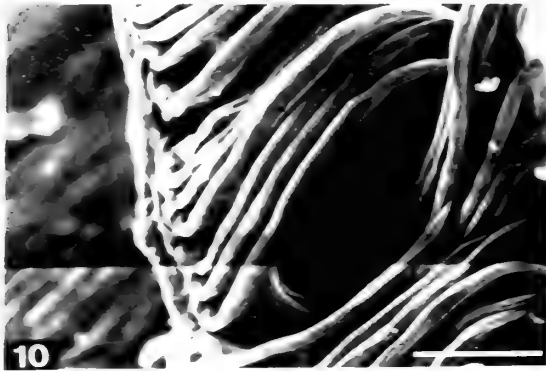
Figure 5. Entire left jaw laid flat showing inner surface.

Figure 6. Mandibular elements from inner face of jaw: a, mid-central group from posterior end of jaw; b, marginal group from anterior end; c and d, mid-central groups from anterior end.

Figure 7. Prostate gland as dissected off bursa copulatrix and laid flat; view of inner surface.

Figure 8. Detail of distal section of vas deferens and penis. Abbreviations: d.v.d., distal vas deferens; p., penis; p.s., penial sac; p.sh., penial sheath.

Figure 9. Diagrammatic view of structure of reproductive organs of a mature adult (ovotestis, nidamental glands, and penial sac not shown). Abbreviations: amp., ampular region of hermaphrodite duct; b.c., bursa copulatrix; p., penis; pr., prostate gland; p.sh., penial sheath; r.s., receptaculum seminis; v., vagina.



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Explanation of Figures 10 to 17

Figures 10 to 17. Radula and jaws of *Bathyberthella antarctica*.

Figure 10. SEM of inner lateral radular teeth. Bar = 100 μ m.

Figure 11. SEM showing detail of cusps of several middle lateral teeth. Bar = 20 μ m.

Figure 12. SEM of outermost lateral teeth from two radular rows. Bar = 100 μ m.

Figure 13. SEM of group of middle lateral teeth from center of radular row. Bar = 100 μ m.

Figure 14. Detail of isolated middle lateral teeth. Bar = 40 μ m.

Figure 15. Photomicrograph of mandibular elements from inner face of jaw; marginal group from anterior end of jaw. Bar = 25 μ m.

Figure 16. Photomicrograph of mandibular elements from inner face of jaw; mid-central group from anterior end of jaw. Bar = 25 μ m.

Figure 17. Photomicrograph of mandibular elements from same region of jaw as Figure 16. Note fine subdenticles flanking cusps. Bar = 25 μ m.

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A New Species of *Aegires* Lovén, 1844
(Opisthobranchia: Doridacea: Aegiretidae)
from the Caribbean Sea: *Aegires ortizi* spec. nov., with
Comparative Descriptions of the North
Atlantic Species of this Genus

by

JOSE TEMPLADO

Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal, 2, 28006 Madrid, Spain

ANGEL A. LUQUE

Departamento de Zoología, Facultad de Ciencias, Universidad Autónoma, 28049 Madrid, Spain

AND

JESUS ORTEA

Departamento de Zoología, Facultad de Ciencias Biológicas, Universidad de Oviedo, Oviedo, Spain

Abstract. *Aegires ortizi*, spec. nov. is described from the Caribbean Sea, and compared with the other two Atlantic species: *Aegires punctilucens* (Orbigny, 1837) and *A. sublaevis* Odhner, 1932. The new species has an inner denticle below the base of the cusp of each radular tooth and conical tubercles over the mantle.

INTRODUCTION

THE GENUS *Aegires* Lovén, 1844, has two Atlantic species: *Aegires sublaevis* Odhner, 1932, and *A. punctilucens* (Orbigny, 1837). The first is a rare species, known only from the Canary Islands, the Mediterranean, Panama, and Bermuda (ODHNER, 1932; MEYER, 1977; ALTIMIRA & ROS, 1979; THOMPSON, 1981; SCHMEKEL & PORTMANN, 1982). The second is widely distributed through the European Atlantic and the Mediterranean Sea (SCHMEKEL & PORTMANN, 1982; THOMPSON & BROWN, 1984). The species of this genus have an elongate body covered by numerous papillae, tubercles or keels, bi- or tripinnate gills, and simple hook-shaped radular teeth.

During the first scientific Cuban-Spanish expedition to Juventud (formerly Pinos) Island and the Canarreos Archipelago in 1984, a specimen of *Aegires* was caught and

initially identified as *A. punctilucens*. A more detailed study proved that it is a new species, which is described in this work and compared with *A. punctilucens* and *A. sublaevis*.

Family AEGIRETIDAE Fischer, 1883
Genus *Aegires* Lovén, 1844

Aegires punctilucens (Orbigny, 1837)
(Figures 1B, 2B, 3B, 4)

Synonyms:

Polycera punctilucens Orbigny, 1837.
Doris maura Forbes, 1840.
?*Aegires leuckarti* Vérany, 1853 (see discussion).
Aegires hispidus Hesse, 1872.

Geographic range: Northeast Atlantic, from Sweden and the British Isles as far as the Mediterranean Sea (SCHME-

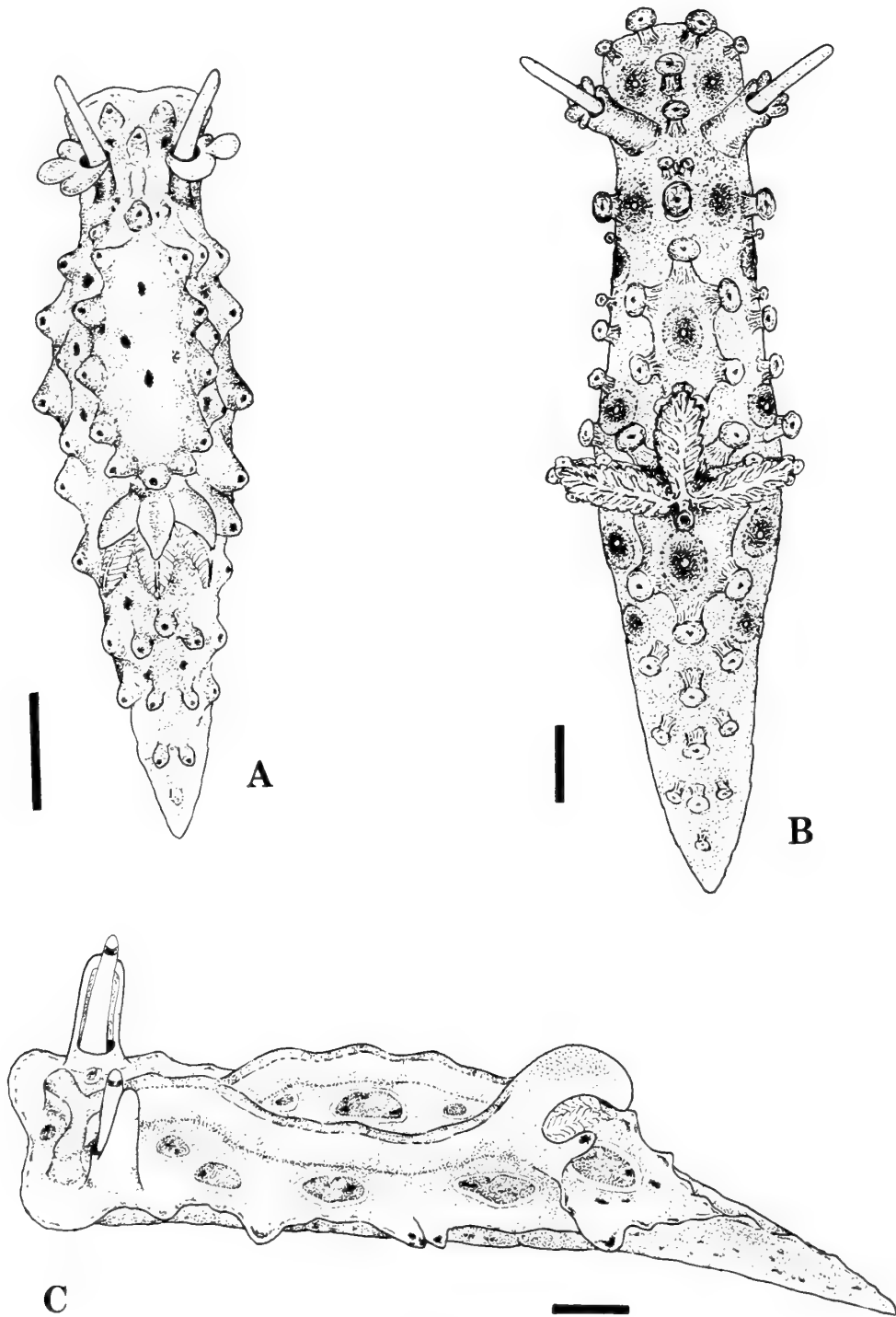


Figure 1

A, *Aegires ortizi*, spec. nov.; B, *A. punctilucens* (Orbigny, 1837); C, *A. sublaevis* Odhner, 1932. Scale = 1 mm.

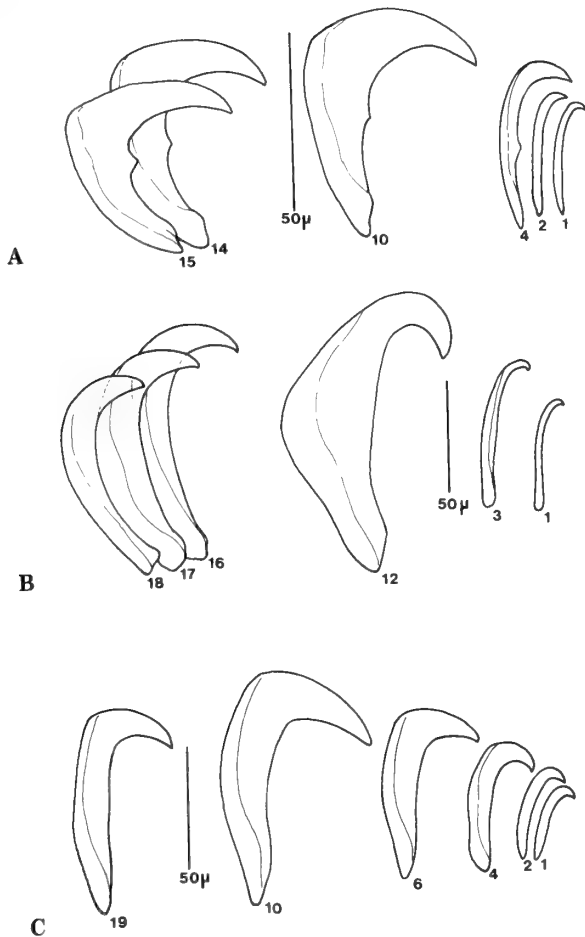


Figure 2

Half row of the radulae of *Aegires ortizi* (A), *A. punctilucens* (B), and *A. sublaevis* (C).

KEL & PORTMANN, 1982; THOMPSON & BROWN, 1984). Only a single record from Japan (BABA, 1974), and one other from Guam (HOFF & CARLSON, 1974).

Material: Asturias (north Spain), 40 specimens from 4 to 15 mm in length, collected between 1976 and 1980. This species is frequent under stones with sponges and bryozoans in tide pools.

Cabo de Palos (Murcia, southeast Spain), 42 specimens from 2 to 9 mm in length, collected between 1979 and 1984. In this zone, *Aegires punctilucens* has been collected between 3 and 23 m of depth, in rhizomes of *Posidonia oceanica* and on shady rocky walls.

La Herradura (Granada, southeast Spain), one specimen 5 mm long, collected by diving on 3 Apr. 1985, in a sample of coralligenous gravel at 20 m of depth.

Description: The studied specimens have a firm body. The dorsum bears abundant mushroom-shaped tubercles.

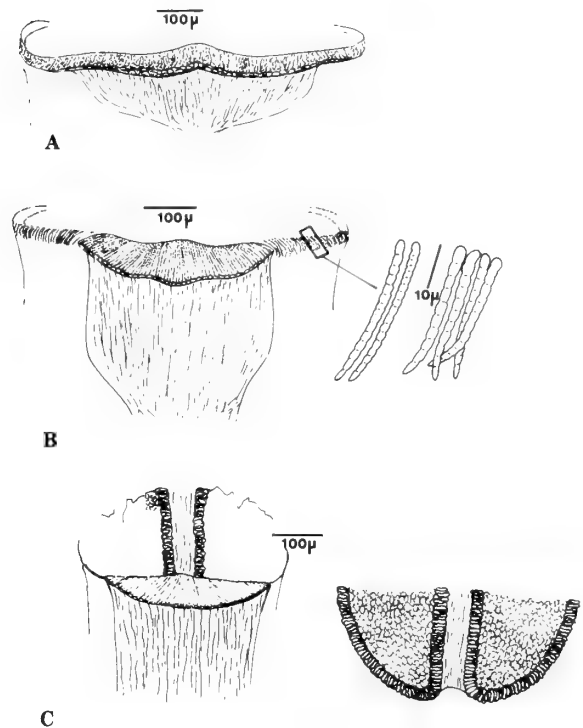


Figure 3

Labial armature of *Aegires ortizi* (A), *A. punctilucens* (B), and *A. sublaevis* (C); right, detail of the posterior mid-ventral part.

The body color is grayish brown, paler in young specimens and darker in adults. There are very small opaque white dots all over the surface, especially on the rhinophores and gills. There is a dark red spot on the top of each tubercle. The rhinophores are smooth and cylindrical, occasionally with an apical dark band. There are three bi- or tripinnate gills just behind the three large tubercles. The dorsum presents ocelli consisting of an orange-yellow area with an iridescent blue, small circle in the center.

Most of the Mediterranean specimens are of small size (3 to 5 mm), of pale color, with more conical tubercles, and without the ocelli characteristic of this species. Only the larger specimens have the typical coloring.

SCHMEKEL & PORTMANN (1982) and THOMPSON & BROWN (1984) give complete descriptions of this species, and KRESS (1981) gives a detailed account of the structure of the tubercles of the mantle.

The labial armature has a well developed mid-dorsal plate, and the lateral areas are armed with rods (Figure 3B). The radula of a 7-mm specimen (Figure 2B) has a formula of 15×18-0-18. All the teeth are hook-shaped and increase in size continuously and regularly from the 1st to the 12th in each row; from the 12th to the 16th they are of the same size, and the 17th and 18th teeth decrease in size.

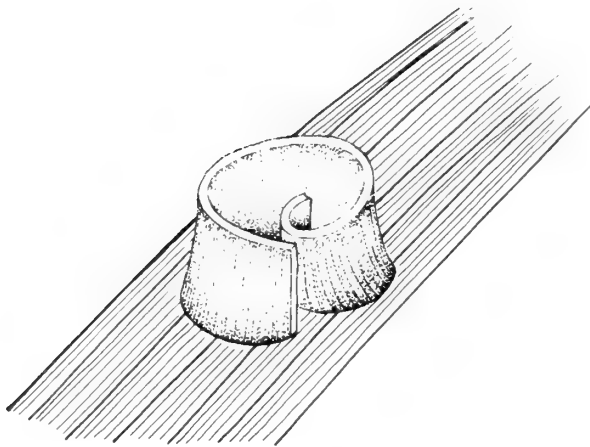


Figure 4

Spawn of *Aegires punctilucens*, on a leaf of *Zostera*.

Biology: *Aegires punctilucens* lives from the intertidal zone to depths of 100 m (FRIELE & GRIEG, 1876), and feeds on encrusting bryozoans (HUNNAN & BROWN, 1975) or sponges of the genus *Leucosolenia* (THOMPSON & BROWN, 1984). The spawn is a simple spiral ribbon of one whorl (Figure 4), with eggs of 90–100 μm diameter. THIRIOT-QUIEVREUX (1977) published a detailed study of the larval development and metamorphosis of this species.

Discussion: Two subspecies of *Aegires punctilucens* are recognized by some authors, e.g., SCHMEKEL & PORTMANN (1982): the nominal subspecies and *A. punctilucens leuckarti* Vérany, 1853. According to HAEFELFINGER (1968), *A. leuckarti* Vérany, 1853, known principally from the Mediterranean Sea, which lacks ocellated markings, is synonymous with *A. punctilucens*. SCHMEKEL & PORTMANN (1982) believe that there are no significant anatomical differences (radula, labial armature, and genital organs) between the two subspecies, but they differ in biological characters: the genital system is completely developed in 3-mm specimens of *A. punctilucens leuckarti*, and only in 7-mm specimens of the nominal subspecies; *A. p. leuckarti* spawns from September to October, and *A. p. punctilucens* from March to April. Also, two-thirds of the specimens of *A. p. leuckarti* live at more than 30 m of depth, whereas 90% of *A. p. punctilucens* live over 20 m of depth. We think that the validity of these two subspecies must be reexamined, because they have a sympatric distribution and, moreover, in some localities (*viz.* Cabo de Palos, Murcia, SE Spain), we have found both in the same habitat. In any case, if reproductive isolation and lack of hybridization were eventually proved, they should be considered as different species.

BABA (1974) recorded *Aegires p. punctilucens* from Japan and HOFF & CARLSON (1974) recorded *A. p. leuckarti* from Guam. The specimen from Japan (BABA, 1974) shows slight morphological and anatomical differences

from the European ones, mainly in radular features. The Japanese specimen is 13 mm long and its radular formula is $15 \times 15-0-15$; a 12-mm specimen from the Isle of Man (Atlantic), described by THOMPSON & BROWN (1984), has a formula of $23 \times 22-0-22$. The outer and inner teeth are similar in the Japanese specimen, whereas the Atlantic specimens have the outer teeth thicker than the inner ones. HOFF & CARLSON (1974) did not give any data for the radula of their specimen.

Aegires sublaevis Odhner, 1932

(Figures 1C, 2C, 3C)

Geographic range: Mediterranean Sea (SCHMEKEL & PORTMANN, 1982) and Canary Islands (ODHNER, 1932; ALTIMIRA & ROS, 1979). Galeta Point, Panama (MEYER, 1977) and Bermuda (THOMPSON, 1981).

Material: Twelve specimens from 3 to 13 mm long collected in Tenerife and Lanzarote (Canary Islands) during the "Plan de Bentos Circuncanario (1980–82)," from the intertidal zone to 6 m of depth, associated with the sponge *Clathrina coriacea* (Montagu), on which it feeds.

One specimen 10 mm in length, from Cabo de Palos (Murcia, southeast Spain), collected on 7 Aug. 1984 at 25 m of depth in a cave.

Description: The body is lemon-yellow, rarely light cream, with minute brown punctae regularly scattered, and large brown spots with white and dark brown minute spots surrounded by lighter areas. The larger spots vary in number and distribution among the different specimens, but usually are aligned in three anteroposterior fringes. The dorsum presents two longitudinal crests that join at the level of the rhinophores in front, and near the gills behind, forming three lobes directed backwards, with the central lobe more developed. Also, there are swellings along the edges and behind the gills. The rhinophoral sheaths have only an external lobe, and the rhinophores are smooth with a brown ring near the apex. The three tripinnate gills are whitish or light yellow, with brown punctae. The Mediterranean specimen has no significant differences from the Canary Islands ones.

The middle plate and lateral areas of the labial armature are thickened; the structure and function of the labial armature have been described by THOMPSON (1981). The radula of a 7-mm fixed specimen has a formula of $14 \times 19-0-19$. The teeth rapidly increase in size from the 1st to the 7th; increase slowly from the 8th to the 10th; are of equal size from the 11th to 17th; and the 18th and 19th decrease.

Aegires ortizi Templado, Luque & Ortea, spec. nov.

(Figures 1A, 2A, 3A)

Material: One specimen 7 mm in length, from the southern slope of the "Bocas de Alonso" Keys ($82^{\circ}30'W$, $21^{\circ}40'N$), SW Cuba, found on a sample of *Thalassia tes-*

tudinum, collected by diving at 4 m of depth, on 18 Apr. 1984. No additional specimens were found in 14 days of sampling in the neighboring waters to the southern region of Juventud (formerly Pinos) Island. The holotype and a permanent mount of the labial armature and radula are deposited in the Museo Nacional de Ciencias Naturales of Madrid, with the number 12-64/1006.

Description: The unique specimen has a firm body, with abundant more or less conical tubercles, arranged in four longitudinal rows. The two inner rows join posterior to the rhinophores, and just anterior to the gills. The rhinophoral sheaths have three large tubercles on the side distal to the rhinophores, which are smooth and cylindrical, light brown, and with a cream-colored apex. There are three gills of cream color, protected by three large anterior tubercles. The general body color is creamy yellow with minute white punctae in the region of the tubercular rows, and is light brown between these rows. The sole of the foot is whitish. There is a dark brown spot on the top of each tubercle, and there are some oval-rounded spots of this color in the center of paler areas distributed over the dorsum (Figure 1A).

The labial armature has a slightly developed mid-dorsal plate (Figure 3A) and lateral areas without differentiated elements. The radula (Figure 2A) has a formula of $15 \times 16-0-16$; the teeth are hook-shaped with a clear denticle in their inner middle part.

Etymology: *Aegires ortizi*, spec. nov. is named in honor of Dr. Manuel Ortiz, Vicedirector of the "Centro de Investigaciones Marinas" of Havana University, for his kind cooperation.

Discussion: *Aegires ortizi* resembles *A. punctilucens*, but clearly differs from this species and the other known species of the genus by the inner denticle of the radular teeth. The conical tubercles of the mantle are also different from the mushroom-shaped ones of *A. punctilucens* and from the keels of *A. sublaevis*, the other two Atlantic species.

The presence of an inner denticle in the radular teeth of this new species is of particular interest, because it represents an intermediate structure between the simple hook-shaped teeth of the known species of *Aegires* and the bifid radular teeth of the related Indo-Pacific genus *Notodoris* Bergh, 1875. The prey of *A. ortizi* is unknown, but other species of *Aegires* are known to prey on calcareous sponges (BERTSCH, 1980).

of Havana University and, especially, Drs. Manuel Ortiz and Osvaldo Gómez and the crew of the research vessel *Felipe Poey*; without their kind cooperation this work would not have been possible. We also thank Drs. Antonio García-Valdecasas and José Luis Viejo for their comments on the manuscript, and Mr. John Kay for his help with the English translation.

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A New Species of *Bunnya*
(Gastropoda: Pulmonata: Humboldtianidae)
from Western Mexico, with Notes on its
Life Cycle and Familial Relationships

by

WALTER B. MILLER

Department of Ecology and Evolutionary Biology, University of Arizona,
Tucson, Arizona 85721, U.S.A.

Abstract. A new species of land snail, *Bunnya naranjoae* Miller, is described from western Mexico. Its unusual life cycle of about one year from birth to maturity, with death after egg laying, is described. Its anatomy places it in the family Humboldtianidae, formerly considered a subfamily of Helminthoglyptidae and recently elevated to familial rank by A. A. Schileyko.

INTRODUCTION

BAKER (1942) described the genus *Bunnya* and its type species, *Bunnya bernardinae* H. B. Baker, 1942, from a single specimen collected on the wall of the old monastery at El Desierto de los Leones at the western outskirts of Mexico City. Since that time, *B. bernardinae* has also been collected by Gonzalo Halffter at Temexcaltepec, Estado de Mexico, and by my graduate student Edna Naranjo Garcia in lower elevations of the Desierto de los Leones, Distrito Federal. Baker stated that "in its genitalia, *Bunnya* appears to approach *Humboldtiana*," but he felt that its shell and external body characters related it closely to *Xanthyx* Crosse & Fischer, 1867. Accordingly, he did not place it in a designated family but merely referred to it as "a new genus of Mexican helicids."

BAKER (1959) subsequently discussed the use of the family names Xanthonychidae, Helminthoglyptidae, Bradybaenidae, and others which have been used for dart-bearing helicoids whose mucus glands are "club-shaped, globular, or irregular (not tubular or finger-shaped)" (PILSBRY, 1939:1). He concluded that because the name Xanthonychidae has priority over the others, it "must be accepted for at least the native American genera of helicoids" (BAKER, 1959:28); he went on to state that "since the sizes of families are matters of convenience and/or custom, we Americans, North and South, can leave to the wisdom of our Old World colleagues the advisability of a separate family for the genera of their home lands." In-

deed, Old World genera belonging to this group of helicoids have been placed in Bradybaenidae, effectively separating them from New World genera.

Baker's recommendation that the name Xanthonychidae be adopted in lieu of the better known name Helminthoglyptidae did not meet with universal acceptance. SOLEM (1983:47) stated that he did not "accept strict nomenclatural priority for names of families and higher level taxa." A. A. Schileyko, in his extensive analysis of the evolution and relationships of pulmonate gastropod mollusks (SCHILEYKO, 1973, 1978, 1979), also continued to use the name Helminthoglyptidae. In his 1978 study of the superfamily Helicoidea based on detailed anatomical characters, he raised the Humboldtianinae Pilsbry, 1939, to familial rank, thereby also separating that group of helicoids from the Helminthoglyptidae. His determinations were summarized in an evolutionary tree (SCHILEYKO 1979:60-61, figure 7) showing the Humboldtianidae in the direct evolutionary line from a common helicoid ancestor, with the Helicidae branching off at an early date, the Helminthoglyptidae at a later date, and the Bradybaenidae branching off at a still later date from the Helminthoglyptidae. He placed these families in the superfamily Helicoidea, named in accordance with Article 29a of the International Code of Zoological Nomenclature.

Pilsbry's Humboldtianinae was a monogeneric subfamily consisting only of the genus *Humboldtiana* Ihering, 1892. ZILCH (1960) added *Lysinoe* H. & A. Adams, 1855,

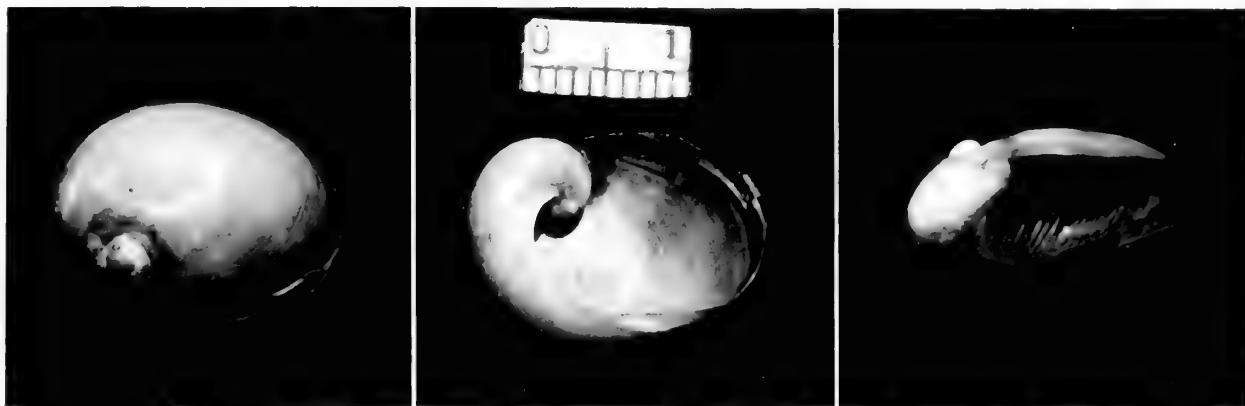


Figure 1

Shell of holotype of *Bunnya naranjoae*, spec. nov. SBMNH No. 34369. Dorsal, ventral, and side views.

to the subfamily. I now report that a new species of the genus *Bunnya*, described below, provides additional evidence that this genus is more closely related to *Humboldtiana* than to *Xanthonyx* and should therefore be placed in the family Humboldtianidae. I concur with Schileyko that the Humboldtianidae are sufficiently distinct anatomically from other Helicoidea to warrant their status as a separate family. The names used here for taxa above the family level also follow his recommendations (SCHILEYKO, 1979).

SYSTEMATICS

Subclass Pumonata

Superorder Stylommatophora

Order Geophila

Suborder Helixina

Superfamily Helicoidea

Family Humboldtianidae

Genus *Bunnya* H. B. Baker, 1942

Bunnya naranjoae Miller, spec. nov.

(Figures 1, 2)

Diagnosis: A sluglike land snail with thin, fragile, depressed, vitriniform shell, overlapped all around by a papillose fold of the mantle, too small to contain entirely the retracted animal. The reproductive system is characterized by 3 bilobed dart-sacs and 3 saccular mucus lands arranged circumferentially around the vagina near the genital orifice, by an epiphallus tightly coiled around the vas deferens, and by a short-ducted spermatheca equipped with a globular appendix at its apex.

Description of shell of holotype: Shell imperforate, thin, fragile and translucent, slightly glossy, light brown colored, vitriniform, with only $2\frac{3}{4}$ whorls, depressed, rounded, and rapidly increasing in size. Embryonic whorls $1\frac{1}{4}$, sculptured with very closely set, parallel, spiral grooves (about 40 per mm) superimposed on closely set radial

riblets (about 10 per mm at lower suture); spiral grooves sparse and widely scattered on subsequent whorls, while radial riblets continue closely set to the end of the second whorl, thereafter becoming more widely spaced, irregular, and weakly rounded. On top of the body whorl, an ovoid, irregular callus marks where the edge of the mantle fold overlapped the shell. Aperture large, ovoid, oblique, much wider than high, in plane about 120° from the shell axis; peristome sharp and thin, very fragile; parietal callus somewhat thick, glossy and granular. Columella sharp, thin and arcuate. Shell diameter 18.0 mm, height 11.3 mm; number of whorls $2\frac{3}{4}$.

Variation in shells of paratypes: Seventeen paratypes had shells that were measurable, having been obtained from freshly killed specimens; shells from dead specimens were generally decalcified, shrivelled, and partially broken. The smallest measurable adult shell had a diameter of 17.0 mm while the largest measured 18.9 mm; the mean was 17.9 mm. Shells had variable amounts of callus deposit on top of the body whorl, marking variable degrees of overlap by the mantle fold; in some shells, the embryonic whorls were completely covered by thick callus. Except for the callus deposits, the shells varied from glossy to dull brown; one shell was light lemon yellow.

Anatomical features: Living animals varied from dark gray to pale brown. All but one, out of 18 live adults, possessed a prominent tail horn; the hornless individual showed no vestige whatsoever of a horn. In some specimens, the body wall at the edge of the foot, as well as on the back of the tail, was colored a pale chartreuse, while in others the color was orange. The mantle edge overlapped the shell all around, to varying degrees, usually including the spire, and secreted a calcareous callus; as the mantle protracted and retracted, the callus tended to form a solid sheet, covering large portions of some shells. In one specimen, the mantle had overlapped the shell entirely and its edges had fused, thereby effectively creating

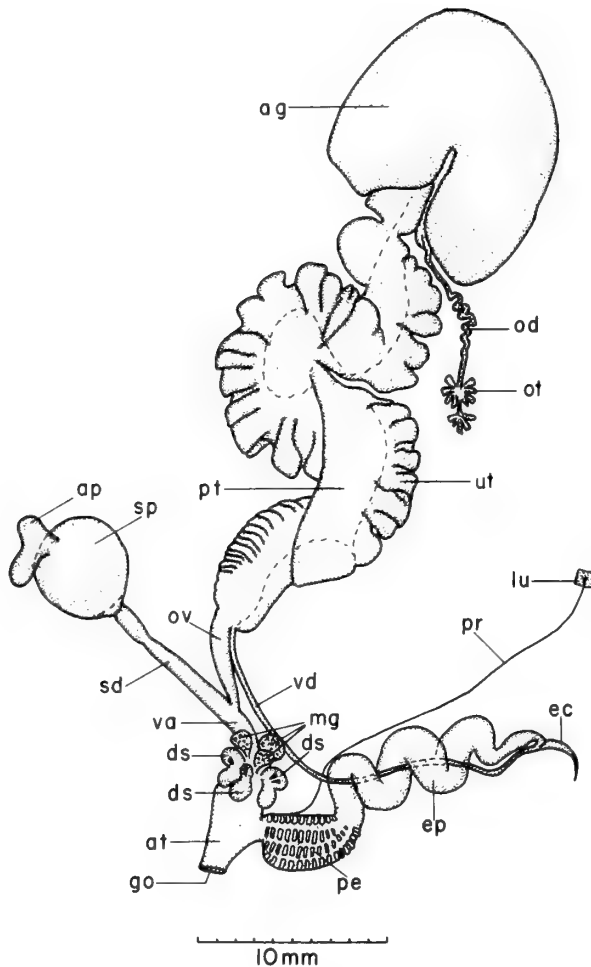


Figure 2

Reproductive system of *Bunnya naranjoae*, spec. nov. Drawing made from projection of stained whole mount, WMB 7473; specimen collected in Sierra de Manantlan, Jalisco, Mexico, along road from El Chante to Guizar, 16 km south of El Chante, by E. Naranjo Garcia & W. B. Miller, 26 Dec. 1984. Abbreviations: ag, albumen gland; ap, appendix of spermatheca; at, genital atrium; ds, dart-sac; ec, epiphallitic caecum; ep, epiphallus; go, genital orifice; lu, portion of floor of lung; mg, mucus gland; od, oviducal duct (hermaphroditic duct); ot, ovotestis; ov, oviduct; pe, penis; pr, penial retractor; pt, prostate; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens.

an internal shell. The mantle overlap was coarsely papillose and pigmented with irregular, black, radial lines. The thin mantle directly over the viscera, under the shell, was maculated with scattered pigment spots around the anterior and lateral edges; the maculae coalesced to form a connected, reticulate pattern over the heart and the white kidney; the mantle over the digestive gland and the ovotestis was clear, without pigment. A dark pigmented groove led from the pneumostome to the mantle edge at the apex of the spire.

The anatomy of the reproductive system (Figure 2) is generally similar to that of *Bunnya bernardinae* in that there are three bilobed dart-sacs located circumferentially around and opening into the vagina at a point about 6 mm posterior to the genital orifice. There are also three saccular, globose, mucous glands just posterior to the dart-sacs, each with its own duct descending into the vagina at the level of, and between, each dart-sac. In 14 specimens dissected, some had two darts per sac, others had only one, and still others had none. The globose spermatheca has an appendix situated at its apex, somewhat ear-shaped or bilobed, and a relatively short (ca. 8 mm) spermathecal duct without diverticulum. The penis is short, bulbous (5 mm long and 3 mm in diameter) with its inner wall consisting of numerous, small, rectangular, glandular alveoli arranged in a reticulate pattern clearly visible on the outer surface. Posteriorly, the lumen of the penis leads into a tightly coiled epiphallus wound helically around the vas deferens, forming from $2\frac{1}{2}$ to $3\frac{1}{2}$ coils; the lumen of the epiphallus is lined with five or six prominent longitudinal pilasters for its entire length; there is a short epiphallitic caecum, about 3–4 mm in length. The penial retractor muscle is extremely thin, long, and attached to the penis. The vagina, in the region of the mucous glands and dart-sacs, is attached by numerous thin strands of connective tissue to the right lateral body wall; its lumen is lined with from 10 to 15 anastomosing longitudinal pilasters. The widely convoluted uterus and prostate, the lobed albumen gland, and the ovotestis of clavate alveoli are as in *B. bernardinae*.

Disposition of types: Holotype: Santa Barbara Museum of Natural History no. 34369. Paratypes: U.S. National Museum no. 859016; Academy of Natural Sciences of Philadelphia no. 360102; Field Museum of Natural History no. 205901; California Academy of Sciences no. 060385; University of Texas at El Paso no. 9386; Florida State Museum no. 80271; Universidad Nacional Autonoma de Mexico (UNAM) no. 1020; Edna Naranjo Garcia Collection no. 526; W. B. Miller (WBM) no. 7473.

Type locality: Sierra de Manantlan, Jalisco, Mexico; along road from El Chante to Guizar, 1.5 km (0.9 mi) south of Rancho Manantlan (or 16 km south of El Chante), under large rocks between road and left bank of Rio Manantlan; $19^{\circ}36.5'N$, $104^{\circ}12.3'W$, elev. ca. 1390 m (4550 ft).

Distribution and habitat: This species appears to be wide ranging along the tropical areas of the western slope of the Sierra Madre Occidental from the vicinity of Mazatlan in the north to the Sierra de Manantlan in southwest Jalisco. Areas farther south and east, in Colima, Michoacan, etc., have not been explored for this species. At its northernmost known locality, a ravine along the Mazatlan–Durango highway 3 km easterly from Santa Lucia (or 15 km westerly from Loberas summit), I obtained several shells and a live adult in December 1962; dissec-

tion of the adult anatomy confirmed its identity (no. WBM 4401). Another locality in Nayarit, a ravine along the Tepic-Puerto Vallarta highway at km-42 marker (measured from Tepic), yielded a single shell in January 1973 (no. WBM 6068). In the Sierra de Manantlan, it is found under rocks, especially rock piles from crumbling rock walls, in the riparian valley of the Rio Manantlan, from the type locality (1.5 km south of Rancho Manantlan) to the vicinity of the abandoned sawmill at Rincon de Manantlan, 1.1 km farther upstream along the river. The dominant trees along the river banks are large alders (*Alnus* sp.), several leguminous trees, a large-leaf oak (*Quercus* sp.), and an occasional five-needled yellow pine.

Comparative analysis: *Bunnya naranjoae* differs from the only other described *Bunnya*, *B. bernardinae*, by its shell which is larger and flatter and by its reproductive anatomy which has a multicoiled epiphallus and a spermathecal appendix, situated at the apex of the spermatheca, instead of a spermathecal diverticulum below the spermatheca, as reported by Baker for *B. bernardinae*.

Etymology: This species is named for my graduate student, M-en-C Edna Naranjo Garcia, whose tireless search and keen eyesight resulted in the discovery of the numerous, minute, live, embryonic specimens that enabled me to study their life cycle as well as obtain, eventually, large numbers of adult animals for dissection.

LIFE CYCLE

Bunnya naranjoae has a most unusual life cycle in that it lives only for one year, hatching near the end of the rainy season, hibernating in its embryonic shell tightly sealed to rocks during the dry season, and then activating and rapidly growing to adulthood during the next rainy season, at the end of which it lays eggs and dies. When first found by Edna Naranjo Garcia, on 26 December 1984, the specimens had only tiny embryonic shells (ca. 3 mm in diameter) and were hibernating, strongly sealed to the underside of large rocks in rock piles. In obtaining two to three dozen specimens, it was impossible to avoid crushing some shells while trying to pry them off the rocks. The young snails were immediately activated in terraria at the UNAM Biological Field Station at Chamela, Jalisco. The terraria were provided with a layer of humus, dead leaves, and stems from the type locality in the event that certain essential food items might occur there; later, however, additional terraria were established, with different forest litter, and no apparent ill effects were noted. The snails were fed fresh romaine lettuce every three or four days, with sliced carrots added occasionally. They ate ravenously, grew rapidly in size, and by April, about four months after activation, they reached adulthood. In early May, some individuals began to die, and large clutches of eggs (25 to 30 eggs each) appeared in the litter. Moribund, emaciated snails lay near the egg masses, with prolapsed genital atrium and shrivelled shell largely devoid of cal-

careous material, as in *Vitrinizonites wuidermis* Pilsbry, 1890. On dissection, it was found that the albumen gland had atrophied and the uterus and spermatheca were lysing. Apparently, the process of forming and laying such large numbers of eggs had robbed the animal of excessive quantities of tissue, nutrients, and minerals. Young snails soon hatched, in about two or three weeks, with strong, ribbed, embryonic shells. At that time, the terraria were allowed to dry out, to simulate a dry season, and the young snails promptly sealed to the walls with strong, calcareous epiphragms. This short life cycle of one rainy season activity explains why no live adults could be found during the dry season and why most dead shells were thin, fragile, and damaged.

FAMILIAL RELATIONSHIP

The shells of *Bunnya naranjoae* collected in 1962 and again in 1973 were originally thought to be a species of *Xanthonyx*. Likewise, the specimens from the Sierra de Manantlan were thought to belong in the genus *Xanthonyx* because their appearance in size, shape, and form resembled published descriptions of species of *Xanthonyx*. Dissection, however, revealed that the anatomy was unquestionably that of *Bunnya*.

Although the shell of *Bunnya naranjoae* is similar to that of *Xanthonyx* spp., this similarity is considered another example of convergent evolution. In numerous instances, reduced, sluglike shells of similar appearance have been shown to belong to animals whose dissimilar anatomy places them in entirely different families, e.g., *Binneya* Cooper, 1963, in Arionidae, *Gaeotis* Shuttleworth, 1854, in Bulimulidae, and *Vitrinizonites* W. G. Binney, 1879, in Zonitidae. LIKHAREV & WIKTOR (1979) reported on an extensive and detailed analysis of parallelism in the structure of slugs and sluglike snails.

Anatomically, *Xanthonyx* is known only from three of the five described species, and in each of these, the reproductive anatomies are significantly different. In *X. sumichrasti* (Brot, 1867), the type species of the genus, FISCHER (1867) showed one mucus gland, no dart-sac, and a spermathecal diverticulum; in *X. cordovanus* (Pfeiffer, 1856), BAKER (1942) reported two "dart-glands with a few tubules" entering the vagina above a rudimentary dart-sac, and a spermathecal diverticulum; in *X. salleanus* (Pfeiffer, 1956), PILSBRY (1900) showed two mucus glands, one dart-sac, and no spermathecal diverticulum. The anatomies of *X. chiapasensis* (Pfeiffer, 1956) and *X. potosiana* Dall, 1907, have not been reported in the literature, to my knowledge. Fred G. Thompson (*in litt.*, 1985) reported that he had an undescribed species from San Luis Potosi whose dart-glands and dart-sacs are sufficiently different from typical *Xanthonyx*, as described by Strebelt, to warrant recognition of a new genus. He added, however, that we know too little about xanthonychid systematics to justify the hasty designation of a new genus for that particular species. It appears obvious that much more work

needs to be done to collect live adult topotypes of the described species of *Xanthyx* in order to study their anatomies and obtain reliable data on which to base satisfactory determinations of their systematic relationships.

In *Bunnya naranjoae*, however, the generic characteristics, namely the arrangement, shape, and position of the three bilobed dart-sacs and three mucus glands, are virtually identical with those of *B. bernardinae*. These characteristics, while establishing concise criteria for generic identity, also indicate a close evolutionary relationship with *Humboldtiana* whose four saccular mucus glands and four dart-sacs are arranged circumferentially around the vagina in a similar manner as in *Bunnya*. Accordingly, the genus *Bunnya* is here placed in the family Humboldtianidae.

ACKNOWLEDGMENTS

I wish to express my gratitude to Edna Naranjo Garcia for her assistance in obtaining the specimens, to my wife Betty Sue for companionship and support in this potentially perilous and at times trying expedition into the Sierra de Manantlan, and to Laurie Vitt and Jan Caldwell, herpetologists at the University of California at Los Angeles, who accompanied us in their vehicle and provided a safety back-up as well as cheerful companionship. I also thank Fred Thompson, friend and colleague at the Florida State Museum, for the loan of a preserved specimen of *Bunnya bernardinae*. I am grateful to Barry Roth, then at the California Academy of Sciences, for notifying me of the results of the expedition of Dennis Breedlove, botanist at the CAS, into the Sierra de Manantlan where he found specimens of *Lysinoe sebastiana* (Dall, 1897), thereby whetting my desire to conduct further explorations. I am also grateful to Dr. Jose Sarukhan, Director of the Institute of Biology at the Universidad Nacional Autonoma de Mexico, who made available to us the excellent laboratory

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Descriptions of the Larvae of Three Species of the *Onychoteuthis banksii* Complex from Hawaiian Waters

by

RICHARD EDWARD YOUNG AND ROBERT F. HARMAN

Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822, U.S.A.

Abstract. Squid larvae from Hawaiian waters that belong to three species of *Onychoteuthis* indicate that the generally recognized single tropical-subtropical species in the genus, *O. banksii*, represents a species complex. The Hawaiian species are easily separated by chromatophore patterns.

INTRODUCTION

THE IDENTIFICATION of cephalopod larvae to species has not been possible in most areas, largely owing to small collections of larvae and the uncertainty about the species composition of the adult fauna. In Hawaii, the adult fauna was thought to be well known; however, during a recently initiated program that involved larval identifications, uncertainty arose concerning larvae belonging to the genus *Onychoteuthis*. Only a single species, *O. banksii* (Leach, 1817), is generally recognized from tropical and subtropical waters of the world's oceans. The *Onychoteuthis* larvae collected around Hawaii, however, clearly represent three distinct species.

Onychoteuthis larvae are easily recognized by a prominent, pointed rostrum on the posterior tip of the gladius that extends well beyond the tip of the muscular mantle. These larvae have been illustrated by a number of authors from a variety of oceanic regions (*e.g.*, PFEFFER, 1912; NAEF, 1923; OKUTANI, 1968, 1974; OKUTANI & MCGOWAN, 1969) and they frequently are among the most abundant squid larvae found in tropical and subtropical regions (*e.g.*, OKUTANI, 1974).

This paper describes the larval stages of the three species of *Onychoteuthis* found in Hawaiian waters, identifies larval characters in the genus that are species-specific, and presents preliminary data on the vertical distributions of the larvae.

MATERIALS AND METHODS

Larvae were collected off the leeward coast of the island of Oahu, Hawaiian Archipelago (about 21°15'N, 158°20'W) during a series of cruises aboard the University

of Hawaii's research ships R/V *Kana Keoki* and R/V *Kila* in 1983 and 1984. Juveniles were taken from collections at the University of Hawaii that were made with mid-water trawls over the preceding 15 years (*e.g.*, see YOUNG, 1978). The sampling program for larvae consisted of both horizontal and oblique tows with both open nets and opening-closing nets. Two series of tows taken from the surface to 300 m examined vertical distribution. The first series was taken in April 1984, and consisted of 40 vertically stratified oblique tows with paired, opening-closing 70-cm bongo nets. The second was taken during October 1984, and consisted of horizontal tows with an open 4-m² net. Both nets were of 0.505-mm mesh and were equipped with flow meters and time-depth recorders.

Vertical distribution profiles from the stratified-oblique (April) series were compiled by apportioning the catch from each tow equally into 10-m depth intervals over the depth range of the tow. The catch rate for a given depth interval was taken as the total catch in that depth interval from all tows divided by the total volume of water (all tows) sampled in that interval. Those catch rates were then combined into 20-m depth strata. For the horizontal (October) series, the entire catch for a tow was assumed to have been caught at the modal fishing depth of the net during that tow. Details of the sampling program are given in HARMAN & YOUNG (1985).

Larvae were fixed in 4% buffered formalin and preserved in 40% isopropyl alcohol. Nearly all onychoteuthid larvae retained their skin and chromatophores through the rigors of capture, and fading of the chromatophore pigment in recently preserved specimens was not serious. Illustrations of chromatophore patterns and counts of chromatophores in some body regions (*e.g.*, chromatophores at

Table 1
Mantle and head chromatophores: mean (range).

<i>Onycho-</i> <i>teuthis</i> species	Gladius length	n	Ventral Mantle, Belly	Ventral Mantle, Margin	Ventral Mantle, Tail	Dorsal Mantle, Midregion	Dorsal Mantle, Margin	Dorsal Mantle, Tail	Dorsal Head
<i>compacta</i>	2.0-2.9	2	4 (1-7)	0	2	0	0	0	3 (0-6)
B	2.0-2.9	6	15.5 (7-20)	3.8 (0-5)	2	0.8 (0-4)	0	0	7
C	2.0-2.9	8	4.2 (3-7)	0	1.9 (1-2)	3.9 (2-5)	0	0	6.8 (6-7)
<i>compacta</i>	3.0-5.9	14	9.0 (5-12)	9.0 (0-11)	2.0 (2-4)	1.5 (0-5)	0.2 (0-3)	0.4 (0-1)	7
B	3.0-5.9	21	26.3 (18-44)	14.3 (2-20)	3.3 (2-5)	6.8 (4-17)	2.7 (0-11)	0.0 (0-1)	10 (7-33)
C	3.0-5.9	20	7.0 (3-12)	5.2 (0-13)	2	6.3 (4-15)	1.5 (0-11)	0	9.0 (7-17)

the mantle margin), however, must be considered incomplete because some types of expanded chromatophores can be extremely difficult to detect, and this problem can be amplified if only a slight amount of fading has occurred.

Specimens illustrated have been deposited in the Santa Barbara Museum of Natural History.

TERMINOLOGY

Larva—convenient designation for the young stages of squids that are effectively caught by plankton nets.

Juvenile—young stage initiated by the appearance of hooks and large numbers of chromatophores.

Chromatophore band—transverse series of chromatophores.

Chromatophore row—longitudinal series of chromatophores.

Simple band or row—a single straight line (series) of chromatophores.

Complex band or row—a single very irregular line, or multiple lines (regular or irregular) of chromatophores.

Chromatophore zones:

Ventral Mantle, Margin—band of chromatophores lying at the anterior margin on the ventral mantle surface. In older larvae where this band may become continuous with chromatophores along the dorsal margin, the separation point of these two series is defined as the lateral point on the mantle that is posterior to the midpoint of the eye.

Ventral Mantle, Belly—a distinct patch of chromatophores on the ventral surface of the mantle, just posterior to the transverse midline of the mantle.

Ventral Mantle, Tail—chromatophores on the lateral surface of the mantle near the narrow posterior end of the mantle, usually ventral to the fins.

Dorsal Mantle, Margin—dorsal counterpart of "Ventral Mantle, Margin."

Dorsal Mantle, Midregion—chromatophores along or on the longitudinal midline of the dorsal surface of the mantle but not reaching to the anterior or posterior margins.

Dorsal Mantle, Tail—small, isolated patch of chromatophores on the dorsal posterior surface of the mantle, often extending slightly onto the dorsal surface of the fins.

Dorsal Head—chromatophores on the dorsal surface of the head from the collar to the arms and laterally to the edge of the eyelid.

Arms and Tentacles, Aboral—chromatophores on the aboral and lateral surfaces of these structures.

Arms and Tentacles, Oral—chromatophores restricted to the oral surfaces of these structures.

Ocular Photophore—a large, often indistinct photophore on the ventral surface of each eye. In some species the photophore first develops as separate anterior and posterior components that later fuse into a single organ.

Visceral Photophores—two photophores lying "beneath" (i.e., dorsal to) the intestine, one at each end. (These

Table 2
Brachial crown chromatophores: mean (range).

<i>Onycho-</i> <i>teuthis</i> species	Gladius length	n	Tentacle Aboral	Tentacle Oral	Arm I Aboral	Arm I Oral	Arm II Aboral	Arm II Oral
<i>compacta</i>	2.0-2.9	2	0	1 (0-2)	0	0	0	0
B	2.0-2.9	6	3.8 (3-5)	3.8 (3-5)	0.1 (0-1)	2.2 (1-3)	0.0 (0-1)	2.2 (1-4)
C	2.0-2.9	8	2.8 (1-4)	2.0 (1-3)	0.2 (0-1)	0.8 (0-1)	0	0.8 (0-2)
<i>compacta</i>	3.0-5.9	14	3.6 (2-5)	3.1 (2-6)	3.0 (0-4)	0.0 (0-1)	1.9 (0-3)	1.5 (0-2)
B	3.0-5.9	21	4.6 (3-11)	8.6 (4-13)	2.2 (0-6)	4.8 (2-9)	1.8 (0-4)	6.2 (3-12)
C	3.0-5.9	20	2.8 (1-5)	2.8 (2-4)	3.1 (1-5)	1.1 (0-2)	1.2 (0-3)	1.9 (0-4)

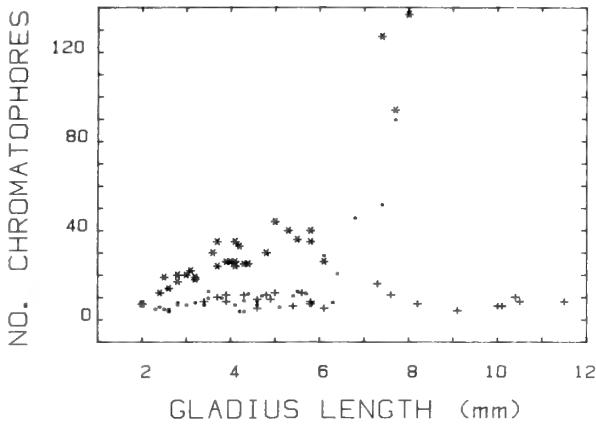


Figure 1

Number of Ventral Mantle, Belly chromatophores. +, *Onychoteuthis compacta*; *, *Onychoteuthis* sp. B; ■, *Onychoteuthis* sp. C.

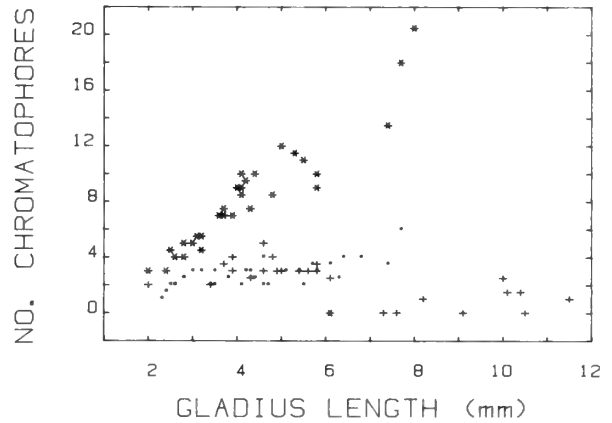


Figure 3

Number of Oral chromatophores on each tentacle. Symbols as in Figure 1.

are often difficult to see in young specimens unless the intestine is removed.)

Hooks, Dorsal and Ventral Series—in young larvae the tentacular club has four series (rows) of suckers. The two middle series will develop into hooks. The more dorsal of these is called the Dorsal Series, and the more ventral is the Ventral Series.

Tentacle Stalk Suckers—suckers are present on the tentacle stalk until, approximately, the appearance of the carpal cluster on the club. These suckers apparently are lost during development.

Gladius Length (GL)—length of the gladius from the anterior tip to the posterior tip. The GL is used as a measure of body length rather than the mantle length because the gladius (a more accurate measure of size than the mantle length) is easily seen in these larvae.

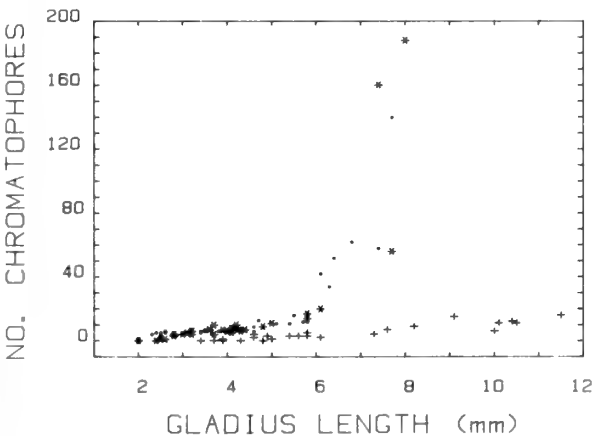


Figure 2

Number of Dorsal Mantle, Midregion chromatophores. Symbols as in Figure 1.

RESULTS

The 280 *Onychoteuthis* larvae captured during the 1983–1984 sampling program constituted 10.1% of the 2763 cephalopod (squid and octopod) larvae taken and 10.6% of the 2628 squid larvae taken.

The chromatophore counts on larvae smaller than 6 mm GL for all three species are summarized in Tables 1 and 2. Chromatophore counts for all sizes of larvae examined are plotted for some chromatophore zones for each species in Figures 1–4.

Onychoteuthis compacta (Berry, 1913)

(Figure 5)

Material examined: This species ranked second in abundance among the three species of *Onychoteuthis* and thir-

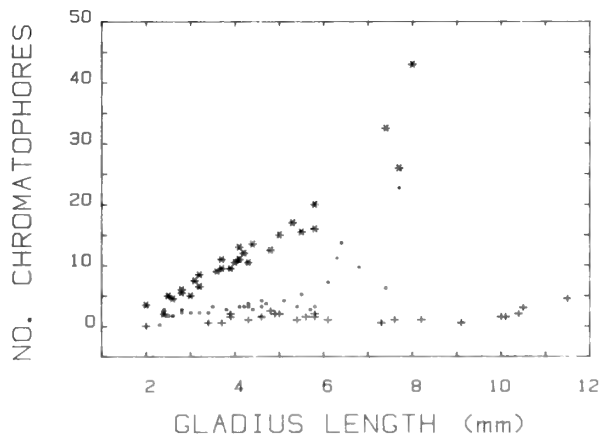


Figure 4

Number of Oral chromatophores on each arm I combined with the number on each arm II.

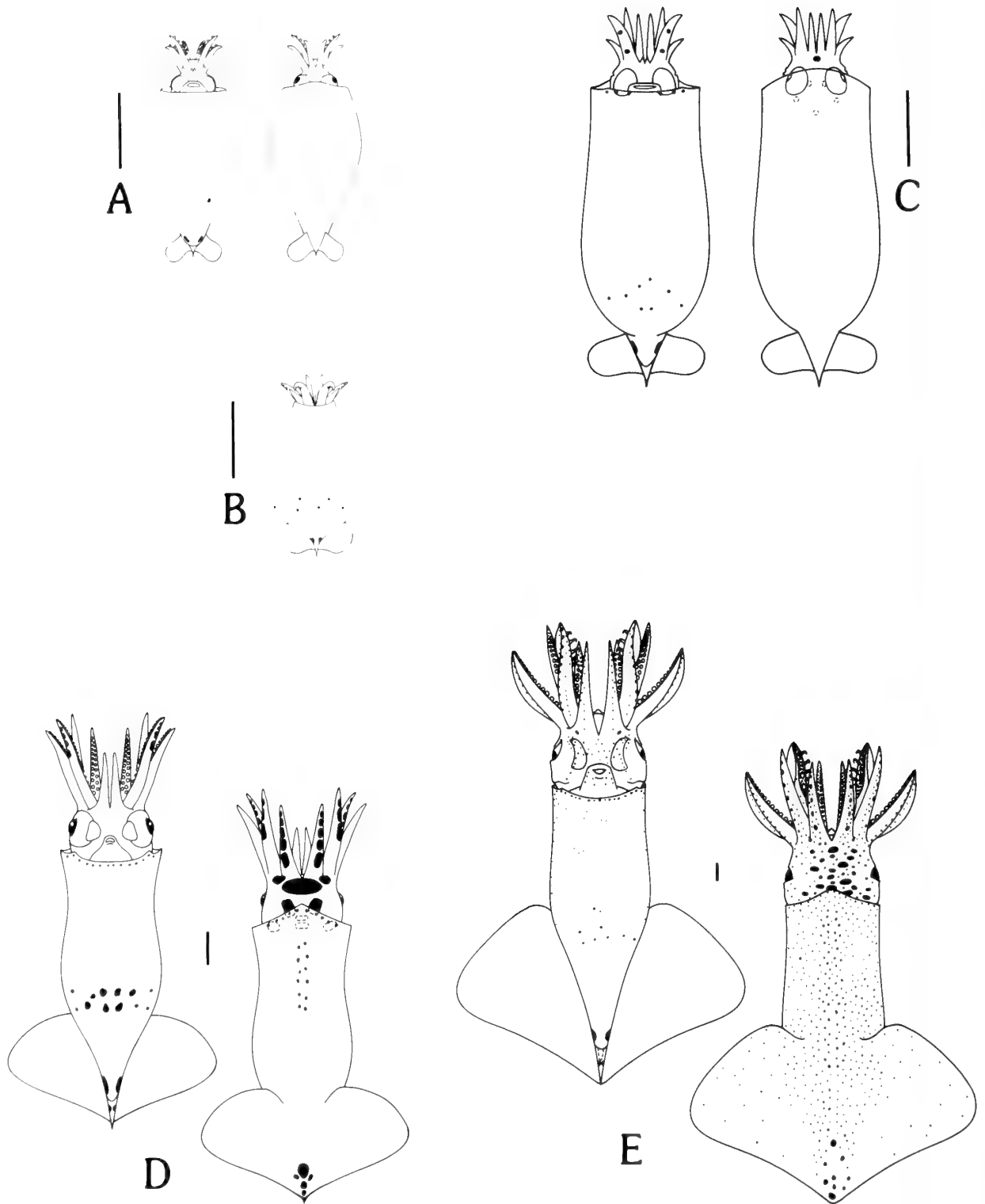


Figure 5

Onychoteuthis compacta. A, ventral and dorsal views of 2.3-mm GL larva; B, ventral view of 4.8-mm GL larva showing retracted position of head; C, ventral and dorsal views of 4.1-mm GL larva; D, ventral and dorsal views of 8.9-mm GL larva; E, ventral and dorsal views of 18.5-mm GL juvenile. Dotted circles represent head chromatophores.

teenth in abundance among all species of squids. The 42 larvae captured constituted 16% of all squids taken during the sampling program. Additional specimens were available from previous sampling. A total of 119 specimens, ranging in size from 2.0 to 21.5 mm GL, was examined.

Chromatophores: *Ventral Mantle, Margin*—chromatophores precisely aligned in a simple band. *Ventral Mantle, Belly*—few chromatophores located well posteriorly at less than 4–5 mm GL. *Ventral Mantle, Tail*—by 6 mm GL, most larvae with 4 chromatophores; anterior pair much larger. *Dorsal Mantle, Midregion*—chromatophores on either side of midline; by 9 mm GL, 10–15 chromatophores clearly in two straight, simple rows, one on each side of midline. Chromatophores very small. *Dorsal Mantle, Tail*—by 5–6 mm GL, one to several chromatophores present; by 9 mm GL, about 5–10 chromatophores present. *Arms and Tentacles, Oral*—present in a single row on each arm until about 13–16 mm GL when double rows appear. *General chromatophore counts*—numbers increase dramatically at 12–16 mm GL.

Photophores: *Ocular Photophores*—present by 9–10 mm GL. *Visceral Photophores*—present by 9–10 mm GL.

Tentacles: *Hooks, Ventral Series*—first appear at 12–14 mm GL. *Hooks, Dorsal Series*—not present in specimen of 20.5 mm GL; hook rudiments present in a 21.5-mm GL specimen. *Tentacle Stalk Suckers*—present in 13.2-mm GL specimen, but only 1 remaining in 16.5-mm specimen.

Other larval characters: Nearly all specimens with head either partially or fully retracted into mantle cavity (Figure 5B); arms and tentacles short; fins large in juveniles.

Vertical distribution: Very few larvae were caught during the April vertical distribution series. In the October series most larvae were caught between 50 and 150 m during the day, while at night most captures came from the upper 25 m (Figure 6).

Onychoteuthis sp. B

(Figure 7)

Material examined: This was the least abundant of the three species of *Onychoteuthis*, and ranked 23rd in abundance among all species of squids taken. The 23 larvae captured constituted 0.8% of all squid larvae taken. Additional specimens were available from previous sampling. A total of 65 specimens, ranging in size from 1.9 to 16.0 mm GL, was examined.

Chromatophores: *Ventral Mantle, Margin*—chromatophores in complex band with either staggered or multiple series; at less than 3 mm GL a few chromatophores, if positioned relatively far from the anterior margin, will indicate the future complex band. *Ventral Mantle, Belly*—numerous chromatophores even in larvae of 1.8–2.0 mm GL. *Ventral Mantle, Tail*—by 4 mm GL, most larvae with 4 chromatophores; by 5–7 mm GL, 6 chromatophores

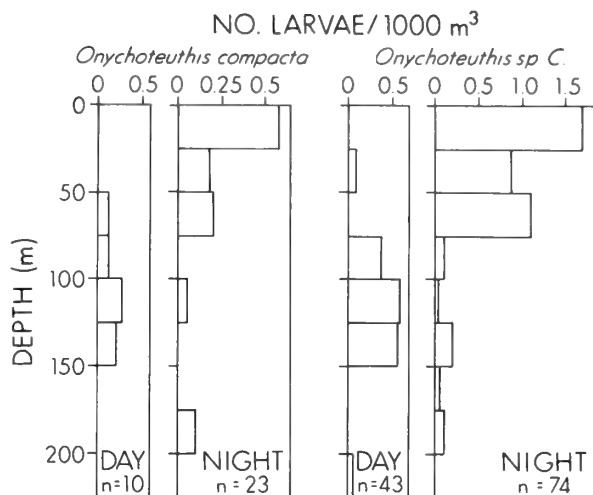


Figure 6

Vertical distribution of larvae of *Onychoteuthis compacta* and *O. sp. C* from the October series with open nets. n = total number of larvae.

present. *Dorsal Mantle, Midregion*—chromatophores on midline; usually in simple, straight row; sometimes with a few additional non-aligned chromatophores by 3.5–4.0 mm GL. *Dorsal Mantle, Tail*—by 6–7 mm GL several chromatophores present. *Arms and Tentacles, Oral*—present in a single row per arm until about 7–8 mm GL when double row appears. *General chromatophore counts*—numbers increase dramatically about 6–8 mm GL.

Photophores: *Ocular Photophores*—posterior component present by 3–4 mm GL; anterior component appears at 5–7 mm GL. *Visceral Photophores*—present by 5–6 mm GL.

Tentacles: *Hooks, Ventral Series*—appears at 7–8 mm GL. *Hooks, Dorsal Series*—not present in a 16-mm GL specimen. *Tentacle Stalk Suckers*—most lost by 7–8 mm GL.

Other larval characters: Specimens rarely with head retracted, even partially, into mantle cavity. Arms and tentacles long; fins large in juveniles.

Distribution: Most of the few larvae caught were taken during the October series. Two day-captures were made in the upper 100 m and five night-captures were made in the same depth zone.

Onychoteuthis sp. C

(Figure 8)

Material examined: This species was first in abundance among species of *Onychoteuthis* and fourth in abundance among all species of squids taken. The 215 larvae captured constituted 8.2% of all squid larvae captured. A total of 260 specimens, ranging in size from 2.2 to 17.0 mm GL, was examined.

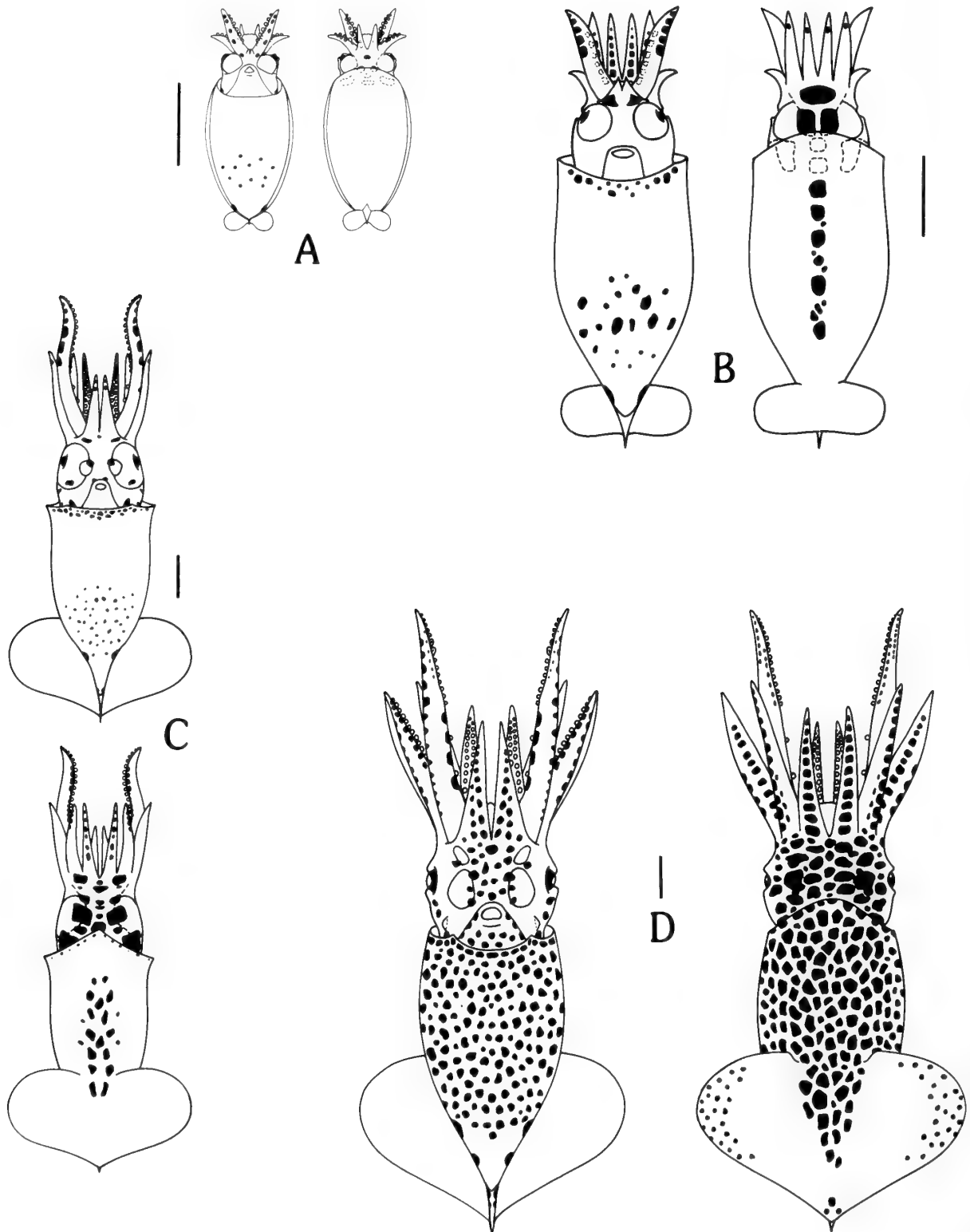


Figure 7

Onychoteuthis sp. B. Ventral and dorsal views of various stages. A, 1.9 mm-GL larva; B, 3.8-mm GL larva; C, 5.8-mm GL larva; D, 8.8-mm GL juvenile.

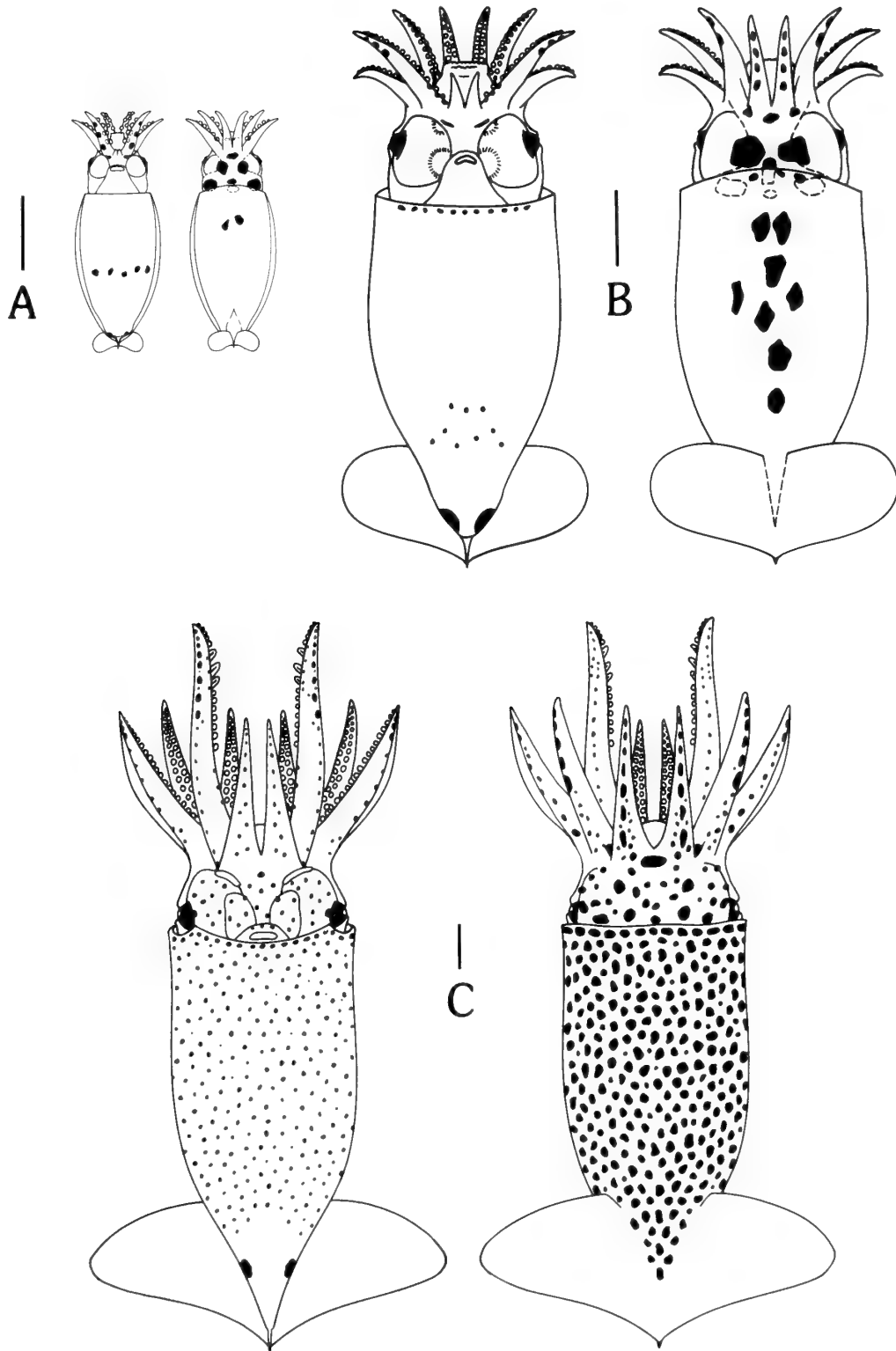


Figure 8

Onychoteuthis sp. C. Ventral and dorsal views of various stages. A, 2.2-mm GL larva; B, 5.2-mm GL larva; C, 9.6-mm GL juvenile.

Table 3
Chromatophore comparisons among the three species of *Onychoteuthis*.

	<i>Onychoteuthis compacta</i>	<i>Onychoteuthis</i> sp. B	<i>Onychoteuthis</i> sp. C
Ventral Mantle, Belly	few	many	few
Ventral Mantle, Anterior Margin	simple band	complex band	simple band
Dorsal Mantle, Midregion	2 rows	"1" row	patch
Ventral Mantle, Tail (>4 mm pL)	2 pr	2-3 pr	1 pr
Dorsal Mantle, Tail (>6 mm pL)	present	present	absent
Arms and Tentacles, Oral	few	many	few
Major increase in chromatophore numbers	14-16 mm GL	6-8 mm GL	6-8 mm GL

Chromatophores: *Ventral Mantle, Belly*—at less than 5–6 mm GL, belly chromatophores often two separate bands; smaller than 2.5 mm GL, belly series a simple band. *Ventral Mantle, Margin*—chromatophores precisely aligned in a simple band. *Ventral Mantle, Tail*—no more than a single pair present in larvae of any size. *Dorsal Mantle, Midregion*—at less than 6 mm GL, chromatophores in a complex row or patch along midline. *Dorsal Mantle, Tail*—no separate patch of chromatophores found in this position. *Arms and Tentacles, Oral*—Present in a single row per arm until about 8–9 mm GL at which size a double row appears. *General chromatophore counts*—numbers increase dramatically at 6–8 mm GL.

Photophores: *Ocular Photophores*—posterior component present at 4–5 mm GL; anterior component present at 7–8 mm GL. *Visceral Photophores*—present by 5–7 mm GL.

Tentacles: *Hooks, Ventral Series*—first appear at 8–10 mm GL. *Hooks, Dorsal Series*—present in a 17-mm GL specimen. *Tentacle Stalk Suckers*—most lost by 10–11 mm GL.

Other larval characters: Specimens rarely with head retracted (even partially) into mantle cavity; arms and tentacles intermediate in length; fins short in juveniles.

Vertical distribution: Larvae were common during both sampling periods and exhibited about the same distribution patterns during both periods. Most catches came from about 50–150 m during the day and from the upper 50 m at night (Figure 6).

DISCUSSION

Only two species of *Onychoteuthis* are generally recognized: *O. borealijaponicus* (Okada, 1927) from the high North Pacific and *O. banksii* from most other areas of the world oceans. YOUNG (1972), however, suggested that *O. banksii* might represent a species complex based on his examination of specimens from off Florida, U.S.A. Because of this uncertainty, he revived the name *O. compacta* (Berry, 1913) for the species occurring in Hawaiian waters (YOUNG, 1978).

In spite of BERRY's brief description (1914) of the unique type of *Onychoteuthis compacta* from Hawaii, a young 21-

mm ML specimen, there is no doubt as to which of the three series of larvae described here represents this species. BERRY's illustration of the holotype shows the head partially withdrawn into the mantle cavity. This feature was characteristic of only one of the three species that we collected. In addition, at comparable GL, the arm, tentacle and fin measurements, as well as hook arrangements of this species, were close to those of BERRY's description of the holotype. The other two species are considered to be new. We see no advantage in naming these before an adequate series of adults or subadults can be obtained and described.

The *Onychoteuthis* larvae from Hawaii were easily separable on the basis of chromatophore patterns (see summary in Table 3). In addition, differences also existed between the species in head retraction, in the size at which the photophores and tentacular hooks first appeared, in the relative lengths of the arms, tentacles and fins, and in the shape of the fins. However, because these latter characters were difficult to measure accurately, we have not emphasized them.

In the smallest larvae examined (2.0–2.5 mm GL) *Onychoteuthis compacta* could be recognized most easily by the "Ventral Mantle, Belly" chromatophore series which, if present, had a few chromatophores arranged in a complex band that was located farther posteriorly than in the other species. *Onychoteuthis* sp. C could be recognized most easily by the simple band in the "Ventral Mantle, Belly" chromatophore series, by usually at least one chromatophore in the "Dorsal Mantle, Midregion" series that was not on the midline, and by the relatively low numbers of oral chromatophores. *Onychoteuthis* species B was recognized by the complex "Ventral Mantle, Belly" chromatophore series, by the arrangement of all "Dorsal Mantle, Midregion" chromatophores (if present) on the midline, and by the large number of oral chromatophores.

Many of the differences in chromatophore patterns vanish on specimens smaller than 2 mm GL. We have yet to determine whether or not the differences described here will allow separation of the smallest larvae.

The sudden increase in chromatophore numbers that correlates with the appearance of hooks apparently marks the end of the larval stage.

Clear evidence for vertical migration was present for *Onychoteuthis compacta* and for *Onychoteuthis* sp. C during the October series.

The presence of the larvae of three species of *Onychoteuthis* from the same locality in Hawaii confirms that "*O. banksii*" is a species complex. Systematic problems with this genus are not surprising because adults avoid most nets and, as a result, adults are rare in most reference collections.

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The Malacological Taxa of Henry Hemphill

by

EUGENE COAN

Research Associate, Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118, U.S.A.

AND

BARRY ROTH

Department of Invertebrate Zoology, Santa Barbara Museum of Natural History,
2559 Puesta Del Sol Road, Santa Barbara, California 93105, U.S.A.

Abstract. Henry Hemphill (1830-1914) was an early malacologist in the western United States, whose specimens formed the basis of the present collection of the California Academy of Sciences. In his papers on mollusks, he introduced some 102 names, mostly for land snails. Eighteen of these are *nomina nuda* or are otherwise unavailable. Of his 84 available names, 50 are now regarded as junior synonyms and 34 are recognized as valid. We have located type material of all but one of the available names. One lectotype designation is made. Other workers introduced 25 names coined by Hemphill, of which 7 are unavailable and 18 are available. A bibliography of Hemphill's papers is provided.

INTRODUCTION

HENRY HEMPHILL (1830-1914) was an early and influential malacologist on the west coast of the United States. He amassed a huge collection of land, freshwater, and marine mollusks, which, when divided, became the nucleus of the present holdings of the California Academy of Sciences and Stanford University.

This article provides a complete bibliography of Hemphill's published works on mollusks and lists the nomenclatural units that were first published by him, or that have been credited to him.

The published information about Hemphill's life is sparse (ANON., 1914a, b; BAILY, 1962; DALL, 1914; HOWARD, 1972). He was born in Delaware in 1830. Beginning around 1861, he traveled in the West, finally settling in San Diego, California, in 1865, where he worked as a bricklayer. However, he also made a number of gold prospecting trips in the western states. He evidently started collecting mollusks as early as 1861, and under the influence of such Californian malacologists as Wesley Newcomb and Robert E. C. Stearns increasingly turned his attention from gold to mollusks.

He collected extensively throughout the western states, Baja California, and Florida. Unfortunately, the only information on the timing and localities of his wanderings

lies in bits and pieces scattered in his writings and on specimen labels.

From the 1870's to 1890 he published small catalogues of shells for sale (HEMPHILL, 187[?], 1875, 1878, 1881c, d, 1890f). Around this time too he began to publish articles in the *Proceedings of the California Academy of Sciences*, *The Nautilus*, and other serials. He sent samples from his collecting to experts in the eastern U.S., including William G. Binney and Henry A. Pilsbry, and they were responsible for the publication of many of his names, variously with and without descriptive text contributed by Hemphill.

Around 1909, he moved to Oakland, California, to live with his daughter. He died 24 July 1914, as a result of contact with arsenic he used in preserving specimens.

In the following list, we have included all the names that were first made available by Hemphill in his publications, new names that appear in his publications as *nomina nuda*, and names—both available and *nomina nuda*—published by others but credited to Hemphill.

Some of Hemphill's practices have caused problems for later systematists. He sorted his material for uniformity (thereby destroying all evidence of population structure), lumped together under a single locality specimens from numerous stations, sold or otherwise sent out material

labeled with unpublished names, introduced many *nomina nuda*, and had a predilection to see "varieties" and dignify them with formal naming. In at least the case of *Epiphragmophora traski* var. *cuyamacensis*, he seems to have sent the shells of the lot to one specialist (Bartsch) and the soft anatomy to another (Pilsbry), with the ultimate result that it was described twice. If part of the problem of the haphazard validation of his manuscript names lay with the exuberance of what has been called the "Descriptive Age of Malacology" (BOSS *et al.*, 1968:1), these foibles of Hemphill's did nothing to discourage the syndrome.

The following are a number of complications and factors that must be kept in mind when using this list.

Trinomials: Particularly in his work on land mollusks, Hemphill proposed a great many trinomials for entities that today are regarded merely as intrapopulational variants. Most have been synonymized by subsequent workers, but they should be kept in mind if it is found that additional taxa can be recognized in the groups involved. His named "varieties" often appear as separate entries in his sales catalogues, suggesting that in part he may have tried to increase the number of his marketable products.

Authorship: Manuscript names accompanying Hemphill material in various collections and the many *nomina nuda* in his sales catalogues suggest that, given the opportunity, he would have proposed a great many more names, mainly for "varieties." Some of these manuscript names were picked up and made available by other authors, who often simply credited them to Hemphill. In reality, the names should be fully credited to these later authors, because they are responsible for the conditions that made the names available (*ICZN Code*, Art. 50). Compilers of the taxa of such authors as Pilsbry have often missed them. These names are cited here in a format of "Pilsbry, *ex* Hemphill MS." The proper identification of authorship of taxa is crucial to decisions about type material (see below).

Authorship of some Hemphill taxa, particularly those in BINNEY (1886), has been difficult to interpret. Our decisions are based on a consideration of each appearance of each name with reference to the criteria of availability in *ICZN Code*, Art. 12. (The distinction between "Jones, *ex* Smith MS" versus "Smith, in Jones" has been discussed by COAN, 1972.)

Type localities: Hemphill is well known for reporting his localities in vague terms (PILSBRY, 1939:449), and it has been speculated that he did so to prevent other collectors from finding the habitats of some of his more unusual taxa. In a number of cases, his labels narrow down the localities; later malacologists have tracked down others.

Type material: Hemphill was a prodigious collector. He amassed huge lots, in part because he made money from the sale of duplicate material. As a result of his sales and exchanges, what must now be interpreted as type material of his taxa ended up in many institutions. His main per-

sonal collection was given to the California Academy of Sciences by his daughter, Mrs. Charlotte Hosmer (ANON., 1915). Large duplicate sets of specimens were purchased by Stanford University and are now housed with the rest of the Stanford mollusk collection at the California Academy of Sciences. He also sent many specimens to the U.S. National Museum of Natural History and to the Academy of Natural Sciences in Philadelphia. Others went to W. G. Binney, whose collections are in the American Museum of Natural History and the U.S. National Museum. Many type specimens are in the University of Colorado Museum in Boulder (WU & BRANDAUER, 1982), possibly obtained through Ida Shepard Oldroyd of Stanford University.

We have examined the material in the American Museum of Natural History, the California Academy of Sciences, the Santa Barbara Museum of Natural History, and the United States National Museum of Natural History. Arthur E. Bogan of the Academy of Natural Sciences of Philadelphia examined the collections under his care. The following published catalogues were consulted: H. B. BAKER (1962, 1964) and JOHNSON & BAKER (1973), Academy of Natural Sciences of Philadelphia; BROOKS & BROOKS (1931), Carnegie Museum, Pittsburgh; J. T. SMITH (1978), Stanford University; WILSON & KENNEDY (1967), San Diego Natural History Museum; WU & BRANDAUER (1982), University of Colorado Museum, Boulder. We have not tried to survey material in other institutions or still in private hands. In light of the fact that abundant type material has been found for most species, we did not make a careful survey of the large duplicate lots in the Stanford University collection.

Hemphill labeled a few lots in the California Academy of Sciences and the Stanford University collections as "types." However, he did not designate individual specimens as holotypes in any of his publications. We therefore regard his labeled "types" as syntypes; they are perhaps the best specimens from which lectotypes might be designated. Certain authors and curators have erroneously recognized Hemphill "holotypes" of species for which only syntypic lots exist.

Later authors have designated lectotypes for some of the taxa, in which case the rest of the type material are paralectotypes. (In one case, there are competing lectotype designations; the earliest takes precedence.)

Hemphill evidently returned to his productive localities repeatedly and collected additional material. Thus, in a number of cases there are more "syntypes" than the number of specimens he claimed he had in hand when he prepared his original descriptions. We have here merely indicated when this is the case, leaving the interpretation of this material and the selection of lectotypes to systematists working on the taxa involved.

If a name was made available by "Hemphill, in Pilsbry," for example, then the type material is all the specimens Hemphill had in hand when he named the species. If, on the other hand, a name was made available by

"Pilsbry, *ex* Hemphill MS," or the like, then the converse is the case: supposed Hemphill syntypes have no standing; the type material is only that which Pilsbry (or some other author) consulted.

Where we have examined and annotated the type material, we have called the specimens what we believe them to be, most often syntypes. Where we have not personally reviewed a museum's holdings, we have generally reported the type status assigned in that institution's register, adding quotation marks (as "paratypes") if our interpretation differs.

This review has resulted in the introduction of three nomenclatural changes:

(1) *Helminthoglypta tudiculata convicta* (Pilsbry, 1913, *ex* Hemphill MS) is a senior synonym of *H. t. angelena* Berry, 1938. *Helminthoglypta t. convicta* was based on specimens with the supraperipheral band very weakly developed. The type locality is recorded only as "Los Angeles County," but the holotype, paratype, and material labeled "*convicta*" by Hemphill in the California Academy of Sciences agree in all other respects with large lots of normally banded specimens that Hemphill collected at "Cerritos" [Signal Hill], California, within the range of the subspecies *H. t. angelena*. They were undoubtedly selected out of such lots.

(2) Authorship of *Helminthoglypta cuyamacensis* is to be attributed to Pilsbry (1895, *ex* Hemphill MS) rather than to Bartsch (1916, *ex* Hemphill MS). PILSBRY (1895) validated the name with a figure of the reproductive system. MILLER (1985:98) has collected probable topotypes of *H. cuyamacensis* and affirms PILSBRY's (1939) suggestion that the anatomy of *Epiphragmophora traski* var. *cuyamacensis* Pilsbry, 1895, and the shells of *E. cuyamacensis cuyamacensis* Bartsch, 1916, came from the same lot.

(3) *Monadenia fidelis flava* (Hemphill, 1892) is a senior synonym of *M. f. beryllica* Chace & Chace, 1935. *Monadenia f. flava* was based on bandless individuals. PILSBRY (1939:40) regarded it as representing "merely an albino or xanthic mutation . . . [which] may occur apparently in any *fidelis* colony," but the only extant type specimen, herein designated lectotype, is from within the range of *M. f. beryllica*, and it is the earliest available name for that subspecies.

Each entry in the following list consists of: (1) the name as originally proposed (except that capitalization has been normalized to modern practice), with authorship, date, and page and figure numbers (keyed to the bibliography); (2) the type locality, including refinements based on label data or subsequent authors' work; (3) the number of specimens if indicated in the original publication; (4) type material, including museum numbers, type status, and number of specimens (in parentheses); and (5) remarks, including current taxonomic assignment, notes on interpretation of authorship, and references to pertinent discussion elsewhere. References are provided in the bibli-

ography for all literature cited and for senior homonyms but not for junior or senior synonyms. (We have found that a number of supposed senior homonyms are really *nomina nuda* or are otherwise unavailable.)

The following abbreviations are used: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; CASGTC, former numbers of the CAS Geology Type Collection; CM, Carnegie Museum; MCZ, Museum of Comparative Zoology, Harvard University; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; SUPTC, former numbers of the Stanford University Paleontology Type Collection; UCM, University of Colorado Museum; USNM, United States National Museum of Natural History, Smithsonian Institution.

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TAXONOMIC LISTING

Class Bivalvia

consanguineum "Prime," *Pisidium*—HEMPHILL, 1890f:20 [*nomen nudum*]. Nevada.

idahoensis, *Anodonta nuttalliana* var.—HEMPHILL, 1891a: 328–329, 337; pl. 10, figs. 3, 4. Spokane River above Post Falls, Kootenai Co., Idaho.

Type material—CAS 058856, syntypes (4), labeled "types" by Hemphill; ANSP 62757a, "figured holotype" (2 valves); ANSP 62757, "paratypes" (4 valves) (see JOHNSON & BAKER, 1973:158).

Remarks—Synonym of *Anodonta nuttalliana* Lea, 1838, according to BURCH (1975:165).

roseum "Prime," *Sphaerium*—HEMPHILL, 1890f:20 [*nomen nudum*]. Washington.

Remarks—Possibly a misspelling of *Cyclas rosacea* Prime, 1852.

subangulata, *Anodonta angulata* var.—HEMPHILL, 1891a: 325, 337; pl. 10, figs. 1, 2 [a primary homonym of *Anodon subangulata* ANTHONY, 1865:158–159, because these generic names are the same (ICZN Opinion 561, 1959)]. Russian River, Putah Creek, and Upper San Joaquin River, northern Calif.

Type material—CAS 058866, syntypes (3), from

Healdsburg, Sonoma Co., Calif., labeled "types" by Hemphill.

Remarks—Synonym of *Gonidea angulata* (Lea, 1838).

Class Gastropoda

aequisculpta, *Alvania*—HEMPHILL, 1875:3, ex Carpenter MS [*nomen nudum*].

Remarks—Made available by KEEP (1887) (COAN, 1985:212).

albida, *Helix* (*Mesodon*) *areolata* var.—HEMPHILL, 1890f: 17 [*nomen nudum*] [*non H. albida* COSTA, 1839: *Helix* 32]. Baja Calif.

albida, *Helix intercisa* var.—HEMPHILL, 1891a:330 [*non H. albida* COSTA, 1839: *Helix* 32] [HEMPHILL, 1890f: 17, *nomen nudum*]. San Clemente Id., Los Angeles Co., Calif.

Type material—CAS 058817, syntypes (7), labeled "types" by Hemphill; CAS 037578 (2), 037840 (2), syntypes; USNM 174540, syntypes (2); ANSP 10799, syntypes (3); AMNH 52117, syntypes (2).

Remarks—Synonym of *Xerarionta intercisa* (W. G. Binney, 1857). Not preoccupied by *Helix albida* RÖDING, 1798:107, a *nomen nudum*.

albida, *Helix kelleetti* var.—Hemphill, in W. G. BINNEY, 1890:220 [*non H. albida* COSTA, 1839: *Helix* 32]. Santa Catalina Id., Los Angeles Co., Calif.; 2 specimens.

Type material—Obviously also representing subsequent collecting: CAS 037311, syntypes (4), labeled "types" by Hemphill; CAS 037679, syntypes (4); ANSP 79744, syntypes (2).

Remarks—Synonym of *Xerarionta kelleetti* (Forbes, 1850).

albida, *Helix tryonii* var.—HEMPHILL, 1891a:332 [*non H. albida* COSTA, 1839: *Helix* 32] [HEMPHILL, 1890f: 17, *nomen nudum*]. Santa Barbara Id., Los Angeles Co., Calif.

Type material—CAS 032758 (4), 037698 (2), syntypes; USNM 174388–174394, syntypes (14); AMNH 52540, syntypes (4); UCM 20678, syntypes (13); SBMNH 33952, syntypes (7).

Remarks—Synonym of *Plesarionta tryoni* (Newcomb, 1864).

albida, *Oreohelix* var.—HENDERSON & DANIELS, 1917:66, ex Hemphill MS [in synonymy of *O. haydeni hybrida* (Hemphill, 1890)].

albida, *Patula strigosa* var.—HEMPHILL, 1890d:17. Near Logan, Cache Co., Utah [Logan Canyon, 5000 ft. (labels)].

Type material—CAS 058875, lectotype (PILSBRY, 1939:494); CAS 058874, paralectotypes (6); USNM 363233, paralectotypes (24); AMNH 52914, paralectotypes (2); SBMNH 33933, paralectotypes (6).

Remarks—Synonym of *Oreohelix subrudis rugosa* (Hemphill, 1890), according to PILSBRY (1939:493–494).

albofasciata, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 31, 32, 47; pl. 2, figs. 3, 4. Banks of Bear River, near Brigham, Box Elder Co., Utah [4500 ft. (PILSBRY, 1939)].

Type material—USNM 102161 (1), 102163 (1), both "orig. type figd."; USNM 102162, "orig. type" (1); CAS 054513 (2), 054517 (2), 054520 (2), 054522 (2), 054586 (2), 054595 (2), syntypes; AMNH 53975, probable syntypes (4); AMNH 61688, syntypes (10 in 3 lots); UCM 20652, "paratypes" (43); SBMNH 33920 (10), 33922 (8), syntypes.

Remarks—Synonym ("color-var.") of *O. peripherica peripherica* (Ancey, 1881), according to PILSBRY (1939: 450–454; figs. 298-5, -18, -19).

avalonensis, *Oreohelix*—Hemphill, in PILSBRY, 1905:283, 284, 285; pl. 11, figs. 4–7. Santa Catalina Id., Los Angeles Co., Calif.

Type material—ANSP 86671a, "holotype"; ANSP 86671, "paratypes" (2); CAS 029012 (18), 032996 (4), syntypes; CAS 058942, ex SUPTC 6162, syntypes (51); USNM 174685, syntypes (6); UCM 20746 (8), 21273 (4), syntypes; SBMNH 33996, syntypes (9); CM 6160, syntypes (3); SDMNH 1376, syntypes (5).

Remarks—*Radiocentrum avalonense* (Hemphill, in Pilsbry, 1905). Hemphill later published a more formal description (HEMPHILL, 1911:104–108; pl. 4—as *Helix* var. *avalonensis*).

bicolor, *Helix kelleetti* var.—HEMPHILL, 1891a:334 [*non H. bicolor* J. ADAMS, 1800:4, 6; pl. 1, figs. 25–27] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif.

Type material—CAS 037172 (7), 037200 (3), 037201 (3), 037232 (4), 037233 (7), 037676 (5), syntypes; USNM 174442–174444, syntypes (6); AMNH 51891, syntypes (2).

Remarks—Synonym of *Xerarionta kelleetti* (Forbes, 1850).

bicolor, *Patula strigosa*—HEMPHILL, 1890a:133. Rathdrum, Kootenai Co., Idaho.

Type material—CAS 058864, lectotype (PILSBRY, 1939:424); CAS 050484 (4), 050492 (5), paralectotypes; ANSP 62387a (1), 62387 (1), paralectotypes; AMNH 53972, paralectotypes (4); SBMNH 33940, paralectotypes (8).

Remarks—Synonym of *Oreohelix strigosa strigosa* (Gould, 1846) and of its "form" *subcarinata* (Hemphill, 1890), according to PILSBRY (1939:419, 424). See also HANNA & SMITH (1939:386, 392; pl. 35, figs. 7–9).

binneyi, *Helix tudiculata* var.—Hemphill, in W. G. BINNEY, 1890:219–220. Mountains near San Diego, San Diego Co., Calif. [Balena, near San Diego (label)]; 1 specimen.

Type material—CAS 058862 (1), 062704 (1), syntypes, labeled "types" by Hemphill. PILSBRY (1939:72) calls the former "unique type."

Remarks—Synonym of *Helminthoglypta (H.) tudiculata tudiculata* (A. Binney, 1843).

binneyi, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 29, 31, 47; pl. 2, fig. 13. Bear River, N of Brigham, Box Elder and Cache cos., Utah [4500 ft. (PILSBRY, 1939)].

Type material—USNM 102172, "orig. type figd." (1); CAS 054449 (2), 054455 (2), 054510 (2), 054511 (2), 054584 (5), 054585 (2), 054588 (2), 054589 (2), 054591 (2), 054593 (2), 054519 (2), syntypes; AMNH 53976 (1), 61671 (7 in 2 lots), probable syntypes; SBMNH 33946, syntypes (37).

Remarks—Synonym ("color-var.") of *Oreohelix peripherica peripherica* (Ancey, 1881), according to PILSBRY (1939:450-454; figs. 298-1-3, -6-8, -11, -13-15, -24).

blandi, *Triodopsis mullani* var.—Hemphill, in W. G. BINNEY, 1892:184 [but not p. 203; pl. 2, fig. 6, according to PILSBRY (1939)] [HEMPHILL, 1890f:16, *nomen nudum*, as *Helix (Mesodon) devius* var.]. Post Falls, and banks of Salmon River, Kootenai Co., Idaho.

Type material—CAS 058841 (6), 058842 (6), syntypes from Post Falls, labeled "types" by Hemphill.

Remarks—Synonym of *Cryptomastix (C.) mullani mullani* (Bland & Cooper, 1861), according to VAGVOLGYI (1968:223) and MILLER *et al.* (1984:7).

buttonii, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1890:220. Box Elder Co., Utah [sandstone ledges, 4500-5000 ft. (labels)].

Type material—CAS 058871, lectotype (PILSBRY, 1939:439); CAS 058869 (1), 058870 (1), paralectotypes; CAS 050332 (5), 050333 (9), 050334 (6), 050335 (5), 050336 (7), 050338 (9), 050388 (5), paralectotypes; USNM 31211, paralectotypes (2); ANSP 10905, paralectotypes (3); AMNH 61672, paralectotypes (16 in 4 lots); SBMNH 33948, paralectotypes (8).

Remarks—*Oreohelix strigosa buttonii* (Hemphill), according to PILSBRY (1939:439-440; fig. 291).

californica, *Helix kellethii* var.—HEMPHILL, 1891a:333 [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif.

Type material—CAS 037191 (3), 037192 (5), 037197 (5), 037216 (5), 037220 (5), 037234 (6), 037577 (4), 037641 (7), 037648 (6), 037678 (6), syntypes; USNM 174457-174462, syntypes (12); AMNH 52548, syntypes (2); UCM 20671, "paratypes" (14).

Remarks—Synonym of *Xerarionta kellethii* (Forbes, 1850).

californica, *Helix tryonii* var.—HEMPHILL, 1891a:332 [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Barbara Id., Los Angeles Co., Calif.

Type material—CAS 037692, syntypes (5); USNM 174375-174377, syntypes (6); ANSP 10828 (1), 86799 (3), 86800 (2), 86801 (2), 86803 (2), syntypes; AMNH 52541, syntypes (4); UCM 20679, "paratypes" (10); SBMNH 33942, syntypes (9).

Remarks—Synonym of *Plesarionta tryoni* (Newcomb, 1864).

carinata, *Micrarionta tryoni*—PILSBRY, 1939:221-222; fig. 110i-o, *ex* Hemphill MS. Santa Barbara Id., Los Angeles Co., Calif.

Type material—ANSP 86804a, holotype; ANSP 86804, paratype (1).

Remarks—Synonym of *Plesarionta tryoni hemphilli* (Edson & Hannibal, 1911). Pilsbry credited *M. t. carinata* to Hemphill, but Pilsbry alone was responsible for its publication. CLENCH & TURNER (1962:27) regarded it as a replacement name for *Helix tryonii subcarinata* Hemphill (*q.v.*), but Pilsbry expressly proposed it as a new subspecies.

carnea, *Patula strigosa* var.—HEMPHILL, 1890d:15-16. Near Salt Lake [City], Salt Lake Co., Utah [probably City Canyon (PILSBRY, 1939)].

Type material—CAS 050405 (11), 050420 (4), 050435 (11), syntypes; USNM 31169, possible syntypes (2); ANSP 10904a (1), 10904 (2), syntypes; AMNH 52770 (4), 52874 (6 in 2 lots), 61674 (2), syntypes; SBMNH 33949, syntypes (11).

Remarks—Synonym ("form") of *Oreohelix strigosa depressa* (Cockerell, 1890), according to PILSBRY (1939:429-430, 435; fig. 286). In HEMPHILL (1890f:15) and on his original labels, both MS and printed, it is "*corneus*" (*q.v.*).

castaneus, *Helix kellethii* var.—Hemphill, in W. G. BINNEY, 1890:220 [non *H. castanea* MÜLLER, 1774, vol. 2: 67-68]. Santa Catalina Id., Los Angeles Co., Calif.

Type material—CAS 037175 (6), 037176 (7), 037183 (6), 037193 (7), 037217 (4), 037221 (2), 037312 (6), 037674 (3), 037677 (2), 037681 (6), 037682 (7), syntypes; USNM 174415-174422, syntypes (16); AMNH 51893 (2), 52031 (2), syntypes.

Remarks—Synonym of *Xerarionta kellethii* (Forbes, 1850).

castaneus, *Helix ptychophorus* var.—HEMPHILL, 1890g:41 [non *H. castanea* MÜLLER, 1774, vol. 2:67-68] [HEMPHILL, 1890f:16, *nomen nudum*, as *H. townsendiana* var.]. Old Mission and Rathdrum, Kootenai Co., Idaho.

Type material—CAS 058851, syntypes (6) from Rathdrum; CAS 058852, syntypes (6) from Old Mission.

Remarks—Synonym of *Allogona ptychophora* (A. D. Brown, 1870), according to PILSBRY (1940:887-891; figs. 509g, h). See also A. G. SMITH (1943:544).

castaneus, *Helix [kellethii var.] redimita* var.—HEMPHILL,

- 1891a:334 [*non H. castanea* MÜLLER, 1774, vol. 2: 67–68] [HEMPHILL, 1890f:17, *nomen nudum*, as *H. kelletti* var. B]. San Clemente Id., Los Angeles Co., Calif.
- Type material—CAS 037790 (5), 037793 (5), 037804 (8), 037805 (2), 037810 (3), syntypes; USNM 174475–174480, syntypes (12); UCM 20668, “paratypes” (11).
- Remarks—Synonym of *Xerarionta redimita* (W. G. Binney, 1858).
- castaneus*, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 31, 32–33, 47 [as *castanea*]; pl. 2, figs. 11, 14. Banks of Bear River near Brigham, Box Elder Co., Utah [4500 ft. (PILSBRY, 1939)].
- Type material—CAS 058848, lectotype (HENDERSON, 1929b:223, 226; pl. 24, fig. 1); CAS 058849 (4), 058850 (4), paralectotypes; USNM 102167, “orig. type figd.” (1); AMNH 58621 (3), 61701 (2), probable paralectotypes.
- Remarks—Synonym (“color-var.”) of *Oreohelix peripherica peripherica* (Ancey, 1881), according to PILSBRY (1939:450–454; figs. 298–16, –17), who also stated (pp. 428–429) that material mentioned in Hemphill’s original description from Celilo, Sherman Co., Oregon, is referable to *O. strigosa variabilis* Henderson, 1929.
- catalinensis*, *Selenites duranti* var.—Hemphill, in W. G. BINNEY, 1890:221. Santa Catalina Id., Los Angeles Co., Calif.; 1 specimen.
- Type material—Undoubtedly also representing subsequent Hemphill collecting: CAS 058853, syntypes (4); CAS 058854, *ex* SUPTC 6196, syntypes (2), both lots labeled “types” by Hemphill; USNM 30506 (3), 38785 (2), 174084 (5), 174085 (2), possible syntypes; SBMNH 33954, possible syntypes (18).
- Remarks—*Haplotrema (H.) catalinense* (Hemphill, 1890), according to PILSBRY (1946:207–208; fig. 99).
- cuyamacensis*, *Epiphragmophora (Helminthoglypta) traski* var.—see under *cuyamacensis*, *E. (H.) traski* var.
- cedrosensis*, *Helix (Mesodon) areolata* var.—HEMPHILL, 1890f:17 [*nomen nudum*]. Baja Calif.
- celo*, *Micrarionta rufocincta* form—PILSBRY, 1939:206–207; fig. 103g, *ex* Hemphill MS. Santa Catalina Id., Los Angeles Co., Calif.
- Type material—ANSP 86653a, holotype; ANSP 86653, paratype (1).
- Remarks—Synonym of *Micrarionta rufocincta* (Newcomb, 1864). Pilsbry credited this form to Hemphill, but Pilsbry alone was responsible for its publication.
- clappi*, *Helix devia* var.—HEMPHILL, 1897:74–75. Salmon River Mts., Idaho Co., Idaho [Lucile (PILSBRY, 1939)].
- Type material—CAS 058821, syntypes (6), labeled “types” by Hemphill; USNM 46905 (4), 58574 (6), possible syntypes; ANSP 71479, syntypes (2).
- Remarks—*Cryptomastix (C.) mullani clappi* (Hemphill). Illustrated by PILSBRY (1940:868–869; fig. 503b, e).
- cockerelli*, *Anadenus*—Hemphill, 1890c:2–3. Cuyamaca Mts., San Diego Co., Calif. [Julian (label)].
- Type material—CAS 020570, syntypes (4), labeled “types” by Hemphill; USNM 120393, syntypes (3); ANSP 63895, syntype (1).
- Remarks—*Anadenulus cockerelli* (Hemphill), according to PILSBRY (1948:703–706; fig. 384).
- cognatus*, *Helix (Mesodon) devius* var.—HEMPHILL, 1890f: 16 [*nomen nudum*] [*non H. (Helicogena) cognata* FÉRUSSAC, 1821:36; FÉRUSSAC & FÉRUSSAC, 1821: pl. 44, fig. 4]. Oregon.
- columbiana*, *Fluminicola nuttalliana*—KEEP, 1887:63, *ex* Hemphill MS [HEMPHILL, 1881c:12, *nomen nudum*]. Rivers of Oregon and Washington.
- Type material—Not found.
- Remarks—*Fluminicola columbiana* Keep, 1887, according to BURCH (1982:22, 93; fig. 145), although he credited the species to “Hemphill, in Pilsbry” (1899: 121, 123, 125). Material in type collections, such as CAS 058880, CAS 058881 (*ex* SUPTC 5831), and ANSP 27767, was based on the assumption that Hemphill published the species and is without type status. See COAN (1985:212).
- columbiana*, *Physella*—KEEP, 1887:120, *ex* Hemphill MS [HEMPHILL, 1881c:12, *nomen nudum*]. Columbia River, Oregon/Washington.
- Type material—Not located.
- Remarks—*Physella columbiana* Keep, 1887, according to BURCH (1982:53, 159; fig. 639), who dated the species from HEMPHILL (1890c:27—in which it is “*Physa* var. *columbiana*”). Material that would have been types of the species if the species had been proposed first by Hemphill had been placed in some type collections (CAS 058939; CAS 058940, *ex* SUPTC 5806; CAS 058941, *ex* SUPTC 5807; ANSP 32940, 32941; and UCM 21826). See COAN (1985:212).
- columbiana*, *Pompholyx costata* var.—HEMPHILL, 1881c:12 [*nomen nudum*]. No locality given.
- concurus*, *Helix dupetithouarsi*—PILSBRY, 1924:55, *ex* Hemphill MS [in synonymy of *Helminthoglypta umbilicata* (Pilsbry, 1898)]. Morro Bay, San Luis Obispo Co., Calif.
- Remarks—See PILSBRY (1939:132–135; fig. 67). BAKER (1962:6) reported a “holotype” in the ANSP (#112425a), but it is without type status because the name was never made available.
- convicta*, *Epiphragmophora tudiculata*—PILSBRY, 1913, *ex* Hemphill MS. San Diego Co. [Los Angeles Co. (label; corrected by PILSBRY, 1939)], Calif.
- Type material—ANSP 86896a, holotype; ANSP 86896, paratype (1). The CAS had Hemphill material

in its type collection, but it is doubtful that Pilsbry saw it.

Remarks—*Helminthoglypta* (*H.*) *tudiculata convicta* (Pilsbry, 1913), and a senior synonym of *Helminthoglypta tudiculata angelena* Berry, 1938 (**new synonymy herein**; see Introduction). PILSBRY (1939:73–75; figs. 43b, b'), credited *convicta* to Hemphill, but Pilsbry alone was responsible for its publication.

corneus, *Helix strigosa* var.—HEMPHILL, 1890f:15 [*nomen nudum*] [*non H. cornea* LINNAEUS, 1758:770]. No locality given.

Remarks—A variant spelling of *Oreohelix strigosa depressa* form *carnea* (Hemphill), according to PILSBRY (1939:430, 435) (*q.v.*).

costata, *Pompholyx*—STEARNS, 1901:291, *ex* Hemphill MS [HEMPHILL, 1881c:12, *nomen nudum*; HEMPHILL, 1890f:19, *nomen nudum*, as *Pompholyx effusa* var.]. Near the Dalles, Columbia River, Oregon/Washington.

Type material—USNM 36616 (4), 36617 (2), 47519–47521 (11), possible syntypes.

Remarks—*Parapholyx effusa costata*, according to F. C. BAKER (1945:164, 466–469; pl. 115, figs. 24–26; pl. 116, figs. 12–14), who credited the species to Hemphill. The name appeared in DALL (1883:202), where we regarded it as being in synonymy because it is not at all clear that Dall thought it separable. It is also a *nomen nudum* in CALL (1884:19). Material in collections labeled as being Hemphill types, including UCM 13023, 13023a (the former termed “syntypes” and the latter “designated as the type” by HENDERSON, 1929a:81–82), CAS 058882, *ex* SUPTC 5824, and ANSP 21871, 21873, 21877, 21884, is without type status because the name was validated by Stearns.

cuyamacensis, *Epiphragmophora traski* var.—PILSBRY, 1895: 197, 199, 362; pl. 59, fig. 87), *ex* Hemphill MS [spelled *cuyamacensis* on pp. 197 and 362; **first revision herein**] [HEMPHILL, 1890f:17, *nomen nudum*, as *Helix* (*Mesodon*) *fidelis* var.]. Cuyamaca Mts., San Diego Co., Calif. (PILSBRY, 1939:145).

Type material.—ANSP 62381a, holotype (animal & shell); ANSP 62381, paratypes (12).

Remarks—*Helminthoglypta* (*Rothelex*) *cuyamacensis cuyamacensis* (Pilsbry, 1895). The name *Epiphragmophora cuyamacensis cuyamacensis* was later proposed by BARTSCH (1916:611, 619; pl. 16, figs. 10–12; pl. 17, fig. 8), *ex* Hemphill MS, who believed that it had not yet been made available, and even PILSBRY (1939) accepted this view. However, PILSBRY's illustration in 1895 suffices to make the name available, and, although he credited the name to Hemphill, he alone was responsible for its publication. See also MILLER (1985:98).

dentata, *Helix* (*Mesodon*) *columbiana* var.—HEMPHILL, 1890f:16 [*nomen nudum*] [*non Mesodon columbiana* var. *dentata* TRYON, 1867:42; pl. 8, fig. 12, nor *M.*

albolabris var. *dentata* TRYON, 1867:39; pl. 7, fig. 6]. Calif.

depressus, *Helix* (*Mesodon*) *columbiana* var.—HEMPHILL, 1890f:16 [*nomen nudum*] [*non H. depressa* MONTAGU, 1803:439–440; pl. 13, fig. 5]. Oregon.

Remarks—Probably what was later named *Vespericola columbiana depressa* (Pilsbry & Henderson, 1936) (see PILSBRY, 1940:895–896; fig. 514).

diegoensis, *Zonites*—Hemphill, in W. G. BINNEY, 1892: 168, 203; pl. 3, fig. 2. Near Julian City, and on Cuyamaca Mt., 4500 ft., both San Diego Co., Calif.

Type material—Not found.

Remarks—In spite of the original figure, this species has not been recognized since its description; PILSBRY (1948:653) placed it with doubt under the genus *Punctum* and commented that the figure somewhat resembled *P. californicum* Pilsbry, 1898. The only specimens we have found that in any way document Hemphill's concept of the species are two adult *Paralaoma caputspinulae* (Reeve, 1852) (CAS 058467) with a label in Hemphill's writing: “*Zonites diegoensis?*/Hemphill/Near Julian City/San Diego Co. Cal.” They are lower spired, less globose, more strongly sculptured than the original figure, which, however, could be taken to represent a juvenile *Paralaoma caputspinulae*. Additional field work in the type areas is needed to resolve the identity of *Z. diegoensis*.

ductor, *Micrarionta intercis*a form—PILSBRY, 1939:224, 225; figs. 111h, i, *ex* Hemphill MS. San Clemente Id., Los Angeles Co., Calif.; fossil.

Type material—ANSP 86747a, holotype; ANSP 86747 (1), 86748 (2), 86749 (2), 86750 (2), 86751 (2), paratypes.

Remarks—Pilsbry credited this synonymic “form” of *Xerarionta intercis*a to Hemphill, but Pilsbry himself was responsible for making the name available. KANAKOFF (1950:82) regarded it as a form of *X. redimita* (W. G. Binney, 1858).

elegans, *Helix intercis*a var.—HEMPHILL, 1891a:330 [*non H. elegans* GMELIN, 1791:3642] [HEMPHILL, 1890f: 17, *nomen nudum*]. San Clemente Id., Los Angeles Co., Calif.

Type material—CAS 037569 (2), 037572 (7), syntypes; CAS 058883, *ex* SUPTC 6200, syntypes (4); ANSP 10807, syntypes (3); AMNH 52539, syntypes (2).

Remarks—Synonym of *Xerarionta intercis*a (W. G. Binney, 1857).

fasciata, *Helix tryonii* var.—HEMPHILL, 1891a:332 [*non H. fasciata* GMELIN, 1791:3646] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Barbara Id., Los Angeles Co., Calif.

Type material—CAS 032737, syntypes (6); USNM

174369–174574, syntypes (12); AMNH 52042 (2), 52542 (2), syntypes; UCM 20681, “paratypes” (13); SBMNH 33953, syntypes (9).

Remarks—Synonym of *Plesarionta tryoni* (Newcomb, 1864). Not a primary homonym of *Cochlea fasciata* DA COSTA, 1778:76–78; pl. 5, figs. 1–5, 8, 14, 19), although *Cochlea* is a synonym of *Helix*.

feralis, *Helix* var. [also as *H. ruficincta feralis*]—HEMPHILL, 1901b:121, 124; pl. 1, fig. 2. San Nicolas Id., Ventura Co. (35 specimens), & Santa Barbara Id., Los Angeles Co. (10 specimens), Calif.

Type material—CAS 058823 (11), syntypes from San Nicolas Id., labeled “types” by Hemphill; CAS 061482 (8), syntypes from Santa Barbara Id., labeled “types” by Hemphill; USNM 174250–174252 (6), 174263–174272 (20), syntypes from San Nicolas Id.; USNM 174254–174262 (18), syntypes from Santa Barbara Id.; SBMNH 33925 (15), 33943 (2), syntypes from San Nicolas Id. Obviously, some of this material was from later collecting.

Remarks—*Micrarionta feralis* (Hemphill, 1901). See PILSBRY (1939:209–211; fig. 105).

flavus, *Aglaja fidelis* var.—Hemphill, in W. G. BINNEY, 1892:185. Chehalis, Lewis Co., and San Juan Ids., San Juan Co., Wash.; Port Orford, Curry Co., Oregon.

Type material—CAS 058840, **lectotype** (herein), from Port Orford, Oregon, labeled “type” by Hemphill.

Remarks—*Monadenia* (*M.*) *fidelis flava* (Hemphill, 1892) and a senior synonym of *M. fidelis beryllica* Chace & Chace, 1935 (**new synonymy herein**). The lectotype, from the third locality mentioned by Hemphill, is the only extant type specimen, and it was accepted as the “type” by PILSBRY (1939:40).

floridana, *Polygyra septemvolva* var.—Hemphill, in W. G. BINNEY, 1892:184–185. Oyster [Estero] Bay, Lee Co., Florida.

Type material—CAS 058839, syntypes (2), labeled “types” by Hemphill.

Remarks—*Polygyra* (*P.*) *cereolus floridana* Hemphill, 1892, according to PILSBRY (1940:586–587; fig. 380).

forbesi, *Helix kelletti* var.—HEMPHILL, 1891a:333 [non *H. forbesii* PFEIFFER, 1845:71–72] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif.

Type material—CAS 037643 (4), 037646 (5), 037665 (4), 037669 (5), syntypes; USNM 174436–174441, syntypes (12); AMNH 52550, syntypes (2); SBMNH 33927, probable syntypes (2).

Remarks—Synonym of *Xerarionta kelletti* (Forbes, 1850).

fragilis, *Patula strigosa* var.—HEMPHILL, 1890d:17–18. Near Franklin, Franklin Co., Idaho; among red sandstone [5000 ft. (label)].

Type material—CAS 058863, lectotype (PILSBRY, 1939:438); CAS 050462 (5), 050464 (3), 050465 (5), 050467 (1), 050468 (4), 050472 (6), paralectotypes; USNM 31164–31165 (4), 58357 (3), 58431 (2), paralectotypes; ANSP 10901, paralectotypes (3); AMNH 61675 (4 in 2 lots), 61686 (2), paralectotypes; SBMNH 33937, paralectotypes (16).

Remarks—PILSBRY (1934:408; 1939:438–439, fig. 289) recognized this as a subspecies of *Oreohelix strigosa*, whereas HANNA & SMITH (1939:389, 392; pl. 36, figs. 4–6) regarded it as a distinct species.

frater, *Helix kelletti* var.—HEMPHILL, 1891a:333 [non *H. (Cochlostyla) frater* FÉRUSSAC, 1821:52; FÉRUSSAC & FÉRUSSAC, 1821:pl. 112, figs. 1, 2] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif. [Isthmus (label)].

Type material—CAS 037195 (4), 037206 (9), 037229 (5), 037667 (5), 037671 (5), 037675 (5), syntypes; USNM 174451–174456, syntypes (12); ANSP 86582 (2), 85683 (2), 86584 (2), syntypes; AMNH 52032, syntypes (2); UCM 20674, “paratypes” (15); SBMNH 33926, probable syntypes (4).

Remarks—Synonym of *Xerarionta kelletti* (Forbes, 1850).

gabbiana, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 30, 34, 47; pl. 2, fig. 9 [HEMPHILL, 1878:2, *nomen nudum*, as *P. haydeni* var.]. Near Salt Lake City, Salt Lake Co., Utah; in a rock pile.

Type material—USNM 102166, “figd type” (1); CAS 054333 (6), 054336 (7), 054341 (3), 054469 (7), syntypes; AMNH 35983 (1), 61703 (2), syntypes; AMNH 35162, probable syntypes (10).

Remarks—Synonym (“form”) of *Oreohelix haydeni oquirrhensis* (Hemphill, in Binney, 1886), according to PILSBRY (1939:464–465, 469–471; figs. 304j, k).

gouldi, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 31, 32, 47; pl. 2, figs. 5, 16. Banks of Bear River, N of Brigham, Box Elder Co., Utah [4500 ft. (PILSBRY, 1939)]; 1000 specimens.

Type material—USNM 102165, “orig. type figd.” (1); CAS 054454 (6), 054523 (2), 054524 (3), 054582 (2), 054587 (2), syntypes; AMNH 56573, syntypes (2); AMNH 61675 (12), 61676 (4), probable syntypes; SBMNH 33947, syntypes (22).

Remarks—Synonym (“size-var.”) of *Oreohelix peripherica peripherica* (Ancey, 1881), according to PILSBRY (1939:450–454; fig. 298–22).

hemphilliana “Binney,” *Helix*—HEMPHILL, 1881c:11 [*nomen nudum*]. No locality given.

holzneri, *Haliotis cracherodii* var.—HEMPHILL, 1907:59–60. Coast of Baja Calif. [presumably northern]; 3 specimens.

Type material—SDNHM 45587, syntypes (3); CAS 058826, possible syntype, labeled “type” by Hemphill,

but this may be a specimen added to his collection later because the SDNHM specimens match the dimensions given by Hemphill.

Remarks—Synonym of *H. cracherodii* Leach, 1814, according to J. H. McLean (personal communication, 26 Jan. 1985).

hybrida, *Helix* [*kelletti* var.] *redimita* var.—HEMPHILL, 1891a:334 [non *H. hybrida* POIRET, 1801:71] [HEMPHILL, 1890f:17, *nomen nudum*]. San Clemente Id., Los Angeles Co., Calif.

Type material—CAS 037787 (6), 037788 (4), 037806 (7), 037809 (5), syntypes; USNM 174469–174474, syntypes (12); AMNH 51894, syntypes (2); UCM 20669, “paratypes” (16).

Remarks—Synonym of *Xerarionta redimita* (W. G. Binney, 1858).

hybrida, *Patula strigosa* var.—HEMPHILL, 1890d:17. Near Logan, Cache Co., Utah [Logan Canyon; about 5000 ft. (labels)].

Type material—CAS 054531 (7), 054532 (13), 054533 (6), syntypes; ANSP 23058, syntypes (3); AMNH 61678, syntypes (6 in 2 lots); SBMNH 33951, syntypes (7). Some additional lots in the USNM from Hemphill placed under this name but not individually labeled as such may also be syntypic.

Remarks—*Oreohelix haydeni hybrida* (Hemphill, 1890), according to PILSBRY (1939:464–469; figs. 340c–f).

hybrida, *Selenites vancouverensis* var.—HEMPHILL, 1890g:42–43 [HEMPHILL, 1890f:13, *nomen nudum*, as *S. concava* var.]. Astoria, Clatsop Co., Oregon.

Type material—CAS 058846, syntypes (4), labeled “types” by Hemphill; AMNH 52883, syntypes (2).

Remarks—Synonym of *Haplotrema (Ancotrema) hybridum* (Ancey, 1888) (B. Roth, in preparation). Ancey did not credit his proposal of this name to Hemphill, but the name probably came to his attention on a Hemphill label.

inconstans, *Micrarionta redimita* form—PILSBRY, 1939:219, 220; figs. 109f–i, ex Hemphill MS. San Clemente Id., Los Angeles Co., Calif.

Type material—ANSP 86761a, holotype; ANSP 86761, paratype (1).

Remarks—Synonym of *Xerarionta redimita* (W. G. Binney, 1858). Pilsbry credited this form to Hemphill, but Pilsbry alone was responsible for publishing it.

intermedia, *Micrarionta facta* form—PILSBRY, 1939:209–210; fig. 105e, ex Hemphill MS. Santa Barbara Id., Los Angeles Co., Calif.

Type material—ANSP 86840, “type and paratype” (2); 86641 (2), 86841 (2), paratypes.

Remarks—*Micrarionta intermedia* Pilsbry, 1939. Pilsbry credited this name to Hemphill, but Pilsbry alone was responsible for its publication. Supposed type

material in other institutions was probably not studied by Pilsbry.

intersum, *Patula strigosa* var.—HEMPHILL, 1890a:135.

Bluffs along the banks of Little Salmon River, Idaho Co., Idaho; in stone piles; rare.

Type material—SBMNH 33929, lectotype (BERRY, 1932:62; figs. 9, 10); SBMNH 33930, paralectotypes (12); CAS 058867, “lectotype” (PILSBRY, 1939:496); CAS 054557 (7), 054558 (8), 054561 (9), paralectotypes; USNM 363248, paralectotypes (4); AMNH 61704 (2), 61705 (2), paralectotypes.

Remarks—*Oreohelix intersum* (Hemphill, 1890). See BERRY (1932:62), HANNA & SMITH (1939:388–389; pl. 36, figs. 1–3), and SOLEM (1975:29–30).

jugalis, *Patula strigosa* var.—HEMPHILL, 1890a:134. Banks of Salmon River, Idaho Co., Idaho; in stone piles [Lucile (PILSBRY, 1934:398)].

Type material—ANSP 62372a, lectotype (PILSBRY, 1934:398); ANSP 62372, paralectotype (1); ANSP 62386 (2), 62391 (2), probable paralectotypes; CAS 053553 (5), 054555 (7), 054556 (6), 058859 (1), paralectotypes; USNM 363251, paralectotypes (5); AMNH 53977 (2), 61679 (2), 61680 (2), paralectotypes; SBMNH 33935 (4), 33936 (9), paralectotypes.

Remarks—*Oreohelix jugalis* (Hemphill, 1890). See PILSBRY (1939:496–497; fig. 322) and SOLEM (1975:27–28; figs. 6a, 7b, 31–36).

keepi, *Selenites vancouverensis* var.—HEMPHILL, 1890g:42 [HEMPHILL, 1890f:13, *nomen nudum*, as *S. concava* var.]. Hills near Oakland, Alameda Co., Calif.; 1 specimen.

Type material—Clearly also representing later collecting by Hemphill: CAS 058847, syntypes (5), labeled “types” by Hemphill; ANSP 77894, syntypes (2); SBMNH 33921, syntypes (2).

Remarks—*Haplotrema (Greggiella) keepi* (Hemphill, 1890), according to PILSBRY (1946:213–214; figs. 104, 108–4, -5).

kelseyi, *Circinaria* var.—HEMPHILL, 1911:103–104; pl. 3. San Mateo Co. (?1 specimen); San Luis Obispo Co. (22 specimens), both Calif.

Type material—Obviously also representing subsequent collecting: CAS 058836 (3), 058837 (5), syntypes from San Mateo.

Remarks—Synonym (“var.”) of *Haplotrema (Ancomena) minimum* (Ancey, 1888), according to PILSBRY (1946:218–221; fig. 107e).

kelseyi, *Oreohelix*—PILSBRY, 1934:408, ex Hemphill MS [in synonymy of *O. pygmaea* Pilsbry, 1913]. Raymond, Big Horn Co., Wyoming.

Remarks—Material in type collections, such as UCM 7063, has no type status because the name was never made available.

labiosa, *Micrarionta rufocincta* form—PILSBRY, 1939:206–207; figs. 103h, i, *ex* Hemphill MS. Santa Catalina Id., Los Angeles Co., Calif.

Type material—ANSP 86665a, holotype; ANSP 86665 (1), 86656 (2), 86657 (2), 86658 (2), 86659 (2), paratypes.

Remarks—Synonym of *Micrarionta rufocincta* (Newcomb, 1864). Pilsbry credited this “form” to Hemphill, but Pilsbry himself was responsible for its publication.

lactea, *Patula strigosa* var.—HEMPHILL, 1890a:134. Rathdrum, Kootenai Co., Idaho; open places in dense pine forests.

Type material—CAS 058857, lectotype (PILSBRY, 1939:424); CAS 050486, paralectotypes (4); ANSP 62390, paralectotypes (2); AMNH 52771, paralectotypes (2).

Remarks—Synonym of *Oreohelix strigosa strigosa* (Gould, 1846), according to PILSBRY (1939:419, 424).

leai, *Goniobasis plicifera* var.—HEMPHILL, 1890f:18 [*nomen nudum*]. Oregon.

Remarks—Material in type collections, such as UCM 17779 and 17780, has no type status because the name was never made available.

maculata, *Helix tryonii* color var.—HEMPHILL, 1901b:123, 124 [*non Helix (Carocolla) maculata* ANTON, 1839:40]. Santa Barbara Id., Los Angeles Co., Calif.

Type material—USNM 174378–174383, syntypes (12); UCM 20685, “paratypes” (14).

Remarks—Synonym of *Plesarionta tryoni* (Newcomb, 1864).

major, *Epiphragmophora traskii*—BARTSCH, 1916:612, *ex* Hemphill MS [in synonymy of *E. traskii traskii* (Newcomb, 1861)].

Remarks—Material formerly in type collections has no type status because the name was never made available.

major, *Helix tryonii*—HEMPHILL, 1901b:123, 124; pl. 1, fig. 1, two center specimens [*non H. major* A. BINNEY, 1837:473–475; pl. 12]. San Nicolas Id., Ventura Co., Calif.; subfossil.

Type material—CAS 058873, syntypes (2), labeled “types” by Hemphill; USNM 174297–174299 (6), 174308–174310 (6), syntypes; SBMNH 33923, syntypes (16).

Remarks—Synonym of *Plesarionta tryoni hemphilli* (Edson & Hannibal, 1911).

meridionalis “Sterki,” *Pupa (Pupilla) californica* var.—HEMPHILL, 1890f:17 [*nomen nudum*]. Calif.

minor, *Helix intercisca* var.—HEMPHILL, 1891a:330 [*non H. epistylum minor* C. B. ADAMS, 1851:97] [HEMPHILL, 1890f:17, *nomen nudum*]. San Clemente Id., Los Angeles Co., Calif.

Type material—CAS 037341 (6), 037626 (2), syn-

types; USNM 174524–174525, syntypes (4); ANSP 10805, syntypes (3); AMNH 51963, syntypes (2).

Remarks—Synonym of *Xerarionta intercisca* (W. G. Binney, 1857).

minor, *Helix (Mesodon) rufocincta* [*sic*] var.—HEMPHILL, 1890f:17 [*nomen nudum*] [*non H. epistylum minor* C. B. ADAMS, 1851:97]. Calif.

minor, *Helix tryonii*—HEMPHILL, 1901b:123, 124; pl. 1, fig. 1, two outer specimens [*non H. epistylum minor* C. B. ADAMS, 1851:97]. San Nicolas Id., Ventura Co., Calif.; subfossil.

Type material—CAS 058819, syntypes (8), labeled “types” by Hemphill; CAS 037701 (5), 037710 (5), syntypes; USNM 174302–174305, syntypes (8).

Remarks—Synonym of *Plesarionta tryoni hemphilli* (Edson & Hannibal, 1911).

morroensis, *Helix* var.—HEMPHILL, 1911:103. San Luis Obispo Co., Calif.; among brush and rocks [near city of San Luis Obispo (ROTH, 1973)].

Type material—Obviously also representing later Hemphill collecting: CAS 058820, syntypes (11), labeled “types” by Hemphill; USNM 174683 (2) [“near Morro”], 174684 (2) [“near San Luis Obispo”], syntypes; UCM 20179, “paratypes” (4); SBMNH 33934, syntypes (6).

Remarks—*Helminthoglypta (H.) walkeriana morroensis* (Hemphill, 1911).

multicostata, *Patula strigosa* var.—W. G. BINNEY, 1886:27, 32, 47; pl. 2, fig. 6, *ex* Hemphill MS. Box Elder Co., Utah [Bear River, N of Brigham; 4500 ft. (PILSBRY, 1939)].

Type material—USNM 102168, “orig. type figd.” (1); AMNH 53974 (6), 56572 (5), 61584 (8), 61684 (10 in 3 lots), syntypes.

Remarks—Synonym (“color-var.”) of *Oreohelix peripherica peripherica* (Ancey, 1881), according to PILSBRY (1939:450–454; figs. 298-4, -10, -12, -20–23. Because we interpret this form as having been made available solely by Binney, other material in collections from the type lot does not have standing as syntypes, including CAS 054452, 054453, 054515, 054525, 054526, 054590; UCM 20654; SBMNH 33945.

multilineatus, *Helix kelletti* var.—HEMPHILL, 1891a:333 [*non H. multilineatus* SAY, 1821:150] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif. [Isthmus (labels)].

Type material—CAS 037166 (2), 037168 (7), 037202 (6), 037205 (6), 037227 (6), 037639 (6), 037645 (6), 037647 (6), 037662 (6), 037688 (6), syntypes; USNM 174430–174435, syntypes (11); AMNH 51895, syntypes (2).

Remarks—Synonym of *Xerarionta kellettii* (Forbes, 1850).

- nebulosa*, *Helix tryonii* var.—HEMPHILL, 1891a:331 [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Barbara Id., Los Angeles Co., Calif.
 Type material—CAS 032735 (6), 037695 (6), syntypes; USNM 174354–174359, syntypes (12); AMNH 51961 (2), 52543 (2), 52573 (2), syntypes; SBMNH 33931, syntypes (10).
 Remarks—Synonym of *Plesarionta tryoni* (Newcomb, 1864). Not preoccupied by *Helix nebulosa* Ziegler, in ROSSMÄSSLER, 1837:31, which is in synonymy. We have not located any other preoccupying use of this specific name in *Helix*.
- nepos*, *Helix intercisa* var.—HEMPHILL, 1891a:330 [HEMPHILL, 1890f:17, *nomen nudum*]. San Clemente Id., Los Angeles Co., Calif.
 Type material—CAS 037571 (2), 037611 (4), syntypes; CAS 058835, *ex* SUPTC 6201, syntypes (4); USNM 174534–174539, syntypes (12); ANSP 86539 (2), 86540 (2), 86541 (2), syntypes; AMNH 51962 (2), syntypes; SBMNH 33955, syntypes (9).
 Remarks—Synonym of *Xerarionta intercisa* (W. G. Binney, 1857).
- neritoides*, *Parapholix effusa*—F. C. BAKER, 1945:468–469; pl. 116, figs. 7–11, *ex* Hemphill MS. The Dalles, Columbia River, Oregon.
 Type material—USNM 36615 (2), 37518 (3), syntypes; ANSP 21883 (3), syntypes; ANSP 21872 (6), possible syntypes.
 Remarks—*Vorticifex neritoides* (F. C. Baker, 1945), according to D. W. Taylor (*in litt.*, 11 Feb. 1985). Baker credited this species to Hemphill, but Baker alone was responsible for publishing it.
- newcombi*, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 30, 32, 47; pl. 2, fig. 8. Mts. N of Ogden [Weber Co.], Utah; steep sides of a gulch facing N.
 Type material—USNM 102171, “orig. type figd.” (1); CAS 050280 (2), 050283 (2), 050284 (2), syntypes.
 Remarks—*Oreohelix peripherica newcombi* (Hemphill, 1886), according to PILSBRY (1939:455–456; fig. 300a).
- newcombiana*, *Paludinella*—HEMPHILL, 1877:49. Humboldt Bay, Humboldt Co., Calif.; abundant in salt marshes.
 Type material—CAS 058872, *ex* SUPTC 6241, syntypes (7); USNM 32725 (1), 127340 (1 “figd.” + 9), syntypes; UCM 20878 (12), 23545 (3), “paratypes”; SDNHM 780 (3), 780A (34), syntypes; SBMNH 33995, syntypes (4).
 Remarks—Type species of *Algamorda* DALL, 1918: 137. *Littorina (Algamorda) newcombiana* (Hemphill, 1877), according to D. W. Taylor (*in litt.*, 11 Feb. 1985). *Assimineia subrotundata* Carpenter, 1864, may prove to be a senior synonym, though either or both may be an introduced Atlantic *Littorina*, perhaps *L. saxatilis* (Olivi, 1792). J. T. Carlton, *in litt.*, 8 April 1985).
- nitidus*, *Helix kelletti* var.—HEMPHILL, 1891a:333 [*non H. nitidus* MÜLLER, 1774:32] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif.
 Type material—CAS 037184 (5), 037207 (6), 037226 (6), 037553 (4), 037666 (6), 037680 (6), 037687 (6), syntypes; USNM 174445–174450, syntypes (12); AMNH 51892, syntypes (2).
 Remarks—Synonym of *Xerarionta kelletti* (Forbes, 1850).
- occidentalis*, *Eulimella* [also as *Bulimulus*]—HEMPHILL, 1894:395–396. San Diego, San Diego Co., Calif.; intertidal zone; mudflats; 20 specimens.
 Type material—Probably also representing later collecting: CAS 058876, syntypes (6); CAS 058877, *ex* SUPTC 6248, syntypes (9); USNM 127551, syntypes (6).
 Remarks—*Schwengelia occidentalis* (Hemphill, 1894), according to J. H. McLean (personal communication, 26 Jan. 1985).
- occidentalis*, *Limnaea stagnalis* var.—HEMPHILL, 1890e:26. Lake Whatcom, Whatcom Co., Wash.; Nov. 1889; 15–20 specimens.
 Type material—CAS 058834, *ex* SUPTC 5817, syntypes (4); USNM 118791, syntypes (2); ANSP 62297, syntypes (3).
 Remarks—*Limnaea occidentalis* Hemphill, 1890, according to McDONALD (1969:13; pl. 1, fig. f).
- occidentalis*, *Selenites concavus* var. [also under *S. vancouverensis*]—Hemphill, in W. G. BINNEY, 1892:165 [HEMPHILL, 1890f:13, *nomen nudum*]. Sonoma Co. to Santa Cruz Co., Calif.
 Type material—CAS 051890, syntypes (17), from near Fish Ranch, Contra Costa Co., Calif.
 Remarks—Synonym of *Haplotrema (Ancomena) minimum* (Ancey, 1888), according to PILSBRY (1946:218–219).
- oquirrhensis*, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 30, 34, 47; pl. 2, fig. 12 [HEMPHILL, 1878:2, *nomen nudum*, as *P. hemphilli* var.]. Oquirrh Mts., Salt Lake Co., Utah; limestone [4300 ft. (label)].
 Type material—CAS 054337 (6), 054338 (15), 054342 (6), 054344 (2), 054345 (8), 054404 (2), 054406 (2), 054545 (7), syntypes; USNM 102164, syntype (1); ANSP 23052, syntypes (3); AMNH 56606 (2), 61683 (6 in 2 lots), syntypes; SBMNH 33944, syntypes (6). PILSBRY’s (1939) reference to Binney’s figure as “representing the type” cannot be taken as a lectotype designation.
 Remarks—*Oreohelix haydeni oquirrhensis* (Hemphill,

- 1886), according to PILSBRY (1939:469–471; figs. 304g–i).
- oregonensis*, *Helix (Mesodon) mullani* var.—ANCEY, 1882: 29, ex Hemphill MS [non *H. oregonensis* LEA, 1838: 100–101; pl. 23, fig. 85]. Eastern Oregon.
Type material—Not searched. CASGTC 4104–4115 were labeled “syntypes” of Hemphill’s species, but they were probably never seen by Ancey.
Remarks—Synonym of *Cryptomastix (Bupiogona) hendersoni* (Pilsbry, 1928). See PILSBRY (1940:866–867) and WEBB (1970:77–78).
- parma*, *Patula strigosa* var.—HEMPHILL, 1890d:17. Near Spokane Falls, Spokane Co., Washington.
Type material—CAS 058861, syntypes (2); ANSP 10898a, “holotype”; ANSP 10898, syntypes (5); AMNH 53973, syntypes (3); SBMNH 33956, syntypes (2).
Remarks—Synonym of *Oreohelix strigosa strigosa* (Gould, 1946), according to PILSBRY (1939:419–424). See also HANNA & SMITH (1939:384, 387, 391; pl. 33, figs. 7–9; pl. 34, figs. 1–3).
- penicillata*, *Physa heterostropha* var.—HEMPHILL, 1890f:19 [nomen nudum]. Calif.
- picta*, *Patula strigosa* var.—HEMPHILL, 1890d:16. Rathdrum, Kootenai Co., Idaho.
Type material—CAS 058860, lectotype (PILSBRY, 1939:424); ANSP 62284a (1), 62284 (1), paralectotypes; AMNH 53978, probable paralectotypes (2).
Remarks—Synonym of *Oreohelix strigosa strigosa* (Gould, 1846), according to PILSBRY (1939:419–421, 424). See also HANNA & SMITH (1939:384, 388, 391; pl. 34, figs. 7–9).
- pilsbryi*, *Limnaea (Leptolimnaea)*—HEMPHILL, 1890e:25–26. Fish Spring[s], Juab Co., “Nevada” [Utah, according to TAYLOR *et al.* (1963)]; June 1868; a few specimens.
Type material—ANSP 62293, syntypes (3).
Remarks—*Stagnicola (Hinkleyia) pilsbryi* (Hemphill, 1890), according to TAYLOR *et al.* (1963:262–263, 265–266; pl. II, fig. 1).
- proles*, *Arionta traski* var.—HEMPHILL, in W. G. BINNEY, 1892:187 [HEMPHILL, 1890f:17, nomen nudum, as *Helix (Mesodon) fidelis* var.]. Near Fraser’s Mill [Mountain Home], Tulare Co., Calif. [6280 ft. (PILSBRY, 1939)].
Type material—SBMNH 33938, lectotype (BERRY, 1938:47, 51; figs. 11, 12); SBMNH 33939, paralectotypes (2); CAS 058816, paralectotypes (8), labeled “types” by Hemphill.
Remarks—*Helminthoglypta (H.) proles* (Hemphill, 1892). Illustrated by PILSBRY (1939:196–197; figs. 99a, b). Some authors have dated this species from BARTSCH (1916:616, 619; pl. 116, figs. 4–6).
- puer*, *Micrarionta intercis* form—PILSBRY, 1939:224, 225; fig. 111-l, ex Hemphill MS. San Clemente Id., Los Angeles Co., Calif.; fossil.
Type material—ANSP 86720a, holotype; ANSP 86720 (1), 86731 (2), 86732 (2), 86733 (2), 86735 (2), 86736 (2), 86737 (2), paratypes.
Remarks—Synonym of *Xerarionta intercis* (W. G. Binney, 1857). Pilsbry credited this form to Hemphill, but Pilsbry alone was responsible for its publication.
- rugosa*, *Patula strigosa* var.—HEMPHILL, 1890d:16–17. “New” [Near] Brigham City, Box Elder Co., Utah [Near Boxelder Canyon; limestone ledges; 5000 ft. (PILSBRY, 1939)].
Type material—CAS 052765 (4), 052766 (5), 053050 (7), syntypes; USNM 31173, probable syntypes (2); AMNH 52772 (2), 53979 (2), 61687 (4 in 2 lots), syntypes; SBMNH 33919, syntypes (6).
Remarks—*Oreohelix subrudis rugosa* (Hemphill, 1890), according to PILSBRY (1939:493–494; figs. 313j, k, n).
- salmonacea*, *Helicodiscus fimbriatus* var.—HEMPHILL, in W. G. BINNEY, 1890:189, 220 [spelled *salmonensis* on p. 220; first reviser: PILSBRY (1948:634)]. Banks of the Salmon River and Old Mission, Kootenai Co., Idaho; Oakland, Alameda Co., Calif.
Type material—CAS 058865, syntypes (9), from Salmon River; CAS 058868, ex SUPTC 6197, syntypes (27), from Salmon River; USNM 58551, possible syntypes (3); MCZ 12752, syntypes.
Remarks—*Helicodiscus salmonaceus* Hemphill, 1890, according to PILSBRY (1948:632–635; fig. 344). Hemphill’s Oakland record was probably based on specimens of *Speleodiscoides spirellum* A. G. Smith, 1957.
- salmonensis*, *Helicodiscus fimbriatus* var.—see under *salmonacea*, *H. fimbriatus* var.
- saucius*, *Epiphragmophora traskii*—BARTSCH, 1916:612–613, 619; pl. 114, figs. 10–12, ex Hemphill MS [in synonymy of *E. traskii traskii* (Newcomb, 1861)]. Los Angeles Co., Calif.
Remarks—Material formerly in type collections has no type status because the name was never made available.
- shepardi*, *Zonites*—HEMPHILL, in W. G. BINNEY, 1892:167. Santa Catalina Id., Los Angeles Co., Calif.
Type material—CAS 058843, syntypes (3); CAS 058844, ex SUPTC 5845, syntypes (24), both lots labeled “types” by Hemphill; ANSP 86664, syntype (1); UCM 21434, syntypes (8); SBMNH 33928, syntype (1).
Remarks—*Pristiloma (Priscovitroeps?) shepardae* (Hemphill, 1892), according to PILSBRY (1946:409; fig. 220). Following the examples given in the 1985 edition of the *ICZN Code* (Art. 32c[ii]), Hemphill’s incorrect

masculine ending on the name, which was dedicated to Ida Shepard [Oldroyd], is to be replaced with the correct termination.

sodalis, *Helix* var.—HEMPHILL, 1901b:122-123, 124; pl. 1, fig. 3 [as *H. ruficincta sodalis* on pp. 123, 124].

San Nicolas Id., Ventura Co., Calif.; subfossil.

Type material—CAS 039383, syntypes (9), labeled "types" by Hemphill; CAS 038315 (3), 038316 (13), 038357 (1), 038359 (7), 039383 (9), 039386 (8), 058818 (12), 061429 (10), syntypes; ANSP 79750, syntypes (6); USNM 107898 (4), 107900 (8), 174151-174156 (14), 332190 (4), syntypes.

Remarks—*Micrarionta sodalis* (Hemphill, 1901).

sonomaensis, *Helix* var. [also as *H. (Triodopsis) loricata* var.]—HEMPHILL, 1911:101. Near Healdsburg, Sonoma Co., Calif.

Type material—CAS 058855, syntypes (5), labeled "types" by Hemphill; ANSP 11144, syntypes (4).

Remarks—*Trilobopsis loricata sonomaensis* (Hemphill, 1911), according to PILSBRY (1940:783; fig. 467c).

stearnsi, *Ocenebra* [*sic*]—HEMPHILL, 1911:100-101. Monterey, Monterey Co., Calif.

Type material—CAS 058824, syntypes (2), labeled "types" by Hemphill; CAS 058825, *ex* SUPTC 6242, syntypes (2).

Remarks—Synonym of *Ocenebra gracillima* Stearns, 1871, according to SMITH & GORDON (1948:188).

straminea, *Ariolimary* [*sic* for *Ariolimax*] *columbianus* var.—HEMPHILL, 1891b:120 [HEMPHILL, 1890f:13, *nomen nudum*, as *Ariolimax*]. Santa Cruz Id., Santa Barbara Co., Calif.

Type material—CAS 021161, syntypes (4), labeled "types" by Hemphill.

Remarks—*Ariolimax (A.) columbianus stramineus* Hemphill, 1891, according to PILSBRY (1948:709, 720-721; fig. 385f).

subangulata, *Helix (Mesodon) fidelis* var.—HEMPHILL, 1890f:16 [*nomen nudum*] [*non H. subangulata* PFEIFFER, 1855:53]. No locality given.

subcarinata, *Aglaja fidelis* var.—Hemphill, in W. G. BINNEY, 1892:185-186 [HEMPHILL, 1892a:314, *nomen nudum*]. Humboldt Co., Calif. [near Eureka (label)].

Type material—CAS 058845, syntypes (3), labeled "types" by Hemphill.

Remarks—*Monadenia (M.) fidelis subcarinata* (Hemphill, 1892).

subcarinata, *Helix tryonii* var.—HEMPHILL, 1891a:332 [*non H. subcarinata* MONTAGU, 1803:438-439; pl. 7, fig. 9]. Santa Barbara Id., Los Angeles Co., Calif.; subfossil.

Type material—CAS 058812, syntypes (5), labeled "types" by Hemphill; CAS 037717, syntypes (4);

USNM 174320-174324, syntypes (10); SBMNH 33924, syntypes (33).

Remarks—Synonym of *Plesarionta tryoni hemphilli* (Edson & Hannibal, 1911), a new name for Hemphill's preoccupied name. PILSBRY (1939) introduced a new taxon because of this homonymy (see under *carinata*), missing Edson & Hannibal's earlier (1911) replacement.

subcarinata, *Patula strigosa* var.—HEMPHILL, 1890a:133.

Rathdrum, Kootenai Co., Idaho.

Type material—CAS 058858, lectotype (PILSBRY, 1939:424); CAS 050483 (4), 050487 (5), 050488 (4), 050489 (5), 050490 (3), 050493 (9), paralectotypes; ANSP 62284 (2), 62321a (1), 62321 (4), paralectotypes; AMNH 53971, paralectotypes (2). PILSBRY's (1893:118) citation of Binney's illustration as "type" does not constitute a lectotype designation.

Remarks—Synonym ("form") of *Oreohelix strigosa strigosa* (Gould, 1846), according to PILSBRY (1939:419-421, 423-424). See also HANNA & SMITH (1939:384, 385, 391; pl. 34, figs. 4-6). ANSP 62284 was also cited as "type" of *Patula strigosa picta* Hemphill, 1890, by PILSBRY (1939:420, fig. 279-28) (*q.v.*).

subdolos, *Helix tudiculata* var.—HEMPHILL, 1890g:41-42 [HEMPHILL, 1890f:16, *nomen nudum*]. San Jacinto [*sic* for Jacinto], San Diego Co. [*sic* for Riverside Co.], Calif.

Type material—CAS 058829 (2), 058830 (2), 058831 (2), syntypes, labeled "types" by Hemphill; SBMNH 33918, syntypes (6).

Remarks—*Helminthoglypta (H.) tudiculata subdola* (Hemphill, 1890), according to PILSBRY (1939:73-74; figs. 34a-d).

subquadrata, *Amphysphyra*—HEMPHILL, 1881c:9, *ex* Carpenter MS [*nomen nudum*].

Remarks—Later made available by KEEP (1887) (COAN, 1985:213).

tenuis, *Selenites vancouverensis* var. [also as *S. concavus* var.]—Hemphill, in W. G. BINNEY, 1892:166 [HEMPHILL, 1890f:13, *nomen nudum*, as *S. concava* var.]. Napa Co., Calif. [Aetna Springs (label)].

Type material—CAS 050632, lectotype (PILSBRY, 1946:221; fig. 109); CAS 058878, paralectotype (1).

Remarks—Synonym ("form") of *Haplotrema (Ancomena) minimum* (Ancey, 1888), according to PILSBRY (1946:218, 221; fig. 109).

tincta, *Tegula gallina*—KEEP, 1887:84, *ex* Hemphill MS. Type locality not given, but presumably southern Calif.

Type material—Not located.

Remarks—Synonym of *Tegula gallina* (Forbes, 1852). This varietal name has sometimes been dated from PILSBRY, 1889:169-170, *ex* Hemphill MS, and several institutions have supposed types of this taxon credited

to Hemphill or to Pilsbry, including ASNP 37967, 40788, 40791, 40793 (see COAN, 1985:213).

transfuga, *Selenites vancouverensis* var.—Hemphill, in W. G. BINNEY, 1892:165 [HEMPHILL, 1890f:13, *nomen nudum*, as *S. concava* var.]. San Diego, San Diego Co., Calif., to Bahía Todos Santos, Baja Calif.

Type material—CAS 051479 (4), 051483 (4), syntypes from near San Diego; AMNH 60676, syntype (1), from near San Diego; UCM 21131, “paratypes or topotypes” (13); SBMNH 33941, syntypes (2), from near San Diego.

Remarks—*Haplotrema* (*Greggiella*) *transfuga* (Hemphill, 1892), according to PILSBRY (1946:214–215; figs. 103–5, 105).

tremperi, *Murex carpenteri*—DALL, 1910:96, ex Hemphill MS. Santa Barbara [San Pedro] Channel off Newport, Orange Co., Calif. [64 m (label, as 35 fm)].

Type material—USNM 219904, holotype.

Remarks—Synonym of *Pteropurpura macroptera* (Deshayes, 1839), according to McLEAN (1978:42). HEMPHILL (1911:99–100; pl. 1) later proposed this name himself. Material formerly in some type collections, such as CAS 058879, was probably not studied by Dall.

tricolor, *Helix kelletii* var.—HEMPHILL, 1891a:334 [non *Helix tricolor* PFEIFFER, 1850:129] [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Catalina Id., Los Angeles Co., Calif.

Type material—CAS 037190 (6), 037203 (6), 037580 (6), 037663 (6), syntypes; USNM 174426–174429, syntypes (8); AMNH 51949, syntypes (2); UCM 20676, “paratypes” (15).

Remarks—Synonym of *Xerarionta kelletii* (Forbes, 1850).

tularensis, *Arionta tudiculata* var.—Hemphill, in W. G. BINNEY, 1892:187 [HEMPHILL, 1890f:16, *nomen nudum*, as *Helix* (*Mesodon*) *tudiculata* var.]. Tulare Co., Calif. [Fraser’s Mill, Mountain Home, Tulare Co., Calif.; 6280 ft. (labels)].

Type material—CAS 058813 (3), 058814 (4), 058815 (1), syntypes, labeled “types” by Hemphill; CAS 058943 (4), 058944 (4), syntypes; AMNH 51904, syntypes (2).

Remarks—*Helminthoglypta* (*H.*) *tularensis tularensis* (Hemphill, 1892).

tularensis, *Epiphragmophora traskii*—PILSBRY, 1895:199; 1897:59, ex Hemphill MS [*nomen nudum*] [not to be confused with *Arionta tudiculata* var. *tularensis* Hemphill, in W. G. Binney, 1892, *q.v.*].

Remarks—A name for this supposed Californian species, *E. traskii tularica*, was first made available by BARTSCH (1916:615, 619; pl. 116, figs. 1–3), in which it was not credited to Hemphill. ROTH (1982) has shown that it was based on material actually from Baja California and is a synonym of *Plesarionta orcutti* (Dall, 1900).

utahensis, *Patula strigosa* var.—Hemphill, in W. G. BINNEY, 1886:27, 30, 33 [locality only on this page (PILSBRY, 1939)] [HEMPHILL, 1878:2, *nomen nudum*, as *P. hemphilli* var.]. Oquirrh Mts., near Salt Lake City, Salt Lake Co., Utah [4300 ft., among limestone rocks (labels)].

Type material—CAS 054343 (5), 054539 (5), 054541 (7), 054542 (6), 054543 (7), 054544 (5), syntypes; ANSP 23051a, “holotype”; ANSP 23051, “paratypes” (2); ANSP 23049 (2), 23050 (3), syntypes; USNM 363232 (4), 31184 (2), 58404 (2), 58441 (2), syntypes; USNM 31179 (2), 31182 (2), 58405 (2), possible syntypes; AMNH 56605 (3), 61702 (4 in 2 lots), syntypes; SBMNH 33932, syntypes (6).

Remarks—Synonym (“form”) of *Oreohelix haydeni oquirrhensis* (Hemphill, 1886), according to PILSBRY (1939:469–471; fig. 304–1), who said that the description on p. 33 is really in part of *O. yawapai magnicornu* Pilsbry, 1916.

varius, *Helix tryonii* var.—HEMPHILL, 1891a:331 [HEMPHILL, 1890f:17, *nomen nudum*]. Santa Barbara Id., Los Angeles Co., Calif.

Type material—CAS 037694, syntypes (6); USNM 174360–174365, syntypes (12); AMNH 51802 (2), 52041 (2), syntypes; UCM 20686, “paratypes” (12).

Remarks—Synonym of *Plesarionta tryoni* (Newcomb, 1864).

verna, *Epiphragmophora traskii*—BARTSCH, 1916:612–613, 619; pl. 114, figs. 13–15, ex Hemphill MS [in synonymy of *E. traskii traskii* (Newcomb, 1861)]. Los Angeles Co., Calif.

Remarks—Material formerly in some type collections, such as CASGTC 2753–2758, has no type status because the name was never made available.

walkeriana, *Helix*—HEMPHILL, 1911:102–103; pl. 2. San Luis Obispo [Co.], Calif. [near Morro Bay (ROTH, 1973)].

Type material—CAS 058838, syntypes (6 + 2 epiphragms), labeled “types” by Hemphill; USNM 174679–174682 (8), syntypes; ANSP 112424, syntypes (4); UCM 20178, “paratypes” (4); SBMNH 33958, syntypes (22). ROTH (1973:148–154; fig. 3), illustrates a CAS syntype.

Remarks—*Helminthoglypta* (*H.*) *walkeriana walkeriana* (Hemphill, 1911). There are additional Hemphill lots in the CAS and SBMNH general collections that may also be part of the original material.

wasatchensis, *Lymnaea stagnalis*—F. C. BAKER, 1911:152, 153, 518; pl. 20, figs. 10–12; text fig. 11, ex Hemphill MS. Near Salt Lake, Utah.

Type material—CAS 058832, syntypes (2); CAS 058833, ex SUPTC 5818 (26), syntypes.

Remarks—*Lymnaea stagnalis wasatchensis* F. C. Baker, according to McDONALD (1969:13; pl. 1, fig. d),

who credited the species to Hemphill as did Baker, but Baker alone was responsible for its publication.

wasatchensis, *Patula strigosa* var.—HEMPHILL, in W. G. BINNEY, 1886:27, 29, 34, 47; pl. 2, fig. 7 [HEMPHILL, 1878:2, as *P. idahoensis* var. "*wassatchensis*," *nomen nudum*]. Wasatch Mts., near Ogden, Weber Co., Utah; among quartzite boulders [4500 ft.; 1877 (labels)].

Type material—USNM 102170, "orig. type figd." (1); CAS 050290 (5), 050291 (4), 050292 (8), 050293 (5), 050295 (5), 050297 (6), 050298 (5), 050299 (5), 050300 (5), 050301 (5), 050302 (5), syntypes; AMNH 35163 (9), 53980 (2), 56610 (1), 56611 (2), 61685 (4 in 2 lots), syntypes; UCM 20656, "paratypes" (24); SBMNH 33950, syntypes (14).

Remarks—*Oreohelix peripherica wasatchensis* (Hemphill, 1886), according to PILSBRY (1939:456–457; figs. 300b–e).

wascoensis, *Tonites* [*sic* for *Zonites*] (*Conulus*?)—HEMPHILL, 1911:102. Wasco Co. and near Salem, Marion Co., Oregon.

Type material—CAS 058828 (2), syntypes from Wasco Co., Oregon, labeled "types" by Hemphill.

Remarks—*Pristiloma (Priscovitrea) wascoense* (Hemphill, 1911), according to PILSBRY (1946:414–415; fig. 224).

Class Polyplacophora

decoratus, *Callistochiton*—HEMPHILL, 1875:6 [*nomen nudum*].

Remarks—Later made available by KEEP (1887) (COAN, 1985:213).

fibriatus, *Callistochiton*—HEMPHILL, 1875:6, *ex* Carpenter MS [*nomen nudum*].

Remarks—Later made available by KEEP (1887) (COAN, 1985:213).

Class Cephalopoda

stearnsii, *Loligo*—HEMPHILL, 1892d:51. Fish markets in San Francisco and Oakland, Calif.

Type material—CAS 021005, syntypes (2) in alcohol; CAS 021006, syntypes (4), dried pens, both lots from a fish market in Oakland, Alameda Co., Calif.

Remarks—Suppressed by the International Commission on Zoological Nomenclature when synonymized with *Loligo opalescens* Berry, 1911 (ICZN Opinion 1122, 1979), and the two are now regarded as synonyms (VOSS, 1974).

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NOTES, INFORMATION & NEWS

A Final Note on *Cancellaria nassiformis* Lesson, 1842,
and *Nassarius corpulentus* (C. B. Adams, 1852)

by

Richard E. Petit

806 St. Charles Rd., North Myrtle Beach,
South Carolina 29582, U.S.A.

CERNOHORSKY's (1986:460) note on the status of *Cancellaria nassiformis* Lesson, 1842, unfortunately requires a reply, as his paper makes it appear that the earlier paper on the subject (PETIT, 1984) was written in ignorance of the International Code of Zoological Nomenclature. Cernohorsky cites Declaration 43 (1970) and declares *Cancellaria nassiformis* to be a *nomen oblitum*. Declaration 43 was superseded by the 1972 changes (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1972:177) in the Code which deleted Article 23(a) and (b), replacing them with Article 23(a-b) which stated: "The Law of Priority is to be used to promote stability and is not intended to be used to upset a long-established name in its accustomed meaning through the introduction of an unused name which is its senior synonym. A zoologist who considers that the application of the Law of Priority would in his judgement disturb stability or universality or cause confusion is to maintain existing usage and must refer the case to the Commission for a decision under the Plenary Powers [Art. 79]." Article 23(b) in the 1985 edition of the Code has slightly different wording, but the intent remains unchanged.

The term *nomen oblitum* has not appeared in the Code since 1 January 1973 except for its definition in the glossary of the 1985 edition (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1985:260).

The purpose of this note is not to make a case for the retention of the earlier name, but to restate my earlier contention that Lesson's name must either be employed as the correct name for the species or it must be rejected by action of the International Commission on Zoological Nomenclature. This statement is in conformity with the Code. CERNOHORSKY's (1986) unilateral action is in violation of Article 23(b) and is unacceptable.

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1985. International code of zoological nomenclature. 3rd ed. 338 pp.

PETIT, R. E. 1984. An earlier name for *Nassarius corpulentus* (C. B. Adams, 1852). *Veliger* 26(4):330.

Soviet Contributions to Malacology in 1981

by

Kenneth J. Boss

Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138, U.S.A.

and

M. G. Harasewych

Division of Mollusks, Smithsonian Institution,
Washington, D.C. 20560, U.S.A.

INTRODUCTION

Following previous synopses of the Soviet malacological literature (see *Veliger* 28[3]:329-337 for the most previous listing and reference to earlier ones), we present in translation, a summary of the papers abstracted by the Referativnyy Zhurnal in 1981. We have utilized the categorical arrangements offered by the Referativnyy Zhurnal although on occasion we have placed a paper in what, to us, appears to be a more appropriate category.

At least two major contributions appeared during the year, one being the extensive treatment of the terrestrial slugs of the USSR by Likharev & Viktor who considered over 100 species from eight different families of stylomatophoran pulmonates. Of considerable interest is the fact that the expression of the sluglike condition, which is characterized by a reduction and/or total loss of the shell in the adult stage, has independently evolved several times from shelled ancestors within the Pulmonata. Examples of parallelism and convergences among these lineages are noted. Incidentally, these numerous sluglike taxa obviously do not include those autochthonous or otherwise independently evolved taxa from the Neotropics, Sub-Saharan Africa, southeast Asia, and Oceania.

Another major work includes Skarlato's exhaustive systematic monograph of the bivalves of the cool-temperate waters of the western Pacific Ocean. He covered almost 300 species distributed among 45 families. Careful descriptions, good illustrations, and extensive biological data are provided for each species and the entire fauna is analyzed to give greater credence to the current divisions of

the zoogeographical provinces of the Far Eastern Seas of the USSR. Of much smaller scope is his handbook to the bivalves, co-authored by Volova, to the obviously more restricted area of the Peter the Great Bay.

Important for our appreciation of the population dynamics of species, indeed for the species concept in the hermaphroditic freshwater pulmonates, are Berezkina's papers, especially where she showed the deleterious effects of continued inbreeding by self-fertilization in *Lymnaea*; she clearly documented decreased fitness in succeeding generations of selfed individuals, not only by a reduction in shell size, but also in decreased reproductive success as reflected, for example, in the increased occurrence of anomalous eggs. It is not possible to imagine that some of the more than 1200 nominal species of lymnaeids are daughter colonies of self-fertilized individuals. Similarly, Kruglov's analysis of the morphological changes in the reproductive systems of lymnaeids indicates that exact measurements of such features as length of the preputium without reference to the age or sexual condition of the specimen are quite meaningless.

Kruglov & Frolenkova have in the spirit of Bondeson described the egg capsules of 24 species of prosobranch and pulmonate freshwater mollusks. In examining the life cycle of *Bradybaena*, Zeifert & Khokhukin have shown how the species optimizes its reproductive potential during the short summers of the Palearctic.

The introduction of new taxa continues apace with: Ivanov on *Caudofoveatus* for an aplacophoran caudofoveate; Kruglov & Starobogatov on *Aenigmomphiscola* for an array of new lymnaeid species convergent on *Lymnaea* (*Ophiscola*); Starobogatov & Andreeva on pyrgulids from the Aral Sea; Stadnichenko for fingernail clams, cycladids or pisidiids, from the Crimea and the Ukraine; Savitskii on Kuril Island *Cyclocardia*; Uvalieva on *Carychium* from Kazakhstan; Izzatullaev on planorbids from Central Asia; and Golikov & Sirenko on archaeogastropods from the Sea of Japan. Lus has provided new data on several deep-sea representatives of the Buccinidae including the genera *Tacita*, *Mohnia*, and *Sipho*.

Introduction of foreign or exotic species or the spread of European species into various parts of the USSR are documented by Popova & Shibanova for some land pulmonates in Siberia, by Izzatullaev for *Deroceras* and *Oxychilus* in Central Asia, and by Alekseev for the supposed Australoid *Potamopyrgus* (*Hydrobia*) *jenkinsi* in the Baltic.

For bivalves, Nevesskaya & Popov recounted the spectacular radiation of certain taxa, mostly cardiids, in the increasingly isolated and brackish waters of the Paratethys during the late Tertiary; not only were numerous morphologies rapidly elaborated, but new niches exploited; many new genera and even subfamilies have been delineated. Leibson & Usheva summarized data on the structure and function of the digestive diverticula and its role in intra-cellular digestion while Makrushin showed, in

two vastly different lineages (e.g., mytilids and tellinids), a probable, general ontogenetic phenomenon for bivalve hemocytes.

For cephalopods, Kondrakov, Moskalev & Nesis, utilizing previously expounded ideas concerning the Pleistocene history of the Arctic Basin, explained the current allopatric distribution of two octopoids, *Benthooctopus sibiricus*, which occupies the eastern Arctic seas from the Kara to the Beaufort, and *Bathypolypus arcticus* of the western Arctic. Nesis & Nikitina studied the presumably long-lived epipelagic, so-called macrotritopic larvae of *Octopus defilippi* and showed them not to belong to *Scaevurg unicirrhus* as previously believed.

ABBREVIATIONS

- BMV—Biologiya Morya (Marine Biology, Vladivostok).
 EKS—Ekol. Zhivotnykh Smolensk. i sopredel'n. obl. (Ecology of the Animal Life of Smolensk and adjacent regions, Smolensk, 1980).
 ES—English summary.
 GERM—Gistofiziol. Effektivn. i retseptorn, mekhanizmov. (Histophysiology of the effector and receptor mechanisms in the nervous system of marine organisms, Vladivostok).
 GZ—Gidrobiologicheskii Zhurnal (Hydrobiological Journal).
 NDVS—Nauch. Dokl. Vyssh. Shkol. Biol. Nauk. (Scientific Reports of the Higher Educational School for Biological Sciences).
 SRF—Nauch. Soobshch. Inst. Biol. Morya. Dal'nevost. Nauch. Tsent. (Scientific Reports of the Institute of Marine Biology, Far Eastern Scientific Center. Acad. Sci., USSR).
 TIO—Trudy Instituta Okeanologii. Akademiya Nauk SSSR. (Transactions of the Institute of Oceanology, Academy of Sciences, USSR).
 ZEBF—Zhurnal Evolyutsionnoi biokhimii i fiziologii. (Journal of evolutionary biochemistry and physiology).
 ZZ—Zoologicheskii Zhurnal (Zoological Journal).

GENERAL

ZATRAVKIN, M. N. 1980. Freshwater molluscan faunas of the central drainage of the northern Donetz River. ZZ 59(11): 1739–1742 (ES).

[71 species of gastropod and bivalve mollusks are reported from the central and upper drainage of this river. Of these 60 are represented in the collections gathered by the author. Included is a list of the molluscan species compositions of the northern Donetz, its tributary the Kazennii Toretz, and flood-plain lakes.]

ZOLOTAREV, V. N. 1980. On some principles for the interpretation of growth temperatures of marine mollusks established by the oxygen isotope method. BMV, no. 4:82–86 (ES).

[The influence of methodology and choice of samples on the results of biogeochemical determinations of growth temperatures of marine mollusks is examined. An example of the utilization of such data as a basis for a model of the evolution of cold water malacofauna (Kafanov, 1979) was shown to contain several errors in the interpretation of results of oxygen isotope analyses.]

CAUDOFOVEATA

IVANOV, D. L. 1981. *Caudofoveatus tetradens*, gen. et sp. n. and a diagnosis of taxa in the subclass Caudofoveata (Mollusca; Aplacophora). ZZ 60(1):18–28 (ES).

[The first critical review of the synonymies of *Chaetoderma* Loven, 1845, and *Crystallophrisson* Möbius, 1875, has resulted in changes of generic names in the superorder Chaetodermatimorpha. Described is *Caudofoveatus tetradens* Ivanov, gen. et sp. n. (Chaetodermatida). Included are diagnoses of all ordinal and family level taxa in the subclass Caudofoveata. These include several that have been separated as new taxa.]

SCAPHOPODA

CHISTIKOV, S. D. & A. YU. SAGAJDACHNII. 1981. Comparative morphology of the shells of two species of *Entalina* (Mollusca; Scaphopoda). *ZZ* 60(1):36-41 (ES).

[Linear regression analysis of the Mediterranean and eastern Atlantic forms of *Entalina quinquangularis* (= *E. tetragona* auct.) has shown that these taxa may be considered different species. The name *E. pentagona* (M. Sars, 1865) (type locality—Lofoten Island, Norwegian Sea) is restored for the Atlantic species. The Mediterranean species retains the name *E. quinquangularis*. The possibility of utilizing regression equations for differential diagnoses of these species is discussed. A description of *E. pentagona* is included.]

GASTROPODA, PROSOBRANCHIA

ALEKSEEV, N. K. 1980. On the occurrence of a freshwater form of *Potamopyrgus jenkinsi* (Mollusca; Gastropoda) in Kaliningrad Province. Tr. Kaliningr. Tekh. In-ta Ryb. Prom-sti i Kh-va (Transactions of the Kaliningrad Technical Institute of Fisheries, Industry and Agriculture), no. 91:28-30.

[The spread of the mollusk *Potamopyrgus*, a representative of the Australian zoogeographic province, into the Baltic Sea and the freshwater drainages of Europe is reported. The ecological plasticity and biological features of this mollusk cause it to be recommended for introduction into fish-breeding ponds, so as to increase the food supply for fish.]

GOLIKOV, A. N. & B. I. SIRENKO. 1980. New species of the subclass Scutibranchia from the Sea of Japan. Issled. Fauni Morei (Studies of Marine Fauna), Leningrad, 25/33:105-108 (ES).

[Based on material collected in 1972 on Moneron Island (Sea of Japan), *Puncturella varicostata* sp. n. and *Scissurella* (*Schizotrochus*) *disciformis* sp. n. are described.]

GUL'BIN, V. V. 1980. The fauna and several ecological features of the littoral gastropod mollusks of the northern portion of the Sea of Japan. Pribrezh. Plankton i bentos sev chasti Yapon. Morya (Coastal plankton and benthos of the northern portions of the Sea of Japan), Vladivostok, pp. 93-105.

[43 species of gastropod mollusks were found in the littoral zone of the northern portion of the Sea of Japan (from off Cape Povorotnii to Moneron Island, and Cape Kril'on, and to the north of the Strait of Nevel'skii). A short bibliography, zonal-geographic affinities, and characters of habitat are presented for each species. There is a predominance of cold-water fauna in the region of Soviet Gavan' (continental shore) and Cape Kuznetsov (SE Sakhalin), while a warm-water fauna predominates in the region of Moneron Island. It is proposed that there are two biogeographic provinces in the Sea of Japan, their boundary passing through Cape Povorotnii and south of Moneron Island and Cape Kril'on. The presence of two biogeographic regions is proposed for the northern province: one envelops the littoral zone of Moneron Island, the other of Capes Povorotnii and Kril'on northward to the Straits of Nevel'skii.]

LUS, V. YA. 1981. On the abyssal species *Sipho* (*Siphonorbis*) *danielsseni* (Friele) and *Mohnia mohni* (Friele) (Gastropoda: Buccinidae). *TIO* 115:126-139 (ES).

[Detailed, illustrated descriptions of shell structure, morphology, and anatomy of two deep-water Arctic species of gastropod mollusks of the family Buccinidae are presented as is information on their geographic and bathymetric distribution. The evolution as well as the systematic relationships of these two species to other members of the family Buccinidae are discussed.]

LUS, V. YA. 1981. A new species of *Tacita* (Gastropoda: Buccinidae), widely distributed in the lower abyssal zone of the northwestern Pacific Ocean. *TIO* 115:140-154.

[A detailed description of the morphology and anatomy of the deep-water buccinid *Tacita arnoldi* sp.n., from seven stations of the R/V *Vityaz* in the northwestern portion of the Pacific Ocean at depths of 5070-6135 m is presented. The genus *Tacita* includes three species, of which two were described earlier, that are distributed in a series of deep-water trenches in the Pacific. The center of species radiation of the genus *Tacita* is here considered to be the Kuril-Kamchatka Trench. The taxonomic and phylogenetic significance of this hypothesis is discussed.]

MANCHENKO, G. P. 1980. Isoenzymes in the gastropod *Haliotis discus*. *BMV*, no. 5:82-85 (ES).

[By the method of vertical starch gel electrophoresis, tissue specificity and molecular polymorphisms of the following isoenzymes of the gastropod mollusk *Haliotis discus* were studied: adenylate kinase, alcohol dehydrogenase, aspartate aminotransferase, hexokinase, glycerol-3-phosphate, dehydrogenase, glucose phosphate isomerase, isocitrate dehydrogenase, acid and alkaline phosphatases, xanthine dehydrogenase, lactate dehydrogenase, leucine aminopeptidase, NAD dependent malate dehydrogenase, NADP dependent malate dehydrogenase, sorbitol dehydrogenase, superoxide dismutase, phosphoglucomutase, 6-phosphogluconate dehydrogenase, and nonspecific esterase. Activity of the enzymes aspartate aminotransferase, glycerol-3-phosphate dehydrogenase, isocitrate dehydrogenase, leucine aminopeptidase, phosphoglucomutase, and alkaline phosphatase was not found in any of the tissues studied. Discovery of multiple molecular forms of the remaining enzymes indicates that they are under the control of at least 20 independent genetic loci.]

STAROBOGATOV, YA. I. & S. I. ANDREEVA. 1981. New species of mollusks of the family Pyrgulidae (Gastropoda; Pectinibranchia) from the Aral Sea. *ZZ* 60(1):29-35 (ES).

[Eight species new to science are described from various regions of the Aral Sea. *Caspiohydrobia kazakhstanica*, *C. behningi*, *C. obrutchevi*, *C. aralensis*, *C. sidorovi*, *C. nikitinskii*, *C. nikolskii*, and *C. bergi* are distinguished from each other and from previously described species by the proportions and form of the shell and by the rate of growth of the whorls. The genus *Caspiohydrobia*, endemic to the Aral-Ponto-Caspian Basin and surrounding arid regions, contains, to date, 29 species.]

YAROSLAVTSEVA, L. M. & L. A. KARPENKO. 1980. Studies of the roles of organismic and cellular mechanisms in adapting to decreases in salinity in several near shore mollusks. *BMV*, no. 3:80-87 (ES).

[Three species of gastropod mollusks (*Collisella dorsuosa*, *C. radiata*, and *C. versicolor*) differing in zonation within the littoral were studied. In upper littoral species, stability during sharp decreases in salinity is provided by a behavioral reaction—the insulating reflex. Absence of differences in osmotic equilibria of cells in the studied mollusks is probably indicative of similar salinity conditions at various levels of the littoral zone. Gradual changes in salinity elicit a different response in littoral mollusks. A higher degree of tolerance, the basis for which is most likely

cellular, is possessed by mollusks from the upper littoral in comparison to species from the mid and lower littoral zones.]

GASTROPODA, PULMONATA, AQUATIC

ARKHIPOV, V. V. & M. A. KOSTENKO. 1981. Mobility and interaction in a culture of isolated neurons taken from adult mollusks. *ZEBF* 17(2):187-190.

[Isolated neurons from brains of the pond snail *Lymnaea stagnalis* and the grape snail *Helix pomatia* were treated with pronase and cultured. The direction of motion and aggregation of neuronal bodies was demonstrated. Observations on the formation of cellular aggregates and on the formation, in culture, of nerve nets, not simply by motion of axons, but in the very bodies of neurons are recorded.]

BEREZKINA, G. V. 1980. Some observations on the development and function of the reproductive system of lymnaeids. *EKS*, pp. 22-32.

[Material representing eight species of *Lymnaea* was collected in the waterways of Smolensk Province. The ontogeny of lymnaeids can be separated into three stages: juvenile, stage of male reproductive maturity, and stage of full hermaphroditism; the first may be further subdivided into three periods. This paper describes each of these stages in detail. Development of the ducts under laboratory and field conditions is compared, and the limits of variability of several taxonomically significant indices of shell and reproductive characters are determined. Influences of several external factors (e.g., size of body of water, illumination) and of the role of self-fertilization in the reproductive process were also investigated. It was shown that with self-fertilization, eggs are deposited later, the number of eggs per clutch decreases, and the number of clutches increases in *Radix transsylvanica*, while in *L. atra* the number of clutches sharply decreases. With increased self-fertilization, the number of anomalous eggs increases and the size of the eggs and of the mollusks decreases. In the field, the negative consequences of self-fertilization appear to be limited to two or three generations. As a result, homozygosity increases.]

BEREZKINA, G. V. 1981. Seasonal changes in the reproductive system of lymnaeids. *ZZ* 60(7):978-983 (ES).

[Studies of the genitalia of five species of *Lymnaea* have shown that the degree of spermatogenesis and oogenesis in the hermaphroditic glands of pond snails depends on the time of year. Laboratory experiments indicate that these may be the reactions of the organism to the duration of daylight.]

BEREZKINA, G. V., A. P. IZAKENAITA, L. N. KISELEVA & T. S. KONSTANTINOVA. 1980. Some observations on calcium levels in lymnaeid shells. *EKS*, pp. 45-49.

[Studied were levels of Ca^{++} in shells of four species of *Lymnaea* collected in waterways within Smolensk Province that have different hydrochemical regimes. As a rule, lymnaeids are limited to waterways that have high levels of the ions Ca^{++} and Mg^{++} . Correlations of the basic components of uncorroded shells of all sizes are similar. Percentage levels of Ca^{++} in the exoskeleton of lymnaeids were the same for all species studied. Entrance of Ca^{++} into the body and its deposition into the shell is actively regulated by the organism in different water hardnesses. At high concentrations of Ca^{++} , its accumulation is increased.]

DVORYADKIN, V. A. 1980. Planorbids (Gastropoda, Pulmonata) and their infestation with the larvae of trematodes in the Amur and Marine [coastal] Districts of the Soviet Union. *Fauna presn. vod Dal'n. Vost.* (Freshwater Fauna of the Far East), Vladivostok, pp. 24-36.

[Included are descriptions and several notes on the density, bi-

ology, and distribution of seven species of planorbids, and of their infection by metacercariae of trematodes in the Amur Basin and the drainages of the Marine Coastal District [Primorsk'e]. Included is a list of 29 species of trematode larvae discovered in these mollusks. Examined are questions of the formation of centers of infection in various regions of the southern Far East.]

IZZATULLAEV, Z. 1980. New and little known species of freshwater mollusks of the molluscan family Planorbidae from Central Asia. *Dokl. AN Tadzh. SSR* (Reports of the Tadzhikistan Academy of Sciences) 23(7):406-410 (Tadzhik Summary).

[During 1976-1978, four new species of planorbids were found in the basins of the Syr Darya and the Amu Darya (Oxus) rivers. *Segmentina aveccenninae* sp. n. (Turkmen SSR, right bank Amu Darya) is similar to *S. distinguenda*, but is distinguished by a more bulging last whorl and a less distinct keel. Dimensions of the holotype (4 whorls): height 1.4 mm, width 4.2 mm, aperture 1.5 mm. The shell *Kolhymorbis dildora* sp. n. (Uzbek SSR, Akkyrgansk Res.) resembles *K. maacki*, but differs in the form of whorl growth. Dimensions of the shell (2.5 whorls): height 0.6 mm, width 1.8 mm, aperture 0.7 mm. *Helicorbis bactriana* sp. n. (Turkmen SSR, right bank Amu Darya) is similar to *H. kozhovi*, but differs in the number of strongly submerged whorls, smaller dimensions, and narrow umbilicus. Shell dimensions: height 1.1 mm, width 3.6 mm, aperture 1.5 mm. *Helicorbis kushanica* sp. n. (type specimen found together with the preceding species) resembles the preceding species, but is sufficiently distinguished by the bulging form of the shell and more submerged upper whorls. Shell dimensions (4.5 whorls): height 1.4 mm, width 4.6 mm, aperture 1.5 mm. *Segmentina distinguenda* (Gredler) is reported from the drainage of Central Asia for the first time.]

KRUGLOV, N. D. 1980. Growth and the functional changes in the morphology of the genitalia during ontogeny of pond snails (Pulmonata Lymnaeidae). *EKS*, pp. 33-45.

[Over 400 specimens representing five species of *Lymnaea* were used in different series of experiments; 200 were dissected. Growth changes in the genitalia are apparent until the onset of hermaphroditic reproductive maturity, prior to which there is more variation both in the morphology of the glandular organs and in the proportions of the copulatory apparatus than in adult mollusks). With reproductive maturity comes stability in the dimensions and proportions of the reproductive apparatus, but not in the glandular organs, which undergo significant functional changes during the reproductive cycle. These natural changes in the genitalia during ontogeny should be taken into account in systematic studies of this group.]

KRUGLOV, N. D. & O. A. FROLENKOVA. 1980. Comparative studies on the morphology of the egg capsules of freshwater gastropods from the European portions of the USSR. I. Subclass Pectinibranchia (Planilabiata, Ectobranchia, Discopoda). II. Subclass Pulmonata (Hygrophila). *EKS*, pp. 49-70.

[Mollusks were collected in the waterways of Smolensk, Moscow, and Kursk provinces. Egg capsules (515) of 24 species from seven families were studied. Features of their external and internal morphologies were used to construct tables to distinguish egg capsules of these species.]

KRUGLOV, N. D. & YA. I. STAROBOGATOV. 1981. A new genus of lymnaeids and the systematics of the subgenus *Omphiscola* of the genus *Lymnaea*. *ZZ* 60(7):965-977 (ES).

[Representatives of *Aenigmomphiscola* gen. n. have a preputial organ divided transversely into two sections. The genus includes three species: *A. europaea* sp. n. (type species) from the waterways of Bashkirii, Yaroslavskii, and Gor'kovskoi provinces; *A. uvalvae* sp. n. from Bashkirii and Kazakhstan; and *A. kazakh-*

stanica sp. n. from Kazakhstan. The systematics of species belonging to the subgenus *Omphiscola* of the genus *Lymnaea* were studied and found to be conchologically convergent with the new genus. This subgenus includes three species limited almost exclusively to the drainages of the Baltic and North seas: *L. (O.) glabra*, *L. (O.) clavata*, and *L. (O.) gingivata*. Both groups evolved independently from the subgenus *Stagnicola* of the genus *Lymnaea*.]

TURKEVICH, V. N. & N. S. YALINSKAYA. 1981. Maintenance of carbohydrates in the fluids of the mantle cavity of pulmonate mollusks at different temperatures. *GZ* 17(3):79-85 (ES). [Material was collected in the summers of 1977-1978 in the cooling reservoir of the Kursk region in the waterways and flood plains of the Seym River and in the ephemeral waterways of the sub-Carpathians. Carbohydrate concentrations in the mantle fluids of *Lymnaea stagnalis* and *Planorbis corneus* were studied, as were the effects of changes in temperature on infection of the mollusks with trematodes. Sugar levels in the mantle fluids of these mollusks ranged from 128 to 368 mg% and glycogen from 47 to 98 mg%. Sugar and glycogen levels were higher in mantle fluids of mollusks collected in zones of higher insolation than in other ecological zones during all seasons. Carbohydrate levels in mantle fluids decrease in mollusks infected with trematodes, when compared to uninfected individuals, and continues to decrease with increasing worm infestation.]

UVALIEVA, K. K. 1981. New mollusks of the genus *Carychium* (Pulmonata; Ellobiidae) from Kazakhstan. *Izv. AN KazCCP, Ser. Biol.* (Proceedings of the Academy of Sciences Kazakhstan SSR, Biology Series), no. 3:35-40 (Kazakh Summary).

[On the basis of an analysis of world malacological literature, characteristics of the genus *Carychium* are reported, as are diagnoses of subgenera described only in foreign sources. Two new species are described and assigned to different subgenera. Their descriptions, systematic affinities, type localities, ecologies, and distributions in Kazakhstan are presented.]

ZHUKOVA, E. V., V. M. SVISTUNOV & B. S. OSIPOV. 1980. The anatomy of the MP-1 neurons of the ramshorn snail *Planorbis corneus*. *Tr. Kaliningr. Tekh. In-ta. Ryb. Prom-sti i Kh-va* (Transactions of the Kaliningrad Technical Institute of Fisheries, Industry and Agriculture), no. 91:39-42.

[One of the larger neurons originates within the limits of the ventral surface of the small parietal ganglion. It has three primary branches emanating from the proximal segment, leading to the right mantle nerve, the visceral, and right pleural ganglia. The geometry of the neuron remains constant, is independent of its location in the ganglion, and may serve as a reliable morphological criterion for its identification.]

GASTROPODA, PULMONATA, TERRESTRIAL

IZZATULLAEV, Z. 1981. Introduced species of land snails new to the fauna of Central Asia. *Dokl. AN Tadzh. SSR* (Reports of the Tadzhikistan Academy of Sciences) 24(3):202-205.

[As a result of investigations conducted in 1977-1979 on four previously recorded species of land snails introduced into Central Asia, two additional introduced species are reported. *Deroceras reticulatum* is first reported from the fauna of Central Asia and *Oxychilus translucidus* is noted as new to the fauna of the USSR. Included are short descriptions of the structural features of the shell, pictures of animals, notes on their harmful effects, and distribution.]

LIKHAREV, I. M. & A. I. L. VIKTOR. 1980. Fauna of the USSR. Mollusks. Vol. 3, no. 5. The Slug Fauna of the USSR

and Contiguous Regions (Gastropoda Terrestria Nuda). Science Press: Leningrad. 437 pp., illustrated.

[This study presents a systematic survey of all species of slugs that occur on the territory of the USSR and adjacent regions: 102 species from 29 genera and 8 families are recognized. Comparisons of the functional morphology of slugs and shelled snails show parallel lines of evolution toward the slug form. Included is a phylogenetic arrangement of the genera and families of slugs and their proper placement within the Gastropoda. A new classification of Holarctic slugs is proposed. Also included is a survey of the basic features of the ecology and physiology of slugs, especially species that menace agriculture. Tables for diagnoses of families, genera, and species are given.]

MATEKIN, P. V., T. N. SOBOLEVA & L. V. PAKHORUKOVA. 1981. Genotypic characteristics of *Bradybaena tzvetkovi* Uvalieva et Soboleva, 1973 (Mollusca: Stylommatophora). *Izv. AN KazCCP, Ser. Biol.* (Proceedings of the Academy of Sciences Kazakhstan SSR, Biology Series), no. 1:25-30 (Kazakh Summary).

[By the use of polyacrylamide gel electrophoresis to separate water soluble proteins, biochemical markers and allelic systems were studied in *Bradybaena tzvetkovi*. Biochemical markers confirm species status for *B. tzvetkovi* and demonstrate the broad conchological polymorphism within *B. plectotropis*.]

POPOVA, S. M. & I. V. SHIBANOVA. 1981. On species of land snails (Gastropoda, Pulmonata) new to the fauna of Siberia. *ZZ* 60(2):305-306 (ES).

[In the basin of the Irkut River (left tributary of the Angara River), three species of land snails new to the Siberian fauna were found: *Cochlicopa lubricella* (Parro), *Pupilla sterri* (Voith), and *Bradybaena* cf. *fructicum* (Muell.). The first species was collected in Siberia in the Recent as well as fossil fauna (Pleistocene terraces). Stations at which these species were collected are described in detail, and the distribution of the species is discussed.]

ZEIFERT, D. V. & I. M. KHOKHUTKIN. 1980. Growth rates of land snails from the Trans-Urals. *Inform. Materiali In-ta Ekol. Rast. i Zhivotnykh. Otchet. Ses. Zool. Lab.* (Informational materials from the Ecological Institute of Plants and Animals. Reports of Zoological Laboratory), Sverdlovsk, pp. 37-38.

[The growth rate of *Bradybaena fructicum* was studied in two natural populations in Sverdlovsk Province, the eastern limit of its range. Animals of the spring generation hatch in the second ten days of May (mid-May); those of the fall generation in the second ten days of August (mid-August). The former become mature in the second year of life; the latter in the third. The early appearance of young is related to the fact that after hibernation, the snails do not mate, but immediately begin laying eggs. At this time, the young of the fall generation are still in hibernation. On the whole, growth of snails stops after early August, with only recently hatched snails growing significantly.]

GASTROPODA, OPISTHOBRANCHIA

ROGINSKAYA, I. S. 1979. Some observations on the fauna and ecology of opisthobranch mollusks of Cape Kanin Point [Kanin Peninsula, Barents Sea]. *Ekol. Don. Naseleniya Shel'fov. Zoni* (Ecology of the benthic fauna of the shelf zone), Moscow, pp. 93-103.

[Material for this study was collected in July 1974 in the littoral zone at the northern end of the Kanin Peninsula. In total, four species of opisthobranchs were found: one species of Sacoglossa (*Limapontia cocksii*) and three species of Nudibranchia (*Eubran-*

chus exiguus, *Ancula cristata* and *Doto* sp.). *Ancula cristata* and *Doto* sp. were abundant; the other two species were rather rare in the region studied. The dynamics of opisthobranch faunal composition were determined in spring and in more severe climatic conditions. Studies were conducted on the appearance of live animals, diet, time of spawning, and on the methods of dispersal of a species in different portions of its range.]

BIVALVIA

BELYAEVA, T. G. 1981. On the secretion of polyphenol oxidase by blood cells in the Far Eastern bivalve mollusks (*Crenomytilus grayanus* and *Modiolus difficilis*). Dokl. Acad. Nauk SSSR (Reports of the Academy of Sciences of the USSR) 256(1):188-190.

GAL'PERINA, G. E. & A. A. L'VOVA. 1980. Observations on the growth of *Dreissena polymorpha* (Pall.) in different parts of its range. Materiali k z-u ves. soveshch. vid. i ego produktivi v areale (Materials of the 3rd All Union Conference on the Species and its productivity within its range, Palanga 1980), Vil'nyus, pp. 10-11.

[A comparative study of the rates of growth of *Dreissena polymorpha polymorpha* (I) from the Uchinsky Reservoir (N of Moscow) and *D. polymorpha andrusovi* (II) from the northern Caspian was conducted. The growth season of I lasts from the end of May until October, of II from April to October. There was good correlation between calculated values of and actual maximum lengths of the mollusks, 40 mm and 38-42 mm for I and 24 mm and 26 mm for II respectively. Lifespan of both subspecies is similar, ranging from 3 to 5 years. It is thought that the principal influence on the growth rate of the investigated subspecies is the salinity regimes of their habitats.]

GOROMOSA, S. A. & V. A. TAMOZHNYAN. 1981. Some kinetic characteristics of transaminases from the tissues of the mussel *Mytilus galloprovincialis*. ZEBF 17(4):337-341 (ES).

[Several kinetic characteristics of cytoplasmic and mitochondrial fractions of aspartate and alanine aminotransferase (AAT and ALAT) were studied in mussel tissues. Differences in pH optima and apparently in Michaelis-Menton constants (Km) were found in the fractions of transaminases from muscles and gills. The pH optima of cytoplasmic fractions lie within the limits 7.5-9.0. Those of mitochondrial fractions are more acidic. Cytoplasmic AAT and ALAT are characterized by a high dependence on alpha-ketoglutarate and low dependence of aspartate and alanine. In mitochondrial fractions the reverse dependence is observed. These data confirm the presence of two isoenzymes of each transaminase in the tissues of mussels.]

KALININA, G. G. 1980. Lipids in the nerve ganglia of the grey mussel. GERM, pp. 44-47.

[Lipids of the nerve cells from cerebropleural, visceral, pedal ganglia were studied using cytochemical and biochemical methods. The maximum level of lipids is found in the fall, declines in winter, and gradually increases in the spring and summer. The phospholipids include: phosphatidylethanolamine, phosphatidylcholine, ceramide 2-aminoethylphosphonate, lysophosphatidylcholine, phosphatidylinositol, lysophosphatidylethanolamine, phosphatidylserine, phosphatidic acid, and phosphoglycerol. Total content of lipids and phospholipids increases during the spawning season, but their qualitative composition does not change.]

KHARAZOVA, A. D., V. I. FATEEVA & N. V. NECHAEVA. 1981. Determination of the rate of protein synthesis in the tissues of

mussels under conditions of reduced salinity. Tsitologiya (Cytology) 23(3):323-327.

[Methodology for determining the rate of protein synthesis while monitoring changes in cell permeability was applied to study protein synthesis in tissues of *Mytilus edulis* under conditions of reduced salinity. It was shown that the rate of protein synthesis was significantly reduced with changes in salinity.]

KHLEBOVITCH, V. V., L. A. YAKOVISHINA & A. YU. KOMENDANTOV. 1981. Changes in electrolyte content in the mantle fluids and hemolymph of the White Sea mussel (*Mytilus edulis*) under the prolonged, complete freshening of the external environment. BMV, no. 2:86-89 (ES).

[After placing White Sea mussels in freshwater, their mantle fluid gradually lost Na⁺, K⁺, and Mg⁺⁺ into the surrounding water (on the ninth day 50, 36, and 45% respectively), despite the isolation reflex. Levels of Ca⁺⁺ gradually increased in the mantle fluid—by 50% on the ninth day. Concentrations of Na⁺ and Ca⁺⁺ were the same in the hemolymph and mantle fluid, while levels of K⁺, and likely Mg⁺⁺, were higher in the hemolymph. The exchange of ions by mussels in freshwater is determined by diffusion outward from the mantle fluid and by the utilization of shell Ca⁺⁺ to increase the buffer capacity of body fluids during anaerobic respiration.]

KOSHELKINA, Z. V. 1980. The family Retroceramidae and the zonal stratigraphy of the Middle Jurassic of the northeastern USSR. Ekosistemi v stratigr. Materiali Vses. Soveshch. (Ecosystems in Stratigraphy. Proceedings of the All-Union Conference, Vladivostok, 1978), pp. 131-135.

[The development of the family Retroceramidae represents an important period in the development of the organismic world of boreal Jurassic seas, even though it was of comparatively short duration. Several stages can be outlined in the developmental history of the retroceramids. These form the basis for distinguishing the sublayers and regional zones. The first stage is characterized by the formation and radiation of the subgenus *Mennericeramus*, the second stage by the appearance and development of the subgenus *Fractoceramus*, and the third includes the origin and radiation of the subgenera *Retroceramus* and *Boreioceramus*. Stage boundaries overlap in some places. In some areas, subgenera appear sequentially through time. In other areas, they continue their development in parallel, appearing as mixtures of species complexes. A burst of adaptive radiation of retroceramids occurs in the Middle Jurassic.]

KUZ'MICHEVA, V. I. & L. V. SANINA. 1981. Caloric content of bivalve mollusks of the Caspian Sea. NDVS, no. 6:44-48.

[The caloric content of four bivalves from the northern and central Caspian Sea were determined and found to vary little in the spring and fall, ranging between 4.5 and 5.5 cal./mg dried body weight. Changes in caloric content are due to the degree of maturity of the gonad. As the gonads mature, caloric content per unit dried body weight increases, then decreases after the gametes are shed. Salt retention increases simultaneously.]

KUZ'MINA (MIKHAILOVA), O. YU. 1981. Effects of potassium concentration and salinity on the electrolyte composition and cell volume of mussel muscle. Tsitologiya (Cytology) 23(4): 461-465 (ES).

[During incubation of adductor muscles in potassium free seawater with salinities of 10, 26, and 40‰, the sodium concentration of muscles increases and potassium levels decrease. Two- and fourfold increases in potassium concentration of seawater with a salinity of 10‰ does not affect potassium levels in adductor muscles nor their hydration. These data demonstrate that sodium-potassium ionic regulatory mechanisms play a signifi-

cant role in stabilizing the ratio of sodium to potassium in cells, and indicate that to function properly, this pump requires certain minimum levels of potassium in the environment. Increases in potassium concentration do not effect the function of the Na-K ionic regulatory mechanism.]

LEIBSON, N. L. & L. N. USHEVA. 1979. Functional morphological characteristics of the digestive gland of bivalve mollusks. SRF, no. 4:5-33.

[This survey investigates the basic questions of structure and function of the principal organ of digestion in bivalve mollusks—the digestive gland or digestive diverticulum. A history of the study of this organ is briefly recounted, and includes the main points of the classical theory of Yonge—the discoverer of intracellular digestion in mollusks—as well as a re-analysis of this theory in the light of more recent data. Included are descriptions of the cellular composition of the epithelium of the ducts and channels, of the dynamics of the currents circulating within them, and of the ultrastructure and function of the different cell types (transport, phagocytic, absorptive, enzyme secreting, and excretory). The characteristics of two types of basophilic cells (secretory and regenerative) are given. The dependence of the digestive cycles of bivalve mollusks on factors in the surrounding medium (primarily tides) is demonstrated. The sources and mechanisms of regeneration of the epithelia of the gland are examined. Summarized is the basic literature on the structure and function of the digestive gland of *Bivalvia*.]

MAKRUSHIN, A. V. 1981. The hemocytes of *Mytilus edulis* and *Macoma baltica*. ZZ 60(2):306-309 (ES).

[Histological studies on the structure of hemocytes in the gills of mussels of different ages were conducted, beginning with the first year of life. Judging by the morphology of the hemocytes, which were identified as amebocytes and lymphocytes, the ontogeny of mussels was divided into two periods. The first (one- to three-yr-old mollusks with shells 1.5-15 mm in length) is characterized by hemocytes of variable form, without granular cytoplasm or sharp division between nucleus and cytoplasm (amebocytes). In the second period (two- to five-yr-old mollusks with 23-25 mm shells) the dominant hemocytes were oval or round in form and had granular cytoplasm (lymphocytes). Similar growth changes in hemolymph composition were found in *M. baltica*.]

MARCHENKO, A. A. 1979. Nerve cells of the cerebropleural ganglia of the edible mussel. SRF, no. 4:46-48.

MOTAVKIN, P. A. & A. A. VARAKSIN. 1979. Histophysiology of the central nervous system of the coastal scallop *Patinopecten yessoensis*. SRF, no. 4:34-45.

MOTAVKIN, P. A. & A. A. VARAKSIN. 1980. Types of axons and synapses in the neuropil of the visceral ganglia of the Maritime Territory scallop *Patinopecten yessoensis* (Jay). GERM, pp. 27-32.

[Several types of axons, each with characteristic vesicles, are described from the neuropil of the visceral ganglion. The most reliably identified are those with choline and monoaminergic (serotonin and dopamine) vesicles. Despite the prevalence of axon-axon synapses on individual nerve cells throughout the neuropil, there are also axon-somatic contacts. Elementary neurosecretory peptide-containing granules may function as synaptic vesicles.]

NEVESSKAYA, L. A. & S. V. POPOV. 1980. Features of the evolution of bivalve mollusks in the intra-continental basins of the Paratethys Sea and their significance for stratigraphy. Ekosistemi v. stratigr. Materiali Vses. Soveshch. (Ecosystems in Stratigraphy. Proceedings of the All-Union Conference, Vladivostok, 1978), pp. 98-101.

[Bivalve mollusks are considered to be a conservative, slowly evolving group, with basic ecological types appearing early in the fossil record. Their Mesozoic expansion is linked to the appearance of siphonate forms and the divergence of epifaunal groups. In the Cenozoic, generic composition remains almost unchanged, with many of the Recent species known from the Oligocene and Miocene. However, the radiation of mollusks in closed, brackish-water basins, where only a few euryhaline taxa are able to survive, provides examples of very rapid "explosive" evolution, with the formation of numerous taxa of specific, generic, and subfamilial rank, often accompanied by a transition into niches unusual for the ancestral group. Stratigraphic boundaries in marine deposits are based on changes in ecological conditions. Correlations are, therefore, less precise than with deposits produced by the breaking up of isolated brackish basins which can be subdivided on the basis of the evolutionary succession of species which rapidly evolved in them.]

SAVITSKII, V. O. 1981. New species of Far Eastern *Cyclocardia* (*Bivalvia*; *Carditidae*). ZZ 60(3):457-461 (ES).

[*Cyclocardia kurilensis* sp. n. and *C. skarlatoi* sp. n. are described from the southern part of the Sea of Okhotsk in the region of Urup and Iturup islands. The following quantitative characters were utilized in the description: length and height of shell, convexity of one valve, number of ribs, coefficient of elongation (ratio of shell height to its length), and coefficient of convexity (ratio of convexity to shell height). Figures and diagnostic characters of the new species are included.]

SHEPEL', N. A. 1980. Influence of environmental conditions on the behavior of the mussels (*Crenomytilus grayanus*) in mats. Izvestiia Tikhookeanskii nauchno-issledovatel'skii institut rybnogo khoziaistva i okeanografii (Proceedings of the Pacific Ocean Scientific Institute of Commercial Fisheries and Oceanography) 104:88-91.

[The method by which adult mussels move within the colony is discussed. This observation changes notions of the solidity, constancy, and stability of mussel colonies. The absence of silt on the substrate and protection from wave action of the regions inhabited by mussels create optimal conditions for their growth.]

SHKORBATOV, G. L. & P. I. ANTONOV. 1980. An ecological-physiological approach to the study of population structure of the subspecies *Dreissena polymorpha polymorpha* (Pallas). Materiali k z-u vses. soveshch. vid. i ego produktivni v areale (Materials of the 3rd All Union Conference on the species and its productivity within its range, Palanga 1980), Vil'nyus, pp. 24-25.

[It is suggested that the potential range of *Dreissena* may be cosmopolitan, its boundaries determined by abiotic factors of habitat. Local populations of *Dreissena* inhabiting isolated waterways are distinguished from macropopulations characteristic of river systems. The latter can be subdivided into meso- and micropopulations. Mesopopulations are synchronized in different climatic zones or regions to various hydrological or biological conditions; micropopulations are associated with specific biocenoses. Comparison of ecophysiological and ecomorphological characteristics of *Dreissena* from various regions within its range confirms the complexity of its intraspecific structure and broad range of adaptive variability. Definition of the stable boundaries of the various meso- and micropopulations of *Dreissena* with basic abiotic factors allows prediction of the development of *Dreissena* in waterways with various thermal, salinity, and oxygen regimes, and outlines the boundaries of its potential range.]

SKARLATO, O. A. 1981. Bivalve mollusks of temperate latitudes

- of the western portion of the Pacific Ocean. Science Press: Leningrad. 497 pp., illustrated.
- [279 species, belonging to 119 genera and 45 families, are discussed in this monograph. Tables for their identification are included. Based on an analysis of bivalve distribution, the biogeographic regions of the Far Eastern seas of the Soviet Union are defined. Several historical features of the formation of the bivalve fauna of the North Pacific are identified. The relationships of bivalves to temperature, substrate, and depth of the habitat are explained. The roles of these mollusks in benthic marine biocenoses are discussed.]
- STADNICHENKO, A. P. 1980. New species of freshwater mollusks (Bivalvia; Cycladidae) in the fauna of the USSR. *Vestn. Zool. (Zoological Herald)*, no. 6:29-34 (ES).
- [From the collections of freshwater mollusks taken in Crimea during 1973-1979, three new species of the genus *Euglesa*—*E. juliae*, *E. crimeana*, and *E. dymy*—are described. An additional new species of the same genus, *E. alexandri*, is based on 40-yr-old material in the collections of The Zoological Institute, Academy of Science, USSR. Detailed descriptions of shell morphology, dimensions of holotypes, and information on type localities are included. Diagnostic characters include external morphology and form of the shell, changes in shell convexity with height of the frontal section, position and form of the umbos, structure of the ligament pits, features of the adductor muscle scar and pallial line, and hinge structure. All four new species are figured. All holotypes are in the collections of the Zoological Institute.]
- STADNICHENKO, A. P. 1981. New and little known species of the family Cycladidae in the fauna of the Ukraine. Report I. *Vestn. Zool. (Zoological Herald)*, no. 2:38-41.
- [Studies are based on materials collected during 1964-1979 in the Ukraine and from several malacological collections. Twenty-two species were found, of which 11 are first reported in the Republic. Shell morphology as well as morphometric characters (height, length, shell convexity, etc.) were used to distinguish these species. Locality data and notes on the ecology are included, as are comparative remarks for several species.]
- TUSHMALOVA, N. A., O. YU. KARULINA & V. V. ASHAPKIN. 1981. Conditioned defensive reflexes in bivalve mollusks of the family Sphaeriidae. *NDVS*, no. 8:51-55.
- [Investigations of different forms of acquired behavior have shown that these mollusks are capable of developing temporary conditioned defensive reflexes to tactile and chemical stimuli. This type of acquired reaction, apparently, is highest for mollusks of this family, and places them at a level of development of the central nervous system comparable to that of gastropods.]
- VARAKSIN, A. A. 1980. Innervation of the walls of the sexual glands of the Maritime Territory scallop *Patinopecten yessoensis* (Jay). *GERM*, pp. 21-26.
- [The walls of the gonads have been found to contain nerve cells, small ganglia, and nerve fibers. The majority of nerve fibers, which form a dense network, contain primarily dopamine and serotonin. Peptide-containing fibers were often found in nerve trunks. Their expansions, filled with secretory granules, are in contact with the walls of neighboring cells. A portion of this peptide-containing neurosecretory material reaches the walls of the gonads via nerve conductors. Cholinergic fibers are found less frequently. There are also sensory conductors with typical receptor endings, most often of the dendritic type.]
- VOLOVA, G. N. & O. A. SKARLATO. 1980. Bivalve mollusks from Peter the Great Bay. Far Eastern Book Press: Vladivostok. 95 pp., illustrated.
- [This guide, intended for professionals and amateurs, includes

all species of bivalves known to the bay, dwelling to depths of 50 m; brackish-water species from the estuaries are not included. All diagnostic tables are based only on the morphology of the shell.]

- ZAITSEVA, O. V. & V. A. SOKOLOV. 1981. Cellular organization of the osphradium in the lamellibranch mollusks *Unio pictorum* and *Anodonta cygnea*. *Arkhiv. anatomii, gistol. i embriol. (Archiv for anatomy, histology and embryology)* 80(5): 90-97 (ES).

[The localization and cellular organization of osphradia in the freshwater lamellibranchiate mollusks *Unio pictorum* and *Anodonta cygnea* were studied. A large number of bipolar primary sensory receptor cells was found in the subepithelial sensory domain of the osphradium using in-vitro staining with methylene blue. Uni-, bi- and multipolar neurons, forming a special branchial ganglion in the proximal part of the osphradium, were found along a branch of the branchial nerve. Elements that conduct impulses in both ascending and descending directions, and that form primary and reverse connections between receptors and the CNS, are believed to be found among these neurons.]

- ZHADAN, P. I., P. B. SEMEN'KOV & N. M. CHEKMASOVA. 1980. Morphological and electrophysiological studies of the sensory system in the mantle edge of the Maritime Territory scallop *Patinopecten yessoensis* (Jay). *GERM*, pp. 33-43.

[Light and electron microscopy were used to study the long mantle tentacles. Epidermal papillae were found to contain two types of cells. Cells of the first type are structural, forming the capsule of the papilla. The free surface of these cells is covered with microvilli. Cells of the second type are distributed within the capsule and carry apical cilia. Electrophysiological studies of the sensitivity of the mantle edge to mechanical and chemical stimuli have shown that the mantle nerve originates a discharge impulse in response to touch and to weak stirring of the water. Chemical stimulation with extracts of tissues of various animals elicits a prolonged increase in impulse production in the mantle edge. Effectiveness of extract depends on the species of animal, and decreases in the sequence starfish, holothurian, sea urchin, mussel, and fish. Action of extracts from external tissues is always greater than from extracts of internal organs.]

CEPHALOPODA

- DEMBITSKII, V. M. 1981. Plasmalogen composition of phospholipid classes in different organs and tissues of an octopod *Octopus* sp. *ZEBF* 17(3):296-298.

[The levels of phosphatidylethanolamine, phosphatidylcholine, and phosphatidylserine and of the plasmalogen forms of these phospholipids in the brain, venous heart, gills, eyes, stomach, liver, and muscle were determined in one species of octopod from Vityaz' Bay, Sea of Japan. Only phosphatidylethanolamine has significant levels of plasmalogen. For phosphatidylcholine and phosphatidylserine, plasmalogen levels do not exceed 10%. Levels of the plasmalogen form of phosphatidylethanolamine are highest in the liver (50%) and lowest in the brain (27.8%). The latter level is greater than that found in bony fish (15.8%), frogs (17.9%), and reptiles (20%), closer to levels found in cartilaginous fish (29%) and birds (26.5%), and lower than levels found in mammals (49-65%).]

- KOBELEV, E. A. 1981. A squid from the White Sea. *Ryb. Khvo (Fisheries)*, no. 4:48.

[A single specimen of the squid *Todarodes sagittus* was caught in October 1980 in nets at a depth of 3 m off Petrominsk, Dvinskaya Guba [Dvinsky Bay]. Length 67 cm, wt. 1.2 kg. This species was previously taken only once in the White Sea (in

1884, two specimens). Its appearance has been erroneously connected to the warming of the water of the White Sea in 1980.]

KONDRAKOV, N. N., L. I. MOSKALEV & K. N. NESIS. 1980.

The octopus *Benthoctopus sibiricus* Loynig endemic in the eastern Arctic. Ekol. Issled. Shel'fa (Ecological investigations of the shelf), Moscow, pp. 42-56.

[*Benthoctopus sibiricus* is re-described on the basis of material collected on the edge of the shelf of the Chukchi Sea at drifting station SP-22 (an adult male) and in the Laptev Sea by expeditions of the vessels *Zare* in 1901 and *Vaygache* in 1914 (juveniles). It is a shallow (38-220 m) cold-water species of the primarily bathyal genus *Benthoctopus* and the only species of benthic octopus in the eastern Arctic seas. It ranges from the Vilkitskii Proliv [S of North Land, Kara Sea] presumably to the Beaufort Sea, with its eastern and western boundaries formed by the range of the large species of the western Arctic *Bathypolyopus arcticus*. These two species of octopus have never been encountered together. The composition and range of the fauna of the Arctic Shelf is discussed. A hypothesis is proposed regarding the limits of the range of *B. sibiricus* in the shelf seas of the eastern Arctic, and suggests that the separation of the ranges of *B. sibiricus* and *B. arcticus* are determined by the same factors that divide the high Arctic and Arctic-Boreal faunas into western and eastern Arctic and American faunistic centers; namely, the different conditions of ice cover during the Pleistocene. In the western Arctic, glaciers dominated to the edge of the shelf, while in the eastern Arctic, the shelf was not subjected to covering glaciers. The biology of *B. sibiricus* is discussed, and a table for diagnosing the Arctic-Boreal species of *Benthoctopus* is presented.]

NESIS, K. N. & I. V. NIKITINA. 1981. Macrotritic planktonic larvae of the benthic octopus *Octopus defilippi*: identification and distribution. *ZZ* 60(6):835-847 (ES).

[A study of 77 macrotritic larvae with mantle lengths ranging from 1.3 to 11.0 mm taken in the Gulf of Mexico, Caribbean Sea, and the east-central Atlantic and Indian oceans established that this is the larvae of the benthic, sublittoral, tropical-subtropical octopus *Octopus defilippi* and not of *Scaevurgus unicolor*, as previously believed. As recently described, larvae hatch with arms of equal length, but different pairs grow at different rates. It is probable that a change in the index of allometry between arm growth and mantle length precedes settling to the bottom. Reproduction occurs year round. Larvae are encountered sporadically, but in some places are abundant. The total number of larvae collected and reported in the literature surpasses the number of young adult and adult individuals of *O. defilippi*. Almost all larvae are epipelagic and encountered beyond the shelf edge. Six regions of larval accumulation were discovered. These were all in regions of closed, quasi-stationary circulation. Very small larvae (mantle length less than 2.5 mm, reflecting growth presumably of less than ten days) were encountered from 100 to 400 km from shore, which is possible only with unusually high speeds of drift. Macrotritic larvae are capable of retarding settling and, presumably, have a chance of crossing the Atlantic.]

Western Society of Malacologists Annual Meeting, 1987

The Western Society of Malacologists will hold its 20th Annual Meeting in San Diego, California, at San Diego State University, 21-25 June 1987. In addition to the regular program of contributed papers on mollusks, two special symposia are planned: "The Imperial Formation

and the Northern Gulf of California—Geology and Recent Mollusks" (Chaired by Judith T. Smith, U.S. Geological Survey, Menlo Park, CA 94025), and "Molluscan Aquaculture" (Chaired by David L. Leighton, Abalone Mariculture Enterprises, 11722 Sorrento Valley Road, San Diego, CA 92121). Abstracts are invited.

For further information and registration materials, contact Carole M. Hertz, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112. Telephone: (619) 232-3821, ext. 228, or (619) 277-6259.

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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.

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b) Books

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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.

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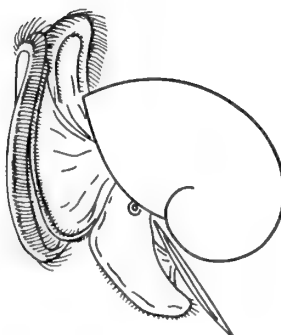
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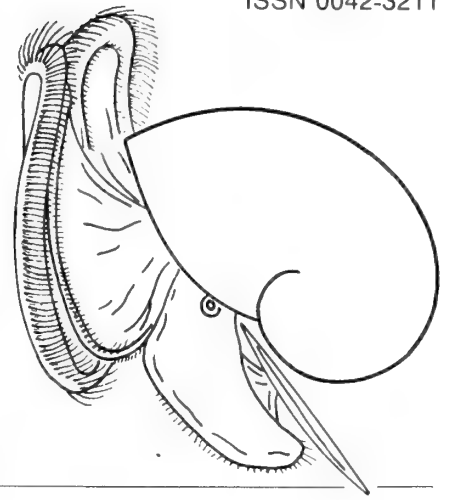
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THE VELIGER

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Anatomical and Taxonomic Characteristics of *Harpa* and *Morum* (Neogastropoda: Harpidae)

by

ROGER N. HUGHES

School of Animal Biology, University College of North Wales,
Bangor, Gwynedd LL57 2UW, U.K.

AND

WILLIAM K. EMERSON

Department of Invertebrates, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024, U.S.A.

Abstract. *Harpa* and *Morum* have similar external and internal anatomies, which are described in detail. Both autotomize the metapodial tip when disturbed. Their radulae are similar. Both probably feed on decapod crustaceans by capturing them in the propodial shield, enfolding them with the metapodium and secreting around them a mucus envelope. The clawed teeth of the minute radula may puncture arthroal membranes of the prey. Saliva injected from the proboscis probably predigests the prey, whose flesh is ingested in liquid form, perhaps using a pumping action of the mid-oesophagus. *Harpa* undergoes indirect and *Morum* direct larval development. Both are predominantly inhabitants of deep-water sediments, but a few species occur in shallow water.

The taxonomic misplacement of *Morum* (*sensu lato*) in the mesogastropod family Cassidae is here rectified. A new subfamily, Moruminae Hughes & Emerson, with *Morum* Röding, 1798, the type genus, is proposed and allocated to the neogastropod family Harpidae (Harpidae of authors).

INTRODUCTION

UNTIL RECENTLY, *Morum* was regarded as a genus within the mesogastropod family Cassidae, a taxonomic arrangement based entirely on the shell. Anatomical studies, however, revealed that *Morum* resembles *Harpa* so closely that the two genera must belong to the same family, namely the Harpidae (HUGHES, 1986; EMERSON, 1986). Although a detailed anatomical description has been published recently for *Morum* (HUGHES, 1986), descriptions of *Harpa* hitherto were confined to the accounts by QUOY & GAIMARD (1832-1835), REYNAUD (1834), and BERGH (1901). These accounts are accurate and, especially in the case of BERGH (1901), quite detailed.

The present paper gives more information on the alimentary system of *Harpa*, more detail of its radular structure, and compares *Harpa* with *Morum*. The taxonomic affinity of *Harpa* and *Morum* is clarified. *Morum* is transferred to the neogastropod family Harpidae and is here proposed as the type genus of a new subfamily.

MATERIALS AND METHODS

Gross external morphology was described from photographs of *Harpa major* Röding, 1798, by Olive Schoenberg (in REHDER, 1973), *Harpa amouretta* Röding, 1798, by R.N.H., *Morum praeclarum* Melvill, 1919, by Bill Liltved, and *Morum oniscus* (Linnaeus, 1776) by Richard Goldberg, Peggy Williams, and Germaine Warmke. Dissections were made of five *Harpa major* collected by Bill Liltved from dredgings of fine sand in 15-20 m of water off Durban harbor and lodged with the South African Museum, Cape Town, registration number A 37012. Dissections also were made of one *Morum kurzi* Petuch, 1979, American Museum of Natural History, registration number 213436, and of six *Morum praeclarum* dredged from about 90 m of water off Durban and donated by Dr. A. D. Connell. Radulae of *Harpa* and *Morum* were prepared by macerating the extreme tip of the proboscis in a drop of 10% sodium hydroxide on a covered glass slide at 70°C for 4 h. Gradually, the solution evaporated, leaving the

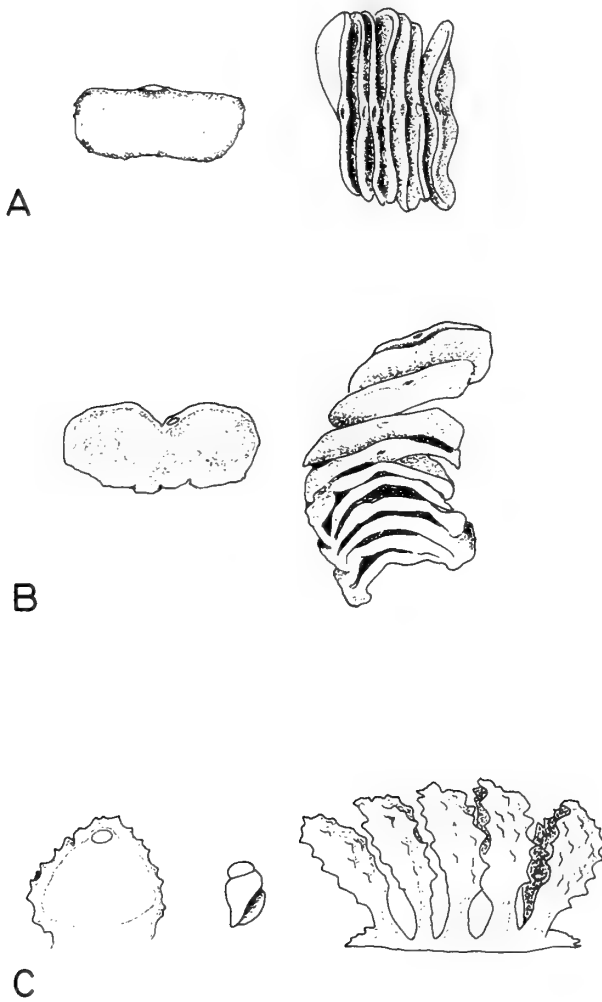


Figure 7

A. Egg capsules of *Harpa major* (after RISBEC, 1932, redrawn from REHDER, 1973). The capsule (left) is about 30 mm wide. B. Egg mass of *Harpa amouretta* (drawn from REHDER, 1973). The capsules (right) are about 40 mm wide. C. Egg capsules of *Morum oniscus* (after WORK, 1969). Each capsule is about 11 mm high. The escapement aperture is subapical on the concave face of the capsule (left). Juveniles emerge at the crawling stage, with a protoconch of about 2.2 mm high (center). Capsules are cemented together on the substratum by a basal layer of capsular material (right).

extremely similar. *Morum* has a propodial shield of slightly smaller proportions than that of *Harpa* and retains a vestigial or reduced operculum. Both are capable of gliding rapidly over the substratum and of efficiently burrowing into sand, and in both genera disturbance is likely to induce autotomy of the metapodial tip. The significance of the large propodial shield, large maneuverable metapodium, and tendency to secrete large quantities of mucus is to be seen in the feeding method of *Harpa*. There are only two reports of this, both recounted by REHDER (1973).

Chabouis and Chabouis (in REHDER, 1973) described the feeding of *Harpa* sp. on small, sand-dwelling specimens of the box crab *Calappa hepatica* (Linnaeus) and the swimming crab *Lupa sanguinolenta* (Herbst). The propodium pins the crab to the substratum while the metapodium glides underneath and wraps itself around the prey (this maneuver probably would be hindered by an operculum). Copious quantities of mucus, with adhering sand grains, form an imprisoning envelope around the crab. Couacaud (in REHDER, 1973) observed *Harpa major* "rolled like a ball" around a decapod crustacean.

Feeding by *Morum* has never been reported, although WORK (1969) on four occasions observed captive *M. oniscus* "with the entire anterior portions of their bodies inserted into the apertures of small gastropod shells which contained small, dead pagurids." He speculated that the *M. oniscus* were scavenging the dead hermit crabs, but it is more likely that they had killed the prey themselves. Perhaps *Harpa* specializes on the more agile brachyurans while *Morum* specializes on the slower moving anomurans, a speculation that could be tested by feeding trials in aquaria. The guts of *Harpa* and *Morum* examined in the present study were mostly empty, but some were full of an orange liquid. QUOY & GAIMARD (1832-1835) found nothing in the guts of some 20 specimens of *Harpa*, concluding that the ingested food must be insubstantial and readily absorbed from the gut.

As was first pointed out by BEU (1976), this conclusion is corroborated by the microscopic buccal apparatus, the extremely narrow part of the oesophagus passing through the nerve ring, and the absence of Lieblein's gland or any organs that would process food before it reaches the digestive gland. The large salivary glands, which are shown in *Morum tuberculosum* (Reeve, 1842) to empty into the buccal cavity via strongly muscular salivary ducts (HUGHES, 1986), probably secrete digestive enzymes that are delivered by the proboscis into the prey. Semidigested fluid could then be ingested, perhaps through pumping action of the mid-oesophagus. The motive force for this might come from contraction and relaxation of the muscular walls of the cephalic haemocoel, transmitted by the muscle-strands connected to the mid-oesophagus. The claw-shaped radular teeth, although microscopic, may serve to pierce the thin arthroal membranes of prey.

Radula

Early descriptions of the radula of *Harpa* (reviewed by REHDER, 1973) were made on flattened specimens mounted for the light microscope. This process evidently splays out the basal segment of the tooth, giving the false impression of a bilateral segmented membrane, sometimes regarded as the vestigial bases of lateral teeth. PEILE (1939) figures the tooth of *H. amouretta* with single lateral cusps, whereas BERGH (1901, cited in REHDER, 1973) figures it with double lateral cusps. Such variation is probably common in *Harpa*. Four specimens of *H. major* examined in

the present study had single lateral cusps, but in the fifth the right lateral cusp was subdivided into three smaller cusps (Figure 4C). Because the radular teeth of *Harpa* do not increase in size as the animal grows, they become proportionately smaller, making it increasingly difficult to locate the radula by dissection. This led some authors (cited by REHDER, 1973) to suggest, erroneously, that the radular teeth disappear in the adult stage.

Spawn and Developmental Mode

Egg capsules of *Harpa* are laid connected in a row on a hard substratum. They are approximately rectangular, laterally compressed, with an escapement aperture midway along the upper edge (Figures 7A, B). Each capsule contains 3000 to 4000 eggs, indicating that the larvae must develop indirectly, passing through a planktonic phase.

Egg capsules of *Morum* are also laid in a row on a hard substratum. They are broadly triangular, with one face convex and covered with blunt spines (Figure 7C).

Each capsule has a subapical escapement aperture on the concave side and contains relatively few eggs (personal observation), which undergo direct development, hatching as crawling young (WORK, 1969).

Habitat

Most species of *Harpa* and *Morum* have been collected from subtidal sediments, predominantly in deep, offshore water, but each genus contains a pair of shallow-water or intertidal species. *Harpa amouretta* has a wide distribution among Indo-Pacific reef flats and the much rarer *H. gracilis* Broderip & Sowerby, 1829, probably uses similar habitat on coral atolls of the central Pacific (REHDER, 1973). *Morum oniscus* inhabits reef flats and shallow water near coral reefs in the Caribbean. It is usually found beneath slabs of rock, but is sparse and requires persistent searching for its discovery. *Morum tuberculosum* occurs at low tide level along the eastern Pacific coast from Baja California, Mexico, to northern Peru. On suitable shores in Panama it may be relatively abundant and can be found at night crawling over mud and stones at extreme low tide level (Royce Hubert, personal communication).

Taxonomy and Systematic Placement

Largely on the basis of shell characters *Morum* (*sensu lato*) has long been classified with the mesogastropods in the Cassidae (formerly Cassididae of authors, see classifications of: TRYON, 1883; FISCHER, 1884; THIELE, 1929; WENZ, 1941; ABBOTT, 1968; BOSS, 1982; EMERSON, 1985). Anatomical studies by R.N.H. (HUGHES, 1986, and herein) and behavioral observations indicate that this genus is referable to the neogastropod family Harpidae (Harpidae of authors). Owing to major differences between *Harpa* and *Morum* in shell morphology and in discrete differences in radular and soft-parts anatomy, we have established below a new subfamily in the Harpidae in which

we place the genus *Morum* (*sensu lato*). We have accepted RAVEN'S (1985) proposal to use Harpidae as an emended name to replace Harpidae Bronn, 1849 (type genus *Harpa* Röding, 1798), not Harpidae Hawle and Corda, 1847 (type genus *Harpes* Goldfuss, 1839, in Trilobita). Final acceptance of the name Harpidae for this gastropod family must await action by the International Commission on Zoological Nomenclature (see RAVEN, 1985).

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Neogastropoda Wenz, 1938

Superfamily Volutacea Rafinesque, 1815

Family Harpidae Bronn, 1849

Subfamily **Moruminae** Hughes & Emerson,
subfamily novum¹

Type genus: *Morum* Röding, 1798

Diagnosis: Shells differ from those of Harpinae by having fewer nuclear whorls ($1\frac{1}{2}$ - $2\frac{1}{2}$ vs. $3\frac{1}{2}$ -5), more post-nuclear whorls ($5\frac{1}{2}$ -6 vs. 4- $4\frac{1}{2}$) with cancellate sculpture present at least on the early postnuclear whorls (except *Morum* s.s. and subgenus *Herculea*), a narrowly constricted aperture with a widely flaring, dentate labrum, and a large raised parietal shield. The gross anatomy differs by having a reduced operculum (Harpinae lack opercula), a relatively smaller propodial shield, a less pronounced expansion of the mid-oesophagus, and radular teeth with relatively shorter cusps.

Genus-group taxa assigned to Moruminae: *Morum* Röding, 1798, type species by monotypy: *Morum purpureum* Röding, 1798 = *Strombus oniscus* Linnaeus, 1767 (syns. *Lambidium* Link, 1807; *Oniscia* Sowerby, 1824; and *Plesioniscia* Fischer, 1844); Plio-Pleistocene to Recent, New World. Non-nominate subgenera: *Oniscidia* Mörch, 1852, type species by monotypy: *Oniscia cancellata* Sowerby, 1824, validated by I.C.Z.N. Opinion 1040 in 1975 (syns. *Pulchroniscia* Garrard, 1961; *Cancellomorum* Emerson & Old, 1963; and *Animusiro* Kira in Kuroda, Habe & Oyama, 1971); Eocene to Recent, New and Old World. *Herculea* Hanley, in H. & A. Adams, 1858, type species by monotypy: *Oniscia ponderosa* Hanley, 1858; Recent, Old World.

In summary: The family Harpidae is expanded to include the newly established subfamily **Moruminae** together with the nominate subfamily Harpinae in which

¹ We have opted to use **Moruminae** in place of "Morinae" to avoid homonymy with the family-group name Moridae Goode & Bean, 1896, in gadiform fishes (see COHEN, 1975). An application will be made to the International Commission on Zoological Nomenclature to set aside the provisions of Article 29 of the Code in this case, to allow the use of the stem *Morum*-, and to place **Moruminae** Hughes & Emerson, herein, on the Official List of Family-Group Names in Zoology.

are placed the extinct genus *Eocithara* Fischer, 1883, and two living genera, *Harpa* Röding, 1798, and *Austroharpa* Finlay, 1931 (see REHDER, 1973:214).

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Morphological Classification of Sibling Species of *Littorina* (Gastropoda: Prosobranchia): Discretionary Use of Discriminant Analysis

by

VICTOR CHOW

Bodega Marine Laboratory, University of California, P.O. Box 247,
Bodega Bay, California 94923, U.S.A.

Abstract. The sibling species *Littorina plena* and *L. scutulata* show considerable intraspecific variation in shell morphology, with wide overlap in shell characters between species. Measures of single characters (length-to-width ratio, apical angle, number of whorls, degree of tessellation, and presence of one spiral amber band in the shell aperture) are not sufficient for accurate separation and classification of specimens. However, discriminant functions that use statistically derived combinations of several easily measured shell characters allow approximately 92% of the snails from the exposed coast near Bodega Bay, California, to be correctly classified, and significantly improve morphological discrimination of these sibling species.

The shell morphology of *Littorina scutulata* and *L. plena* varies geographically and between habitats. Variability in morphological characters may be as great within a species as between species when individuals are considered from several sites. Only 47% of individual *L. plena* are correctly classified when the discriminant functions derived for open coast populations are applied to snails from nearby protected habitats. Although discriminant analysis is a powerful technique for distinguishing between morphologically similar species, such variation in morphology emphasizes the need to derive and evaluate discriminant functions for specific populations.

INTRODUCTION

TAXONOMIC STATUS has been the subject of study for several species of marine littoral gastropods in the genus *Littorina*. Intraspecific variation in shell characters and wide overlap between species have at times made morphological identification of species complicated and ambiguous, and taxonomists have had to rely upon other sources of information to detect or confirm the presence of sibling (morphologically similar) species of *Littorina*. Differences in mode of reproduction (HELLER, 1975a), morphology of genitalia (WHIPPLE, 1965; HELLER, 1975a; GOODWIN & FISH, 1977), characteristics of spawn (WHIPPLE, 1965; BORKOWSKI & BORKOWSKI, 1969), and allele frequencies at certain gene-enzyme loci (HELLER, 1975a; WARD & WARWICK, 1980; WILKENS & O'REGAN, 1980; MASTRO *et al.*, 1982) have been used to establish the existence of separate species in cases where morphological data on shell characters alone were insufficient.

Within populations, many *Littorina* species exhibit con-

siderable variation in shell size, shape, sculpture, color, and color pattern (for examples: BORKOWSKI, 1975; RAFFAELLI, 1979). Further morphological variation within a species can be attributed to environmental gradients in temperature (HUGHES, 1979), substratum (HELLER, 1975b), and exposure to wave action (STRUHSAKER, 1968; NEWKIRK & DOYLE, 1975; HYLLEBERG & CHRISTENSEN, 1977). Distinguishing between sympatric sibling species on the basis of shell morphology alone is tenuous when such intraspecific variability is present.

Where sympatric sibling species do occur, morphological classification of individuals is improved by removing interhabitat variation in shell characters. Separate diagnostic characters can be selected for each habitat in which the species coexist. If necessary, statistically derived combinations of shell characters can be employed to discriminate between sibling species in the same habitat.

Littorina plena Gould, 1849, and *Littorina scutulata* Gould, 1849, occur in sympatry along the west coast of North America. They are abundant microalgal grazers on

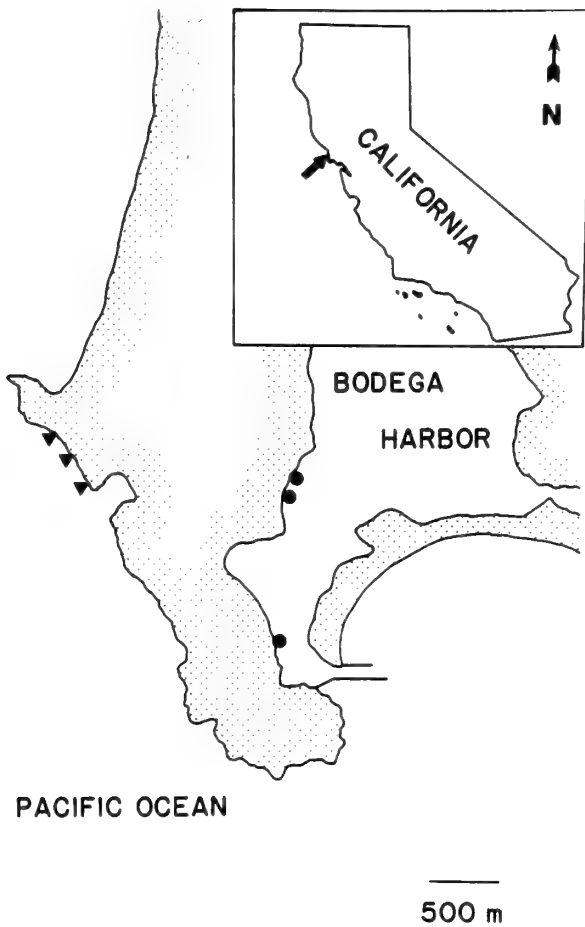


Figure 1

Location of study area on the biological reserve of the University of California Bodega Marine Laboratory: triangles indicate open coast sites and circles indicate protected harbor sites from which *Littorina* specimens were collected.

rocks and pilings in sheltered bays as well as on rocky shores of the exposed open coast. Reproductive distinctions detailed by MURRAY (1979) and patterns of genetic differentiation described by MASTRO *et al.* (1982) have verified the taxonomic status of *L. scutulata* and *L. plena* as separate sibling species. Both species, however, possess variable shell characteristics, and consistent differences in shell morphology have yet to be defined completely for these snails.

MURRAY (1982) uses the statistical techniques of discriminant analysis for morphological classification of *Littorina plena* and *L. scutulata* from a few locations along the west coast of the United States. However, satisfactory species characterization of the morphology of *Littorina* is likely to require control of local environmental (habitat) variables. This study describes in detail the morphology of snails from several populations near Bodega Bay, California, using techniques similar to those of MURRAY

(1982), and emphasizes the potential hazards of using discriminant functions for organisms that show widespread geographical and habitat variation in morphology.

MATERIALS AND METHODS

Exposed Coast Populations of *Littorina*

Specimens of *Littorina plena* and *L. scutulata* were collected from exposed rocky shores northwest of Horseshoe Cove on the biological reserve of the University of California, Bodega Bay, California (Figure 1). Individuals were separated by species and sex according to the characters described by MURRAY (1979) and MASTRO *et al.* (1982). Male snails were identified by penis morphology and female snails by the type of egg capsule produced while isolated in individual containers. Only identifiable snails (spawning females and males with shell lengths greater than 4 mm) were used in this study of shell morphology.

Statistical analyses of morphological data were conducted on several shell characters, which included shell length, shell width perpendicular to the long axis, apical angle, number of whorls, degree of tessellated color pattern, and presence of one amber spiral band in the aperture. These characters were chosen for their ease of determination and for their initial promise in distinguishing *Littorina plena* from *L. scutulata*. Linear dimensions were measured to the nearest 0.01 mm with dial calipers held under a dissecting microscope and the apical angle was determined to the nearest degree with a protractor. The degree of tessellation and the appearance of the amber band were scored as either (0) absent, (1) obscure, or (2) distinct. All measurements were made on live animals with the aperture oriented upwards (Figure 2).

Discriminant Analyses for Exposed Coast Populations

An optimal set of shell characters for classifying exposed coast specimens of *Littorina plena* and *L. scutulata* was obtained by discriminant analysis. Discriminant analysis is a procedure that weights and linearly combines characteristics for which groups are expected to differ; the result is a discriminant function that maximizes statistical separation of the groups. It is then possible to identify those characteristics that contribute most to differentiation between the groups, and to derive functions that classify cases of unknown membership.

Discriminant analyses were performed on several subsets of the data, using a stepwise method of entering and removing shell characters as discriminating variables. The computer program for discriminant analysis obtained from the Statistical Package for Social Sciences (NIE *et al.*, 1975) began by selecting that character that best distinguished *Littorina plena* from *L. scutulata*. A second character was then selected as the variable best able to improve the power of discrimination when combined with the first char-

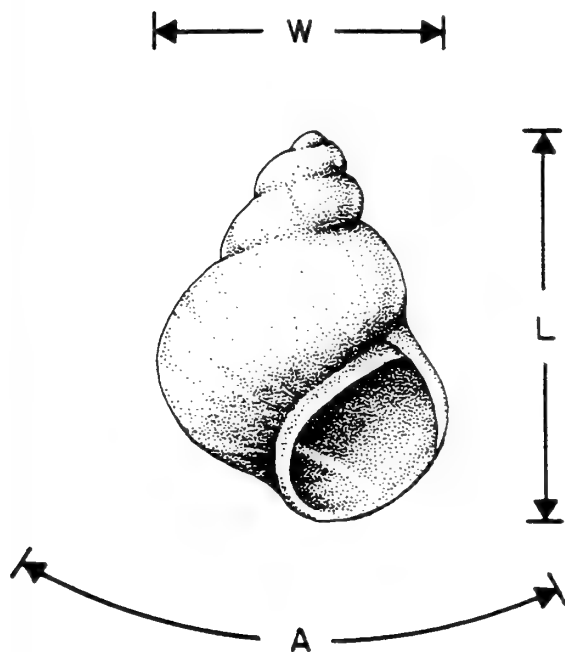


Figure 2

Morphological measurements made on each shell. L = shell length; W = shell width; A = apical angle. (Shell shown with amber band present inside the aperture.)

acter. The third and subsequent characters were selected similarly in order of their explanatory power until all characters were selected. At each step, characters could be removed if they acted to reduce discrimination in combination with more recently selected characters. Standardized (weighting) coefficients were eventually produced that indicated the relative importance of each of the characters finally chosen. COOLEY & LOHNES (1971) and TATSUOKA (1971) have described the mathematical techniques involved.

Snails from exposed coast populations were used to derive discriminant functions for *Littorina plena* and *L. scutulata*. From samples collected monthly during the period September 1980 to December 1981, a subsample of 275 *L. plena* and 253 *L. scutulata* was selected randomly for discriminant analyses. Smaller sample sizes were used for some analyses, and individuals selected were restricted to shell lengths less than 13 mm because all snails larger than 13 mm were *L. scutulata*.

Suitability of Derived Discriminant Functions

Specimens were collected between May 1984 and October 1984 from the exposed coast study site and from additional sites inside a protected harbor located 1.5–2.0 km from the exposed coast site (Figure 1). These samples were used to test the general applicability of the previously derived discriminant functions. Thirty-four *Littorina plena*

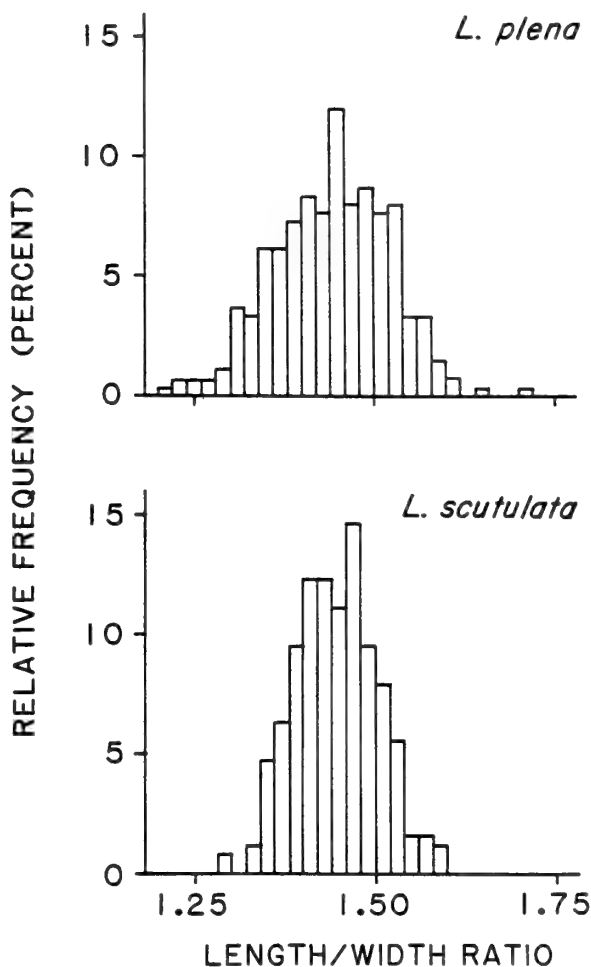


Figure 3

Frequency histograms of length-to-width ratios for *Littorina plena* ($n = 275$) and *L. scutulata* ($n = 253$). Distributions for the two species are not statistically different. Kolmogorov-Smirnov two-sample test: DMAX = 0.1001; $P > 0.10$.

and 33 *L. scutulata* were obtained from the exposed coast habitat to examine the usefulness of the discriminant functions over long periods of time. The capacity of the discriminant functions to classify individuals from a different habitat was measured on a sample of 57 *L. plena* and 22 *L. scutulata* obtained from the protected harbor habitats. Harbor snails were identified and measured using the same methods as described for exposed coast snails.

RESULTS

Exposed Coast Populations of *Littorina*

Littorina plena and *L. scutulata* from the exposed coast exhibited considerable overlap in all shell characters examined in this investigation. Frequency histograms of length-to-width ratios (Figure 3) failed to reveal any sta-

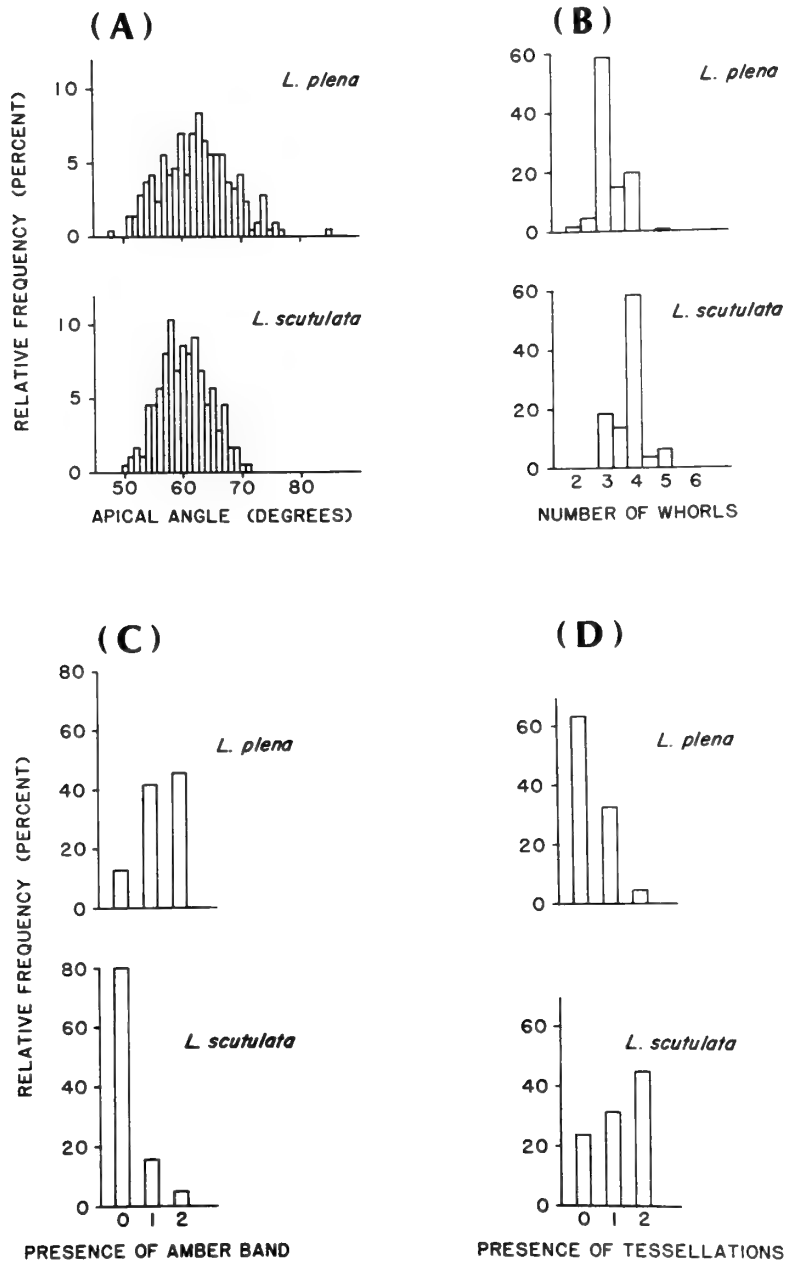


Figure 4

Frequency histograms of shell characters for *Littorina plena* and *L. scutulata*. n_p = sample size for *L. plena*; n_s = sample size for *L. scutulata*. Species differences in all shell characters are significantly different (Kolmogorov-Smirnov two-sample tests; all $P < 0.01$). A, apical angles ($n_p = 216$; $n_s = 174$; DMAX = 0.2208); B, number of whorls ($n_p = 333$; $n_s = 315$; DMAX = 0.4783); C, occurrence of amber band in the aperture (0 = absent; 1 = obscure; 2 = distinct) ($n_p = 280$; $n_s = 272$; DMAX = 0.6692); D, occurrence of tessellated color patterns on shell (0 = absent, 1 = obscure; 2 = distinct) ($n_p = 92$; $n_s = 122$; DMAX = 0.4073).

tistical differences in general shell shape between these two sibling species. However, specimens of *L. scutulata* attained a larger size than those of *L. plena* (snails with shell lengths greater than 13 mm were invariably *L. scutulata*). Moreover, shells from these populations of *L. plena*

and *L. scutulata* displayed statistically significant differences in the apical angle, number of whorls, degree of tessellation, and presence of an amber band in the aperture (Figure 4).

Individual *Littorina plena* generally had larger apical

angles, and the population as a whole showed greater variation ($F = 1.95$; d.f. = 215, 173; $P < 0.01$), than *L. scutulata*. The average apical angle (mean \pm SD) for *L. plena* was 62.6 ± 6.0 while apical angles averaged 60.2 ± 4.3 for *L. scutulata*. Figure 4A presents sample sizes and distributions of apical angles for each of the sibling species.

Shells of *Littorina plena* usually had fewer whorls than those of *L. scutulata* (Figure 4B). Only 20% of the *L. plena* specimens examined ($n = 335$) had four or more whorls, while 68% of the *L. scutulata* shells ($n = 315$) had at least four whorls.

Littorina plena shells were more likely to possess an amber band in the aperture (Figure 4C), but less likely to show tessellations (Figure 4D) than those of *L. scutulata*. In 87% of the *L. plena* specimens ($n = 280$) the band was present to some extent; the band was observed in only 20% of the *L. scutulata* shells ($n = 272$). Thirty-seven percent of the *L. plena* shells inspected ($n = 92$) displayed at least some degree of tessellation; in contrast, a tessellated pattern was present on 76% of the *L. scutulata* shells ($n = 122$), and this pattern was more often very prominent than on *L. plena* shells.

Discriminant Analyses for Exposed Coast Populations

Although the differences between *Littorina plena* and *L. scutulata* in some shell characters were statistically significant, no one character accurately separated individuals to species. Reliability of identification was enhanced by simultaneously using several characters through discriminant analysis. Table 1 lists discriminant functions for three analyses using the following subsets of shell characters: (1) length, width, presence of amber band, and number of whorls; (2) length, width, presence of amber band, number of whorls, and presence of tessellations; and (3) length, width, presence of amber band, number of whorls, and apical angle. A discriminant score was computed for each individual by multiplying each of the snail's shell characters by the corresponding coefficient and adding together these products. The resulting discriminant score represented the number of standard deviations that snail was away from the mean of all snails (both species)

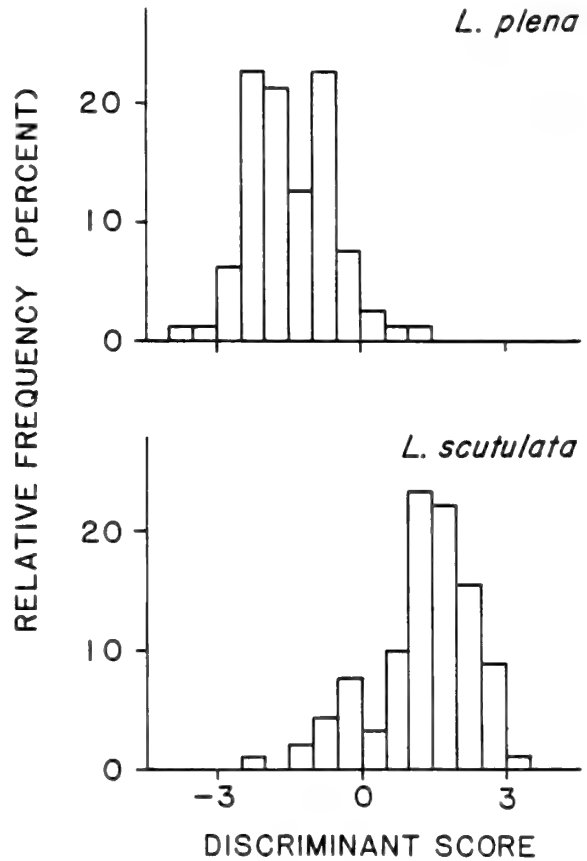


Figure 5

Frequency histograms of discriminant scores for *Littorina plena* ($n = 80$) and *L. scutulata* ($n = 90$). Discriminant score = $-0.882L + 1.662W - 1.274B + 0.821WH + 0.473T - 4.644$ where: L = shell length in mm; W = shell width in mm; B = presence of amber band in aperture; WH = number of whorls; T = extent of tessellated color pattern. B and T are scored (0) absent, (1) obscure, or (2) distinct. Distributions are significantly different. Kolmogorov-Smirnov two-sample test: DMAX = 0.7972; $P < 0.01$.

Table 1

Discriminant functions for three sets of shell characters: L = shell length in mm; W = shell width in mm, B = presence of amber band in aperture, scored 0-2; WH = number of whorls; T = extent of tessellated color pattern scored 0-2; A = apical angle in degrees. Sample sizes (n) indicate the numbers of each species from open coast populations used in the analysis. Mean discriminant scores indicate the species' means for each function. SD = standard deviation.

Anal- ysis	Function	<i>Littorina plena</i>			<i>Littorina scutulata</i>		
		n	Mean	SD	n	Mean	SD
1	$D = -0.732L + 1.599W - 0.983B + 1.306WH - 6.952$	256	-1.128	0.940	215	1.343	1.067
2	$D = -0.882L + 1.662W - 1.274B + 0.821WH + 0.473T - 4.644$	80	-1.459	0.920	90	1.297	1.066
3	$D = -1.369L + 2.514W - 0.812B + 1.514WH - 0.064A - 3.798$	156	-1.119	0.923	125	1.396	1.089

Table 2

Standardized discriminant function coefficients for each analysis of *Littorina plena* and *L. scutulata*. See text for explanation.

Analysis	Coefficients for each shell character					
	Shell length	Shell width	Amber band	Whorls	Tessellations	Apical angle
1	-1.003	1.409	-0.615	0.629	—	—
2	-1.036	1.299	-0.704	0.398	0.331	—
3	-1.991	2.338	-0.530	0.702	—	-0.351

on the given discriminant function. Table 1 indicates the number of snails used in the analyses and the mean discriminant scores for *L. plena* and *L. scutulata* for each of the discriminant functions. The extent to which the two species were separated by discriminant analysis is shown in Figure 5 (for the function that utilized shell length, width, presence of amber band, number of whorls, and degree of tessellation as discriminating variables).

Standardized (weighting) coefficients for each discriminant function are given in Table 2. The absolute value of a coefficient indicates the relative contribution of the associated shell character to that particular function. (The sign of the coefficient simply denotes whether the character is making a positive or negative contribution.) In all three analyses, shell width and shell length had the greatest importance in separating *Littorina plena* from *L. scutulata*. Apical angle and degree of tessellation were least important.

Individuals were assigned to species through the use of classification functions. Classification functions are usually employed to classify new individuals with unknown identities, but were used in this analysis to test the adequacy of the discriminant functions. As with the discriminant functions, classification scores were obtained by multiplying character values by the appropriate coeffi-

cients and summing these products. For each analysis, there was a separate equation for each species; the resulting classification scores quantified the likelihood that an individual belonged to the corresponding species, and the individual was then assigned to the species for which it had the greatest likelihood of membership (the highest classification score). Classification functions and the percent of correct classifications (*i.e.*, those confirming the reproductive characters) are given in Table 3 for each species for the three statistical analyses. (Additional specimens from exposed coast populations, not included in the initial analyses, were added to the samples of snails classified.) The best classification of species was obtained when length, width, presence of an amber band, number of whorls, and presence of tessellations were employed as discriminating characters; better than 95% of the *L. plena* and 89% of the *L. scutulata* were correctly identified.

Suitability of Derived Discriminant Functions

Discriminant and classification functions derived for exposed coast populations of *Littorina plena* and *L. scutulata* (using length, width, presence of an amber band, number of whorls, and presence of tessellations as discriminating characters) correctly identified high proportions of snails collected from the same location three years later. The average discriminant score (mean \pm SD) for *L. plena* collected at the later date was -1.492 ± 0.854 and 97% of the individuals ($n = 34$) were properly classified. The average discriminant score for *L. scutulata* was 0.845 ± 1.092 and 82% of the individuals ($n = 33$) were properly classified.

The same functions successfully classified 86% of the *Littorina scutulata* collected from protected harbor habitats (average discriminant score = 1.063 ± 0.872 ; $n = 22$). However, only 47% of the *L. plena* from protected harbor habitats were correctly classified (average discriminant score = -0.063 ± 0.971 ; $n = 57$). Individuals of both species tended to have more whorls and a higher degree of tessellation when collected from the harbor compared

Table 3

Classification functions for each discriminant analysis. Also shown are the percentages of correct identifications for each species and for each analysis. (Sample sizes are given in parentheses and include additional open coast snails to those used in the initial analysis.) C_p = classification score for *Littorina plena*; C_s = classification score for *L. scutulata*. Other abbreviations the same as for Table 1.

Analysis	Classification functions	Percent correctly identified		
		<i>L. plena</i>	<i>L. scutulata</i>	Total
1	$C_p = -11.76L + 24.63W + 5.07B + 18.13WH - 53.86$ $C_s = -13.57L + 28.58W + 2.64B + 21.36WH - 71.31$	89.82 (275)	88.14 (253)	89.02 (528)
2	$C_p = -8.35L + 23.09W + 8.43B + 18.20WH - 0.33T - 67.71$ $C_s = -10.78L + 27.67W + 4.92B + 20.46WH + 0.97T - 80.29$	95.65 (92)	89.34 (122)	92.06 (214)
3	$C_p = 38.40L - 49.21W + 5.49B + 9.00WH + 4.54A - 174.95$ $C_s = 34.94L - 42.89W + 3.45B + 12.81WH + 4.38A - 184.84$	92.64 (163)	85.50 (131)	89.46 (294)

to snails found on the exposed coast. These morphological changes in the harbor habitat increased the likelihood that any particular snail would be classified as *L. scutulata* by discriminant analysis, and thus significantly increased the probability of mistakenly classifying harbor specimens of *L. plena* (adjusted chi-square = 43.87; d.f. = 1; $P < 0.001$).

DISCUSSION

For gastropods that show as much intraspecific variability in shell morphology as *Littorina* (WHIPPLE, 1965; BORKOWSKI, 1975; RAFFAELLI, 1979), morphological discrimination of sibling species becomes a difficult task. Morphological features of the shell are usually the most convenient, rapid, and inexpensive means for classifying individuals from different species, being applicable to living snails and dried shells alike. In the case of sibling species, however, specific diagnostic characters may be lacking. It may be necessary to rely upon statistical techniques that incorporate several shell characters in order accurately to identify species by morphology.

Adult *Littorina plena* and *L. scutulata* from the exposed coast near Bodega Bay differ significantly in several shell characters, supporting previous conclusions (MURRAY, 1979, 1982; MASTRO *et al.*, 1982) that the two species are indeed separate taxonomic entities. Individual *L. scutulata* reach a larger size, and usually possess more whorls and tessellations than *L. plena*. Yet, classification of these individuals based on shell morphology alone requires measurements of many morphological variables and a statistical procedure for evaluating these variables. Using four or five variables, the discriminant analyses performed in this study correctly assign snails to species in approximately 90% of the cases. Discriminant scores further measure the reliability of identification on an individual by individual basis; greater confidence can be placed in individual identifications that have extreme discriminant scores.

However, the plasticity of shell morphology in single species of *Littorina* can result in distinct morphological alterations along environmental and geographic gradients (COLMAN, 1932; STRUHSAKER, 1968; VERMEIJ, 1973; NEWKIRK & DOYLE, 1975; HUGHES, 1979). In fact, the shells of both *L. plena* and *L. scutulata* from Bodega Bay reach larger sizes, possess more whorls and tessellations, and have taller spires as populations occupy more sheltered habitats. As a result, *L. plena* from sheltered habitats begin to look like *L. scutulata* from exposed habitats, while *L. scutulata* from sheltered habitats look like more extreme forms of *L. scutulata* from exposed habitats. Such variation in shell features with changes in habitat reduces the utility of the specific discriminant functions derived in this study. Clearly, systematic biases in classification occur when discriminant functions for exposed coast populations are applied without adjustment to individuals from nearby sheltered bays. Specimens of one species from one habitat

overlap in morphology with specimens of the second species from a different habitat.

Taxonomic separation of species based on morphology usually assumes that differences between species are greater than differences within a species. COLMAN (1932) states that two morphs are not separate species unless it is shown, "after the examination of sufficient numbers collected over a wide area, that there is not a series of overlapping intergrades between the two differing forms." However, this stipulation for species status is conservative and makes no allowance for the existence of sibling species. Morphological overlap increases between the sibling species *Littorina plena* and *L. scutulata* when specimens are considered from a variety of habitats.

Morphological characterizations of sibling species of *Littorina* are likely to lack discriminating power if considered for the full geographic range of the species. MURRAY (1982) presents a discriminant analysis for *L. plena* and *L. scutulata* morphologies that is based on small samples combined from several sites along the western coast of the United States. Such an analysis may obscure important interhabitat shell variation if a wide variety of environments is considered, or may seriously bias the morphological descriptions if samples from particular habitats are unduly represented. Snails from the exposed rocky shores near Bodega Bay differ significantly in morphology and are less accurately classified to species when methods developed by MURRAY (1982) are utilized. The discrepancies between MURRAY'S (1982) results and the results of this study are likely due, at least in part, to the general phenomenon of variation between populations in different localities. In the case of sibling species, variability in morphological characters may be nearly as great within species as between species when individuals are examined over a wide range of habitats.

Statistical techniques such as discriminant analysis can be powerful methods for distinguishing between morphologically similar species when other means are available initially to verify taxonomic status. Discriminant functions can be derived for particular habitats in cases where interhabitat variation in morphology is high, although other possible sources of variation (sex, season, parasitism) may still create difficulties in some circumstances. Ideally, specific techniques should be developed for specific applications. Discriminant analyses performed for certain local populations are not suitable for species as a whole, nor are analyses for species as a whole likely to be useful for specific local populations. Discriminant functions are potentially important tools for discriminating between specimens of *Littorina plena* and *L. scutulata* and other sibling species of gastropods but they should be used with caution and frequent re-evaluation.

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Continuous Reproduction in the Protobranch Bivalve *Solemya reidi* (Cryptodonta: Solemyidae)¹

by

RICHARD G. GUSTAFSON,² BARBARA D. GUSTAFSON,² AND ROBERT G. B. REID

Department of Biology, University of Victoria, Victoria, B.C., Canada V8W 2Y2

Abstract. Specimens of *Solemya reidi* Bernard, 1980, were obtained at regular intervals from a population in Alberni Inlet, Vancouver Island, Canada, between August 1982 and October 1983. Mature individuals of both sexes (≥ 25 mm in shell length) were examined for their degree of reproductive development based on gonad histology. Female reproductive condition was also analyzed on the basis of oocyte size frequencies. Several lines of evidence indicated that spawning occurred throughout the year within this population. A synchronous bimodality in individual oocyte size frequencies persisted during the study period and a resting phase was not apparent in female gonads. Oocyte size-frequency distributions revealed that oocyte development was asynchronous within the population. Mature spermatozoa were present in males in all seasons except for the occasional partially spent individual. In addition, spawning of laboratory held specimens occurred in all seasons of the year. We conclude that *S. reidi* reproduces year round in Alberni Inlet, with a proportion of the population capable of spawning at any time of year.

INTRODUCTION

Solemya reidi Bernard, 1980, is a gutless protobranch bivalve found from southern California to the Alaskan panhandle, at depths ranging from 40 to 600 m (BERNARD, 1980), in marine habitats where oxygen and reduced sulfur compounds are simultaneously available, such as near sewage outfalls (FELBECK, 1983; FELBECK *et al.*, 1983) and beneath log-booming grounds in the Pacific Northwest (REID, 1980; REID & BERNARD, 1980). Chemoautotrophic bacterial symbionts, found in certain cells (bacteriocytes) of the large gills of all solemyids thus far examined, are proposed to provide nutrition to the clams via synthesis of reduced carbon and nitrogen compounds (FELBECK, 1983; FELBECK *et al.*, 1983).

As a consequence of its relatively easy accessibility and maintenance, *Solemya reidi* is increasingly being used as a representative species in studies of the association between chemoautotrophic endosymbionts and host animals from sulfide-rich habitats (FELBECK, 1983; FELBECK *et al.*, 1983;

HAND & SOMERO, 1983; FISHER & CHILDRESS, 1984; McMAHON & REID, 1984; POWELL & SOMERO, 1985, 1986). However, its reproduction has remained largely unexplored. The present study was designed to provide a description of the reproductive cycle in *S. reidi* in its natural habitat.

Numerous methods have been employed to measure the reproductive condition of bivalve gonads (see SASTRY, 1979 for a partial review). The vast majority of studies have relied on the subjective grading of histological sections of gonads to produce a "maturity index" (GRANT & TYLER, 1983a). A more objective utilization of female gonad sections in bivalves is to measure the oocytes and group them into size classes for analysis (SASTRY, 1979; GRANT & TYLER, 1983b). In this study, the reproductive cycle of *Solemya reidi* was investigated through analysis of gonad histology and oocyte size frequencies.

MATERIALS AND METHODS

Specimen Collection

Adult specimens of *Solemya reidi* were collected from August 1982 to October 1983 from a depth of 40 m with a Van Veen grab in the vicinity of log-booming grounds number 27 and 29 in Alberni Inlet on the west coast of Vancouver Island, B.C., Canada (49°12'N, 124°49'W). Specimens were processed for histology within 24 h of

¹ Harbor Branch Oceanographic Institution Contribution No. 532.

² Present address: Division of Applied Biology, Harbor Branch Oceanographic Institution, 5600 Old Dixie Highway, Fort Pierce, Florida 33450, U.S.A.

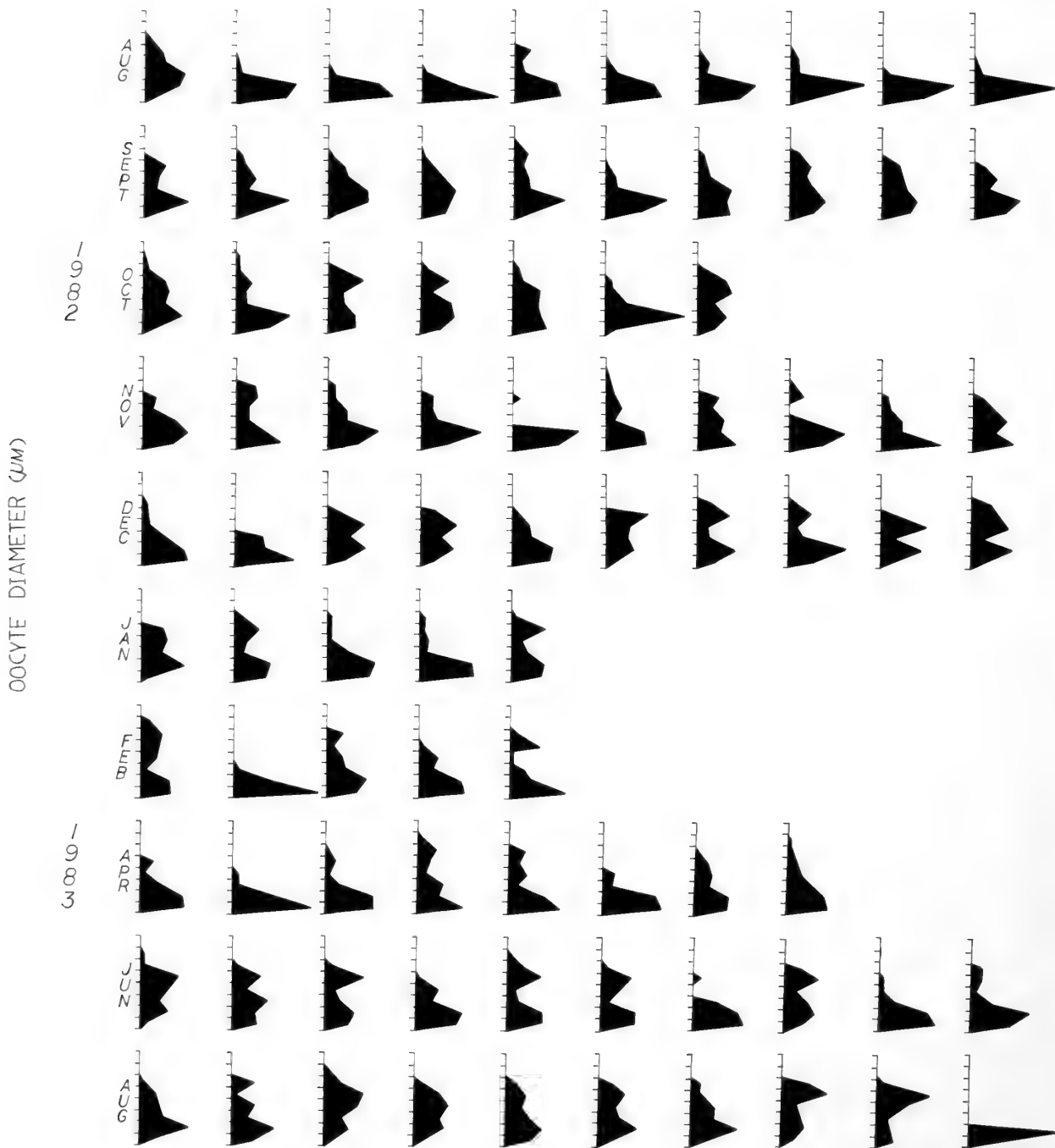


Figure 1

Solemya reidi. Monthly size-class distributions of oocytes in individuals from August 1982 to August 1983. Significant within monthly variation in distribution exists in all months (heterogeneity G-test, $P < 0.001$). Variation in distributions between months is also significant (heterogeneity G-test, $P < 0.001$). Oocyte diameter increments and percent distribution as in Figure 2.

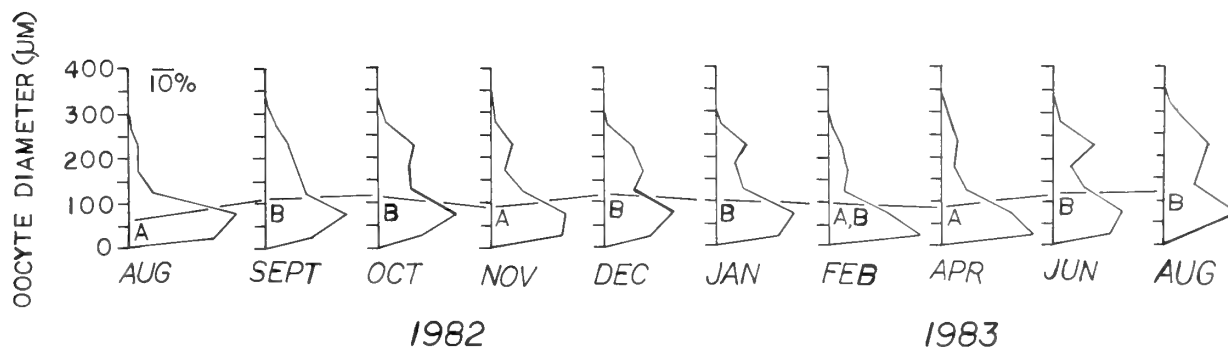


Figure 2

Solemya reidi. Size-class distributions of oocytes from August 1982 to August 1983, with individuals pooled within each month. Variations in distributions between months is significant (heterogeneity G-test, $P < 0.001$). Horizontal line connects mean monthly oocyte diameter values. Mean values labelled with different letters (a or b) are significantly different (Newman-Keuls multiple-range test, $P < 0.05$).

acquisition. All specimens of at least 25 mm in total shell length were sexually mature. Only individuals equal to or greater than this size were utilized.

Histological Procedures

Five to ten specimens of *Solemya reidi* of each sex from each collection were processed for histological analysis. Tissue pieces, containing gonad, were fixed in Bouin's fluid, dehydrated, embedded in paraffin wax (56–58°C), and sectioned at 7–10 μm . Slides were stained with standard eosin-hematoxylin (HUMASON, 1972). Oocyte size-frequency distributions were compiled for 5–10 females from each collection. The first 50 oocytes encountered that displayed nuclei were measured with the aid of an ocular micrometer. Mean oocyte diameters were calculated as the average of measurements along the longest and shortest axes of each oocyte. Statistical methods were used to test the significance of observed variations of oocyte size frequency between individuals within each sample, as well as between pooled monthly oocyte size frequencies (ZAR, 1974; SOKAL & ROHLF, 1981; GRANT & TYLER, 1983b).

RESULTS

Size-frequency distributions of oocyte diameters for individual female *Solemya reidi* are presented in Figure 1. The same data with individuals pooled within months are shown in Figure 2. Significant differences in size-class distributions of oocytes were observed between individuals in all months (heterogeneity G-test, $P < 0.001$) and among months ($P < 0.001$) (SOKAL & ROHLF, 1981). The presence of two separate, concurrent populations of oocytes in each individual is indicated by double peaks in many of the individual size-frequency distributions (Figure 1).

An analysis of variance showed no obvious trend in mean oocyte diameter over the period of collection (Figure 2). Mean oocyte diameters in August 1982, November

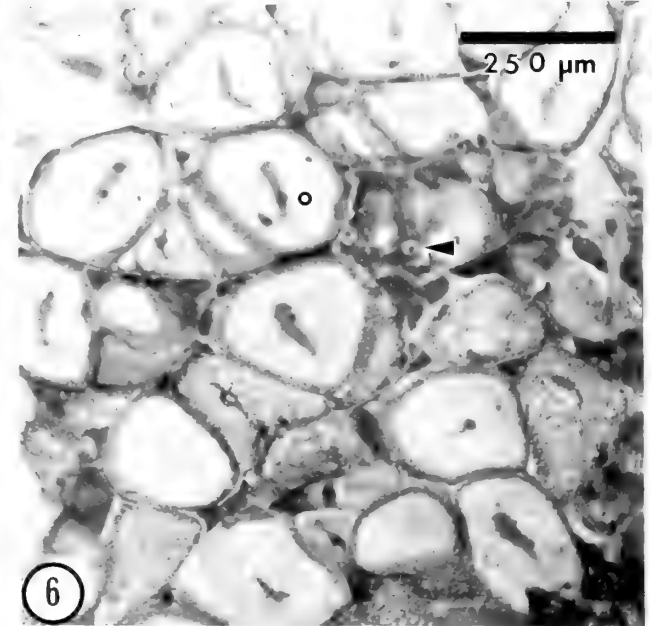
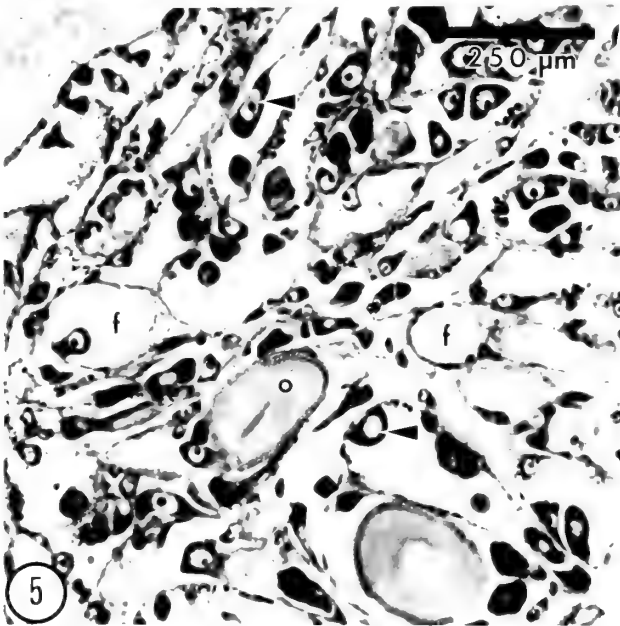
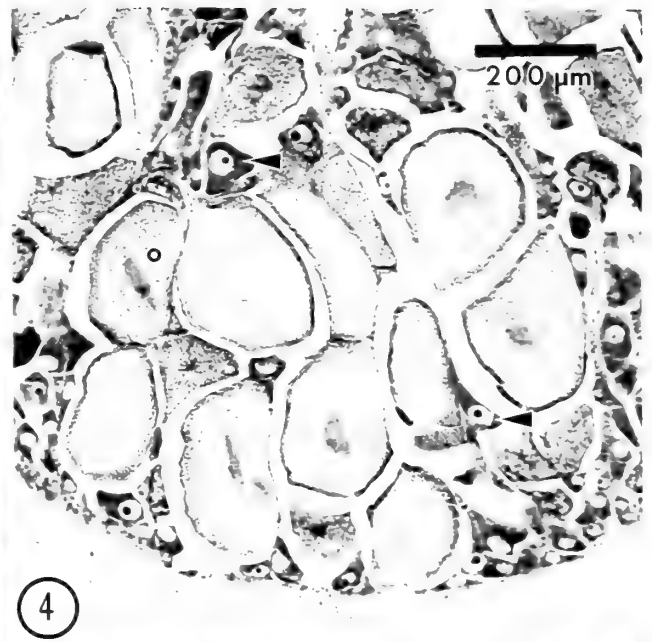
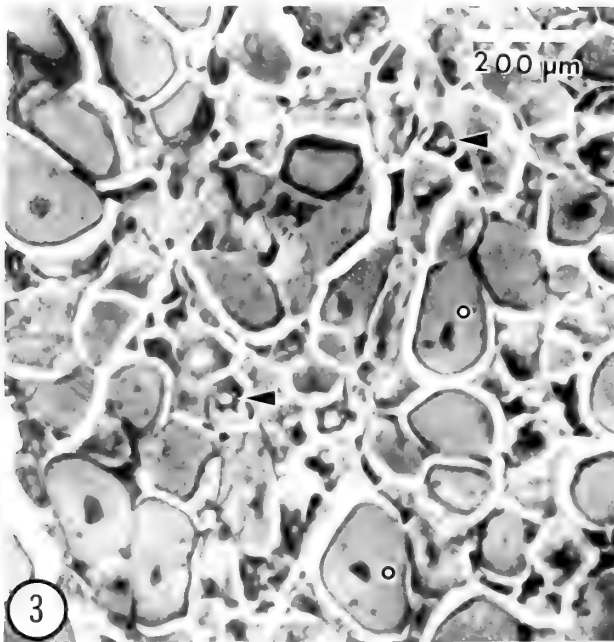
1982, and April 1983 were significantly different from those in September 1982, October 1982, December 1982, January 1983, June 1983, and August 1983 (Newman-Keuls multiple range test, $P < 0.05$).

The gonad of *Solemya reidi* is located deep within the base of the foot and extends alongside the posterior margin of the anterior adductor muscle. It was deemed inappropriate to construct stages of ovary development based on qualitative characters, as used previously in many studies of bivalve reproduction (SASTRY, 1979), owing to the wide range of oocyte diameters encountered in individuals, ranging from 24 to over 300 μm , and to the presence of two distinct populations of oocytes in each individual female (Figures 3–6). In rare cases, partially spent females were encountered (Figure 5). Even in these cases two populations of oocytes were apparent.

Histology of testes resembled that in other bivalves (SASTRY, 1979). No qualitative classification of the reproductive state of the testes was attempted, because the majority of the individuals were identical in histological appearance, with spermatogonia and mature spermatozoa present in almost all specimens (Figures 7, 8). In rare cases, testes were noted that were partially spent (Figures 9, 10). Ovaries were orange in color when ripe and full of eggs, but were black when less than ripe. Testes ranged from olive-green to white in color.

DISCUSSION

Several lines of evidence, including yearly data on the oocyte size frequencies, indicate that reproduction of *Solemya reidi* in Alberni Inlet, B.C., is continuous. Spawning of laboratory held *S. reidi* was observed in all seasons of the year (GUSTAFSON & REID, 1986). A "resting" or "inactive" phase of the gonads, common in many seasonally reproducing bivalves, was not observed. Mature spermatozoa were present in virtually all males throughout the



Explanation of Figures 3 to 6

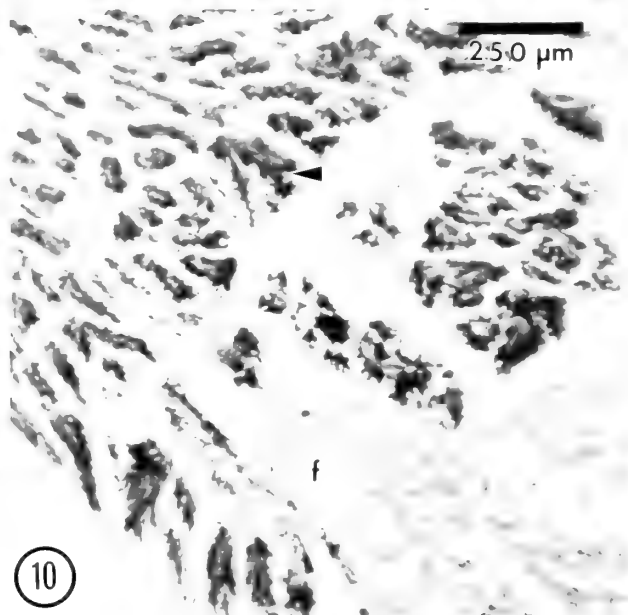
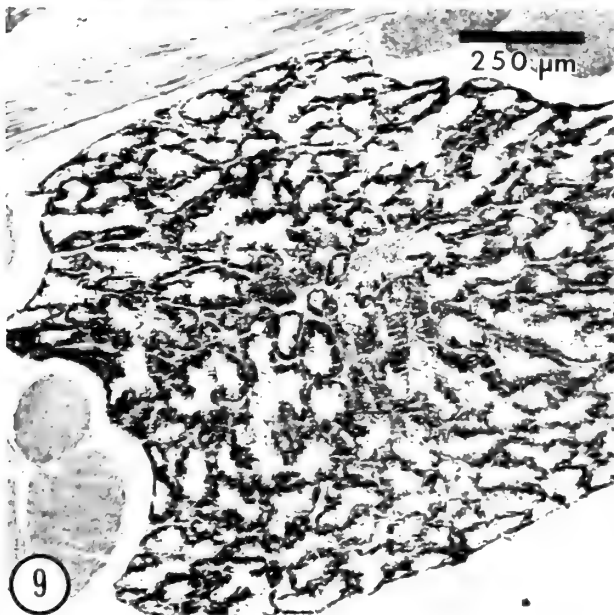
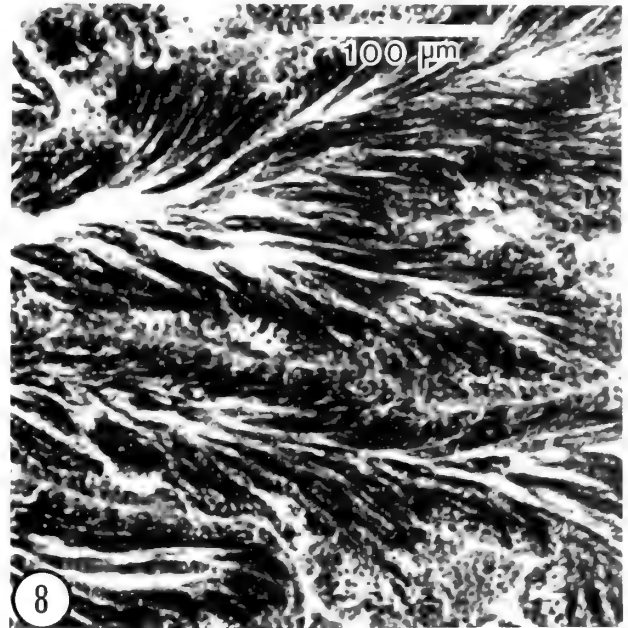
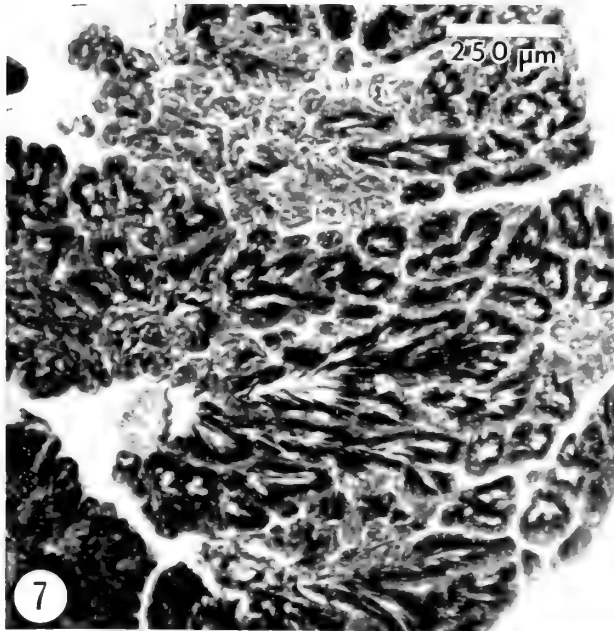
Figure 3. *Solemya reidi*. Photomicrograph of ovary showing development of two populations of oocytes; one large, over 150 μm in diameter (o) and one smaller, less than 50 μm (arrowheads).

Figure 4. *Solemya reidi*. Photomicrograph of ovary. Large ripe oocytes (o) fill the follicles, while small oocytes belonging to a second, developing population of oocytes, line the follicle walls (arrowheads).

Figure 5. *Solemya reidi*. Photomicrograph of partially spent ovary.

The large empty spaces in the follicles (f) indicate that spawning has recently occurred. A few remaining ripe oocytes (o) are spread throughout the ovary, while a second population of developing oocytes (arrowheads) line the follicle walls.

Figure 6. *Solemya reidi*. Photomicrograph of ripest ovary encountered. Large, ripe oocytes (o) are numerous; arrowhead points to developing oocytes of the next oocyte generation.



Explanation of Figures 7 to 10

Figure 7. *Solemya reidi*. Photomicrograph of testes showing follicles filled with mature spermatozoa.

Figure 8. *Solemya reidi*. Photomicrograph of ripe testes showing detail of follicles full of mature, tailed spermatozoa.

Figure 9. *Solemya reidi*. Photomicrograph of partially spent testes. Centers of follicles are depleted of spermatozoa.

Figure 10. *Solemya reidi*. Photomicrograph of partially spent testes showing some follicles (f) full of mature spermatozoa (arrowheads) and others totally depleted of germ cells.

year, except in those rare cases where partially spent individuals were noted.

Ovary histology (Figures 3–6) and oocyte size-frequency distributions (Figure 11) indicate that two readily distinguishable oocyte populations are present in each fe-

male, with the smaller oocytes being located along the follicle walls. Development of each population of oocytes within individuals is therefore synchronous, with spawning of the larger population of oocytes being more or less complete in each individual. Oogenesis is, however, asyn-

chronous within the population as illustrated by bimodal peaks of oocyte size-frequency distributions in each month (Figure 1) and the lack of a significant seasonal pattern in mean oocyte diameters or in pooled monthly oocyte size-frequency distributions (Figure 2). The concurrent development of two populations of oocytes in individual *Solemya reidi* indicates an ability to begin production of a future batch of oocytes before the current population is fully ripe.

Reproductive cycles may occur in populations of bivalves on an annual, semiannual, or continual basis. Continuous reproduction in a bivalve population can follow one of two patterns. A portion of the population can either be in a ripe reproductive state throughout the year, as in *Nucula cancellata* Jeffreys, 1881 (SCHELTEMA, 1972) and *Solemya reidi* (this study), or each individual can display all stages of gametogenesis simultaneously, as in *Nuculana pontonia* (Dall), *Nucula darella* Dall, and *Bathycarca* sp. (ROKOP, 1979). In the first case, each individual is capable of spawning out completely, whereas in the latter case individual gametogenesis is non-cyclic and year-round reproduction occurs both at the population and the individual levels.

In the tropics, where the temperature remains above the critical levels for spawning and food supplies are non-cyclic, many bivalves reproduce continuously (SASTRY, 1979; BRALEY, 1982; WALTER, 1982; LOPEZ & GOMEZ, 1982a, b). Likewise, in the deep sea where similar conditions prevail, many bivalves, particularly deposit-feeding protobranchs, spawn continuously (SCHELTEMA, 1972; ROKOP, 1974, 1979). Some degree of continuous breeding has also been reported for the temperate-zone and continental-shelf bivalves *Thyasira gouldi* (Philippi) (BLACKNELL & ANSELL, 1975), *Modiolus modiolus* (Linnaeus) (BROWN, 1984), *Abra nitida* (Müller) (BROWN, 1982) and *Lucinoma borealis* (Linnaeus) (TUNBERG, 1984).

Although *Solemya reidi* breeds continuously, some deep-sea (LIGHTFOOT *et al.*, 1979) and most continental-shelf protobranchs (LEBOUR, 1938; OCKELMANN, 1958; ANSELL, 1974; ANSELL & PARULEKAR, 1978; DAVIS & WILSON, 1983) breed on an annual basis. On the other hand, *Nucula nitidosa* Winckworth (= *N. nitida* Sowerby) from the German Bight are reproductively active from September to April and, in addition, young *N. nitidosa* can be found in all seasons (RACHOR, 1976).

In contrast to *Solemya reidi*, the shallow-water species *S. velum* Say reportedly spawns seasonally in late spring to mid-summer on the northeast coast of the U.S.A. (J. Pechenik, personal communication), whereas larvae of this species were found to settle only in winter and early spring in Bogue Sound, North Carolina, U.S.A. (WATZIN, 1986).

In the past, there has been considerable confusion as to the location of the gonad in *Solemya* spp. PELSENEER (1891) and STEPELL (1899) stated that the gonad of *S. togata* Poli occupies the interior of the basal part of the foot, whereas YONGE (1939:95) figures the gonad as dorsal to

the gills and hypobranchial gland in the same species. Furthermore, MORSE (1913:269) incorrectly identifies the gonad as "hepatic follicles" in *S. velum*. Descriptions of the habits and nutritive capabilities of *S. parkinsoni* Smith (OWEN, 1961) and *S. reidi* (REID, 1980) agree that the gonad occupies a large part of the interior of the foot and in the latter species extends into the tissue bordering the anterior adductor.

Much of the confusion over the location of the gonad in *Solemya* spp. is likely due to the unusual coloration and consistency of the ovary when in an unripe condition. The developing ovary of *S. reidi* is often black with few or no visible oocytes, whereas the ripe ovary is orange. REID (1980) commented on the dark color of the "gonad" in *S. reidi*, which "had a resemblance to digestive diverticula" of other bivalves. The present study has determined that the gonad of *S. reidi* occupies the interior of the basal part of the foot and extends into the mantle tissue bordering the posterior aspect of the anterior adductor muscle.

In conclusion, no reliable evidence was found of synchronization of breeding activity between individuals in a population of *Solemya reidi* from Alberni Inlet, B.C., Canada. Consequently, spawning in this population most likely occurs on a continuous basis throughout the year.

ACKNOWLEDGMENTS

We thank boat captains Donal Horn, Chuck Dillen, and Sigurd Tuet for their able assistance in collecting *Solemya reidi*; Dawna Brand for assistance and perseverance in the field on many foul weather days; Dr. Robert D. Burke of the University of Victoria Biology Department for allowing use of his holding facilities; and Diarmaid O'Foighil and Dawna Brand for critically reading the manuscript. This research was supported by a University of Victoria Graduate Fellowship to the first author and an operating grant of the National Research Council of Canada to the third author.

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The Ecology of *Cyclocardia ventricosa* (Gould, 1850) (Bivalvia: Carditidae) on the Southern California Borderland

by

GILBERT F. JONES AND BRUCE E. THOMPSON¹

Department of Biological Sciences, University of Southern California,
Los Angeles, California 90089, U.S.A.

Abstract. The pelecypod *Cyclocardia ventricosa* (Gould, 1850) is a widely distributed member of the benthos of the southern California borderland. It is particularly prominent in three borderland habitats: the northern portion of the mainland shelf (Point Conception to Pitas Point); the slope adjacent to the central portion of the mainland shelf (Mugu Submarine Canyon to Dana Point), and the shelf of San Miguel and Santa Rosa islands. Its depth range on the borderland was 14 to 574 m, but 75% of the locations where it was collected were in depths of 200 m or less. Within the *Amphiodia-Cyclocardia* community on the northern portion of the mainland shelf, the dispersion of *C. ventricosa* was aggregated; elsewhere, where densities were lower, randomness characterized its distribution. Aggregated dispersion may be a function of the mode of reproduction of this species, which broods its young rather than having planktonic larvae. *Cyclocardia ventricosa* is associated with a diverse array of macrofaunal taxa which differ markedly from one habitat to another.

INTRODUCTION

THE PELECYPOD *Cyclocardia ventricosa* (Gould, 1850) is a prominent faunal element of the benthos of the southern California borderland. It has been collected in most of the major quantitative studies of the benthic macrofauna of this area (AHF:USC, 1965; HARTMAN, 1955, 1956, 1963, 1966; FAUCHALD, 1971; FAUCHALD & JONES, 1979a, b, 1983). The purpose of this paper is to review these findings and to document the distribution, abundance, spatial and temporal variation, feeding, reproduction and size distribution, and faunal associates of *C. ventricosa* in the region.

The present paper is based on data gathered during three major studies of the benthos of southern California. The Allan Hancock Foundation Survey of the Southern California Mainland Shelf (the State Project) was conducted between 1956 and 1961 (AHF:USC, 1965). This comprehensive survey was supported by the California State Water Pollution Control Board (now termed the

State Water Quality Control Board) and the late Captain G. Allan Hancock. The two other major studies of the benthos of southern California were funded by the Bureau of Land Management: the Baseline Study (1975-1976) and the Benchmark Study (1976-1977). These two studies together are the largest investigations ever made in this marine region (FAUCHALD & JONES, 1979a, b, 1983).

MATERIALS AND METHODS

During the State Project, deep-water samples were collected aboard the research vessel *Velero IV* by a modified Hayward standard orange-peel bucket (OPB) with an areal coverage of about 0.25 m². The nearshore portion of the shelf was sampled from the motor launch of the R/V *Velero IV* using a 1/10-m² Van Veen grab. The animals collected were limited by the size of the mesh, 1-mm, through which the sediment was screened aboard ship before preservation and sorting (AHF:USC, 1965; JONES, 1967, 1969).

Quantitative determinations were based on 335 OPB samples completely analyzed for all molluscan specimens larger than 1 mm from depths of 14 to 480 m (mean = 93.0 m). Van Veen grab samples were collected at 121

¹ Current address: Southern California Coastal Water Research Project, 646 W. Pacific Coast Highway, Long Beach, California 90806, U.S.A.

nearshore locations, in depths of 2.4 to 10.1 m (mean = 6.7 m).

In both the Baseline and Benchmark studies, samples were collected with a modified, $\frac{1}{16}$ -m², USNEL-Reineck spade (or box) corer (HESSLER & JUMARS, 1974) aboard the R/V *Veleiro II* and the R/V *Thomas G. Thompson*. A subsample of each core was removed for sedimentary analysis. Benthic samples were screened through 1.0-mm and 0.5-mm stainless-steel screens using the "overflow-barrel method" (FAUCHALD & JONES, 1983). The benthic macrofaunal invertebrates were narcotized for 20 min in 6% magnesium chloride in seawater prior to killing and fixation; specimens were killed and fixed in 10% buffered seawater-formalin; after 36 h, samples were transferred to 70% ethanol for preservation.

A rapid identification procedure was used to analyze the benthic samples (FAUCHALD & JONES, 1983). Some taxa were identified to the specific level, whereas others were identified only to the familial or generic level under the limitations of this method. All taxa were identified to species (where possible) for 165 of the 712 samples collected during the Baseline Study and for all of the 318 samples collected during the Benchmark Study.

The diet and mineral particle-size range used by *Cyclocardia ventricosa* were analyzed (THOMPSON, 1982). The gut contents of six specimens were examined microscopically (10–1000 \times) and the material categorized into five food groups: (1) detrital aggregates, (2) single mineral particles, (3) particulate organic material, (4) animal remains, and (5) Foraminifera. The proportion of each of the food groups in total sample volume was estimated visually to the nearest 10%. The sizes of mineral particles ingested were measured to the nearest 10 μ m.

The spatial dispersion of *Cyclocardia ventricosa* was determined using an Index of Dispersion (FISHER, 1970; JUMARS, 1975).

The macrofaunal associates of *Cyclocardia ventricosa* on the slope adjacent to the central portion of the mainland shelf and the insular shelf were determined by classification analysis of the Baseline Study data. For this inverse classification, in which species were grouped according to their distribution among stations, the Bray-Curtis Index (BRAY & CURTIS, 1957) was used as the measure of ecological distance (SMITH, 1976). For the taxa associated with *C. ventricosa* in the *Amphiodia-Cyclocardia* community those listed in this paper are from table 9 of BARNARD & ZIESENHENNE (1961).

Sedimentary analyses were made by geologists at California State University, Northridge (Baseline Study) and University of California, Los Angeles (Benchmark Study).

The benthic macrofauna was sampled at over 700 locations during the Baseline Study; 546 of these sampling locations were grouped in 11 regular grids termed High Density Sampling Areas (HDSAs) and varying in size from 16 to over 100 sampling stations. Within these grids stations were arranged on 1.7-km (1-nautical mile) centers. Four of these HDSAs were on the mainland shelf

and its slopes, one on the Santa Catalina Ridge, two on the insular shelf of the Channel Islands, and four on the Santa Rosa-Cortes Ridge.

During the Benchmark Study, replicate sampling was conducted at 21 sampling stations in six areas of the borderland: off Coal Oil Point and the slope of the Santa Barbara Basin (3 stations); off San Pedro, on the slope of the San Pedro Basin and within the basin (6 stations); south of San Miguel Island (2 stations); south of Santa Rosa Island (1 station); on the northern portion of the Santa Rosa-Cortes Ridge south of Santa Rosa Island, the slope of Santa Cruz Basin, and within the basin (3 stations); and on the southern portion of the Santa Rosa-Cortes Ridge, including Tanner Bank, the slope of San Nicolas Basin, and within the basin (6 stations). Sampling was conducted twice during the year, once in the period of low water temperature (early spring) and once in the period of high water temperature (early fall). Eight replicate samples were collected at each station during each sampling period.

RESULTS AND REVIEW

Geographic Distribution

The type locality of *Cyclocardia ventricosa* is Puget Sound, Washington (COAN, 1977). COAN (1977) indicated that the range of this species is from Kasitsna Bay, Cook Inlet, Alaska, south to Punta Rompiente, Baja California Sur.

Cyclocardia ventricosa is distributed throughout the borderland where it is a faunal element of several major habitats (Figure 1). With the ophiuroid *Amphiodia urtica*, *C. ventricosa* co-dominates a major faunal assemblage on the northern portion of the mainland shelf; this community inhabits about 11% of the area of the mainland shelf. To the south *Cyclocardia ventricosa* becomes increasingly more important as a member of the slope assemblages and less important as a member of the biota of the mainland shelf (BANDY, 1958; FAUCHALD & JONES, 1983). It is a frequent and abundant member of the benthos on the insular shelf of the outer Channel Islands: the shelf of San Miguel and Santa Rosa islands. Although it occurs on the ridge north of Santa Catalina Island, the Santa Rosa-Cortes Ridge, and Tanner Bank, it is neither frequent nor abundant on the ridges and banks. It was reported from one deep basin, the San Pedro Basin, but this single specimen probably does not represent a resident population (FAUCHALD & JONES, 1979b).

Cyclocardia ventricosa was collected at 75 (16%) of the 456 locations sampled during the State Project. Population densities ranged from 4 to 388 per m² (mean = 72 m⁻²). During the Baseline Study it was collected at 85 (11.9%) of 712 stations. Densities were highest on the northern portion of the mainland shelf—mean, 179.4 m⁻² (range, 40–329 m⁻²)—but were similar on the slope adjacent to the central portion of the mainland shelf—41.6

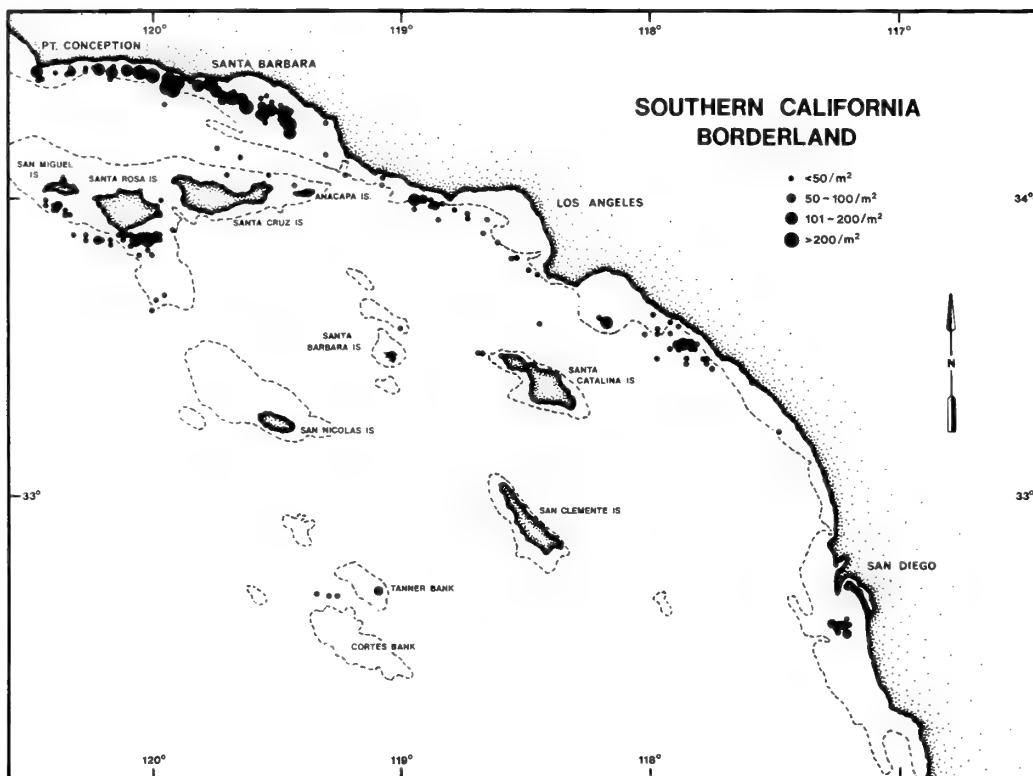


Figure 1

Chart of southern California borderland showing locations where *Cyclocardia ventricosa* was collected. Circle size reflects population density (see legend).

m^2 (range, 16–128/ m^2)—and the insular shelf—40.7/ m^2 (range, 16–272/ m^2) (Table 1).

The northern portion of the mainland shelf is an equilibrium environment² only slightly altered by human activities. Except for areas of rock and relic sediments, sediments in this area are finer, lower in calcium carbonate, and higher in total organic content than on the insular shelf. Neither strong currents nor major upwelling are important factors in the area except near Point Conception. Slopes are characterized by sediment instability. Sediment is frequently transported downslope by turbidity currents or mass sediment flows creating unstable conditions. The insular shelf of the outer Channel Islands is primarily a nondepositional environment. Relatively strong currents result in winnowing of finer detrital sediments and the development of ripple marks. Sediments are frequently coarse and relatively high in calcium carbonate content. The area may be influenced by the persistent upwelling centers of the Point Conception area (EMERY, 1960; FISCHER *et al.*, 1983; R. C. DUGDALE, personal communication).

Distribution by Depth

Cyclocardia ventricosa inhabits primarily the shallower parts of the continental borderland in depths ranging from 14 to 574 m (Figure 2). Seventy-five percent of the stations where *C. ventricosa* was collected were in water depths of 200 m or less, with highest densities in depths less than 100 m (mean depth, 93 m). Mean depths varied by area: northern portion of the mainland shelf, 78 m; the insular shelf, 147 m; and the slope, 410 m (Table 1).

Distribution in Relation to Sediments

Sediments where this species was most frequent and abundant were coarsest on the insular shelf (average mean ϕ = 3.4; range, 1.4–4.4), were intermediate on the northern portion of the mainland shelf (average mean ϕ = 4.1; range, 3.3–5.4), and were finest on the slope adjacent to the central portion of the mainland shelf (average mean ϕ = 5.0; range, 3.6–7.2) (Table 1). An important difference between the insular shelf environment and the mainland shelf and its slopes is that the calcium carbonate content of the island shelves is much higher (23% compared to 2.8 and 2.9%).

² An equilibrium environment is one in which deposition and erosion are balanced.

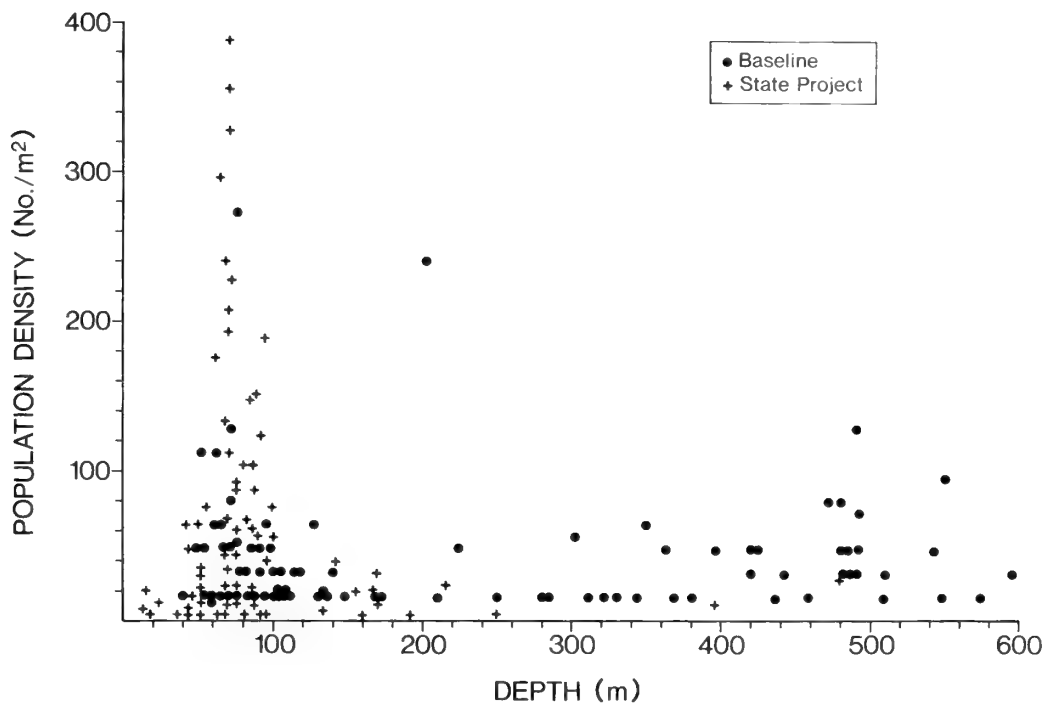


Figure 2

Depth distribution of *Cyclocardia ventricosa* on the continental borderland of southern California. The symbol (+) indicates the distribution of the samples collected during the State Project and the symbol (●) indicates the samples collected during the Baseline Study.

Temporal and Spatial Variation

Limited information is available on the temporal variation of *Cyclocardia ventricosa* populations. Only a single-year sequence was analyzed in each study (the State Project, JONES, 1964; AHF:USC, 1965; and the Benchmark Study, FAUCHALD & JONES, 1979b).

During the State Project 36 seasonal samples were collected at a nine-station grid within the *Amphiodia-Cyclocardia* community. The grid was located about six miles (9.7 km) offshore at a depth of 270 feet (93.9 m). Each grid consisted of three lines of three stations approximately 300 m apart. Sampling was conducted in September 1958, December 1958, March 1959, and June 1959.

A total of 1286 specimens of *Cyclocardia ventricosa* was collected in these samples, representing a mean population density of 144/m² (range, 0–268/m²). Densities for each seasonal sample-set were fairly consistent: 124 to 156/m². However, within sample-set variation was substantial, as indicated by the ranges, standard deviations, and coefficients of variation (Table 2).

Cyclocardia ventricosa accounted for half of the total standing crop of the community (based on the grid sample annual means, 52.4 of 103.2 g/m²). The mean standing crop values were nearly the same for each of the four seasonal sample-sets, 50.8 to 61.6 g/m² or 45 to 64% of the total standing crop.

The other community dominant, the smooth, red ophiuroid *Amphiodia urtica*, had a mean density of 144/m² (range, 12–232). The mean density in December (172/m²) was the highest and the density in June (96/m²) was the lowest. Ophiuroid standing crop (principally *A. urtica*) ranged from 0.8 to 16.8 g/m² with an annual mean of 7.2 g/m².

During the Benchmark Study, replicate samples were collected seasonally (winter and summer) at selected sampling locations (Table 3). Stations where *Cyclocardia ventricosa* was collected were located off Coal Oil Point (the northern portion of the mainland shelf), off San Pedro (the central portion of the mainland shelf), and south of San Miguel Island (the insular shelf). Generally, population densities were higher in the winter than in the summer. At two locations, one on the slope off San Pedro (Benchmark Station 827) and the other on the slope off Coal Oil Point (Benchmark Station 803), *C. ventricosa* was absent in the summer samples.

Within the *Amphiodia-Cyclocardia* community *C. ventricosa* had an aggregated dispersion pattern (Table 2). In other areas—the margin of the community (Benchmark Station 801), the insular shelf (Benchmark Station 806) and the slope adjacent to the mainland shelf (Benchmark Stations 803, 825, and 827)—eight of ten sample-sets exhibited insignificant departure from random dispersion (Table 3). The two exceptions were the summer sample-

Table 1

A comparison of the habitat, depth, and sediment characteristics of *Cyclocardia ventricosa* on the northern portion of the mainland shelf, the slope adjacent to the central portion of the mainland shelf, and the insular shelf of the Channel Islands. Mean, range, and number of stations sampled are given for each variable.

Environmental variable	Insular shelf	Northern mainland shelf*	Slope†
Number/m ²	40.7 16-272 (35 stations)	179.4 40-329 (13 stations)	41.6 16-128 (25 stations)
Depth (m)	147.0 48-472 (35 stations)	77.6 64-94 (13 stations)	410.2 127-594 (25 stations)
Mean <i>phi</i>	3.4 1.4-4.4 (28 stations)	4.1 3.3-5.4 (13 stations)	5.0 3.6-7.2 (18 stations)
Percent gravel	1.2 0.0-28.0 (28 stations)	0 0-0 (13 stations)	0 0-0 (18 stations)
Percent sand	83.0 54.0-94.0 (28 stations)	39.5 1.0-71.6 (13 stations)	18.8 1.0-73.0 (18 stations)
Percent silt	15.3 4.0-36.0 (28 stations)	49.7 19.2-91.1 (13 stations)	57.6 19.0-78.0 (18 stations)
Percent clay	4.0 2.0-11.0 (28 stations)	10.0 6.5-20.1 (13 stations)	18.2 5.0-33.0 (18 stations)
Percent CaCO ₃	23.0 10.4-49.4 (28 stations)	2.8 1.1-8.2 (13 stations)	2.9 1.3-8.5 (12 stations)

* Thirteen representative samples collected from the *Amphiodia-Cyclocardia* community; State Project Data (BARNARD & ZIESENHENNE, 1961; AHF:USC, 1961).

† Slope = the slope adjacent to the central portion of the mainland shelf.

set at Station 806 and the winter sample-set at Station 803.

Mode of Life and Diet

Our observations of *Cyclocardia ventricosa* are consistent with those of YONGE (1969). In the laboratory *C. ventricosa* remains at the sediment-water interface only partially buried in the sediments, anterior end downward and valves partially separated. We suggest that this species obtains its food either from the sediment surface or the water column.

THOMPSON (1982) has described the diet of *Cyclocardia ventricosa*. The largest proportion of the gut contents of six specimens was detritus (detrital aggregates = 71%); the remainder of the contents included single mineral par-

ticles (19%) and foraminiferans (8%); 2% was not identified (Figure 3).

Reproduction and Population Structure

Unlike many pelecypods *Cyclocardia ventricosa* lacks a pelagic larval stage and instead broods its young from eggs to juveniles (JONES, 1963). The brood chambers of *C. ventricosa* are located in the ctenidia. The young are brooded in the interlamellar space in both the inner and outer demibranchs but are usually confined to only the inner demibranchs (Figure 4a). The mode of transport of the eggs from the gonads to the ctenidia is unknown.

The number, location, and stage of development of the brooded young may vary within the same female. The most frequently observed situation in *Cyclocardia ventricosa* is to contain a similar number of young at a similar developmental stage in both the right and left inner demibranchs and to be without young in the outer demibranchs. The mean number of young was 37.3 (range, 14-93). One case was observed where young were present on only one side, the left, of an individual. When young are contained in the outer demibranchs their numbers are fewer than in the inner demibranchs. The maximum number of brooded young in an outer demibranch was 12, while the inner demibranchs of the same specimen contained about 50 young each. No females were observed in which young were present in the outer demibranchs without also being present in the inner demibranchs.

Although different developmental stages may occur in the inner and outer demibranchs of the same individual, young within a single demibranch were always at the same stage of development. Differences between the right and left ctenidia were not observed. Females of *Cyclocardia ventricosa* from the same sample may contain young at very different stages of the developmental cycle.

Figure 4b is an illustration of the young of *Cyclocardia ventricosa* showing D-shaped differentiation of prodissoconch I and II and the initiation of the dissoconch with radial sculpture, and is typical of the most mature stage of brooded young.

Maternal care may be extended beyond brood protection. In a number of samples very young "free-living" specimens were observed to be attached to adults by byssal threads.

Reproducing females of *Cyclocardia ventricosa* were collected in all months of the year except June. Inasmuch as females may brood young of more than one developmental stage, and females from the same sample may have young of very different stages of development, it may be assumed that *C. ventricosa* reproduces continuously in southern California. The minimum size of females with brooded young is 10 mm. If males are sexually mature at this size, then the reproducing population would be nearly half (47%) of the population (JONES, 1964).

A size-frequency distribution was constructed for *Cyclocardia ventricosa* based on the 1286 specimens collected

Table 2

Amphiodia-Cyclocardia intracommunity variation in standing crop (wet weight, g/m²) and population density (number, m⁻²) based on 36 samples from a nine-station grid: \bar{X} = mean; SD = standard deviation; C.V. = coefficient of variation; and I.D. = Index of Dispersion. * = significant values ($\chi^2 \geq 20.1$), $\alpha = 0.01$.

		September	December	March	June	All seasons
<i>Cyclocardia ventricosa</i> Standing crop (g/m ²)	\bar{X}	57.2	50.8	61.6	51.2	52.4
	SD	34.0	31.2	22.4	20.8	30.0
	C.V.	61	52	43	40	58
	I.D.	71.2*	96.0*	40.6*	94.8*	—
Ophiuroid standing crop (g/m ²)	\bar{X}	6.0	11.6	6.4	5.2	7.2
	SD	2.4	2.8	3.2	2.4	3.6
	C.V.	27	24	42	63	44
<i>Cyclocardia ventricosa</i> (number/m ²)	\bar{X}	148	140	156	124	144
	SD	76	72	56	76	68
	C.V.	52	54	37	63	50
<i>Amphiodia urtica</i> (number/m ²)	\bar{X}	144	172	160	96	144
	SD	36	32	56	48	52
	C.V.	29	19	37	51	38
	I.D.	21.8*	39.5*	10.9	18.6	—

in 36 samples from the nine-station grid on the Santa Barbara shelf (JONES, 1964). The result was an inverted pyramid with the <4-mm size class having the least number of individuals and the 10–12-mm size class having the most (Figure 5). This population structure may be the result of the brood protection method of reproduction in this species with significantly fewer young being produced than in species with pelagic larvae.

Macrofaunal Associates

Determination of the organisms associated with *Cyclocardia ventricosa* has been made for three dissimilar borderland habitats where it is frequent and abundant: the *Amphiodia-Cyclocardia* community on the northern portion of the mainland shelf, the slope adjacent to the central portion of the mainland shelf, and the southern insular shelf of San Miguel and Santa Rosa islands. *Cyclocardia ventricosa* lives with a large number of taxa that differ from habitat to habitat (Table 4).

Only one other species, the pelecypod *Acila castrensis*, was an inhabitant of all three environments. Three species were common to both the *Amphiodia-Cyclocardia* community and the slope: the polychaetes *Pectinaria californiensis* and *Paraprionospio pinnata* and the pelecypod *Adontorhina cyclicia*. Only one species, the pelecypod *Psephidia* sp., was common to both the *Amphiodia-Cyclocardia* community and the island shelf. Except for *Acila castrensis* no species was common to both the insular shelf and the slope.

SUMMARY

The pelecypod *Cyclocardia ventricosa* is distributed along much of the length of the coast of western North America,

from Alaska to Baja California. In southern California it is a widely distributed member of the benthos. It is particularly prominent in three dissimilar habitats: the northern portion of the mainland shelf, the slope adjacent to the central portion of the mainland shelf, and the insular shelf of the outer Channel Islands. Densities are highest by far (mean = 179.4/m²) on the northern portion of the mainland shelf where *Cyclocardia* co-dominates an outer-shelf assemblage with the ophiuroid *Amphiodia urtica*. In the other two environments the mean densities of this species average only about 25% of the north shelf value. The environmental conditions of these three environments differ substantially. The northern shelf is an equilibrium

Table 3

Average densities (\bar{X} /m²) and Indices of Dispersion (I.D.) and seasonal comparisons of *Cyclocardia ventricosa* at Benchmark Study sampling sites for the winter and summer of 1977. * = significant values (3 d.f.), $\alpha = 0.05$, indicates clumped distribution.

Location and station (depth)	Winter 1977		Summer 1977	
	\bar{X} /m ²	I.D.	\bar{X} /m ²	I.D.
Mainland shelf and slope; Coal Oil Point				
801 (68 m)	64	5.5	24	7.3
803 (503 m)	144	9.2*	0	—
Mainland shelf and slope; San Pedro Bay and slope				
825 (256 m)	20	5.4	20	0.6
827 (504 m)	8	2.0	0	—
Insular shelves				
806 (99 m)	64	5.0	72	8.2*

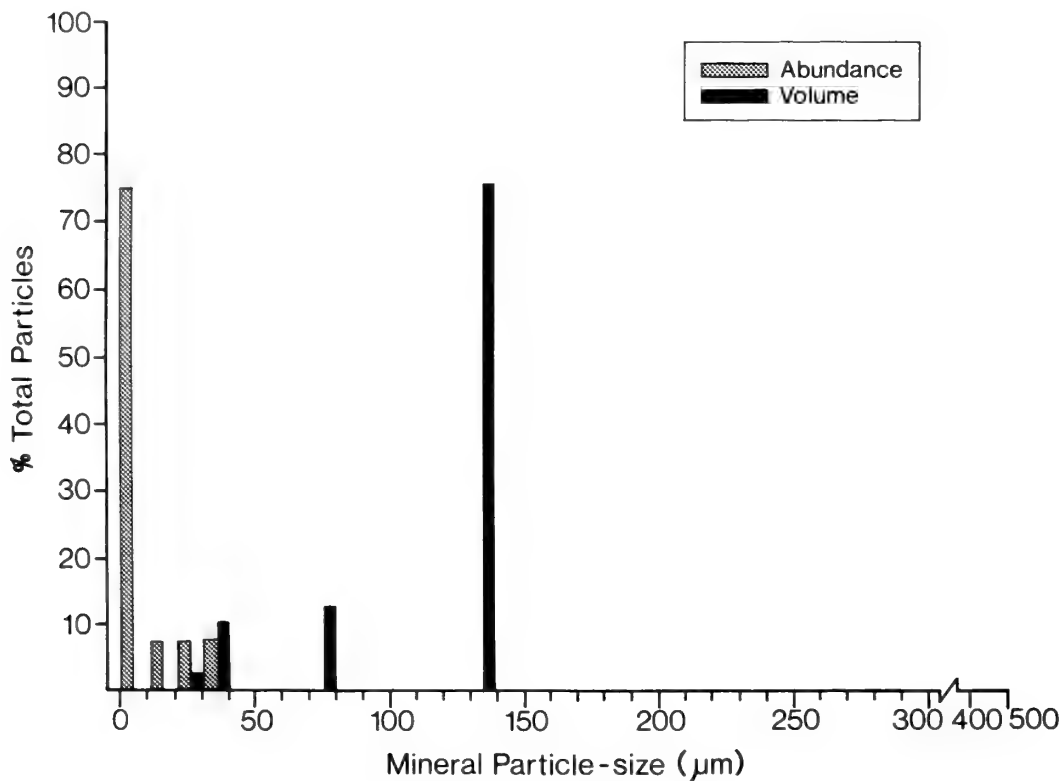


Figure 3

Average mineral particle-size distribution from guts of *Cyclocardia ventricosa*.

environment where deposition and removal of sediments are balanced. Sediments here are finer, lower in calcium carbonate and higher in total organic content than on the insular shelf. Unstable sediment conditions characterize the slope. In this environment, frequent transport down-slope is caused by turbidity currents and mass sediment flows. Nondepositional environments characterize the insular shelf. Here relatively strong currents exclude the deposition of fine detrital sediments and lead to the development of ripple marks and the development of sediments with relatively high biogenic calcium carbonate. This area may be influenced by persistent upwelling.

The depth distribution of *Cyclocardia ventricosa* on the borderland was 14 to 574 m, but 75% of the locations where it was collected were in depths of 200 m or less.

Data are inadequate to make firm conclusions about the temporal variation of the population densities. Two estimates are available: one from the State Project and one from the Benchmark Study. Each represents observations from only a single year. The nine-station grid in the *Amphiodia-Cyclocardia* community on the northern portion of the mainland shelf sampled quarterly during the State Project revealed little seasonal variation; mean densities ranged from 124 to 156/m². During the Benchmark Study, densities were higher in the winter than in the summer

at three locations, and at two sites on the slope *C. ventricosa* was absent in the summer.

A marked difference was evident in the spatial distribution of *Cyclocardia ventricosa*. Within the *Amphiodia-Cyclocardia* community its dispersion was aggregated. However, in the more marginal situations on the borderland, outside this community (the slopes adjacent to the mainland shelf and the insular shelf) where densities are lower, randomness characterized its distribution. Aggregation may be a function of the mode of reproduction of this species; brood protection and attachment of released young by byssal threads to the female parent might contribute to this mode of distribution. The areas where *C. ventricosa* distributions are random may be due to reduced reproductive activity.

Evidence suggests that *Cyclocardia ventricosa* lives at or near the sediment-water interface and feeds either in the water column or at the sediment surface or both. It may be classified as a filter feeder or surface deposit feeder but may functionally fill both roles.

Cyclocardia ventricosa is associated with a diverse array of macrofaunal associates in the three borderland habitats that were examined in detail. Prominent taxa associated with *C. ventricosa* varied considerably from location to location. Only one species, the pelecypod *Acila castrensis*,

Table 4

The macrofaunal associates of *Cyclocardia ventricosa* in three areas of the continental borderland: the northern portion of the mainland shelf, the slope adjacent to the central portion of the mainland shelf, and the insular shelf of the Channel Islands. Data for the northern portion of the mainland shelf from BARNARD & ZIESENHENNE, 1961, table 9.

Taxa	Amphi- odia- Cyclo- cardia com- munity	Slope*	Insu- lar shelf
Polychaetes			
<i>Aricidea</i> sp.	X		
<i>Chloeia pinnata</i>	X		
<i>Glycera capitata</i>	X		
<i>Onuphis</i> sp.	X		
<i>Pectinaria californiensis</i>	X	X	
<i>Pista</i> sp.	X		
<i>Prionospio steenstrupi</i>	X		
<i>Paraprionospio pinnata</i>	X	X	
<i>Sternaspis fossor</i>	X		
<i>Terebellides stroemi</i>	X		
<i>Travisia</i> spp.	X		
<i>Glycera branchiopoda</i>		X	
<i>Maldane glebifex</i>		X	
<i>Maldane sarsi</i>		X	
<i>Prionospio peruana</i>		X	
<i>Amphiteis scaphobranchiata</i>			X
<i>Asabellides lineata</i>			X
<i>Euchone</i> sp.			X
<i>Schistocomas hiltoni</i>			X
Mollusks			
<i>Acila castrensis</i>	X	X	X
<i>Adontorhina cyclia</i>	X	X	
<i>Axinopsida serricata</i>	X		
<i>Bittium subplanatum</i>	X		
<i>Mysella</i> spp.	X		
<i>Nucula</i> spp.	X		
<i>Psephidia</i> sp.	X		X
<i>Bathymedon roquedo</i>		X	
<i>Bittium paganicum</i>		X	
<i>Haliophasma geminata</i>		X	
<i>Limfossor fratulata</i>		X	
<i>Mitrella permodesta</i>		X	
<i>Alvinia rosana</i>			X
<i>Micronellum crebricinctum</i>			X
<i>Nemocardium centrifiliosum</i>			X
<i>Nuculana hamata</i>			X
<i>Turbonilla (Chemnitzia) sp.</i>			X
Crustacea			
<i>Amelisca macrocephala</i>		X	
<i>Leucon subnasica</i>		X	
<i>Pseudomma berkeleyi</i>		X	
<i>Scleroconcha trituberculata</i>		X	
<i>Westwoodilla acutifrons</i>		X	
<i>Gnathia crenulatifrons</i>			X
<i>Melphisana bola</i>			X
<i>Pinnixa schmitti</i>			X

Table 4 (Continued)

Taxa	Amphi- odia- Cyclo- cardia com- munity	Slope*	Insu- lar shelf
Echinoderms			
<i>Amphiodia urtica</i>	X		
<i>Amphipholis squamata</i>	X		
<i>Brisaster latrifrons</i>		X	
Echiuroid			
<i>Listriolobus hexamyotus</i>		X	

* Slope = the slope adjacent to the central portion of the mainland shelf.



Figure 4

a. Adult female *Cyclocardia ventricosa* (Gould, 1850), with the left valve and mantle removed to show the inner demibranch with brooded young; length, 13.7 mm (after JONES, 1963). b. Young of *C. ventricosa* showing D-shaped differentiation of prodissoconch I and II and the initiation of the dissoconch with radial sculpture; length, 1.04 mm (after JONES, 1963).

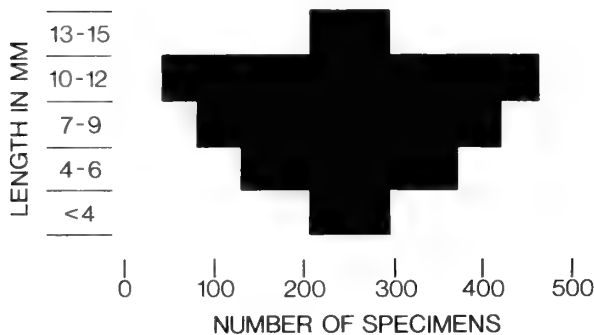


Figure 5

Pyramid graph showing the size distribution of *Cyclocardia ventricosa* in the *Amphiodia-Cyclocardia* community on the northern portion of the mainland shelf (based on length measurements of 1286 specimens from 36 OPG grid samples) (after JONES, 1964).

also occurred in all three areas. Only four co-occurring species were common to two of the three areas.

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In Situ Measurement of Radular Movements of Three Species of *Littorina* (Gastropoda: Littorinidae)

by

PETER S. PETRAITIS AND LAELA SAYIGH

Biology Department, University of Pennsylvania, Philadelphia, Pennsylvania 19104, U.S.A.

Abstract. Radular movements of the periwinkle species *Littorina littorea*, *L. obtusata*, and *L. saxatilis* were measured *in situ* by an underwater microphone. The rates of activity are similar in all three species and are between 28 and 42 rasps/min. The rate of radular activity of *L. littorea* is reduced in larger animals, in animals from the lower intertidal zone, and on surfaces encrusted with *Semibalanus balanoides*. The greatest decline in radular activity is 30% and occurs on irregular surfaces such as those of *S. balanoides*.

INTRODUCTION

ON ROCKY intertidal shores of New England, periwinkles (*Littorina littorea* Linnaeus, *L. obtusata* Linnaeus, *L. saxatilis* Olivi) are the most abundant of the herbivorous gastropods. Impact of periwinkle grazing activity is greater on smooth surfaces (LUBCHENCO, 1983), in protected sites (LUBCHENCO & MENGE, 1978), in tidal pool (LUBCHENCO, 1978, 1982), and on lower intertidal shores (LUBCHENCO & MENGE, 1978; LUBCHENCO, 1983). Yet, periwinkles feed only when submerged or moistened (NEWELL, 1958a, b; Petraitis, personal observations), and NEWELL *et al.* (1971), by timing rasps per minute for 15-30 sec on the sides of aquaria, showed that *L. littorea* from the upper shore have a higher rate of radular activity than those from the lower shore. NEWELL *et al.* (1971) suggested that differences in rates reflected a compensation for differences in the amount of time spent submerged, so that the per individual impact was the same regardless of intertidal position. Thus, it is not clear whether longer duration of submersion or higher densities of snails accounts for their greater impact in tidal pools and on lower intertidal shores. Furthermore, on irregular surfaces, such as in crevices and among barnacles, better success of perennial algae may be due not only to ineffective grazing by periwinkles but also to higher recruitment of algae and lower mortality of germlings as a result of physical factors such as reduced desiccation of germlings in crevices.

Therefore, it was of interest to measure directly the rate of radular activity of *Littorina littorea*, *L. obtusata* and *L. saxatilis* in the field using techniques developed by KITTING (1979).

MATERIALS AND METHODS

All observations and experiments were done at two locations on Swan's Island in Hancock County, Maine, U.S.A. Most of the work was done on Long Cove (44°8'10"N, 68°26'15"W). A south-facing shore, this site is a very protected, nonestuarine, cobble beach with occasional granite outcrops. *Semibalanus balanoides* (Linnaeus) is the most common organism on the upper and lower shore. The mid-intertidal zone is dominated by the alga *Ascophyllum nodosum* (Linnaeus) LeJolis, *Mytilus edulis* Linnaeus and *Chondrus crispus* Stackhouse. Each accounts for less than 10% of the cover in the low intertidal zone. The second site is about 1.0 km west of the Long Cove site on the southern edge of Mill Pond Point. This site is a semiprotected boulder beach but shows similar composition of species and zonation to the Long Cove site. The exception is *M. edulis* which is more common and accounts for 57% of the cover at Mill Pond Point.

Radular activity of *Littorina* species was recorded with a portable cassette tape recorder (Radio Shack Realistic, CTR 48, Model 14-802) and an underwater microphone. All recordings of snails were done without removing the snails and on smooth, bare surfaces unless otherwise noted. The microphone was held 2-3 cm from each periwinkle. Because a snail would usually stop grazing when first approached, a recording was started when a snail resumed grazing and continued for about 20 rasps. Each recording was timed with a stopwatch, and the data were converted to rasps/min.

From 10 June to 2 August 1982, 121 successful recordings were made of individuals of the genus *Littorina*

Table 1

Means and standard deviations for 1982 recordings. Locations (LC for Long Cove, MP for Mill Pond) and dates (month/day) of sampling are grouped by intertidal position and are for Low: LC-6/11, MP-6/15; for Mid: LC-7/27, LC-8/4; for High: LC-6/10, MP-7/28, LC-8/2. Sample sizes are given in parentheses. Snails were recorded on either bare rock, *Semibalanus balanoides*, or *Ascophyllum nodosum*.

Intertidal position	<i>L. littorea</i>			<i>L. saxatilis</i>	<i>L. obtusata</i>
	Bare rock	<i>S. balanoides</i>	<i>A. nodosum</i>	Bare rock	<i>A. nodosum</i>
Low	30.6 ± 5.8 (13)	22.2 ± 3.9 (8)	—	—	—
Mid	31.0 ± 3.4 (8)	25.0 ± 4.0 (2)	33.0 ± 7.1 (22)	—	35.6 ± 7.2 (17)
High	34.8 ± 5.1 (29)	—	19.9 (1)	37.4 ± 4.2 (9)	41.8 ± 10.3 (12)

(83 of *L. littorea*, 29 of *L. obtusata* and 9 of *L. saxatilis*). The position of each snail in the intertidal zone was noted. Most observations were made on the incoming tide and on snails that had been covered for less than 30 min. Although data were collected under a variety of conditions, four comparisons were planned: among samples for *L. littorea* on bare surfaces, between *L. littorea* and *L. saxatilis*, between *L. littorea* on rock and *L. obtusata* on *Ascophyllum nodosum*, and for *L. littorea* on bare versus barnacle-covered rock. For all tests, Bartlett's test for homogeneity of variances was not significant, and data were analyzed by analysis of variance (SOKAL & ROHLF, 1981).

In 1983 only individuals of *Littorina littorea* were recorded and all 157 recordings were done in June. No snail was recorded more than once. The position of each snail relative to fixed markers on the shore was noted. The shore was divided by the markers into three roughly equal zones (low: less than 0.7 m above MLW; mid: 0.7 to 1.6 m above MLW; high: more than 1.6 m above MLW). After each recording, the height of the snail's shell was measured to the nearest millimeter. We also noted whether the snails had just been covered by the tide (less than 5 min) or covered for more than 30 min. The category of more than 30 min includes some animals that were re-

corded on the outgoing tide. Kruskal-Wallis tests were used to examine differences in radular activity because variances were not homogeneous. A regression of activity on length of snail was also done.

The radular activity of *Littorina littorea* on *Semibalanus balanoides* and on bare surfaces was also compared. Snails were removed from the lower shore and placed on a submerged rock that was either bare or covered with *S. balanoides*. The rasping rate of each snail was recorded on both types of surfaces, and the order of presentation of surfaces to each snail was random. Pairs of recordings were successfully obtained for 19 snails during 16 to 18 June 1982 and 16 snails during 20 to 28 July 1983. Because periwinkles were only intermittently active on *S. balanoides*, it was impossible to get good sequences of 20 rasps. Data were therefore tallied as the number of rasps in the first 30 sec after the first rasp, and analyzed as a paired *t*-test (SOKAL & ROHLF, 1981).

RESULTS

Observations of radular activity in 1982 are summarized in Table 1. The rate of radular activity of *Littorina littorea* on bare surfaces varied with date and location of sampling

Table 2

Summary statistics for 1983 recordings. Means and standard deviations are given for rasps/min, for lengths of snails that were recorded, and for residuals from overall regression. Snails were recorded within 5 min of submersion (<5) or after 30 min of submersion (>30).

Intertidal position	Time	Sample size	Rasps per min	Length	Residual
Low	<5	31	34.1 ± 11.0	10.4 ± 3.6	-2.96 ± 10.56
	>30	25	35.7 ± 6.8	11.4 ± 3.5	-0.84 ± 6.78
Mid	<5	30	33.5 ± 5.8	10.7 ± 3.2	-3.38 ± 5.00
	>30	12	40.5 ± 9.8	10.5 ± 2.6	+3.53 ± 8.94
High	<5	32	40.6 ± 5.7	12.2 ± 3.7	+4.48 ± 5.35
	>30	27	37.0 ± 4.9	12.6 ± 3.6	+1.06 ± 5.26

($F = 3.00$, with 5 and 44 d.f., error mean square = 23.6). Significant treatment effect was caused by one sample from Mill Pond that had a much lower mean (27.6 rasps/min), and all unplanned comparisons among samples were not significant. We cannot reject the null hypothesis of no difference for snails from different intertidal zones, for snails from Long Cove versus Mill Pond, and for snails from early (June) versus late (July and August) summer. Both *L. obtusata* and *L. saxatilis* showed rates of radular activity similar to *L. littorea*. Only when found on barnacle-covered rocks, did *L. littorea* graze more slowly ($F = 16.73$, with 1 and 29 d.f., error mean square = 21.2).

For the data collected in 1983, radular activity of *Littorina littorea* was higher for animals from the high intertidal zone (Table 2). The Kruskal-Wallis test was significant ($T = 9.74$, d.f. = 2); however, the effect could have been due to variation of activity with the size of the animal because the high intertidal snails were also larger. The regression of activity on length was significant ($F = 8.40$, with 1 and 155 d.f., residual mean square = 58.83), and shows that larger animals graze more slowly. The model is rasps/min = $42.4 - 0.5(\text{length})$. To correct for effects of body size, the Kruskal-Wallis test among low-, mid- and high-zone snails was re-done using the residuals from the regression. There remained a significant difference ($T = 14.73$).

No difference in activity was detected for animals just covered by the tide versus those covered for more than 30 min (Table 2). Kruskal-Wallis tests were not significant for either the raw data ($T = 0.08$) or the residuals from the regression ($T = 0.05$).

In the paired comparison experiment, periwinkles showed about a 30% decline in the number of rasps when placed on a barnacle-covered surface. The overall mean rate on *Semibalanus balanoides* was 10.2 rasps/30 sec (SD = 4.44) while on bare surfaces the rate was 13.9 rasps/30 sec (SD = 3.86). For pairs of observations of the same snail on both surfaces, the mean difference was 4.0 rasps/30 sec (SD = 5.21), and the paired t -test is significant ($t = 4.54$, $n = 35$).

Our observations suggest that periwinkles have difficulty when grazing among barnacles. A snail frequently stopped moving its radula. During these stops, a snail would move its head from side-to-side, and it appeared that the snail was searching for a better surface upon which to graze. Continuous activity on barnacles occurred only on smaller *Semibalanus balanoides* and in small open patches among the barnacles.

DISCUSSION

NEWELL *et al.* (1971) showed that *Littorina littorea* from upper intertidal shores had a higher feeding rate than those from lower shores. Our results are not as striking. Although snails from the high intertidal do graze at a faster rate, the difference is not large. The percent differ-

ence is 16% ($[(40.6 - 34.6)/40.6]$; data from Table 2). We thus infer from our data that the individual impact of *L. littorea* should be greater in areas that are submerged for longer periods even though there is some compensation of radular activity. Although this is consistent with observed damage to algae (LUBCHENCO, 1978, 1982, 1983; LUBCHENCO & MENGE, 1978; MENGE, 1976), both NEWELL *et al.* (1971) and our results are based on the assumption that rates of activity are constant, or at least vary in a similar fashion, over the tidal cycle. Confirmation requires *in situ* measurements throughout the tidal cycle.

NEWELL *et al.* (1971) reported maximal feeding rates of 16 to 36 rasps/min for animals from low to high intertidal levels (fig. 5 in NEWELL *et al.*, 1971), and much lower average rates than ours (6.1 to 28.4 rasps/min from table 3 in NEWELL *et al.*, 1971). We found, however, average rates of 33.9 to 38.8 rasps/min (Table 2). It is possible that the lower rates found by NEWELL *et al.* were due to handling the snails. When we recorded radular activity of snails that had been handled, we found a mean rate of 23.6 rasps/min (SD = 3.68, unpublished data). This rate is similar to rates observed by NEWELL *et al.* (1971) and when compared to our *in situ* measurements, which ranged from 27.6 ± 2.0 (one sample from Mill Pond) to 38.8 ± 6.2 (Table 2), is quite low.

We did not find any variation in radular activity at different times during the tidal cycle as reported by NEWELL *et al.* (1971). This is consistent with results for patellid limpets (BOYDEN & ZELDIS, 1979). A good predictor of activity is body size and even this explains only 5% of the variation observed in the data.

Our direct measurements of radular activity on barnacle-covered surfaces and bare rocks are quite consistent across experiments. *In situ* measurements show a 31% decline in activity on *Semibalanus balanoides*; this is an average reduction of 10.3 rasps/min (Table 1). Paired observations of the individual on bare versus *Semibalanus*-covered rocks show a 27% reduction or about 8 rasps/min. Assuming that each movement of the radula clears the same amount of material, the refuge from grazing that is provided by crevices is substantial. We consider this 30% reduction a minimum estimate because rasps by *Littorina littorea* on *S. balanoides* tend to be shorter in duration, and we suspect less material may be taken per rasp.

On *Ascophyllum nodosum*, *Littorina obtusata* shows a similar rate of radular movement to *L. littorea* on bare rock (Table 1). *Littorina obtusata* is commonly found on submerged plants of *A. nodosum* at both of our sites. Recordings indicate that *L. obtusata* is grazing on *A. nodosum*, and inspection of plants shows that *A. nodosum* is damaged by grazing activity. On bare surfaces, *L. saxatilis* appears to graze at slightly higher rates than *L. littorea*, although the difference is not significant (Table 1).

Although we found a large amount of variation among individuals in the rate of radular movement, it is clear

that surface conditions have a far greater effect than body size or intertidal position on the rate of rasping. Comparison of individuals on the high shore with those on the low shore shows only a 4–16% decline in activity (Tables 1, 2). Body size has a similar effect; our regression model predicts a 15% decline in activity when the smallest (6 mm) and the largest snails (17 mm) are compared. Compared to these data, the 30% decline we observed when *Littorina littorea* grazes on barnacle-encrusted surfaces is quite striking. Given the amount of variation we have seen among individual snails, it is possible that subtle differences in surface conditions and their effect on effectiveness of *L. littorea* grazing may be as important as changes in density of grazers.

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Habitat and Food Preferences in Six Eastern Pacific Chiton Species (Mollusca: Polyplacophora)

by

RICHARD D. PIERCY

Loma Linda University, Department of Biology, Riverside, California 92515, U.S.A.

Abstract. Habitat and diet were analyzed for six sympatric chiton species (*Mopalia hindsii*, *M. muscosa*, *M. ciliata*, *Katharina tunicata*, *Tonicella lineata*, and *Lepidochitona dentiens*) on a rock outcrop on Deception Island, Washington, U.S.A., using quadrat sampling and gut contents. Species showed significant differences in tidal height distribution, substratum slope, exposure, associations, and gut contents, although considerable overlap of food types occurred. *Katharina tunicata*, composing 72% of the chiton population in the study area, was a generalist, having a wide tidal height distribution and occurring on substratum slopes from 0 to 90 degrees. Its diet consisted of a variety of algal types including diatoms, *Ulva*, filamentous algae, and macrophytes. *Tonicella lineata*, composing 17% of the chiton population, was more specialized in microhabitat, having the highest percent cover of *Lithothamnion* and preferring slopes greater than 45 degrees and tidal heights below MLLW. *Lepidochitona dentiens*, the smallest and most specialized of the species, occurred only above MLLW and had a diet of almost exclusively diatoms (94%). *Mopalia ciliata* and *M. hindsii* had the highest percentages (25% and 18%) of invertebrates in their gut contents, while *M. muscosa* (4%) was more herbivorous. Differences in diet and microhabitat among these chiton species suggest that mechanisms such as resource partitioning or "indirect commensalism" may help maintain chiton diversity.

INTRODUCTION

CHITONS (Mollusca: Polyplacophora) are common members of intertidal communities. Many studies of the distribution, movement, interactions, and food preferences in chitons have concentrated on single species (BARNES, 1972; CAPLAN, 1970; DEMOPOLUS, 1975; DETHIER & DUGGINS, 1984; LYMAN, 1975; MOOK, 1983; NISHI, 1975; SMITH, 1975; WESTERSUND, 1975). Others have considered two or more species, but usually in relation to a limited number of ecological parameters (ANDRUS & LEGARD, 1975; CHELAZZI *et al.*, 1983; CONNOR, 1975; FITZGERALD, 1975; GLYNN, 1970; LANGER, 1978; MURDOCH & SHUMWAY, 1980). Studies comparing microhabitat and diet, two closely related ecological parameters, in a large number of sympatric species are almost lacking with the exception of those done by BARNAWELL (1954, 1960) and more recently by KANGAS & SHEPHERD (1984). Because many chiton species frequently inhabit the same locality, more such studies are needed to examine species differences and determine ecological mechanisms that would support such diversity.

The purpose of this study was to test for differences in habitat and food in six sympatric species of chitons. The

species examined were *Mopalia hindsii* (Reeve, 1847), *M. ciliata* (Sowerby, 1846), *M. muscosa* (Gould, 1846), *Katharina tunicata* (Wood, 1815), *Lepidochitona dentiens* (Gould, 1846), and *Tonicella lineata* (Wood, 1815).

MATERIALS AND METHODS

General

This study was conducted during the summer of 1983 at Walla Walla College Marine Station near Anacortes, Washington, U.S.A. The primary study site was on the south side of Deception Island near Deception Pass, located off Whidbey Island at the eastern end of the Strait of Juan de Fuca. A rock outcrop (approximately 8 × 4.5 m) perpendicular to the shoreline and jutting out into the water was selected at this site. All six chiton species were found on the outcrop.

Transect lines were placed 0.5 m apart across the rock surface. Numbered tags were fastened to these lines at 0.5-m intervals providing a grid system that was used in sampling. Two sizes of quadrats were used in sampling: a 0.5 × 0.5-m quadrat and a 0.25 × 0.25-m quadrat. The smaller or "sampling quadrat" was a quarter section of the main, larger quadrat.

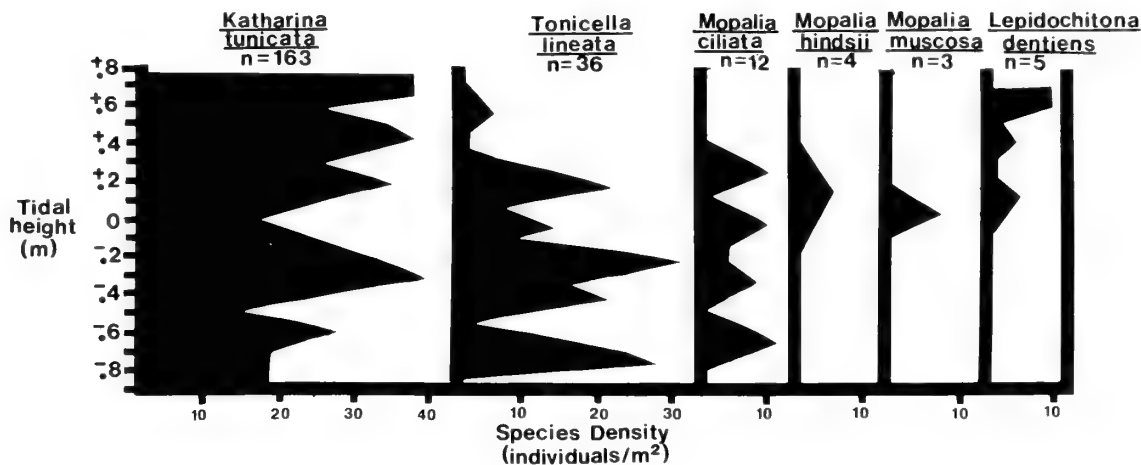


Figure 1

Density of six species of chitons at different tidal heights. Species density was computed from the total area sampled at 0.1-m intervals and the number of individuals of each species occurring in that interval.

Habitat

Habitat parameters evaluated and compared among the chiton species included tidal height, substratum type and slope, position and exposure to light on the rock surface, and percent cover of algae and invertebrates. The rock outcrop was sampled by placing the larger quadrats consecutively along transect lines over the rock surface. For each large quadrat, percent covers of algal species and invertebrates were estimated. One of the four quarter sections (*i.e.*, sampling quadrat) was randomly selected. All chitons in the sampling quadrat were identified following KOZLOFF (1974) and measured to the nearest millimeter. Tidal height was also determined for each sampling quadrat.

For each chiton within the sampling quadrat, the microhabitat was further characterized. Substratum slope was measured using a Brunton compass. Substratum type (rock, gravel-cobble, algae), degree of exposure (being in a pit, crack-crevice, groove, under algae, or fully exposed), position on the rock surface (top, side, bottom), and the presence of large barnacles (primarily *Balanus cariosus* [Pallas, 1788]) were recorded.

Because early sampling revealed that the greatest diversity of chiton species occurred on the sloping sides of the rock outcrop, the total sloping perimeter of the rock was sampled. The top horizontal surface of the rock was less completely sampled with quadrats placed only between alternate transect lines.

Food

Gut contents were examined to determine food preferences of the chiton species. Specimens were collected near the rock outcrop during both low and high tides. SCUBA

was used during high tides. After collection, animals were initially preserved in a 10% formalin solution, and later transferred to 70% alcohol. The stomach and intestine of each animal were dissected out and the contents removed. In those species in which material was abundant, samples were spread over three microscope slides. However, in *Tonicella lineata* and *Lepidochitona dentiens*, gut contents were often sufficient for only 1 or 2 slides. This was partly due to the small size of the animals.

Material in the gut contents was identified, measured, and compared among the chiton species. The gut contents on each slide were scanned three times from left to right. Each time a food item was seen, an estimate of its projected surface area was obtained by counting the number of 0.5-mm squares it covered on a 1 × 1-cm ocular grid. From this area value, the percent of that food in the diet was calculated for each individual and species.

Specific identification of gut contents was not always possible. Most algal material was identified to genus. Invertebrates were identified to general taxonomic group, such as amphipod, barnacle, hydroid, or polychaete.

Individual food items were placed in food categories for species comparison. Food categories, similar to those of STENECK & WATLING (1982), were established. These included diatoms, filamentous algae (*e.g.*, *Polysiphonia*, *Pterosiphonia*, *Antithamnion*, and *Cladophora*), *Ulva*, soft encrusting red algae (*e.g.*, *Hildenbrandia* and *Petrocelis*), hard encrusting algae (*Lithothamnion*), macrophytes consisting of algae with several cell layers and forming large erect thalli usually branching or blade-like (*e.g.*, *Gigartina*, *Hedophyllum*, and *Fucus*), and invertebrates (*e.g.*, bryozoans, hydroids, barnacles, bivalves, gastropods, polychaetes, and various larvae). The algal groupings were at least partially designed to reflect size, structure, toughness, and resistance to being scraped off the rock surface.

Table 1

Summary of species comparisons based on statistical tests and subjective interpretations of observations.

	<i>Mopalia hindsii</i>	<i>Mopalia ciliata</i>	<i>Mopalia muscosa</i>	<i>Katharina tunicata</i>	<i>Tonicella lineata</i>	<i>Lepidochitona dentiens</i>
Habitat study						
Percent of total sampled	<i>n</i> = 4 (2%)	<i>n</i> = 12 (6%)	<i>n</i> = 4 (2%)	<i>n</i> = 163 (72%)	<i>n</i> = 36 (16%)	<i>n</i> = 5 (2%)
Average length (cm)	6.3	4.4	5.6	5.9	2.7	1.1
Tidal range (m)	0-+0.4	-0.8-+0.4	0-+0.3	-0.9-+0.8	-0.9-+0.7	0-+0.8
Distribution†	narrow	broad (-)	narrow	broad (+)	broad (-)	narrow
Substratum slope >45°	X	X			X	
<45°			X	X		X
0-90°						
Position or exposure						
Sides	X	X	X	X	X	
Top				X		X
Under overhang	X	X			X	
Among barnacles	X	X		X		X
Associations						
Diatoms	X	X	X	X	X	X
Soft encrusting	X	X	X		X	X
<i>Lithothamnion</i>					X	
<i>Ulva</i>				X		X
Filamentous			X			
Macrophytes						
Invertebrates	X	X	X			X
Diet study*						
Diatoms	X	X	X	X	X	X
Soft encrusting						
<i>Lithothamnion</i>					X	
<i>Ulva</i>			X	X		
Filamentous	X	X				
Macrophytes				X		
Invertebrates	X	X				

* Diet was determined from gut contents removed from different individuals not included in the habitat study. In the diet study, the sample size was eight for all species except *Lepidochitona dentiens* in which it was six.

† For each distribution listed as broad, the center of abundance is indicated as - or + for centers below or above MLLW, respectively.

RESULTS

Habitat

Katharina tunicata was clearly the dominant species at the study site, composing about 72% of the chiton population (Table 1). *Tonicella lineata* was the next most common species composing 17% of the population, while the remaining four species were considerably less abundant.

Chiton species showed significant (Chi-square tests, $P < 0.005$) differences in tidal height distribution at 0.1-m intervals through the sampling range (Figure 1). Although both had wide distributions, *Katharina tunicata* was more abundant above 0 m tidal height or mean lower low water (MLLW), whereas *Tonicella lineata* was more abundant below MLLW. *Lepidochitona dentiens* appeared limited in its distribution to above MLLW.

Chiton species differed further relative to substratum angle (Table 1). To determine species differences, substratum angle was divided into 15-degree intervals from

0 to 90 degrees. The number of individuals of each species occurring at each slope interval was computed. A significant (Chi-square test, $P < 0.005$) difference existed in species distribution relative to substrate slope. *Tonicella lineata*, *Mopalia hindsii*, and *M. ciliata* seemed to prefer slopes of greater than 45 degrees. In contrast, *Lepidochitona dentiens* occurred on more horizontal substrata. *Katharina tunicata* appeared to have an almost normal distribution centered around 45 degrees.

Position or exposure on the rock outcrop differed among the chiton species (Table 1). Preference for position and exposure on the rock surface was tested using Chi-square tests. Six tests were performed independently on the number of individuals of each species associated with each of the following categories: being under a rock or rock overhang, on the sides of a rock, on the top of a rock, under algae, in a groove-crack-crevice, or among large barnacles. Significant ($P < 0.05$) species differences were found in three of the six categories: presence on the top of the rock,

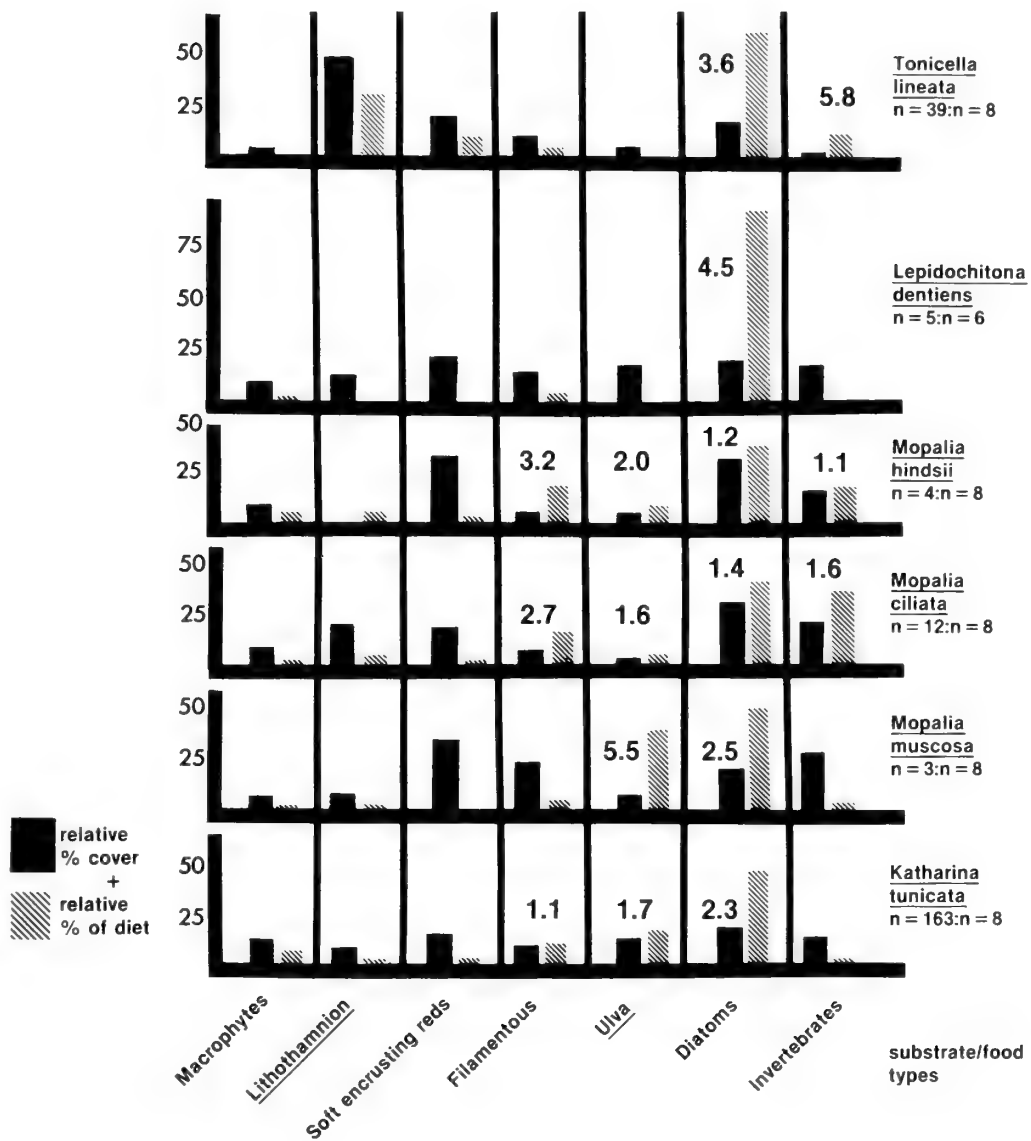


Figure 2

Comparison of percent of diet (crosshatched bars) with percent cover (solid bars) for the seven food groups and six chiton species. Values in some boxes are ratios >1, which suggest "selective feeding." The first *n* value given is for percent cover, the second for diet.

under a rock or rock overhang, and among large barnacles. *Lepidochitona dentiens* was limited exclusively to the top horizontal surface of the rock outcrop. In contrast, *Tonicella lineata*, *Mopalia ciliata*, and *M. hindsii* were found primarily on the sloping sides and under rock overhangs. *Katharina tunicata* was found more uniformly both on the sloping sides and top horizontal surface.

Owing to the topography of the rock outcrop, the tidal height, substratum slope, and position or exposure on the rock surface may be confounding variables at the study

site. Results suggesting significant species differences in all three parameters may therefore be due to but a single factor or some combination of the three.

Microhabitat differences also existed among the chiton species in associations with algae and invertebrates (Table 1; Figure 2, solid bars). Species differed with respect to *Ulva*, to *Lithothamnion*, and to invertebrates (one-way ANOVA, $P < 0.001$) and to soft encrusting red algae (one-way ANOVA, $P < 0.05$). Particularly note the high association of *Tonicella lineata* with *Lithothamnion*.

Food

The guts of chiton species differed (one-way ANOVA, $P < 0.05$) in their contents of *Ulva* and diatoms (Table 1; Fig. 2—crosshatched bars) and possibly ($P < 0.09$) in their contents of *Lithothamnion*, filamentous algae, and invertebrates. Invertebrates, primarily worms and amphipods, were frequently associated with filamentous red algae in the gut contents of *Mopalia hindsii* and *M. ciliata*. Perhaps living among the filaments, such worms and amphipods are ingested with the algae. Whole barnacles and barnacle plates were common in the gut contents of *Mopalia* spp. Separation of invertebrates into several separate food categories would be helpful in distinguishing chiton feeding differences within this broad category.

Figure 2 permits a comparison for each chiton species of percent of food type in the diet to percent cover in the microhabitat. Ratios greater than one suggest positive selectivity in feeding as opposed to random browsing. All species of chitons had a larger proportion of diatoms in their diets than in the microhabitats. This is particularly noticeable for *Tonicella lineata* and *Lepidochitona dentiens*, the two smallest species. In addition to positive selection, such high ratios could result from easier identification and/or greater preservation in the gut as compared with other foods.

In *Mopalia ciliata* and *M. hindsii* the high gut content to microhabitat ratios of filamentous algae also suggest selective feeding. Similarly, *M. muscosa* appeared to select *Ulva*. The particularly high ratio of invertebrates in *Tonicella lineata* was primarily due to a single chiton with a large crustacean in its gut. Hence, this value may not reflect a real food preference for invertebrates. Direct comparisons of food types in the microhabitat with gut contents for individual chitons, a closer examination of less conspicuous food items in the microhabitat (smaller algal and invertebrate species), large sample sizes, and performing food preference experiments are needed to further confirm dietary differences and the presence of selective feeding.

DISCUSSION

Differences in microhabitat (*i.e.*, tidal height, position and exposure on the rock surface, substratum slope, and chiton-algal or chiton-invertebrate associations) may ecologically separate the chiton species studied. Because a limited area and tidal range were sampled, the observed relation of chiton species with intertidal height may not hold for other localities. LANGER (1978) found a spatial separation of three species of chitons in relation to depth. My study and investigations by ANDRUS & LEGARD (1975) and BARNAWELL (1954) suggest that other differences besides tidal height (*i.e.*, exposure or associations) may also be important in spatially segregating chiton species.

ANDRUS & LEGARD (1975) found *Tonicella lineata* to occur only in the presence of encrusting coralline algae. This same association appears in my study. *Tonicella li-*

neata always occurred on or near the encrusting calcareous alga *Lithothamnion*, for which it had the highest percent cover (48%). This factor alone clearly separated it spatially from the other species.

Significant differences in specific food items or food groups found in gut contents indicate that diet varies among these species. The high percent of *Lithothamnion* in the gut contents of *Tonicella lineata* agrees with similar findings of DEMOPOLUS (1975), BARNES (1972), and BARNES & GONOR (1973). The higher percent contribution of animal versus plant material in the gut contents of *Mopalia ciliata* (25%), and *M. hindsii* (18%) than in *M. muscosa* (4%) is in striking agreement with observations by BARNAWELL (1954, 1960). This difference appears especially important in ecologically separating *M. hindsii* and *M. ciliata* from *M. muscosa*, which were quite similar in other niche dimensions.

GAINES (1985) has found that *Katharina tunicata* readily feeds on the relatively large, foliaceous red alga *Iridaea*. DAYTON (1975) has observed that *K. tunicata* browses extensively on large *Hedophyllum*. My findings that *K. tunicata* had the highest percentage (although still small) of macrophytes in its diet agree with this association.

Diet appears to be an important ecological parameter separating sympatric chiton species. Diet differed among 16 species of chitons examined on a boulder slope in south Australia (KANGAS & SHEPHERD, 1984). Six were herbivores, seven omnivores, and three carnivores. Within these feeding types some were generalists, others specialists. A similar range of feeding strategies was found in the six species I studied. The smallest chiton, *Lepidochitona dentiens*, appeared quite specialized in diet, relying almost exclusively (94%) on diatoms. The next smallest species, *Tonicella lineata*, had a greater variety of both plant and animal food types in its gut contents, although it did have the highest percentage (16%) of *Lithothamnion*, clearly distinguishing it from all other species. The remaining species tended to be omnivorous, having a wide variety of both plant and animal material in their guts. However, *Katharina tunicata* and *Mopalia muscosa*, with 99% and 96% plant material in their diets respectively, were clearly more herbivorous than *M. hindsii* (82%) and *M. ciliata* (75%). These latter two species had the highest percentages of animal material (primarily barnacles and amphipods) of all six chiton species. Differences in diet as well as microhabitat could result from resource partitioning.

With niche overlap in both microhabitat and food among the chiton species in this study, competition might result. Indirect evidence for space competition was suggested by the drop in density of *Katharina tunicata* near MLLW where three other species had high densities (Figure 1). To test for competition, however, experiments involving both addition and removal of individual chiton species would be necessary.

An alternative relationship to competition might exist among certain of these chiton species as suggested by the work of DETHIER & DUGGINS (1984) who demonstrated

an "indirect commensalism" between *Katharina tunicata* and two limpet species. Although these species are potential competitors due to partial food type overlap, Dethier and Duggins showed that the presence of *K. tunicata* actually benefited the limpets. *Katharina tunicata* fed on competitively dominant macroalgae (as well as diatoms), thus enhancing the growth of diatoms, which are the primary food of limpets.

That *Katharina tunicata* may have a similar role with certain chiton species is suggested by comparing the Deception Island observations with preliminary observations at a second ("Dock") site near the Anacortes State Ferry Dock. Diatoms had a high percent cover and were a major prey species at the Deception Island site (Figure 2), whereas macroalgae (such as those consumed by *K. tunicata*) were relatively less abundant. The large population of *K. tunicata* may be removing dominant macroalgae species, thus facilitating diatom growth. In contrast, at the "Dock" site, macroalgae (including *Ulva* sp.) had a high percent cover while diatom growth was greatly reduced. At this site, the population density of *K. tunicata* was considerably lower than at Deception Island (4/m² vs. 22/m²). Two species, *Tonicella lineata* and *Lepidochitona dentiens*, that appeared to rely heavily on diatoms for food (Figure 2), also had lower densities (3/m² vs. 6/m² and 0/m² vs. 1/m² respectively) at the "Dock" site than at Deception Island while the density of the remaining chitons (*Mopalia* spp.) remained the same. Thus, extensive grazing by *K. tunicata* on macroalgae might enhance diatom and other microalgal growth for use by other chiton species, and indirectly help to sustain or increase chiton diversity.

The interactions and relationships among the chiton species in my study that maintain diversity are certainly not clear. Further manipulative experiments are needed to better define them.

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Factors Affecting the Rate of Flashing and Loss of Luminescence in an Asian Land Snail, *Dyakia striata*

by

J. J. COUNSILMAN,¹ D. LOH,¹ S. Y. CHAN,¹ W. H. TAN,¹
J. COPELAND,² AND M. MANERI²

¹Department of Zoology, National University of Singapore, Kent Ridge 0511, Republic of Singapore

²Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53201, U.S.A.

Abstract. The Asian snail *Dyakia striata* is the only terrestrial gastropod known to produce light. Fifteen experiments tested the effects of selected social, environmental, and reproductive factors on its rate of flashing and on the loss of luminescence in some individuals; the factors were age, group size, photoperiod, temperature, diet, starvation, and reproductive maturity. An additional experiment provided data on survival of non-luminescent individuals for comparison with luminescent individuals maintained under identical conditions. Flashing rates were (1) lowest among all experiments for a cool temperature, (2) highest among three diets for a highly proteinaceous vegetable, (3) higher for grouped than isolated snails, (4) higher for groups of five individuals than groups of 2, 10, or 15, and (5) higher for young than old snails. Loss of ability to produce light did not affect survival. It occurred most often in isolated snails under extremes of photoperiod (*i.e.*, continuous light) and temperature (*i.e.*, a cool temperature), and was not, as reported by earlier workers, associated with reproductive maturity.

INTRODUCTION

AMONG TERRESTRIAL gastropods, bioluminescence is known only for the Asian snail *Dyakia striata* (Godwin-Austen, 1891) (formerly in *Quantula*) (HANEDA, 1946). Light is produced by a discrete photogenic organ located near the undersurface of the foot and behind the mouth. It is yellowish green and appears as simple or modulated flashes that usually last a second or two but may last as long as 6 sec. Flashes may be repeated up to 30 times/min during peak activity just after dark (PARMENTIER & BARNES, 1975). They are mostly given by snails of 5 to 15 mm in shell width (HANEDA, 1963), although the maximum size of adults is at least 27 mm. Nearly all flashing is performed by feeding or moving snails while fully extended. The intensity of light is very low: even in complete darkness only the brightest flashes can be seen by human eyes from more than several meters or from behind the shell.

Light is reportedly also produced by luminous cells scattered over the foot and mantle. It differs from light produced by the photogenic organ in being extremely faint and continuous (HANEDA & TSUJI, 1969). It is recorded

as being found in all newly hatched snails but in only 20-30% of adults (HANEDA, 1981). PARMENTIER & BARNES (1975) did not mention this type of luminescence.

Little is known about the function or functions of flashing by *Dyakia striata*. MARTOJA & BASSOT (1970) reported that the photogenic organ is replaced by a non-functional "reabsorption cyst" before the gonads mature. HANEDA (1963) had earlier observed that some snails did not luminesce, but he and TSUJI (1969) considered this phenomenon to be an individual characteristic of adults. The recent finding that some very large snails may possess both a functional photogenic organ and well-developed reproductive systems (COPELAND & MANERI, in press) further suggests that light production is not tied to reproduction. Nor does it appear to serve as a warning of the performer's unpalatability (CHAN, 1984), as does the glow of firefly larvae (CARLSON & COPELAND, 1978). Local illumination is unlikely because the light is not directional and flashes are not given when the foot is raised or when an obstacle is encountered (PARMENTIER & BARNES, 1975). Similarly, most other functions proposed for other luminescent organisms (see BUCK, 1978) are apparently not applicable to *D. striata*. For example, jamming, repelling,

and concealment are difficult to imagine as roles for flashing because the light is so weak.

Several workers have tried to evoke luminescence in *Dyakia striata* by artificial means. HANEDA (1981) subjected snails to electrical and mechanical stimulation, and to injury. As well as these methods, PARMENTIER & BARNES (1975) tried food, pure oxygen, and several neurotransmitters. All these efforts failed. COPELAND & MANERI (in press), on the other hand, reported being able to stimulate approaching and flashing responses with artificial flashes. On the basis of this evidence, these authors hypothesized that luminescence in *D. striata* facilitates aggregating behavior. However, the observed instances of approaching and flashing were few; and, the basic social and environmental conditions that may influence flashing, and could thereby promote or inhibit communication (or some other activity), were not investigated.

In this study we examine the effects of a variety of conditions on the rate of flashing by the photogenic organ and its loss of function in some snails. Two factors, age and group size, were chosen to test the hypothesized relationships of flashing with maturity (HANEDA, 1963) and with aggregating (COPELAND & MANERI, in press). Four others were selected as likely influences on the behavior of *Dyakia striata*: they were diet, starvation, photoperiod (see HODASI, 1982), and temperature (see CAMERON, 1970). An experiment was also conducted to test further the hypothesized effects of reproduction on loss of luminescence (MARTOJA & BASSOT, 1970).

MATERIALS AND METHODS

Table 1 identifies the 16 experiments that were conducted. The snails used here were collected during the period of 21 May to 11 July 1984 from several localities in the Republic of Singapore. Most came from one small area of a northeast-facing slope near a large drainage canal in Clementi New Town. An additional 798 animals were collected solely for an examination of the photogenic organ. They were obtained during the period of 20 May to 7 October 1985 from the old campus of the National University of Singapore in Bukit Timah.

Before the experiments were begun (and fortnightly thereafter), the experimental animals were examined for luminescence—whether or not the organ is flashing at the moment, it nevertheless fluoresces under UV irradiation. They were also measured for shell width. The size measurement was presumed to indicate age, because shell growth in captive snails was constant with time (LOH, 1984). Snails used in the experiments on temperature, continuous light, and continuous dark were housed in specially prepared cabinets. In the first two of these treatments, lighting was provided by single 40-W incandescent bulbs. Snails in the remaining experiments (except that on reproductive maturity) were housed in a small light-sealed room with controlled photoperiod and constant temperature. Lighting here consisted of two 40-W incan-

descent bulbs. In the study of reproductive maturity, snails were kept under natural shaded light conditions (of about 12 h of light per day) and natural temperatures (of 24–30°C).

The first 15 experiments were run for 13 weeks, from 1 August to 31 October 1984. The last experiment was run for 12 weeks, from 17 July to 11 October 1984.

Effects of Non-social Factors on Rate of Flashing and Loss of Luminescence (Experiments 1–8)

Because *Dyakia striata* is found in the field as lone animals and in small groups, these experiments were conducted on both isolated and grouped snails. For each experiment, 20 snails were kept separately in round plastic containers of 6.5 (height) × 9 cm (diameter); and 20 were kept in two groups of 10 in rectangular plastic containers of 16 (height) × 12 × 18 cm. All grouped snails were color-coded with nail polish. Every other day the containers were cleaned, fresh food was provided, and the wet paper towels used to keep the animals moist were replaced. Mean shell widths for these eight treatments varied from 16.6 to 17.8 mm, with individual snails ranging from 11.7 to 20.9 mm.

Because pulmonates in general survive and reproduce best on a mixed diet (RUNHAM, 1975), the control diet consisted of several foods. It was composed of frequently replenished pieces of carrot, cucumber, lettuce, and rat-chow, and an occasional piece of *Achatina fulica* (Bowdich, 1822), a large land snail on which *Dyakia striata* scavenges in the field. Table 2 gives a partial nutritional analysis of these foods.

Flashing was observed by a dark-adapted person, with the aid of a dim UV light (NIS FL4 BLB) to enhance the brightness of flashes. Whether simple or modulated, flashes were distinct from one another, and each was counted as a single flash. Data on flashing were collected every third day just after the start of the daily dark cycle (at 0900 h). Among active, non-feeding snails in each experiment, five were chosen at random from isolates and five from groups, for observations of 1 min each. Non-luminescent snails were, of course, not included; and neither were snails fed the *Achatina fulica* diet because all died within 10 days. Only a small number of observations were made on starved snails during the two weeks when most were still alive.

Effects of Group Size and Age on Rate of Flashing (Experiments 9–15)

These experiments differed from no. 1 to 8 in that isolates were not used, and dead snails or those that had become non-luminescent were replaced with luminescent snails of similar size. Maintenance conditions were the same as those for grouped snails in the control experiment. Data on flashing were collected in a similar manner as experiments 1–8 but on every second day.

Table 1
Conditions for experiments on *Dyakia striata*.

Experiment	Presence of luminescence	Diet	Photoperiod (L:D)	Temp. (°C)	Sample size*
1. Control conditions	initially	control	12:12	30	40
2. Non-luminescence	no	control	12:12	30	40
3. Cucumber diet	initially	cucumber	12:12	30	40
4. <i>Achatina</i> diet	initially	<i>Achatina</i>	12:12	30	40
5. Cool temperature	initially	control	12:12	20	40
6. Continuous light	initially	control	24:0	30	40
7. Continuous dark	initially	control	0:24	30	40
8. Starvation	initially	control	12:12	30	40
9. Groups of 2	throughout	control	12:12	30	4
10. Groups of 5	throughout	control	12:12	30	10
11. Groups of 10	throughout	control	12:12	30	20
12. Groups of 15	throughout	control	12:12	30	30
13. Young snails	throughout	control	12:12	30	20
14. Middle-age snails	throughout	control	12:12	30	20
15. Old snails	throughout	control	12:12	30	20
16. Reproductive maturity	initially	control	natural	natural	120
Total:					564

* For experiments 1-8, these are initial sample sizes, because dead snails were not replaced.

Mean shell widths for treatments 9-12 varied from 16.1 to 17.4 mm, with individual snails ranging from 13.5 to 21.3 mm. For experiments 13-15, young snails averaged 13.6 mm (10.0-14.6), middle-age snails 17.0 mm (15.8-17.7) and old snails 20.0 mm (18.8-21.1).

Effects of Reproductive Maturity on Loss of Luminescence (Experiment 16)

Forty isolated snails and 40 pairs, all initially luminescent, were kept in small round containers (see above) with soil for egg-laying. The soil was examined for eggs every other day and changed if fouled. All snails were fed the

control diet. Their mean shell width was 18.8 mm (11.9-25.5). Unfortunately, too few animals were available to run a parallel experiment on breeding by non-luminescent

Table 3
Flashing rates per minute by *Dyakia striata*.*

Experiment	Number of minutes (n)	Mean	SE	Mini-mum	Maximum
Isolates					
1. Control conditions	165	24.8	0.34	16	38
3. Cucumber diet	165	27.6	0.36	18	38
5. Cool temperature	135	13.6	0.33	6	19
6. Continuous light	208	22.4	0.28	16	35
7. Continuous dark	220	22.7	0.28	15	33
Groups					
1. Control conditions	165	26.7	0.38	18	42
3. Cucumber diet	165	30.1	0.38	19	48
5. Cool temperature	165	13.6	0.29	7	25
6. Continuous light	213	22.2	0.30	13	34
7. Continuous dark	220	24.1	0.30	17	35
9. Groups of 2	184	22.0	0.31	14	34
10. Groups of 5	480	25.5	0.23	16	42
11. Groups of 10	960	23.1	0.14	13	39
12. Groups of 15	1440	20.6	0.11	12	38
13. Young snails	960	27.4	0.14	17	39
14. Middle-age snails	960	23.2	0.14	14	36
15. Old snails	960	20.8	0.15	13	37

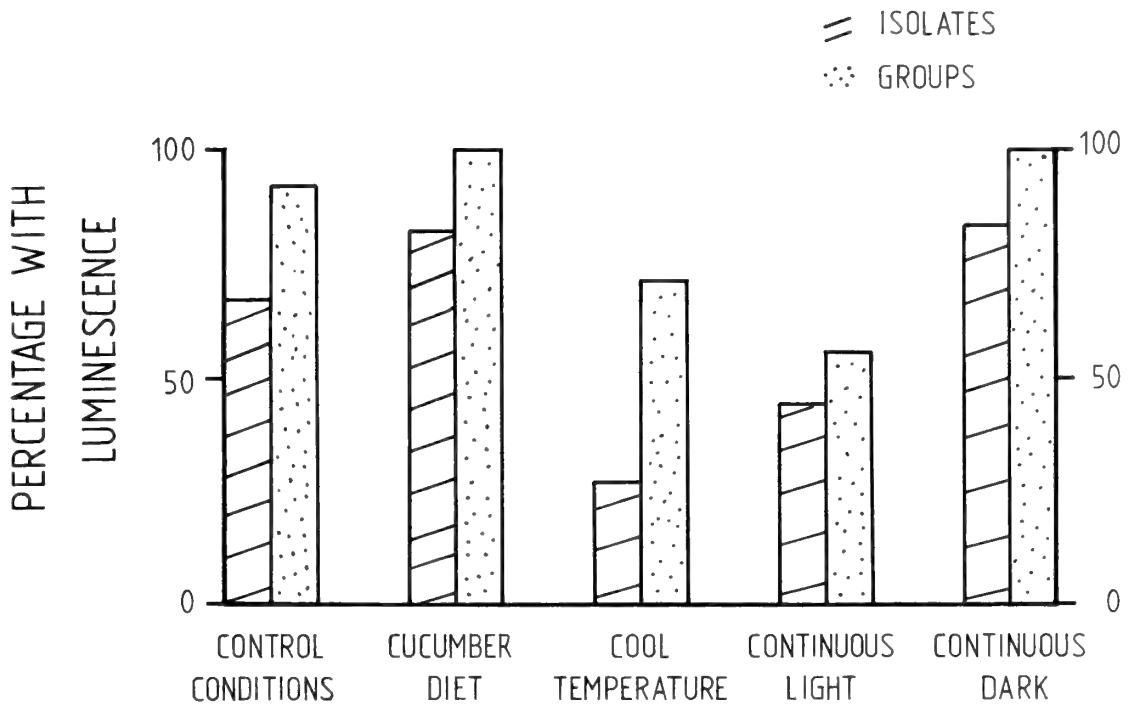
* Excludes experiments on *Achatina fulica* diet (no. 4) and starvation (no. 8), because all snails soon died, and experiment on non-luminescence (no. 2).

Table 2

Nutritional analysis of diets fed *Dyakia striata*, in percent.

Constituent	Food				
	Cucumber	Carrot	Lettuce	<i>Achatina</i>	Rat-chow
Moisture	96.9	92.5	95.6	84.3	12.5
Dry matter	3.1	7.5	4.4	15.7	87.5
	100.0%	100.0%	100.0%	100.0%	100.0%
Crude protein	18.8	6.7	24.4	60.8	24.0
Crude fat	6.1	5.1	4.6	6.6	3.0
Ash	15.2	13.5	15.8	12.4	8.5
Nitrogen-free extract*	59.9	74.7	55.2	20.2	64.5
	100.0%	100.0%	100.0%	100.0%	100.0%

* Primarily carbohydrates.



EXPERIMENT

Figure 1

Percentages of luminescent snails, *Dyakia striata*, among 117 snails surviving until the end of the study.

individuals. *Dyakia striata* is a simultaneous hermaphrodite.

RESULTS

Mortality

Numbers of dead snails were recorded for the first eight experiments. All snails fed the *Achatina fulica* diet died within four weeks; and most of those not fed at all died within five weeks, although one snail survived seven weeks. Among the remaining experiments, there were no significant differences, whether isolates and groups were combined in a one-sample test ($\chi^2 = 6.0$; d.f. = 5; $P > 0.05$) or separated into a two-sample test ($\chi^2 = 1.4$; d.f. = 5; $P > 0.05$). Thus luminescent and non-luminescent snails had similar mortality rates.

Flashing Rates

Among the non-social treatments for which data were in adequate numbers (*i.e.*, control conditions, cucumber diet, cool temperature, continuous light, and continuous dark), the number of flashes per minute varied considerably, although not in the same manner for both group sizes (*i.e.*, isolates and groups of 10). This finding was

revealed by a highly significant interaction between experimental type and group size ($F = 6.3$; d.f. = 4, 1811; $P < 0.001$). A further analysis, using a Student-Newman-Keuls multiple range test, was conducted on the 10 combinations of group size and experimental type. The test identified five significantly separate subsets: (1) groups on cucumber diet, (2) isolates on cucumber diet and groups under control conditions, (3) isolates under control conditions and groups in continuous dark, (4) isolates in continuous dark, and isolates and groups in continuous light, and (5) isolates and groups under the cool temperature. Table 3 gives the basic statistics for these classes and shows that the first subset had the highest flashing rate and the last subset had the lowest.

Although the sample of flashing from starved snails was, we judged, too small for detailed comparisons with other experiments, the mean number of flashes per minute for both isolates and groups combined ($\bar{X} = 14.8$; SE = 0.37; $n = 80$ min) indicated that these snails flashed comparatively little. Their rate was only slightly higher than the combined rate for isolated and grouped snails under the cool temperature ($\bar{X} = 13.6$; SE = 0.31; $n = 300$ min).

Snails in groups of five had the highest rate and those in groups of 15 had the lowest (Table 3). A one-way analysis of variance on the number of flashes per minute

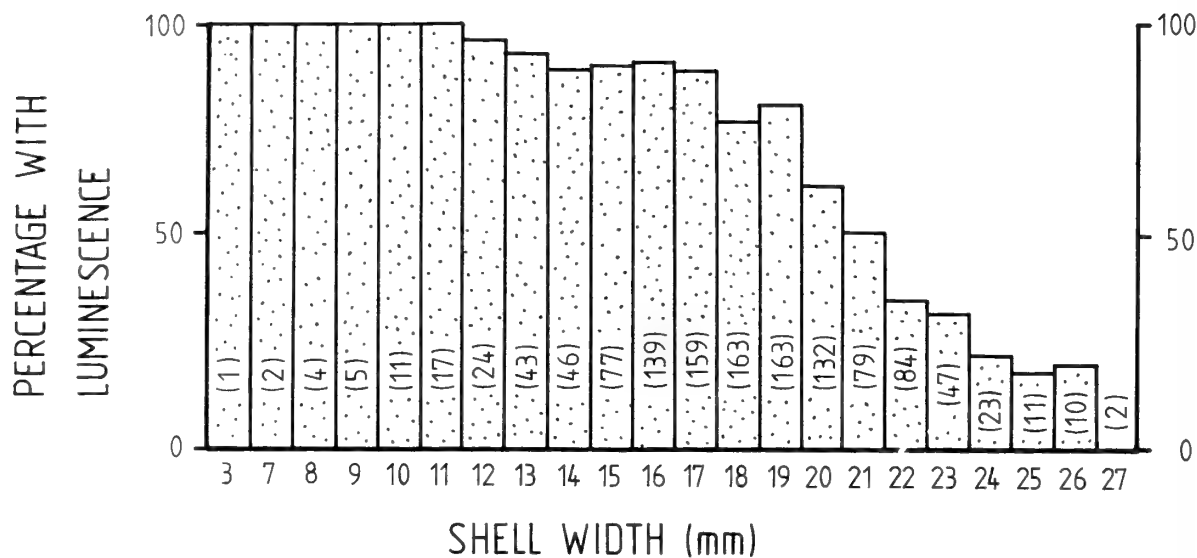


Figure 2

Percentages by shell width of luminescent snails, *Dyakia striata*, among 1242 newly captured snails (sample size per mm in parenthesis).

by snails in groups of different sizes was highly significant ($F = 170.4$; d.f. = 3, 3060; $P < 0.0001$), and a Student-Newman-Keuls test revealed that every group size differed significantly from every other size.

For the experiments on age, young snails flashed most and old snails flashed least (Table 3). A one-way analysis of variance on number of flashes per minute was highly significant ($F = 564.1$; d.f. = 2, 2877; $P < 0.0001$), and the Student-Newman-Keuls test revealed significant separation of all three age classes.

Loss of Luminescence

Excluding the experiment on non-luminescent snails, five treatments among the first eight had snails surviving until the end of the study (Figure 1). Neither the variations among experiments (Friedman test: $\chi^2_r = 7.3$; d.f. = 4; $P > 0.05$) nor those between the two group sizes (sign test: $x = 0$; $n = 5$; $P > 0.05$) were significant. However, in the latter test isolates and groups were nearly significantly different ($P = 0.06$), and within every experiment isolates accounted for a larger proportion of non-luminescent animals than did groups. Moreover, among snails fed the *Achatina fulica* diet and those starved, only isolates (eight and four respectively) had become non-luminescent before and during.

No snail within the first eight experiments regained the ability to luminesce after having lost it. This finding is supported by data on snails examined immediately after capture, which showed that the proportion of luminescent animals decreased with increasing shell size (Figure 2). In total, 73.4% of the sample was luminescent just after capture.

In the experiment to test the effects of reproductive

maturity (no. 16 in Table 1), six isolates (ranging in size from 17.8 to 21.5 mm) laid three clutches of over 20 eggs each and four clutches of 1–4 eggs each. The large clutches were laid by snails that were luminescent both before and after laying. All three produced some live young. Three of the small clutches were also laid by luminescent snails that retained their ability to luminesce after laying, but one was produced by a non-luminescent animal. None of these clutches was viable.

Among the 40 pairs in the experiment on reproduction, only one snail (19.6 mm) became non-luminescent; neither it nor its companion laid eggs. Eighteen of the other pairs laid 34 clutches of 4–38 eggs, and one pair laid single eggs on two occasions. Except for three clutches eaten by adults and the single eggs, all clutches produced live young. Five of the 18 pairs laid three or four clutches each, which revealed that even multiple laying by an individual snail did not result in loss of luminescence. Members of pairs that laid viable eggs ranged in size from 16.5 to 25.5 mm.

DISCUSSION

Our results strengthen four previous, unsubstantiated conclusions regarding luminescence in *Dyakia striata*, namely, that (1) it is present in all young snails but in decreasing proportions of snails with increasing age (HANEDA & TSUJI, 1969), (2) its loss, once having occurred, is permanent (MARTOJA & BASSOT, 1970), (3) it is not influenced by reproductive development (COPELAND & MANERI, in press), and (4) it most likely serves an intraspecific social function (COPELAND & MANERI, in press). The experiments also revealed a considerable sensitivity by *D. striata* in its flashing behavior to a wide

range of social and environmental conditions. Some of the results for loss of luminescence were less clear; but they appeared to indicate that functioning of the photogenic organ is affected by some adverse conditions (*i.e.*, isolation, and perhaps also cool temperatures and excessive light) but not others (*i.e.*, starvation and diet).

As mentioned in the Introduction, MARTOJA & BASSOT'S (1970) hypothesis that *Dyakia striata* becomes non-luminescent when the gonads mature seemed unlikely on recent evidence. The finding that luminescent snails can repeatedly lay clutches of viable eggs disproves it—indeed, whether non-luminescent snails can reproduce successfully remains to be seen. Rather, our results support HANEDA & TSUJI'S (1969) unquantified assertion that loss of luminescence is an individual characteristic of adult snails. For example, within the collection of freshly captured snails, one snail had become non-luminescent by 12 mm, while two were still capable of producing light at 26 mm, nearly the maximum size for this species (see Figure 2). Both luminescent and non-luminescent forms of *D. striata* had identical growth rates during the three months of study (LOH, 1984), as well as similar mortality rates.

HANEDA (1963, 1979) reported that snails from 5 to 15 mm flash most. Our experiments on body size confirmed that flashing declines with age, at least in snails of 10 mm and over. In addition, the few snails under 10 mm that we observed had brighter flashes than those of reproductive size, and many luminescent animals over 20 mm had very dim lights.

A social role for luminescence in *Dyakia striata* is supported by results from our experiments on control conditions, cucumber diet, and continuous dark, in which grouped snails flashed more than did isolated snails (see Table 3). In addition, fewer grouped than isolated snails in every one of the first eight experiments (except, of course, that on non-luminescent snails) lost the ability to flash (see Figure 1 and text). Some of the experiments may even be interpreted as providing evidence for an ecological link between flashing and grouping behaviors. In the experiment on group size, groups of five flashed most; and five is a common, if not the most common, number of snails found together in the field on rotting meat, fruit, or vegetables. Among the food-related treatments (including starvation), rates of flashing varied considerably (see Table 3 and text), but losses of luminescence did not (see Figure 1 and text). Lastly, among all experiments rates were highest for the cucumber diet.

Taken together, our findings suggest that flashing in *Dyakia striata* promotes the aggregation of young snails on sources of food that are probably widely scattered in space or time, or both. We stress, however, that the experiments were not designed to give direct evidence of light communication. Moreover, any hypothesis on communication among non-reproductive *D. striata* faces a major theoretical problem: according to present theory (*e.g.*, TRIVERS, 1985), it requires kin selection, or the unlikely alternative explanation that flashing snails are behaving

altruistically towards other snails that may or may not be relatives. There is currently no information on kin-selected behavior in *D. striata*. The few data available on the reproductive biology and ecology of this species (*e.g.*, large clutches and restricted microhabitats) do not preclude the possibility.

ACKNOWLEDGMENTS

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Review of the Nudibranch Genus *Melibe* (Opisthobranchia: Dendronotacea) with Descriptions of Two New Species

by

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. Two new species of the genus *Melibe* are described. *Melibe liltvedi* sp. nov. is known from the Atlantic coast of South Africa while *M. megaceras* sp. nov. is recorded from the Hawaiian Islands. The morphologies of *M. leonina* (Gould, 1852), *M. pilosa* Pease, 1860, and *M. rosea* Rang, 1829, are also described. A review of morphological variability within the genus is provided.

INTRODUCTION

THE DENDRONOTACEAN GENUS *Melibe* consists of 13 described species from throughout the world. Most species have been superficially described, with an emphasis on external morphological features. For example, the reproductive morphology of the type species, *Melibe rosea* Rang, 1829, remains largely undescribed. Several species, *M. capucina* Bergh, 1875, *M. engeli* Risbec, 1937, *M. maugiana* Burn, 1960, *M. ocellata* Bergh, 1888, and *M. rangi* Bergh, 1875, are known only from their original descriptions. Collections of two apparently undescribed species from South Africa and Hawaii have prompted a review of the genus in order that adequate morphological comparisons can be made.

Family TETHYIDAE

Melibe Rang, 1829

Melibe leonina (Gould, 1852)

(Figures 1A, 2, 8D, 9C)

Chioraera leonina GOULD, 1852:310, pl. 26, fig. 404.

Melibe leonina (Gould, 1852): BERGH, 1875:364.

Melibe pellucida BERGH, 1904:11, pl. 4, figs. 33, 34;

O'DONOGHUE, 1922:148.

Chioraera dalli HEATH, 1917:137, pls. 11-13; O'DONOGHUE, 1922:148.

Melibe dalli (Heath, 1917): ODHNER, 1936:1117.

Material: Three specimens, California Academy of Sciences, CASIZ 061504, collected intertidally, on *Zostera marina* Linnaeus, Limantour Estero, Marin County, Cal-

ifornia, 28 December 1967, T. M. Gosliner. One specimen, collected from 16 m depth, on outer side of breakwater, Monterey Harbor, Monterey Bay, Monterey County, California, 4 August 1978, T. M. Gosliner.

Description: External morphology: The preserved specimens are a maximum of 50 mm in length. The living animals (Figure 1A) are translucent yellowish with small opaque white spots present on the notum. A single specimen photographed by the author in Friday Harbor, Washington, had large, scattered opaque white spots, approximately 2 mm in diameter. The large circular oral hood contains an inner and outer row of papillae along its entire margin. The papillae on the outer row of the hood are significantly longer than those of the inner row. The rhinophore sheaths (Figure 8D) are relatively large and are flattened. The rhinophores are perfoliate with 4-6 lamellae. There are 3-6 cerata on either side of the body. Each ceras (Figure 9C) is flattened and ovoid in shape. The anteriormost cerata are largest. The anus is located anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The single gonopore is ventral to the anteriormost right ceras. The foot is relatively narrow with an entire anterior margin.

Digestive system: The buccal mass is thick, muscular, and devoid of jaws or a radula. A short salivary gland is present near the middle of either side of the buccal mass. From the posterior end of the buccal mass a short esophagus expands into the muscular stomach. The stomach contains no chitinous plates. On the dorsal side of the stomach is a pair of glandular folded pouches, each of

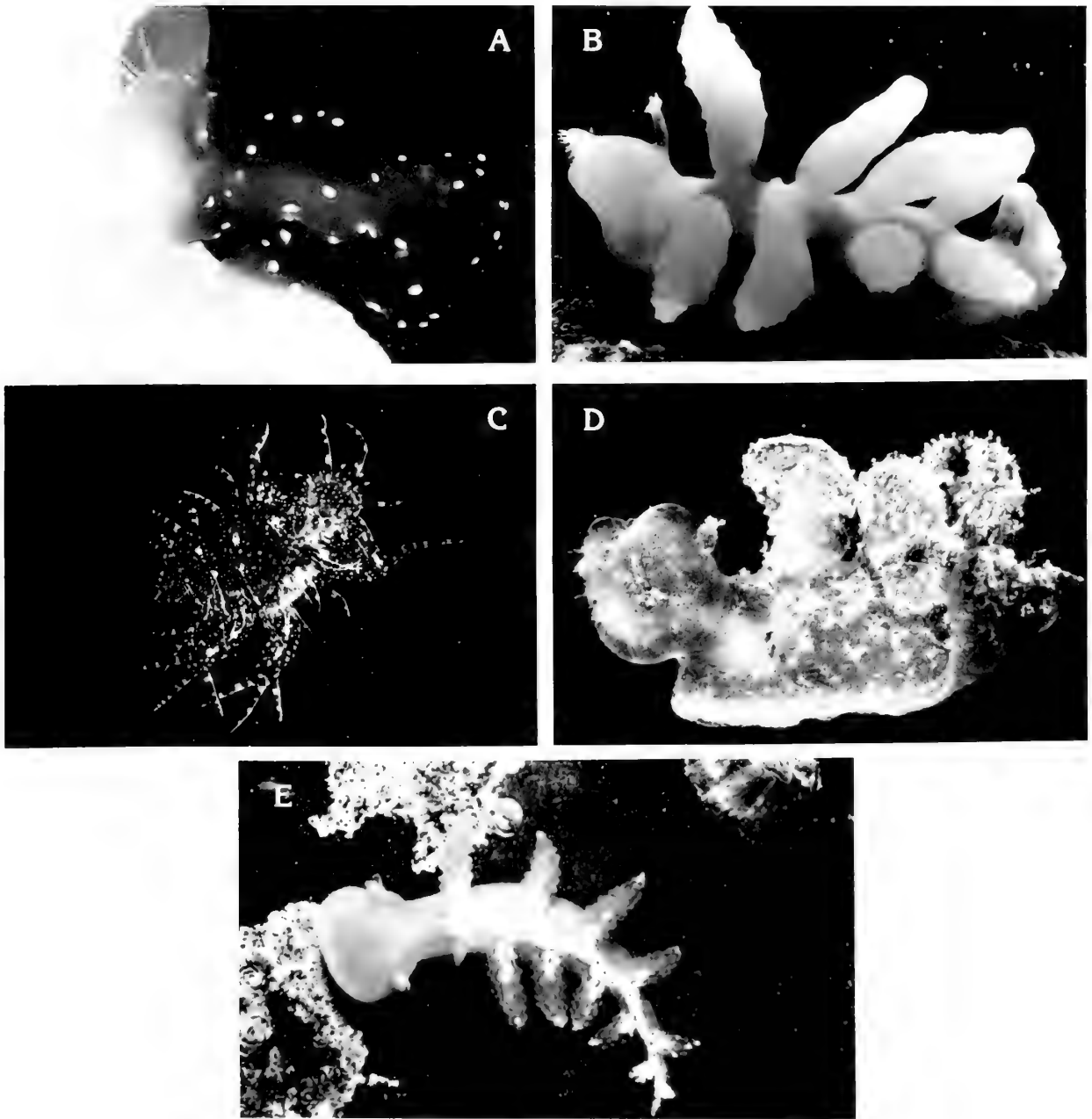


Figure 1

Living animals. A. *Melibe leonina* (Gould, 1852). B. *Melibe liltvedi* sp. nov. C. *Melibe megaceras* sp. nov. D. *Melibe pilosa* Pease, 1860. E. *Melibe rosea* Rang, 1829.

which expands into digestive gland ducts. The right duct is undivided and extends to the base of the anteriormost right ceras. The left duct bifurcates, with an anterior branch joining the base of the anteriormost left ceras and a posterior branch extending to the bulk of the digestive gland. This digestive gland mass branches to each of the posterior cerata. The posteroventral portion of the stomach is a lobed glandular region that is contiguous with the

intestine. The intestine extends ventrally and recurves dorsally, terminating at the anus.

Central nervous system (Figure 2A): The arrangement of ganglia is identical to that described for *Melibe megaceras*, with a few notable exceptions. The cerebral ganglia are bilobed anteriorly and there is a prominent bulge near their posteromedial margin. Similarly, the pedal ganglia are prominently bilobed.

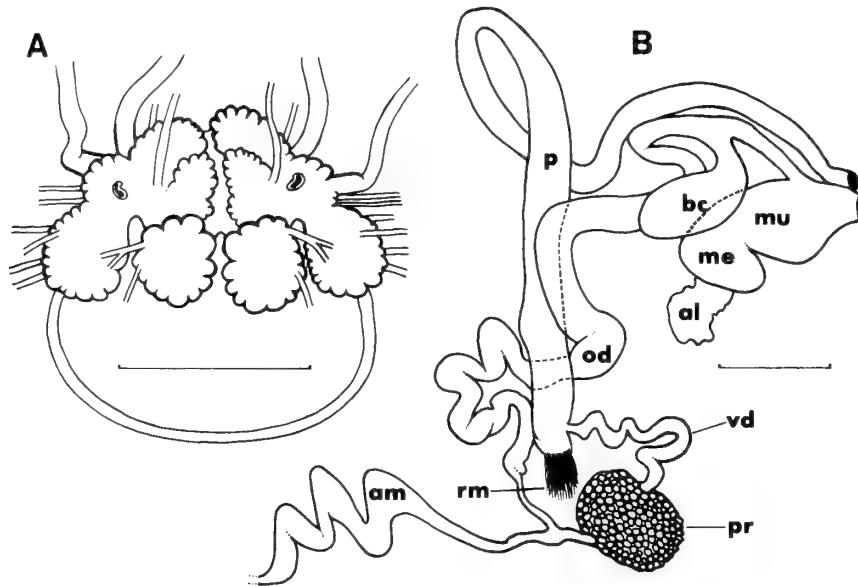


Figure 2

Melibe leonina (Gould, 1852). A. Central nervous system, scale = 1.0 mm. B. Reproductive system, scale = 2.0 mm. al = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; p = penis; pr = prostate; rm = retractor muscle; vd = vas deferens.

Reproductive system (Figure 2B): All of the reproductive organs are elongate. The ampulla is narrow with approximately four convolutions. It divides distally into the vas deferens and the oviduct. The oviduct abruptly widens and consists of numerous convolutions. It continues to widen distally and curves adjacent to the penis. The oviduct contains numerous tubules within its walls. Near its base, the oviduct branches into a short duct which leads to the pyriform bursa copulatrix. The oviduct continues distally and joins the female genital opening. The albumen gland is situated near the proximal limit of the female gland mass. It merges with the membrane gland and the larger mucous gland. The mucous gland joins the oviduct at the female gonopore. The vas deferens enters the prostate a short distance after the branching of the ampulla. The prostate is spherical and consists of numerous small flocculent bodies. From the distal end of the prostate the vas deferens again emerges as a muscular, highly convoluted ejaculatory portion. The vas deferens enters the penial sac laterally. From the posterior end of the penial sac is attached a short penial retractor muscle. The penis is exceedingly elongate and flattened for most of its length. It is unarmed and terminates at the male gonopore.

Natural history: Specimens have been collected from the intertidal region on eel grass, *Zostera marina* Linnaeus, to a depth of 18 m, where they frequently are encountered on the kelp *Macrocystis pyrifera* (Linnaeus) Agardh. Gut contents of specimens collected from Limantour Estero indicate that *Melibe leonina* feeds on gammaridean and

caprellid amphipods. AJESKA & NYBAKKEN (1976) have studied in detail the biology of *Melibe leonina*.

Distribution: Specimens have been collected from Dall Island, Alaska, to Punta Abrejos, on the Pacific coast of Baja California, and into the Gulf of California (MC-DONALD, 1983).

Melibe liltvedi Gosliner, sp. nov.

(Figures 1B, 3, 8E, 9D, 10D)

Type material: Holotype: South African Museum, Cape Town, SAM A35776, collected in 20 m of water, Bakoven, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 21 March 1981, W. R. Liltved.

Paratypes: SAM A35773, one specimen, collected in 18 m of water, Hottentot's Huisie, Oudekraal, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 18 February 1981, W. R. Liltved. SAM A35772, one specimen, collected in 25 m depth, Llandudno, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 17 September 1982, W. R. Liltved.

Etymology: This species is named for my friend and colleague, Bill Liltved, for his assistance in all aspects of my opisthobranch research in southern Africa.

Description: External morphology: The preserved specimens (Figure 3A) range from 19 to 55 mm in length. When alive the animals (Figure 1B) are uniformly opaque white in color. The entire, circular oral hood is large

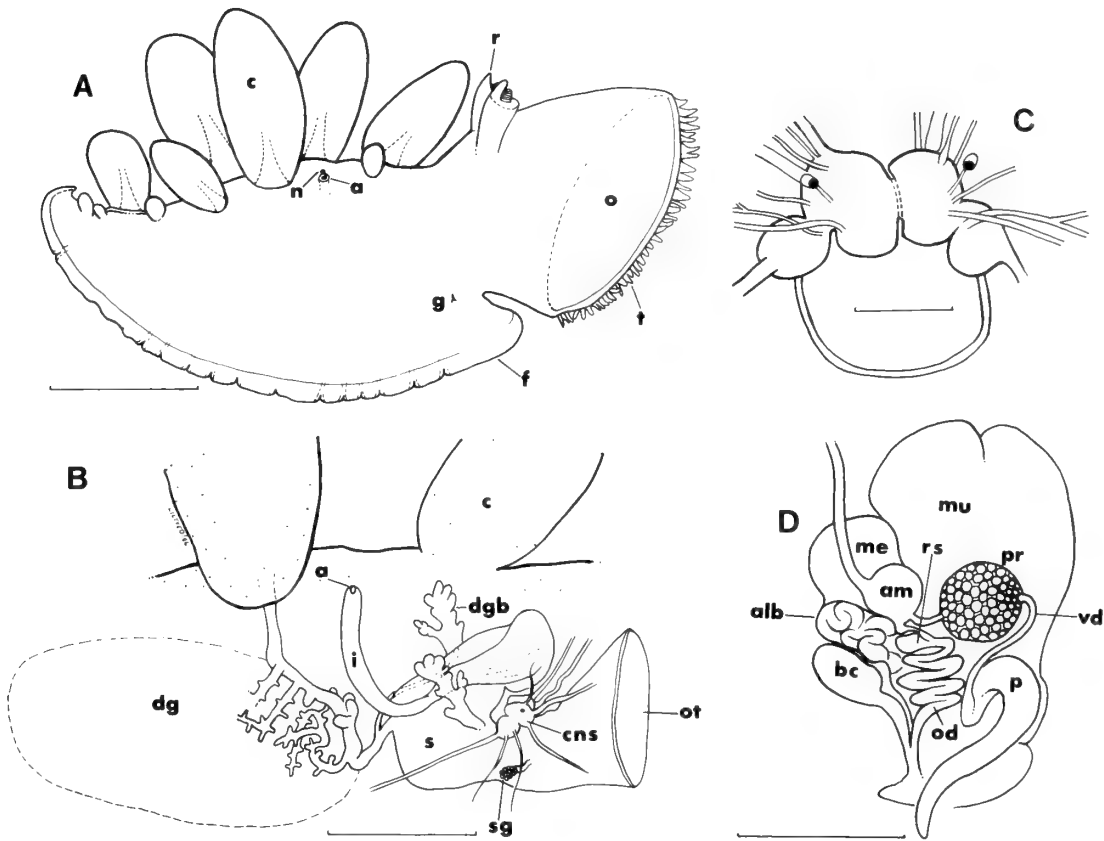


Figure 3

Melibe liltvedi sp. nov. A. Right lateral view of juvenile preserved specimen, scale = 3.0 mm. a = anus; c = ceras; f = foot; g = gonopore; n = nephroproct; o = oral hood; r = rhinophore; t = tentacle. B. Digestive system, scale = 2.0 mm. a = anus; c = ceras; cns = central nervous system; dg = digestive gland; dgb = digestive gland branch; i = intestine; ot = oral tube; s = stomach; sg = salivary gland. C. Central nervous system, scale = 1.0 mm. D. Reproductive system, scale = 1.0 mm. alb = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; p = penis; pr = prostate; rs = receptaculum seminis; vd = vas deferens.

relative to the remainder of the body. It contains 2 to 3 rows of elongate papillae along its margin. The innermost row contains the longest papillae. The rhinophore sheath (Figure 8E) is simple, with an expanded margin that possesses a single triangular papilla at its posterior end. The rhinophores are perfoliate with 6 or 7 lamellae. There are 5 or 6 cerata on either side of the body. Each ceras (Figure 9D) is pyriform with low tubercles scattered over its surface, giving the entire ceras a nodular appearance. The anus is situated on the right side of the body, anterior to the second ceras. The nephroproct is immediately dorsal to the anus. The single gonopore is ventral to the anteriormost right ceras. The anteriorly rounded foot is narrow relative to the rest of the body.

Digestive system (Figure 3B): The buccal mass is muscular throughout its length. No vestige of jaws or a radula is present in any of the three specimens examined. Extending from the posterior portion of either side of the

buccal mass is a short, lobate salivary gland. From the posterior limit of the buccal mass the short esophagus widens into the stomach. The posterior end of the stomach is muscular and lined with 5 or 6 chitinous plates (Figure 10D). There is a single glandular duct emerging from either side of the stomach. The right duct enters the base of the anteriormost right ceras. The left duct is bifurcate, with the anterior branch entering the anteriormost left ceras and the posterior duct giving rise to the bulk of the lobate digestive gland. The posterior digestive gland branches to the base of each of the posterior cerata. The intestine emerges from the posterodorsal end of the stomach, curves ventrally, recurves dorsally, and terminates at the anus.

Central nervous system (Figure 3C): The arrangement of ganglia within the nervous system is identical to that described for *Melibe megaceras*. The ganglia are smooth in texture and rounded.

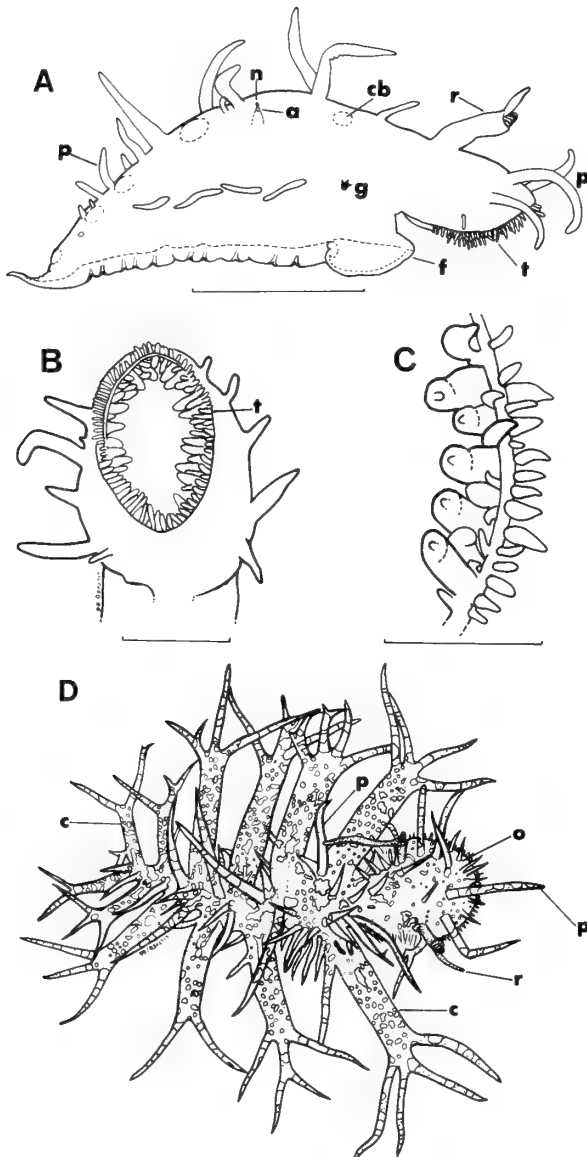


Figure 4

Melibe megaceras sp. nov. A. Right lateral view of preserved animal, scale = 10 mm. a = anus; cb = ceratal base; f = foot; g = gonopore; n = nephroproct; p = papilla; r = rhinophore; t = tentacles. B. Oral hood, scale = 2.5 mm. t = tentacles. C. Detail of oral hood, scale = 2.0 mm. D. Dorsal view of living animal. c = cerata; o = oral hood; p = papilla; r = rhinophore.

Reproductive system (Figure 3D): The preampullary duct is elongate and expands into an S-shaped ampulla. The ampulla bifurcates into the oviduct and vas deferens. The oviduct is narrow and convoluted, widening gradually more distally. The proximal end enters a blind sac that probably functions as a short receptaculum seminis. More distally the oviduct joins the duct of the bursa copulatrix near the bursa's junction with the common genital

atrium. The bursa copulatrix is pyriform, with a relatively short duct in all three specimens examined. The female gland mass is well developed. The albumen gland is the most proximal portion, consisting of several large ovoid bodies. The membrane gland is immediately distal to the albumen gland and is highly folded. The mucous gland forms the largest portion of the nidamental glands. The vas deferens continues proximally from its junction with the oviduct and ampulla. After a short distance it enters the globular prostate gland, which is composed of numerous large spherical bodies. The vas deferens emerges again from the prostate as a wider, muscularized ejaculatory duct, which gradually widens into the curved, conical penis.

Natural history: Specimens have been found from 15 to 45 m depth, where they generally inhabit crevices near the bases of cliffs. Frequently, they have been seen in small aggregations of 3–5 individuals.

Distribution: Animals have been found only along the Atlantic coast of the Cape Peninsula from Bakoven to Haut Bay.

Melibe megaceras Gosliner, sp. nov.

(Figures 1C, 4, 5, 8G, 9F, 10E)

Melibe sp.: KEMPF, 1984.

Type material: Holotype: California Academy of Sciences, CASIZ 061507, collected in 3 m of water, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 12 February 1986, by Terrence M. Gosliner.

Paratypes: CASIZ 061508, 14 specimens, collected in 3 m of water, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 12 and 13 February 1986, Terrence M. Gosliner and Michael T. Ghiselin. CASIZ 061509, 6 specimens, collected in 3 m of water, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 15 February 1986, Terrence M. Gosliner and Michael T. Ghiselin.

Etymology: The epithet *megaceras* refers to the large cerata, which may be almost as long as the body proper.

Description: External morphology: The preserved animals (Figure 4A) are a maximum of 30 mm in length. The living animals (Figures 1C, 4D) are translucent white with brown spots, which represent concentrations of zooxanthellae. Alternating bands of brown and opaque white pigment are present on the rhinophores, cerata, and on the elongate papillae on the head, notum, and sides of the body. Irregularly spaced on the body and cerata are patches of opaque white pigment. The oral hood (Figure 4B) is circular and entire along its margin. It is small for the size of the animal, reaching about 7 mm in diameter. There are two rows of tentacles along the margin of the oral hood (Figure 4C). The tentacles forming the outer row are all similar in size. The inner row alternates between small, medium, and large tentacles. The largest

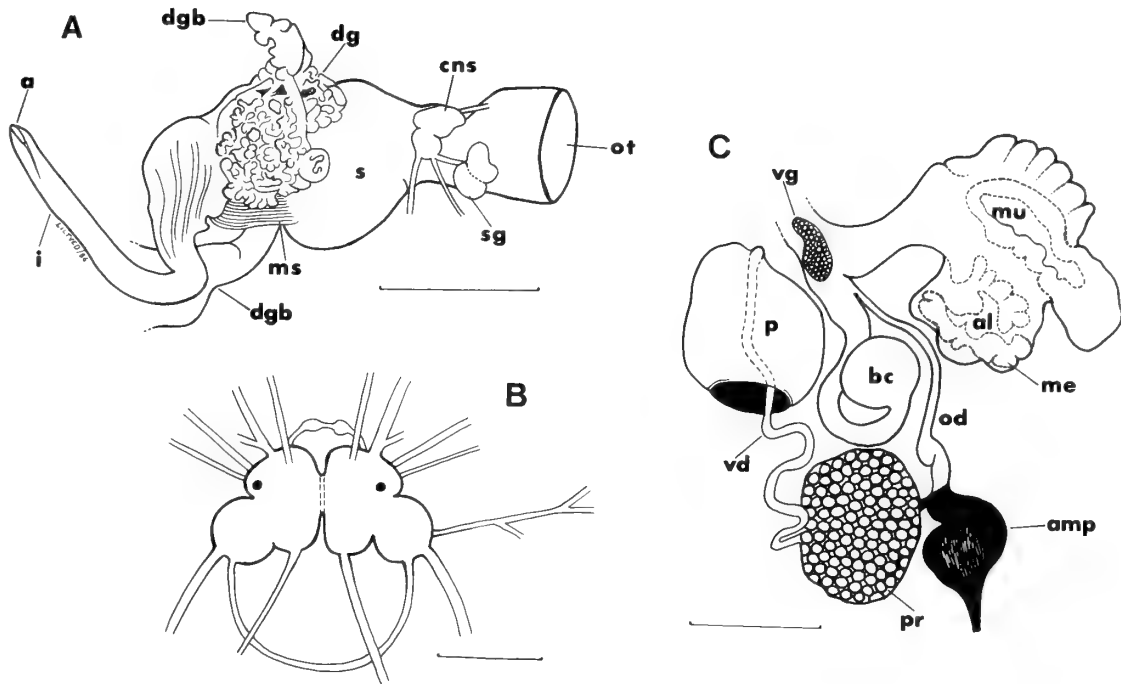


Figure 5

Melibe megaceras sp. nov. A. Digestive system, scale = 2.0 mm. a = anus; cns = central nervous system; dg = digestive gland; dgb = digestive gland branch; i = intestine; ms = muscular portion of stomach; ot = oral tube; s = stomach; sg = salivary gland. B. Central nervous system, scale = 0.5 mm. C. Reproductive system, scale = 1.0 mm. al = albumen gland; amp = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; od = oviduct; p = penis; pr = prostate; vd = vas deferens; vg = vaginal glands.

tentacles of this row are larger than those forming the outer row. The rhinophore sheath (Figure 8G) is tall and cylindrical. At its posterior apex is a single elongate appendage. The rhinophores are perfoliate, consisting of 7–9 lamellae. There are 5 or 6 elongate cerata along either side of the body. The longest are the anteriormost, which may reach 25 mm in length. Each ceras (Figure 9F) terminates in 1–5 elongate apices, which may equal the basal portion of the ceras in their length. Numerous unbranched papillae are situated around the body. From 8 to 17 of these papillae are randomly distributed on the dorsal surface of the oral hood. Another 11–20 papillae are situated along either side of the notum and 6–9 papillae are present along either side of the body. The anus (Figure 4A) is situated between the first and second cerata of the right side of the body. The nephroproct is located immediately dorsal to the anus. The single gonopore is ventral to the anteriormost ceras. The foot is narrow, about 6 mm in width. Its anterior margin is rounded and entire.

Digestive system (Figure 5A): The buccal mass is broad and muscular, without any jaws or radula, in the five specimens dissected. A fold where the jaws are usually situated is devoid of any chitinous tissue. There is a single globular salivary gland on either side of the buccal mass. The esophagus is exceedingly short and expands abruptly into the saccate stomach. The posterior half of the stomach

is lined with approximately 20 chitinous plates (Figure 10E), which are highest posteriorly. The digestive gland is situated largely on the dorsal surface of the stomach. A tubule of dense digestive gland tissue enters both of the anteriormost cerata. Emerging from the bifurcation of the left digestive gland is a duct that leads posteriorly to the diffuse digestive gland, which interdigitates with the ootestis. A portion of this diffuse digestive gland enters the base of each of the posterior cerata. The intestine emerges from the posterior end of the stomach, bends ventrally, and recurves dorsally to the anal opening.

Central nervous system (Figure 5B): The cerebral and pleural ganglia are almost entirely fused. The pedal ganglia are smaller than the cerebral and pleural ganglia and are connected by an elongate commissure. The buccal ganglia are situated on the ventral surface of the buccal mass and are joined to the cerebral ganglia by thin, short nerves. The eyes are situated on short nerves that join the dorsal surface of the cerebral ganglia.

Reproductive system (Figure 5C): The ampulla is S-shaped and black in color in the five specimens examined. The pigment was retained in specimens, regardless of the preservative in which they were placed; thus it is not a fixation artifact. At its distal end the ampulla bifurcates into the vas deferens and the oviduct. The oviduct is thick and muscular and joins the female gland mass and bursa

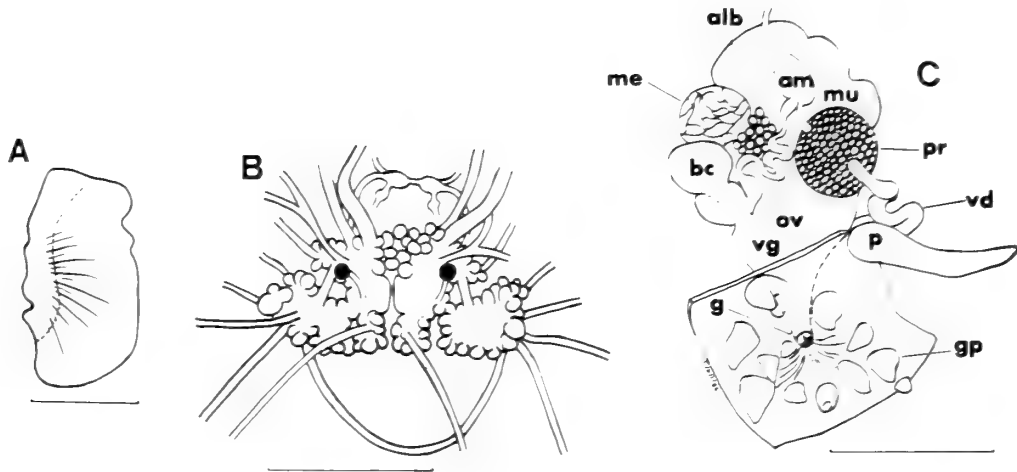


Figure 6

Melibe pilosa Pease, 1860. A. Jaw, scale = 0.25 mm. B. Central nervous system, scale = 1.0 mm. C. Reproductive system, scale = 2.0 mm. alb = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; ov = oviduct; p = penis; pr = prostate; vd = vas deferens; vg = vaginal glands.

copulatrix near the single gonopore. The largest portion of the female gland mass is the mucous gland. The albumen and membrane glands are approximately the same size. The spherical bursa copulatrix joins the oviduct and female glands by means of a thick, elongate duct. There is a small, pyriform glandular area at the junction of the three female ducts. The vas deferens, following its origin from the ampulla, expands into a large prostate gland, consisting of numerous follicles. At the distal end of the prostate the vas deferens narrows into a muscular ejaculatory segment, containing a few convolutions. Here the vas deferens enters the paddle-shaped penis and terminates at the common gonopore.

Natural history: Specimens of *Melibe megaceras* have been found on shallow-water sand flats and may be seasonally common. Specimens in Kaneohe Bay were found sympatrically with *M. pilosa*. When actively crawling, the cerata are held horizontally and the animal is exceedingly flat. The translucent brownish color with opaque white spots makes this animal virtually invisible on a sandy substratum. Fragments of small crustaceans were present in the feces (Steve Kempf, personal communication). When disturbed the animals swim by means of rapid, lateral flexure of the body.

Development: The white egg mass is a broad, coiled ribbon that is attached to the sand substratum by a mucous thread. There are 1–3 eggs per capsule. The zygotes are 72 μm in diameter. From oviposition to hatching at 24–26°C requires 3 days. The shell of the planktotrophic larvae is 128 μm in length and is type-1. Development times and measurements were provided by Steve Kempf (personal communication).

Distribution: Specimens of *Melibe megaceras* have been found on several occasions within Kaneohe Bay, Oahu. A few specimens have been collected from Kauai and Maui (Steve Kempf, personal communication). This species is not known outside the Hawaiian Islands, but this may be a result of its cryptic appearance.

Melibe pilosa Pease, 1860

(Figures 1D, 6, 8H, 9I, 10H, 11A)

Melibe pilosa PEASE, 1860:34.

Jacunia papillosa DE FILIPPI, 1867:233; ODHNER, 1936:1116.

Melibe vexillifera BERGH, 1880:162, pl. 2, figs. 1–11, pl. 3, figs. 1–3; ODHNER, 1936:1116.

Material: California Academy of Sciences, San Francisco, CASIZ 061506, one specimen, intertidal, Diamond Head Beach Park, Oahu, Hawaii, 8 February 1986, Michael T. Ghiselin. CASIZ 061501, one specimen, 2 m depth, on west side of sand bar, Kaneohe Bay, Oahu, Hawaii, 10 February 1986, Terrence M. Gosliner. CASIZ 061505, one specimen, Inhaca Island, Mozambique, July 1955, William Macnae.

Description: External morphology: The preserved specimens range from 30 to 120 mm in length. Living animals (Figure 1D) are translucent white with various amounts of brown pigment, owing to the presence of symbiotic zooxanthellae. Large, isolated spots of dark brown may be present on the cerata. Scattered small spots of opaque white are distributed over most of the body's surface. The oral hood is entire, circular, and of moderate diameter. There are four rows of tentacles along the margin of the oral hood, with the innermost row containing the longest ones. The rhinophore sheath (Figure 8H) widens near its

free end. Several papillae are present along the posterior margin of the sheath, including a multifid papilla at the posterior apex. The perfoliate rhinophores possess 9-11 lamellae. The triangular cerata (Figure 9I) are arranged in alternating rows with 5-8 cerata per side. The cerata have numerous elongate papillae scattered over their surfaces. Similar unbranched or branched papillae are present on the notum and sides of the animal. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is directly anterior to the anus. The gonopore is situated ventral to the anteriormost ceras and is surrounded by several conical papillae. The foot is narrow and rounded anteriorly.

Digestive system: The thick muscular buccal mass contains a pair of jaws (Figures 6A, 11A) with approximately 35 irregular denticles along the elongate masticatory border. A radula is entirely absent. The esophagus is elongate and wide, widening even more posteriorly, where it expands to form the stomach. The stomach is muscular posteriorly and contains 16-30 narrow, laterally compressed chitinous plates (Figure 10H). The arrangement of the branches of the digestive gland is identical to that described for *Melibe liltvedi*, except that the digestive gland is more highly branched, with finer tubules.

Central nervous system (Figure 6B): The arrangement of the ganglia is identical to that described above for other members of the genus. The major morphological difference is that all of the dorsal ganglia of *Melibe pilosa* have a highly nodular appearance, owing to the fact that most of the large neuronal cells are located peripherally on the ganglia. The buccal ganglia are rounded in appearance and possess smaller peripheral ganglia near the major buccal bodies.

Reproductive system (Figure 6C): The ampulla is short and saccate, branching distally into the oviduct and vas deferens. The oviduct is narrow and highly convoluted. It joins the female atrium at a glandular expansion at the base of the bursa copulatrix. This gland is circular and situated at the proximal end of the female atrium. The bursa copulatrix is short and spherical. The female gland mass is composed of the yellow follicular albumen gland, the sinuous membrane gland, and the large, smooth mucous gland. A short distance from the bifurcation of the ampulla, the vas deferens enters the spherical prostate. The prostate consists of numerous small spherical bodies. The vas deferens emerges again from the distal portion of the prostate as a thicker ejaculatory duct. It expands into the conical, unarmed penis.

Natural history: Specimens have been found commonly in the Hawaiian Islands (present study), where they inhabit intertidal and shallow subtidal reef and sand flats. The animals are very cryptic on mixed sand, rock, and algal substrata. The single specimen from Mozambique examined in this study contained a gravid female portunid crab in its stomach. The egg mass consists of several whorls (BERTSCH & JOHNSON, 1981).

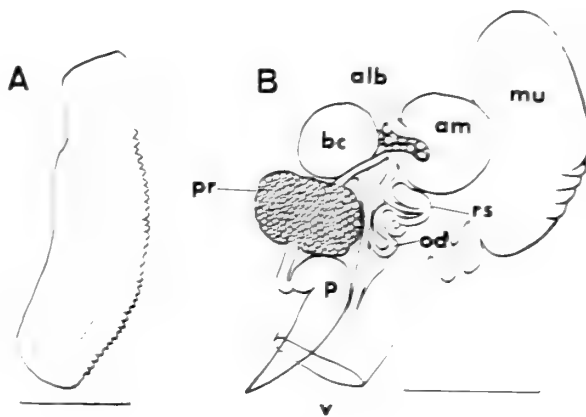


Figure 7

Melibe rosea Rang, 1829. A. Jaw, 0.25 mm. B. Reproductive system, scale = 1.0 mm. alb = albumen gland, am = ampulla, bc = bursa copulatrix, mu = mucous gland, od = oviduct, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina.

Melibe rosea Rang, 1829

Figures 1E, 7, 8J, 9J, 10J, 11B

Melibe rosea RANG, 1829:130, pl. 3, fig. 3.

Material examined: SAM A33980, four specimens, collected intertidally under rocks, Dale Brook, False Bay, Cape Province, South Africa, 18 November 1979. T. M. Gosliner, CASIZ 061503, two specimens, 10 m depth, Phillips Reef, Algoa Bay, Cape Province, South Africa, 14 May 1984. W. R. Liltved.

Description: External morphology: The preserved animals range from 6 to 80 mm in length. The living animals (Figure 1E) are uniformly light: rose pink to orange. Frequently a linear swath of opaque white pigment may be present on the notum, between the cerata and extending on to the bases of the cerata. Most of the surface of the animal is covered with small rounded tubercles. The circular oral hood is entire along its margin. There are 2 or 3 rows of papillae along the margin of the oral hood. There are 3 rows of papillae along the posterior half of the oral hood, which diminish to 2 rows in the anterior half of the hood. The innermost papillae are the thickest and longest. The rhinophore sheaths (Figure 8J) are rounded apically, without any papillae. The perfoliate rhinophores possess 5-9 lamellae. There are 6 or 7 cerata on either side of the body. Each ceras (Figure 9J) is pyriform with dense rounded tubercles, giving the entire ceras a nodular appearance. The anteriormost cerata are largest. The anus is situated directly anterior to the second ceras on the right side. The nephroproct is immediately dorsal to the anus. The gonopore is ventral to the anteriormost ceras. The foot is narrow and rounded anteriorly.

Digestive system: The buccal mass is thick and muscular. The chitinous jaws (Figure 7A, 11B) have a mas-

Table 1
Morphology of species of *Melibe*.

Species	Distribution	Jaws	Rhinophore sheaths	Oral hood	Stomach plates	Penis	References
<i>M. australis</i> (Angas, 1864)	New South Wales, Victoria, Australia	absent	simple without papillae	with single row of tentacles	unknown	unknown	ALLAN, 1932; BURN, 1957; THOMPSON, 1972
<i>M. bucephala</i> Bergh, 1902	Thailand, Red Sea	small with undulate margin	flattened leaf-like	incised anteriorly, 5 rows of tentacles innermost longest	20	large conical	BERGH, 1902; O'DONOGHUE, 1929
<i>M. capucina</i> Bergh, 1875	Cebu, Philippines	with 22 or 23 coarse denticles	small simple without papillae	4 rows of tentacles	10	simple conical	BERGH, 1875
<i>M. engel</i> Risbec, 1937	New Caledonia	with small denticles	flattened with large papillae	2 rows	12	broad conical	RISBEC, 1937, 1953
<i>M. fimbriata</i> Alder & Hancock, 1864	Zanzibar, India, Japan, Mediterranean	thin cuticular	simple without papillae	incised anteriorly, outer row shortest	28	elongate	ALDER & HANCOCK, 1864; ELIOT, 1902, 1913; THOMPSON & CRAMPTON, 1984
<i>M. japonica</i> Eliot, 1913	Japan	with undulate margin	simple with posterior tubercle	2 or 3 rows posteriorly, 9 or 10 rows of tentacles	24	"broad"	ELIOT, 1913; BABA, 1949
<i>M. leonina</i> (Gould, 1852)	Alaska to Baja California	absent	flattened leaf-like	2 rows of tentacles, outer rows longer	absent	elongate flattened	ODHNER, 1936; MACFARLAND, 1966; present study
<i>M. liltvedi</i> sp. nov.	Atlantic Ocean, southern Africa	absent	simple with posterior papilla	2 or 3 rows of tentacles	5 or 6	elongate conical	present study
<i>M. maugeana</i> Burn, 1960	Victoria, Australia	unknown	with posterior papillate margin	single row of tentacles	unknown	unknown	BURN, 1957, 1960
<i>M. megaceras</i> sp. nov.	Hawaiian Islands	absent	with elongate posterior papilla	2 rows, inner row longer but alternating	20-24	broad spatulate	present study
<i>M. mirifica</i> (Allan, 1932)	Queensland, Australia	with undulate margin	simple funnel-shaped	incised anteriorly, 4 rows of tentacles	about 40	unknown	ALLAN, 1932; WILLAN & COLEMAN, 1984
<i>M. ocellata</i> Bergh, 1888	Indian Ocean, Polo-Edam	smooth	unknown	2 or 3 rows of tentacles	24	conical	BERGH, 1888
<i>M. pilosa</i> Pease, 1860	Mozambique-Hawaii	with undulate margin	with 1-3 posterior papillae	4 rows of tentacles, inner row longest	about 30, 16-20 present study	conical	ODHNER, 1936; EDMUNDS & THOMPSON, 1972; present study
<i>M. rangi</i> Bergh, 1875	Red Sea	25-30 denticles	with posterior papilla	2 rows of tentacles	26-31	broad conical	BERGH, 1875
<i>M. rosea</i> Rang, 1829	temperate South Africa	large with 22 denticles	simple without papillae	2 or 3 rows posteriorly, 2 rows anteriorly but subequal	7-8	elongate conical	BERGH, 1907; THOMPSON & CRAMPTON, 1984; present study

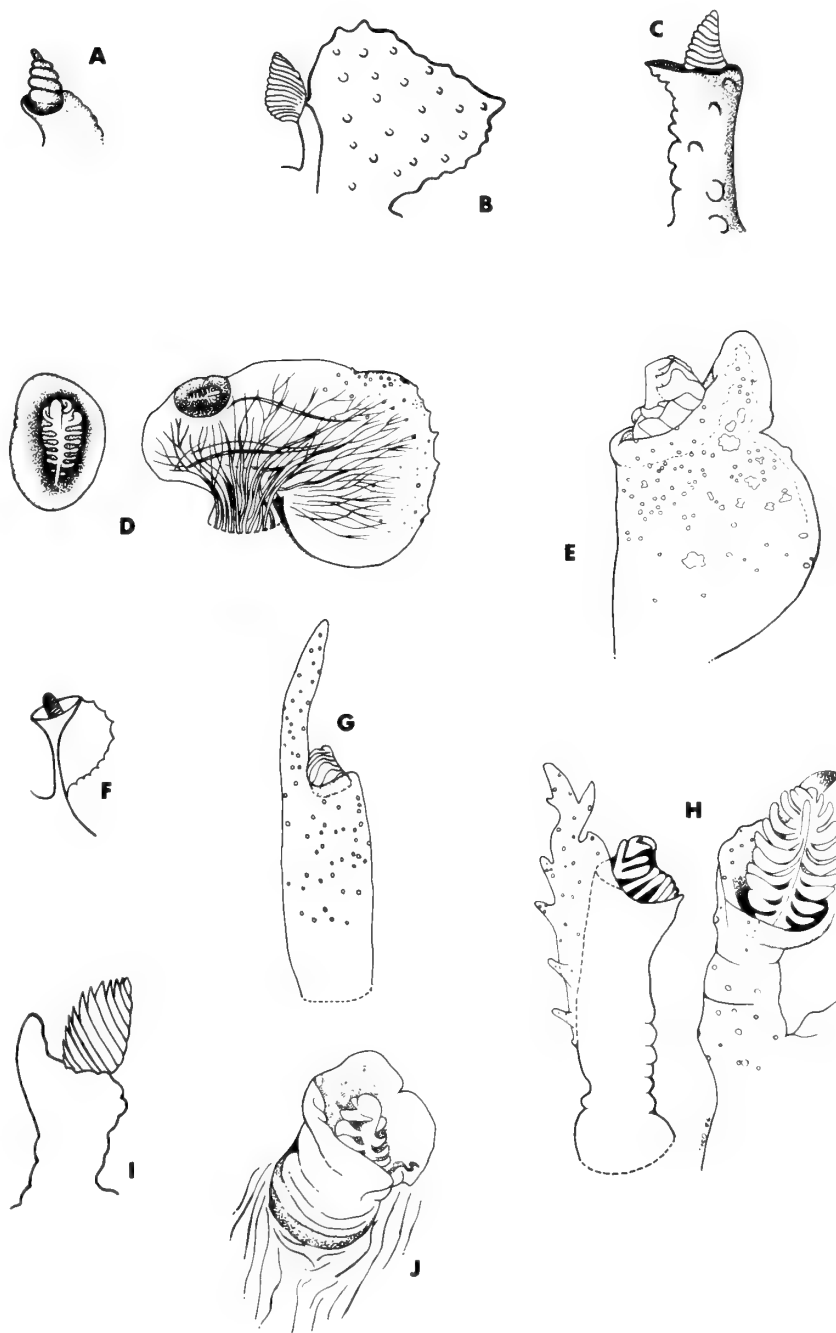


Figure 8

Rhinophores of *Melibe*. A. *Melibe australis* (Angas, 1864) (after THOMPSON, 1972). B. *M. bucephala* Bergh, 1902 (after O'DONOGHUE, 1929). C. *M. fimbriata* Alder & Hancock, 1864 (after THOMPSON & CRAMPTON, 1984). D. *M. leonina* (Gould, 1852). E. *M. liltvedi* sp. nov. F. *M. maugeana* Burn, 1960 (after BURN, 1957). G. *M. megaceras* sp. nov. H. *M. pilosa* Pease, 1860. I. *M. rangi* Bergh, 1875 (after BERGH, 1875). J. *M. rosea* Rang, 1829.

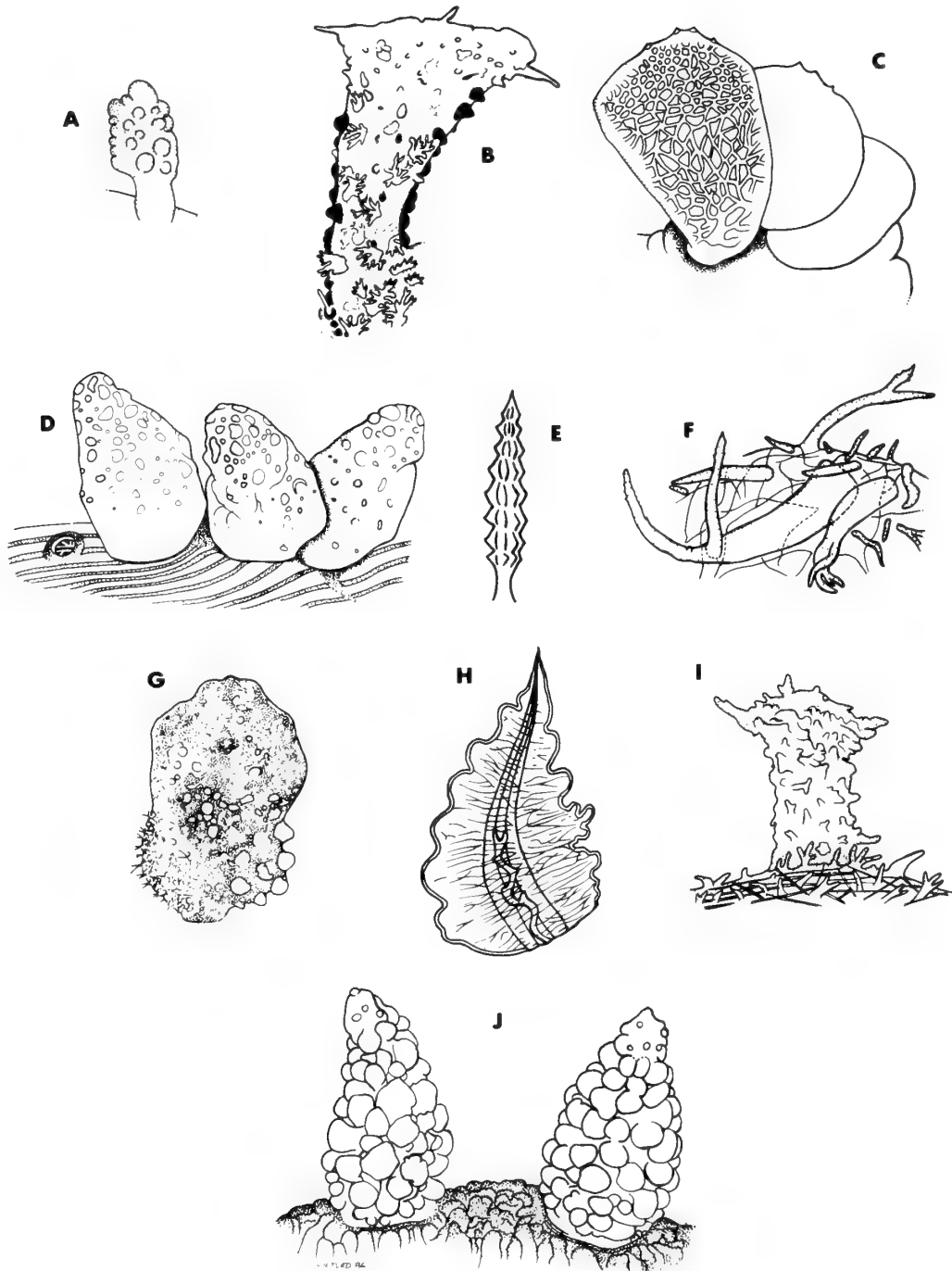


Figure 9

Cerata of *Melibe*. A. *Melibe australis* (Angas, 1864) (after THOMPSON, 1972). B. *M. fimbriata* Alder & Hancock, 1864 (after THOMPSON & CRAMPTON, 1984). C. *M. leonina* (Gould, 1852). D. *M. liltvedi* sp. nov. E. *M. maugeana* Burn, 1960 (after BURN, 1957). F. *M. megaceras* sp. nov. G. *M. mirifica* (Allan, 1932) (after ALLAN, 1932). H. *M. ocellata* Bergh, 1888 (after BERGH, 1888). I. *M. pilosa* Pease, 1860. J. *M. rosea* Rang, 1829.

ticatory border containing 22 denticles in one specimen observed. A radula is entirely absent. The remainder of the digestive system is virtually identical to that described

for *Melibe liltvedi* with one notable exception. In *M. rosea*, 7 or 8 chitinous plates are within the stomach (Figure 10J).

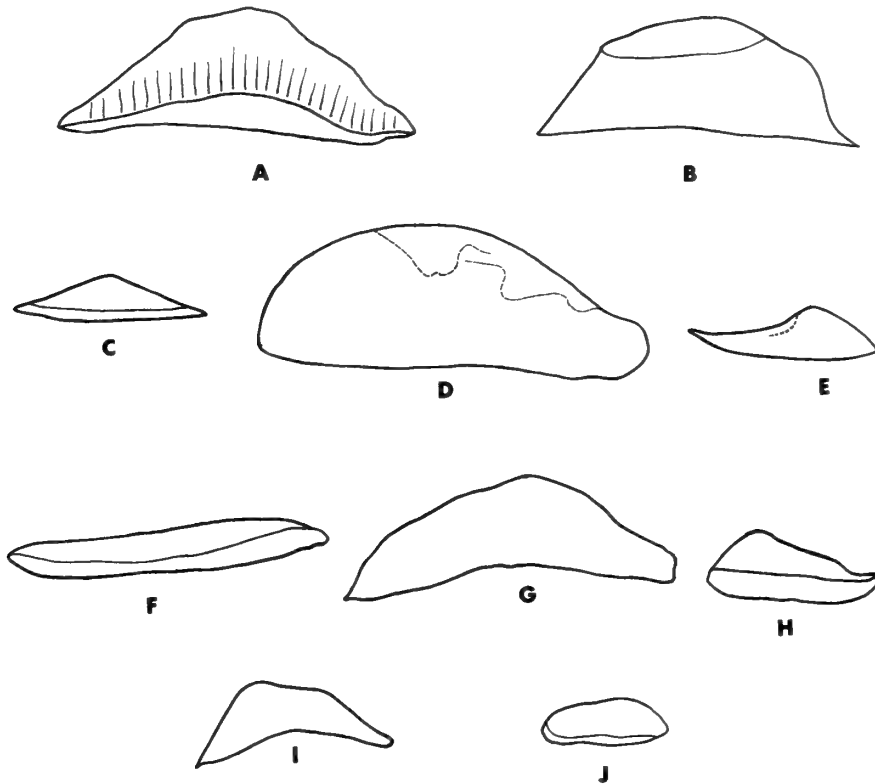


Figure 10

Stomach plates of *Melibe*. A. *Melibe bucephala* Bergh, 1902 (after BERGH, 1902). B. *M. capucina* Bergh, 1875 (after BERGH, 1875). C. *M. fimbriata* Alder & Hancock, 1864 (after THOMPSON & CRAMPTON, 1984). D. *M. liltvedi* sp. nov. E. *M. megaceras* sp. nov. F. *M. mirifica* (Allan, 1932) (after ALLAN, 1932). G. *M. ocellata* Bergh, 1888 (after BERGH, 1888). H. *M. pilosa* Pease, 1860. I. *M. rangi* Bergh, 1875 (after BERGH, 1875). J. *M. rosea* Rang, 1829.

Central nervous system: The arrangement of simply rounded ganglia is identical to that described for *Melibe liltvedi* and *M. megaceras*.

Reproductive system (Figure 7B): The narrow preampullary duct widens into the short, curved ampulla. The ampulla narrows again and divides into the vas deferens and oviduct. The oviduct is thick and convoluted. At its proximal end is an expanded muscular portion, which probably functions as a receptaculum seminis. More distally the oviduct enters the duct of the bursa copulatrix near the middle or at the base of the bursa duct. The duct of the spherical bursa copulatrix is elongate, almost half of the length of the entire genital mass. The albumen gland is a small tightly convoluted mass. The membrane gland is slightly larger and consists of larger folds. The mucous gland is the largest portion of the genital mass and is folded several times. The vas deferens enters the spherical prostate after a moderate distance. The prostate consists of numerous small glandular spheres. From its distal end the muscular vas deferens emerges again and widens into the conical, unarmed penis.

Natural history: Specimens commonly have been found under rocks in the mid-intertidal zone to a depth of 10 m. The specimens were in the open rarely during the day and are likely to be nocturnal.

Distribution: This species appears to be endemic to southern Africa and has been found on the Atlantic coast from Port Nolloth to Port Alfred on the Indian Ocean.

DISCUSSION

The Tethyidae are dendronotacean nudibranchs with an expanded oral hood that is used to capture crustacean prey. In *Fimbria*, the oral hood is less well developed and accessory gills are present at the base of the cerata. The external morphology of *Melibe* is conservative (Table 1). All known species possess an oral hood with 1-10 rows of tentacles around the margin, 4-9 cerata per side, an anus and nephroproct anterior to the second ceras, and a gonopore ventral to the first ceras.

The oral hood is indented anteriorly in *Melibe fimbriata*, *M. mirifica*, *M. japonica*, and *M. bucephala*, but is entire

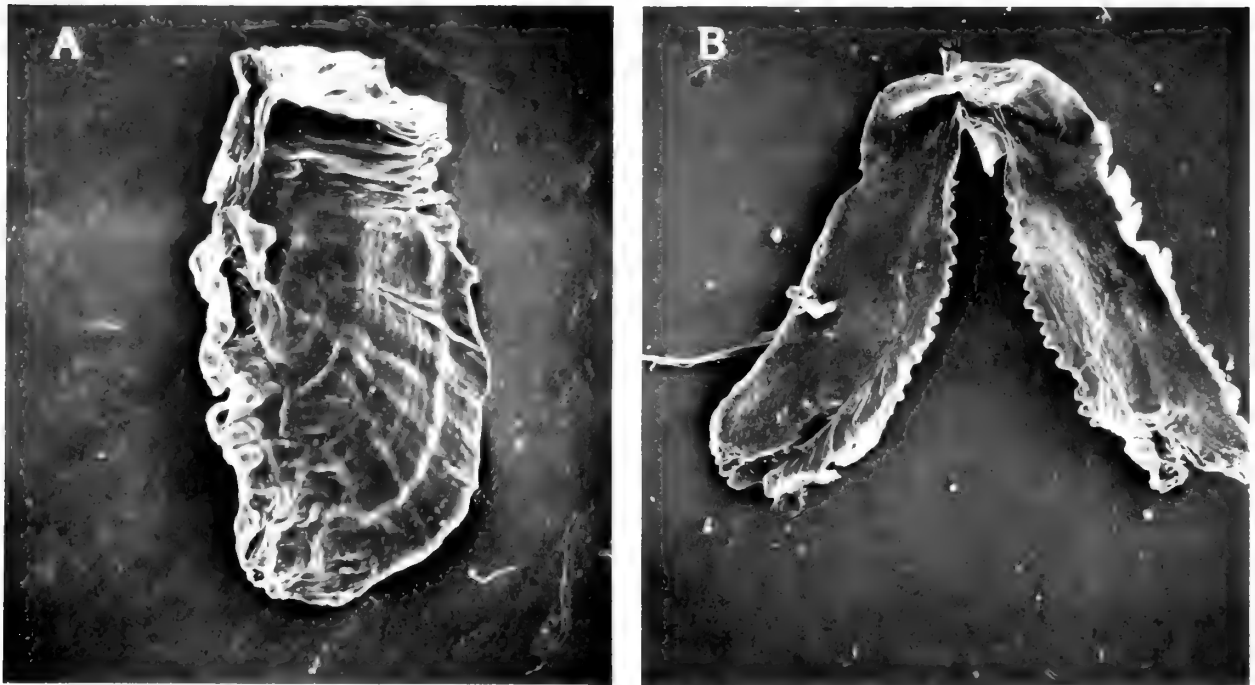


Figure 11

Scanning electron micrographs of jaws. A. *Melibe pilosa* Pease, 1860, $\times 110$. B. *M. rosea* Rang, 1829, $\times 60$.

in the remaining species. The number of rows of tentacles and their relative lengths differ significantly among species (Table 1). *Melibe liltvedi* has alternately large medium and small tentacles forming the inner row of the oral hood. The elaboration of the rhinophore sheaths differs considerably among species (Figure 8). *Melibe leonina* (Gould, 1852), *M. bucephala* Bergh, 1902, *M. engeli* Risbec, 1937, and *M. maugiana* Burn, 1960 (a new name proposed by Burn for *M. pellucida* Burn, 1957, which is a junior homonym of *M. pellucida* Bergh, 1904) have broad flattened rhinophore sheaths, whereas they are cylindrical or funnel-shaped in the remaining species. In some species, *M. rangi* Bergh, 1875, *M. liltvedi*, *M. megaceras*, and *M. pilosa* Pease, 1860, the rhinophore sheath may bear papillae on its posterior margin. In *M. megaceras* the rhinophoral papilla is elongate, almost equaling the remainder of the sheath in its length.

The shape of the cerata may vary considerably among species of *Melibe* (Figure 9). *Melibe ocellata* Bergh, 1888, and *M. rangi* Bergh, 1875, are the only species known to possess acutely pointed cerata. *Melibe rosea* Rang, 1829, *M. australis* (Angas, 1864) and *M. liltvedi* all have rounded tuberculate cerata, similar in appearance to those found in species of *Doto*. In *M. fimbriata*, *M. engeli*, *M. japonica*, *M. mirifica*, *M. bucephala*, and *M. pilosa* the cerata are wedge-shaped with numerous tubercles or papillae, some of which may be highly ramified. The cerata of *M. mau-*

geana are acutely pointed with several distinct rows of tubercles. In *M. megaceras* the cerata have 1–5 acutely pointed apices. The cerata of *M. leonina* are flattened and foliaceous.

The notum is smooth in *Melibe leonina*, *M. maugiana*, and *M. liltvedi* and tuberculate to papillate in the remaining species.

A radula is absent in all members of the genus, although jaws may be present in some species and absent in others. Jaws are absent in *Melibe australis*, *M. leonina*, *M. liltvedi*, and *M. megaceras*. Distinct denticles may be present along the masticatory border of the jaws of *M. capucina*, *M. engeli*, *M. rangi*, and *M. rosea*, whereas the border is undulate or smooth in the remaining species. The esophagus is short in most species but is far more elongate in *M. pilosa* (present study).

A series of chitinous gastric plates is present in the posterior portion of the stomach of all species of *Melibe*, with the exception of *M. leonina*, where they are entirely wanting. The number of plates varies intraspecifically, but *M. rosea*, *M. capucina*, *M. engeli*, and *M. liltvedi* have far fewer plates than do other species. The shape of the plates is somewhat variable, but some species such as *M. megaceras* have plates of a consistently distinct shape (Figure 10).

Most of the digestive gland tissue of *Melibe megaceras* is concentrated around the stomach. In all other species

where it is known, the digestive gland is distributed far more evenly in the posterior portion of the body, where it interdigitates with the ovotestis.

The relative shape of the ganglia forming the central nervous system varies somewhat among species. In *Melibe japonica* and *M. pilosa* the ganglia have a nodular appearance owing to the presence of peripheral nerve cells (ELIOT, 1913; present study). In *M. leonina* the cerebral ganglia are bilobed anteriorly with prominent medial lobes. In the remaining species that have been studied all the ganglia are uniformly rounded.

The reproductive morphology varies within *Melibe*, but has not been described fully in the majority of species. The entire genital mass of *M. leonina* is elongate (MACFARLAND, 1966; present study), but forms a distinct genital mass in the other species where it has been described. The ampulla of *M. megaceras* is black in all specimens examined. BERGH (1875) described the presence of a fan-shaped organ in *M. rangi*. This represents a dilation that contains numerous convolutions or lobes of the oviduct and may function as a receptaculum seminis. This expansion of the oviduct was evident in most species of *Melibe* examined in this study but was most pronounced in specimens of *M. liltvedi* and *M. rosea*. It is also illustrated for *M. leonina* (MACFARLAND, 1966:pl. 54, fig. 1). In other species the oviducal folds are not contained in a distinct dilation. The relative position and elaboration of the bursa copulatrix also seems to vary intraspecifically. *Melibe pilosa* and *M. megaceras* are the only described species that have a dilated vaginal atrium. They also possess a discrete mass of vaginal glands near the gonopore. The relative size of the glandular bodies forming the prostate varies interspecifically and may be useful in separating closely allied species. The penis is conical in most species but is broad and spatulate in *M. megaceras*.

Comparison of several similar taxa is difficult owing to incomplete descriptions or inadequate attention to intraspecific variability. WILLAN & COLEMAN (1984) suggested that *Melibe mirifica* (Allan, 1932) may be synonymous with *M. japonica* Eliot, 1913. The external body form of *M. fimbriata* Alder & Hancock, 1864, is also similar to the above taxa, as all three taxa have an indented anterior margin of the oral veil and papillate cerata. Although it is likely that the three species may in fact be synonymous, inadequate material and incomplete descriptions prevent a detailed comparison at this time. *Melibe bucephala* can be readily differentiated from the other species with an indented anterior margin of the oral hood by its broad rhinophore sheath with an undulating posterior margin. *Melibe capucina*, *M. engeli*, *M. japonica*, *M. ocellata*, and *M. rangi* are known only from the descriptions of preserved material. Their status is open to question until further comparative material is available.

The two species of *Melibe* described here can be readily distinguished from all other previously described species. *Melibe liltvedi* is most closely allied to *M. rosea* and *M. australis*. All three taxa have *Doto*-like cerata and are found

only in southern oceans. There are several consistent morphological differences that distinguish these species. *Melibe australis* bears only a single row of tentacles around the margin of the oral hood, while *M. rosea* and *M. liltvedi* have 2 or 3 rows. *Melibe liltvedi* has a triangular extension on the posterior end of the rhinophore sheath that is absent in the other two species. There are numerous elongate dendritic papillae along the medial portion of the notum in *M. australis*. In *M. rosea* there are scattered simple tubercles over the entire body while in *M. liltvedi* the body surface is entirely smooth. The number of cerata per side of the body differs between the three species. In *M. australis* there are 4 or 5 rows, in *M. liltvedi* 5 or 6 rows, and in *M. rosea* 6 or 7 rows. These differences are not size dependent. The cerata of *M. rosea* and *M. liltvedi* are more elongate than those of *M. australis*. There are dense tubercles covering the surface of the cerata in *M. rosea* while in *M. liltvedi* the tubercles are far more scattered. *Melibe liltvedi* is uniformly opaque white in color while the other two species are yellowish, orange, or pink with scattered opaque white pigment.

There are also internal differences that separate these three taxa. *Melibe rosea* has distinct jaws with a well developed, denticulate masticatory border, which are entirely absent in *M. australis* and *M. liltvedi*. There are more stomach plates in *M. rosea* (7 or 8) than in *M. liltvedi* (5 or 6). The stomach plates of *M. australis* are undescribed. The bursa copulatrix in *M. rosea* is spherical, with an elongate duct, while in *M. liltvedi* it is small and pyriform, with a short duct. These differences are consistent and are independent of size and maturity. The prostate of *M. rosea* is composed of small glandular bodies while those of *M. liltvedi* are much larger.

Melibe megaceras differs markedly from all other described members of the genus. It has elongate cerata with up to five apical branches. It is the only species known to possess a papilla on the posterior end of the rhinophore sheath, which approximates the basal portion of the sheath in length. Internally, it lacks jaws, as in *M. australis*, *M. leonina* and *M. liltvedi*. The digestive gland mass largely surrounds the stomach in *M. megaceras* while in the other species it is far more developed posteriorly. *Melibe megaceras* is the only known species with a broad, spatulate penis and a darkly pigmented ampulla. Together with *M. pilosa*, *M. megaceras* is the only species with a muscular vaginal atrium and vaginal glands. In *M. megaceras* the vaginal glands form a mass on the outer surface of the atrium, while in *M. pilosa* they are located within the atrium.

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A New *Trivia* (Triviidae) and *Primovula* (Ovulidae) (Gastropoda: Prosobranchia) from the South Atlantic and Southwest Indian Oceans

by

WILLIAM R. LILTVED

Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. Two new species of mesogastropods are described from the south Atlantic and southwest Indian oceans. Only the shell is known in the case of *Trivia vemacola* sp. nov. Descriptions of the shell and radula are given for *Primovula diaphana* sp. nov.

INTRODUCTION

VEMA SEAMOUNT is a submerged volcanic peak about 640 km off the Atlantic coast of South Africa, at approximately 31°38'S, 8°20'E. During the first scientific expedition to Vema in the early 1960s by Simpson and Heydorn, a number of ascidians were collected and later described by MILLAR (1968). Among these samples were the shells of a new species of *Trivia* here described. Initially, the shells were misidentified within the collections of the University of Cape Town where they remained for two decades. Recently the material was recognized to represent an undescribed species of *Trivia*.

In 1985, Dr. Allan D. Connell of Durban, South Africa, dredged specimens of a species of *Primovula* also believed to be undescribed. Here I describe these two new taxa and compare them with previously known taxa.

Trivia vemacola Liltved, sp. nov.

(Figure 1)

Shell (Figure 1): Small for *Trivia*, peripherally almost circular, anterior terminal only slightly produced. Dorsum domed and evenly corrugate. Labrum wide, protruding beyond body whorl throughout its entire length. Inner edge of labrum with 9-11 coarse, evenly spaced apically rounded denticles with wide semicircular interstices. Ribs coarse, even, mostly extending continuously around body whorl, over columellar peristome into aperture. Eight to ten denticles arising as thickened portions of transverse ribs crossing columellar peristome. A secondary row of denticles occurs within aperture, forming continuous row

merging with fossular denticles. Fossular area moderately wide and concave. Aperture narrow, recurved at extremities, slightly dilated anteriorly. Spire not visible. Base flattened. Color off-white to pale pink.

Measurements:

	<u>length (mm)</u>	<u>width (mm)</u>	<u>height (mm)</u>
Holotype	4.7	3.9	3.1
Paratype A	5.6	4.7	3.6
Paratype B	5.8	5.2	3.6
Paratype C	3.9	3.5	2.5
Paratype D	5.5	4.7	3.6
Paratype E	5.3	4.7	3.5
Paratype F (subadult)	4.8	4.2	3.2

Type locality: Vema Seamount, approximately 640 km off the Atlantic coast of South Africa (approximately 31°38'S, 8°20'E).

Type deposition: Holotype (SAM A37238) and paratypes B-F (SAM A37243) South African Museum, Cape Town. Paratype A: California Academy of Sciences, San Francisco (CAS 060451). Type material collected during the Simpson and Heydorn Expedition to Vema Seamount in 1960.

Habitat and distribution: Holotype and paratypes B-F: Vema Seamount (31°37.8'S, 8°19.3'E), 61 m, bottom temperature 15.30°C. Paratype A: Vema Seamount (31°37.85'S, 8°20.4'E), 54 m.

All specimens were collected by using an airlift pump.

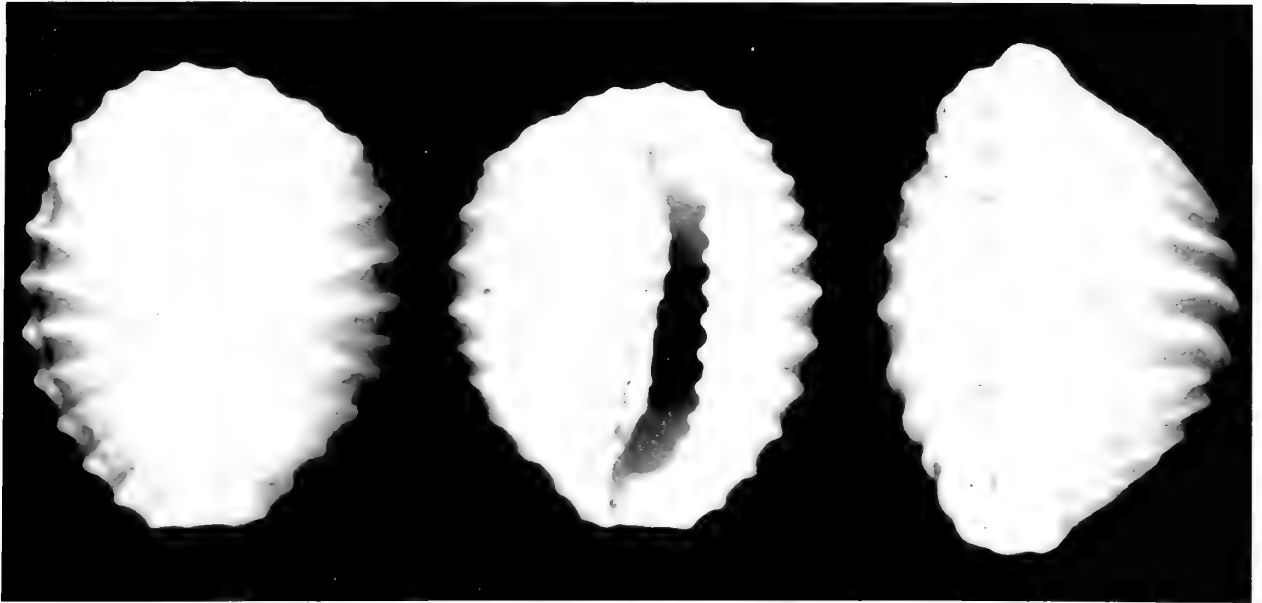


Figure 1

Truva vemacola sp. nov. Holotype shell, 4.7 mm long. Left, dorsal; middle, ventral; and right, lateral views.

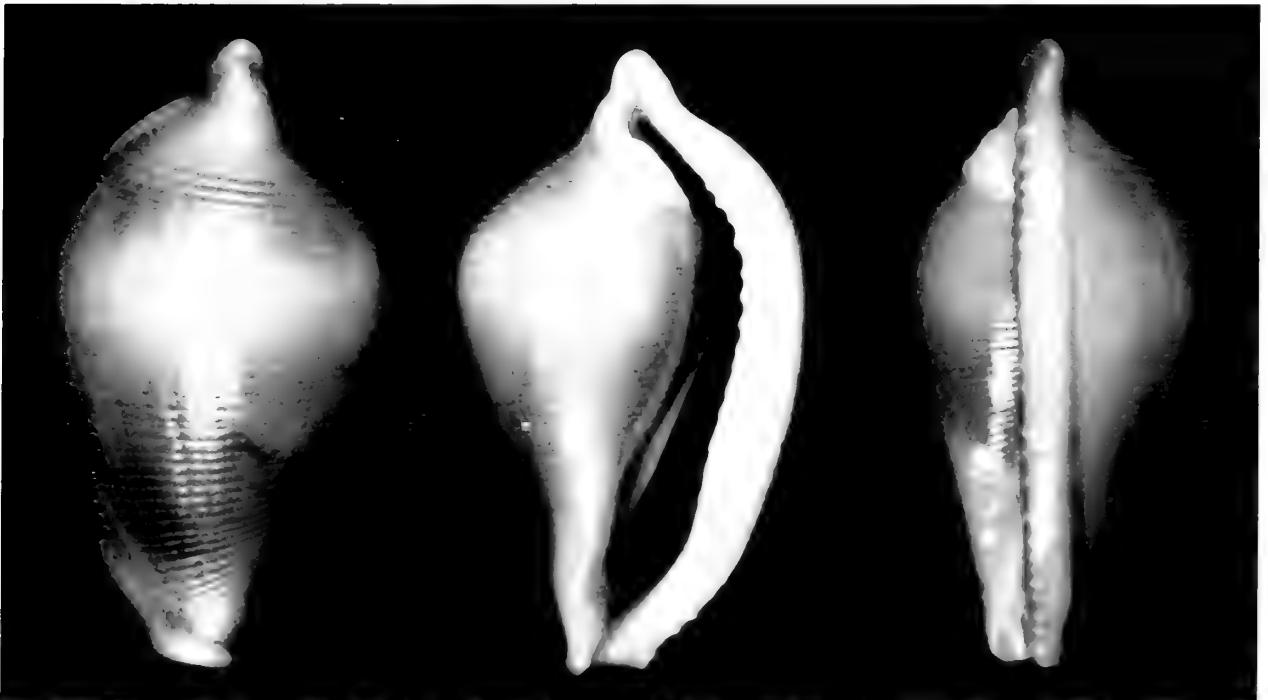


Figure 2

Primovula diaphana sp. nov. Holotype shell, 10.5 mm long. Left, dorsal; middle, ventral; and right, lateral views.

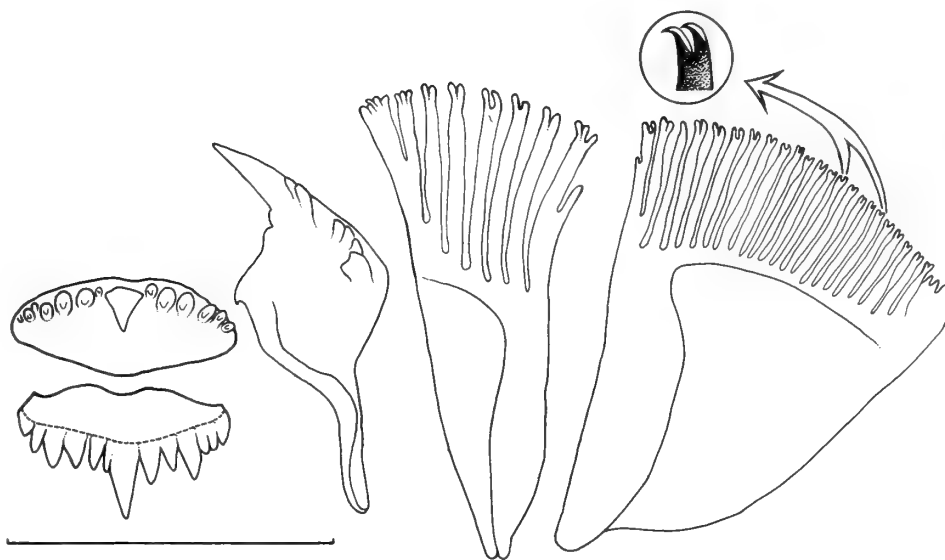


Figure 3

Primovula diaphana sp. nov. Half row of radular teeth, with lateral and dorsal view of rachidian tooth and enlarged tip of flabella. Scale bar = 100 μ m.

Along with the specimens of *Trivia vemacola* sp. nov., the following tunicate species were collected: *Synoicum atlanticum* Millar, *Aplidium vemense* Millar, *Distaplia capensis* Michaelsen, *Pseudodistoma michaelseni* Millar, *Polyclinum neptunium* Hartmeyer, *Eudistoma renieri* (Hartmeyer), *Lissoclinum marpum* Millar, and *Didemnum* sp. It is possible that *T. vemacola* lives in association with one or more of the aforementioned species.

Etymology: The new name is derived from the Latin *cola*, meaning "to inhabit," and Vema Seamount, the type locality.

Discussion: Conchologically, *Trivia vemacola* most closely resembles *Trivia dartevellei* Knudsen, 1955, known from the intertidal and shallow subtidal of Zaire and Angola. The fossil species *Trivia grateloupi* Schilder, 1941, from the Helvetian Miocene, with a distribution in the Netherlands and NW France is also conchologically similar to *T. vemacola*. *Trivia vemacola* lacks the pronounced dorsal sulcus with surrounding tubercles of *T. dartevellei*. The shell of *T. vemacola* is off-white to pale pink, whereas that of *T. dartevellei* is uniformly grayish brown. At maturity *T. vemacola* attains approximately only one-third the size of *T. dartevellei*. Conchologically, *T. vemacola* corresponds closely with features of *Discotrivia* Cate, 1979. It is impossible, however, by comparing shell morphology only, to determine whether or not these two species are truly related subgenerically. Until such time as living animals of *T. vemacola* and *T. dartevellei* are secured and anatomical features compared, it will be difficult to assign the new species to a subgenus. The holotype shell of *T. grateloupi*, measuring 6.0 mm in length, is superficially

similar to that of *T. vemacola*. The labral denticles and transverse ribs of *T. grateloupi* are more numerous than in *T. vemacola* and the posteriormost end of the aperture in *T. grateloupi* is expanded to form an almost circular portion (CATE, 1979:fig. 26), not present in shells of *T. vemacola*.

Primovula diaphana Liltved, sp. nov.

(Figures 2, 3)

Shell (Figure 2): Medium sized for *Primovula*, angularly pyriform. Dorsum thin, subtranslucent and finely transversely striate, abruptly elevated at one-third posteriorly into acute transverse ridge, tapering gradually toward anterior terminal. Aperture constricted and curved posteriorly, straighter along medial portion, widely dilated anteriorly, becoming constricted to form abapical canal between terminal ridge and inner edge of labrum. Triangular funiculum consisting of two fused ridges present at posterior end of base, forming left wall of adapical canal. Fossula well developed, smooth, "bladelikey," widest anteriorly, tapering into rounded carinal ridge. Labrum moderately wide with ventrally flattened surface. Inner and outer edges of labrum denticulate. Fine tubercle-like denticles somewhat connected by calcified transverse corrugations. Denticles situated one-third posteriorly on inner edge of labrum acutely produced, becoming crenulate in anterior two-thirds. Denticles on outer labral edge strongly developed posteriorly and anteriorly, but to a lesser degree medially. Entire basal surface calloused over by translucent white nacreous layer. Posterior terminal beak rounded, anterior terminal obliquely cut. Color white, with

fine sulfur-yellow line along upper edge of labrum, peripherally encircling terminal calluses. Holotype and paratype shells exhibit small irregularly shaped sulfur-yellow stain above labrum posterior to subcentral transverse ridge.

Radula (Figure 3): One hundred and three rows including seven nascentes present. The rachidian teeth are approximately 70 μm wide, squat with rounded base. Central cusp markedly longer than 6 or 7 denticles flanking it on either side. Outer cutting edges of central cusp and denticles flanking it apically rounded and straight at sides. Inner lateral teeth wide with long spatulate basal appendage. Pointed, straight main cusp flanked by 6 clawlike cusps situated on outer surface of tooth. Inner marginal teeth long slender and comblike, possessing approximately 9 flabellae. Outer marginals broad and shorter with approximately 25 flabellae. Bifurcate hooks present at distal extremities of flabellae.

Measurements:

	<u>length (mm)</u>	<u>width (mm)</u>	<u>height (mm)</u>
Holotype	10.5	6.0	5.1
Paratype	7.9	4.2	3.4

Type locality: Off Richard's Bay, northern Natal Province, South Africa (29°3.8'S, 32°9.5'E).

Type deposition: Holotype: California Academy of Sciences, San Francisco (CAS 060450). Paratype: South African Museum, Cape Town (SAM A37244). Type material collected 8 May 1985 by A. D. Connell of Durban, South Africa.

Habitat and distribution: The holotype and paratype were dredged at the type locality at 110 m on a sand and rubble bottom with soft corals and other sedentary invertebrate organisms.

Etymology: The new name is derived from the Latin *diaphanus*, meaning delicate and translucent.

Discussion: *Primovula diaphana* spec. nov. somewhat resembles the east African species *Primovula beckeri* (Sowberby, 1900) (CATE, 1973). Apart from attaining a greater

size at maturity, *P. diaphana* may be easily distinguished from *P. beckeri* by comparing the following features in the two species. The funiculum of *P. diaphana* is smooth and composed of two fused ridges, whereas that of *P. beckeri* is multiridged and serrate. The ventral surface of the labrum of *P. diaphana* is flattened, giving rise to two distinct rows of denticles, one on the inner and one on the outer edge of the labrum. In *P. beckeri* the denticles are restricted to the inner edge, apart from occasional denticles that extend over the posteriormost and anteriormost outer portions of the labrum. The innermost row of labral denticles in *P. diaphana* are crenulate anteriorly two-thirds of the length of the labrum. In *P. beckeri* the denticles are strongly formed throughout. When magnified the transverse striae of *P. diaphana* are evenly incised lines; in *P. beckeri* they are irregular, often almost "zig-zag" in design. The radular configuration of *P. diaphana* corresponds closely to that of *Primovula* Thiele, 1925 (AZUMA, 1976).

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A New Species of *Rabdotus*
(Gastropoda: Pulmonata: Bulimulidae) from
Sonora, with a Description of the Reproductive
Anatomy of *Rabdotus nigromontanus*

by

JAMES E. HOFFMAN

Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

Abstract. A new species, *Rabdotus milleri* Hoffman, is described from eastern Sonora, Mexico, on the basis of shell and anatomical evidence. A map of the range and drawing of the reproductive system of *Rabdotus nigromontanus* (Dall, 1897) are included.

INTRODUCTION

Rabdotus nigromontanus (Dall, 1897) is an extremely widespread species, as indicated by my collection and that of Dr. Walter B. Miller. It occupies much of eastern Sonora, Mexico, entering Arizona at one point (Figure 1); it ranges in elevation from 200 to 1240 m. The species was described from shells in poor condition taken from the summit of Black Mountain (now known as La Loma Colorada; 31°14.2'N, 109°17.5'W) at an elevation of ca. 1240 m, the highest elevation at which I have collected this species. To date, no one has published a drawing of the reproductive tract of this widespread species, although at least one new species has been compared to it (MILLER & REEDER, 1984). The type locality appears to be marginal habitat for *R. nigromontanus*, and I have been able to find only a few complete shells, and no live individuals there. However, I have obtained reproductive anatomies from *R. nigromontanus* collected at La Angostura (ca. 150 km south), Magdalena (ca. 175 km west-southwest), and Alamos (ca. 480 km south of the type locality), and found that they do not differ from each other in any significant way. Among these three localities, the length of the penes varied from 10.6 to 11.2 mm, the penial sheaths varied in length from 3.9 to 4.1 mm, the variation in the epiphal-luses was from 3.6 to 3.8 mm, the variation in epiphallic ceca was from 4.0 to 4.9 mm, and the length of penial retractor muscles varied from 1.9 to 2.8 mm in length (Figure 2).

Shells of *Rabdotus* that appeared to be slightly different from those of *R. nigromontanus* were found near Sahu-

ripa, Sonora, Mexico, by Walter B. Miller in August of 1965, while on a collecting trip with his son. These lay, unnamed, in his collection until I became his graduate student and decided to study Bulimulidae in Sonora. In November 1983, we returned to the locality where the shells had been found, only to find that the area had been washed by recent rains, destroying both snails and habitat. On 26 November, the last day of the expedition, a locality rich in shells was located, and just before we had to leave, a single live adult was found by Dr. Miller.

SYSTEMATICS

Family BULIMULIDAE

Genus *Rabdotus* Albers, 1850

Subgenus *Rabdotus* Albers, 1850

Rabdotus milleri Hoffman, sp. nov.

(Figures 3, 4)

Description of shell of holotype: Shell small, umbilicate, the diameter about six-tenths of the height; uniformly colored light tan, slightly glossy. Embryonic whorls 2 in number, rounded with strong, closely spaced, axial riblets; closely set, fine, spiral threads faintly visible between the riblets of only the first whorl. Post-embryonic whorls moderately rounded, with irregularly spaced growth ribs, and occasional, randomly placed minute pits. Outer lip of peristome sharp, slightly reflexed, inner lip broadly reflected around the umbilicus. Maximum height 16.6 mm, diameter 8.4 mm; 5.4 whorls.

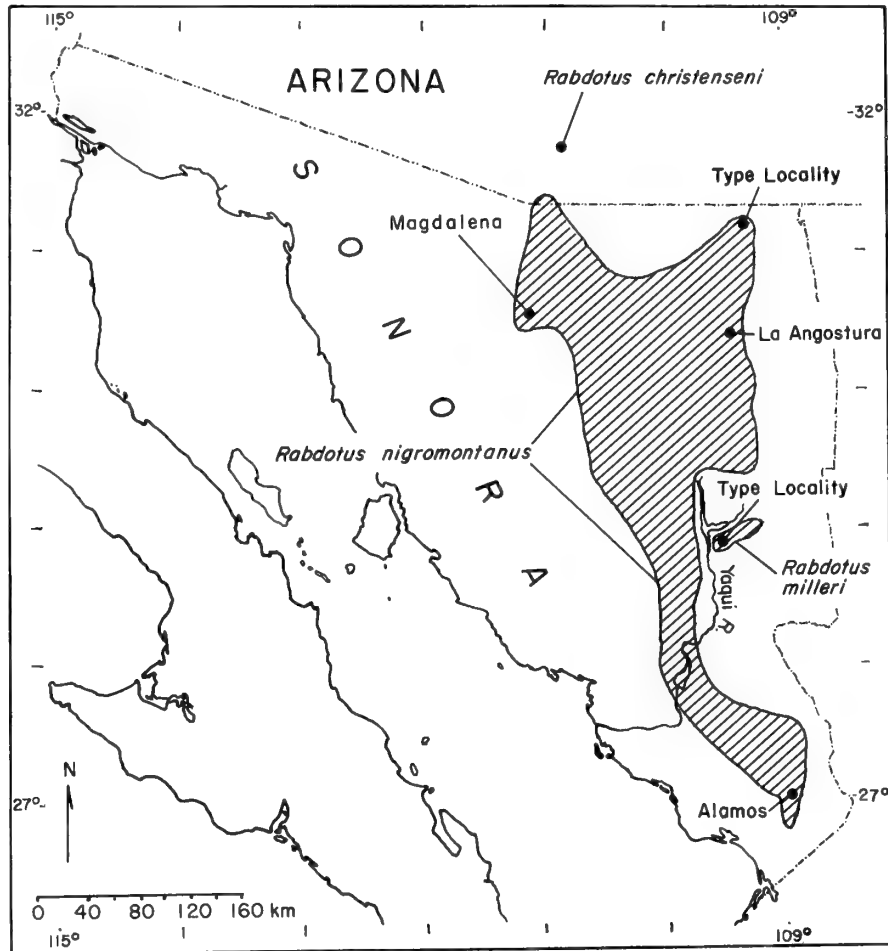


Figure 1

Map of Sonora, Mexico, indicating the ranges and type localities of *Rabdopus milleri* sp. nov., *R. nigromontanus* (Dall, 1897), and *R. christenseni* Miller & Reeder, 1984.

Reproductive anatomy of holotype: Diagnostic characters are in the penial complex. Penis 4.5 mm in length, largely covered by a thick penial sheath 3.8 mm long; the proximal 1.7 mm of the penis contains highly convoluted glandular diverticula. Epiphallus 4.2 mm long, the lumen of which is lined by shallow longitudinal folds. Epiphallic cecum 2.8 mm long; short penial retractor muscle 2.3 mm long attached to apex of the epiphallic cecum. Vas deferens runs free from approximately 3.5 mm below its origin at base of prostate gland, along free oviduct and vagina, and enters the penial sheath at about 1.3 mm from the genital orifice; it continues proximally within the penial sheath, but externally to the penis, exiting the distal end of the sheath and running alongside the penis and epiphallus until its insertion at the junction of the epiphallus and epiphallic cecum.

Variations in paratypes: A total of 28 adult entire shells and 23 immature or damaged shells was collected. Of the

undamaged adult shells, the largest was 18.1 mm in height and 9.4 mm in diameter, and the smallest measured 15.0 mm in height and 8.1 mm in diameter; the mean height was 16.1 mm, and the mean diameter was 8.98 mm. All specimens show all of the characteristics of the holotype except that, among the adult, entire shells, there is variation in the reflection of the outer lip from slight to none.

Disposition of types: Holotype: Santa Barbara Museum of Natural History no. 34490. Paratypes: Universidad Nacional Autonoma de Mexico no. 1203; Academy of Natural Sciences of Philadelphia no. 360593; National Museum of Natural History no. 859066; Field Museum of Natural History no. 215141; University of Texas at El Paso no. 9505; W. B. Miller Collection no. 7340; J. E. Hoffman collection no. 30.

Type locality: Sonora, Mexico; 5.4 km west of the Yaqui River bridge at La Estrella on road to Sahuaripa. In can-

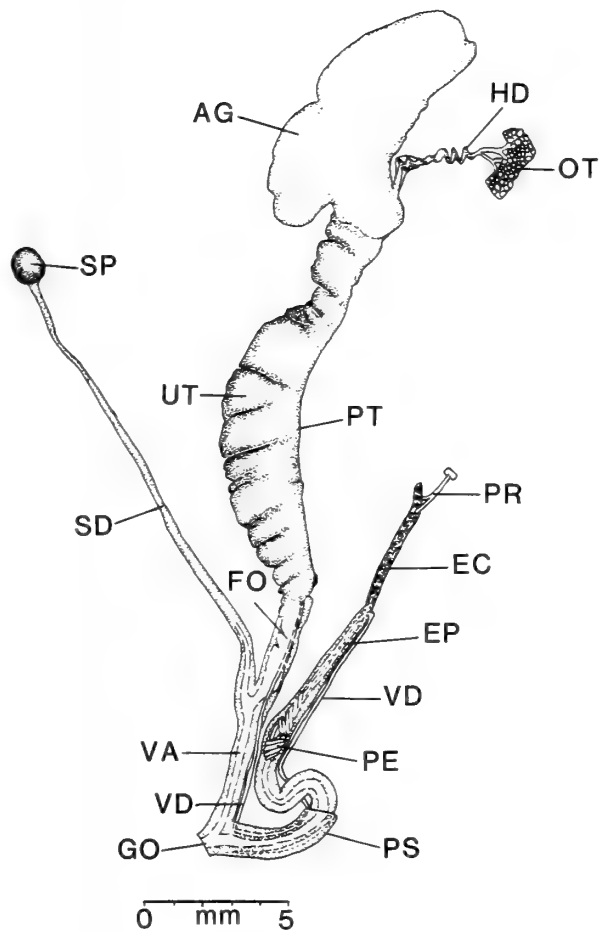


Figure 2

Genitalia of *Rabdodus nigromontanus*, J. E. Hoffman Collection no. 52a. AG, albumen gland; EC, epiphallic cecum; EP, epiphallus; FO, free oviduct; GO, genital orifice; HD, hermaphroditic duct; OT, ovotestis; PE, penis; PR, penial retractor muscle; PS, penial sheath; PT, prostate; SD, spermathecal duct; SP, spermatheca; UT, uterus; VA, vagina; VD, vas deferens.

yon extending north from road, in leaf litter below a rockslide; 28°57.1'N, 109°36.7'W; elevation ca. 340 m.

Remarks: *Rabdodus milleri* is most closely related to *R. nigromontanus* and probably evolved from a common ancestor over a long period of geographical isolation. Its shell differs from that of *R. nigromontanus* only in being somewhat more slender, with a height-diameter ratio of about 1.8, whereas *R. nigromontanus* has an average ratio of 1.54 as determined from 31 specimens from nine lots collected in many parts of the species' range. *Rabdodus milleri* is more readily distinguished from *R. nigromontanus* by its reproductive anatomy. It has a much shorter penis, almost entirely enclosed by a sheath, which is also much shorter than that of *R. nigromontanus*, whereas the longer sheath of *R. nigromontanus* encloses only the distal

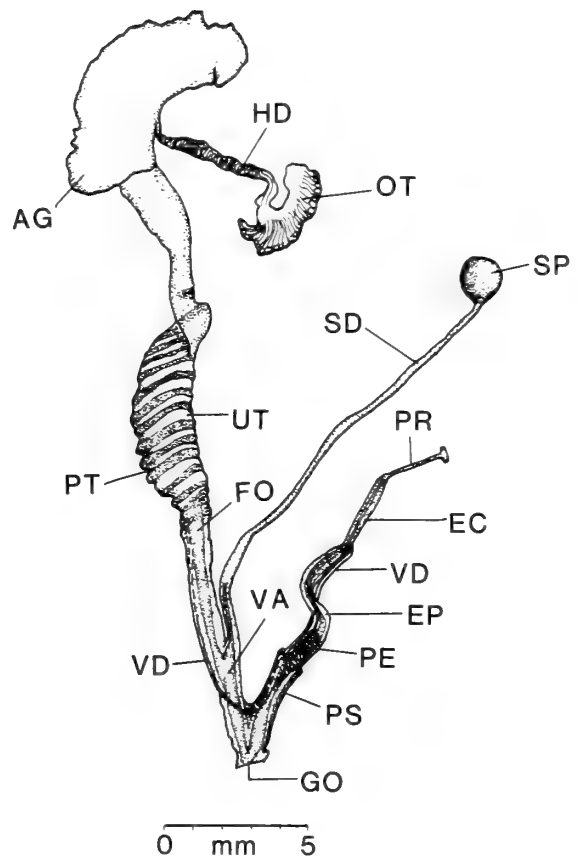
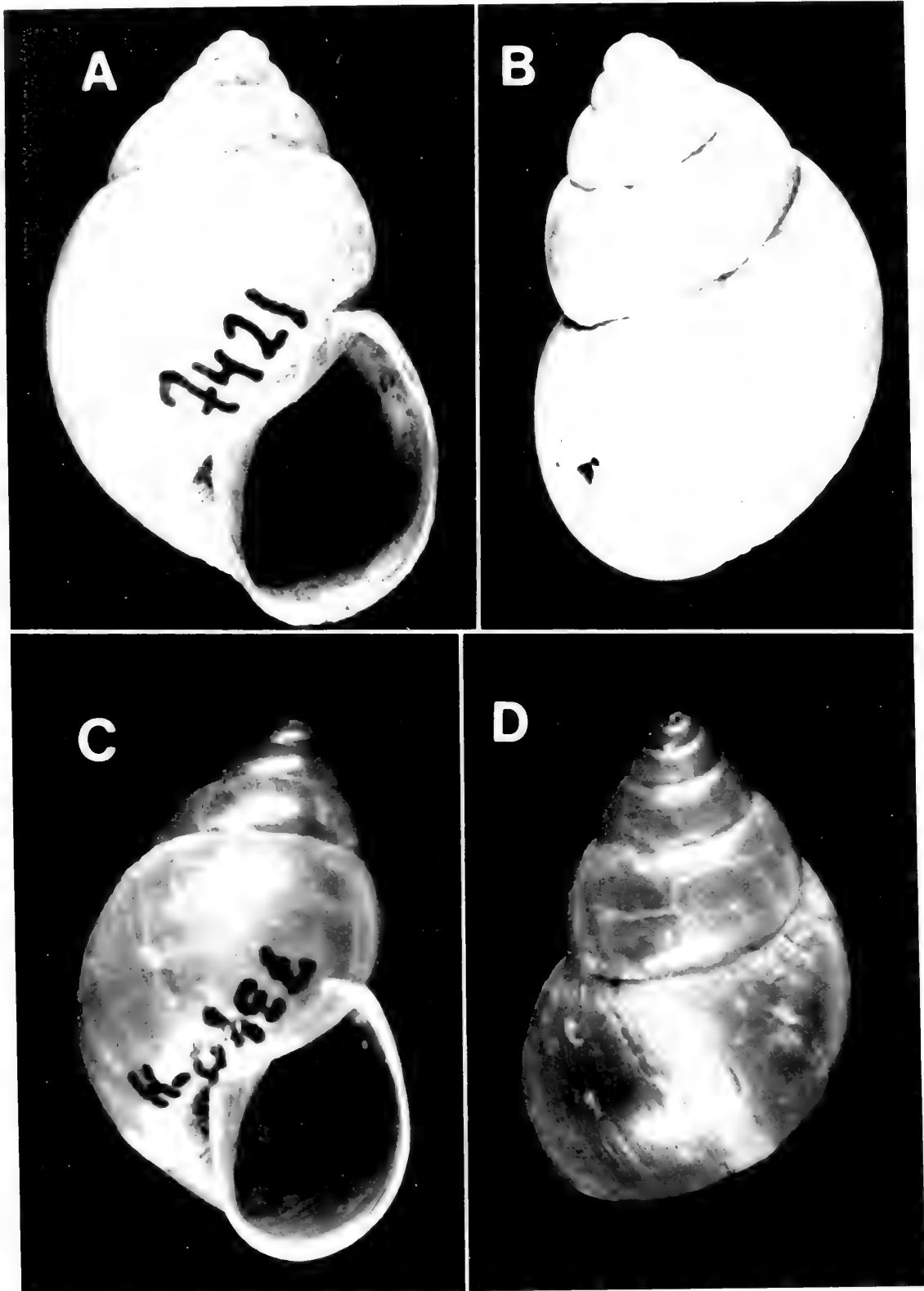


Figure 3

Genitalia of *Rabdodus milleri*, holotype, W. B. Miller Collection no. 7340. AG, albumen gland; EC, epiphallic cecum; EP, epiphallus; FO, free oviduct; GO, genital orifice; HD, hermaphroditic duct; OT, ovotestis; PE, penis; PR, penial retractor muscle; PS, penial sheath; PT, prostate; SD, spermathecal duct; SP, spermatheca; UT, uterus; VA, vagina; VD, vas deferens.

one-third of the penis. In addition, its penial retractor muscle inserts at the end of the epiphallic cecum, whereas that of *R. nigromontanus* inserts approximately 1 mm distally from the end.

There has been some disagreement regarding whether the glandular diverticula in the penial complex of *Rabdodus* should be considered part of the penis or part of the epiphallus. The penis is considered to be the part of the penial complex that is evaginable during copulation (VAN MOL, 1971); this definition works in theory but is, in fact, almost impossible to apply. PILSBRY (1946) considered the diverticula to be part of the epiphallus, and MILLER & REEDER (1984) agreed with him owing to the extreme length of the lower duct in both *R. nigromontanus* and *R. christensenii* as well as because a "pronounced constriction of the lumen" occurred in the latter. On the other hand, CHRISTENSEN (1978), BREURE (1979), and VAN MOL (1971) considered the glandular diverticula to be part of



the penis. Primarily owing to VAN MOL's (1971) histologic evidence, and for the sake of consistency (more species have been described using their terminology), I must side with the latter authors and consider the glandular diverticula to be part of the penis.

Habitat and distribution: Shells of *Rabdotus milleri* have been collected in several localities in the Sierra Santo Niño, in addition to the type locality. They have been collected also in the Sierra Chiltepin, 7.8 km west of Sahuaripa. All were collected at elevations between 300 and 400 m in the Sinaloan thornscrub biome (BROWN, 1982). The land rises steeply to the east and southeast, soon entering Madrean evergreen woodland; to the west, the species seems to be limited by the Yaqui River and we were unable to find any sign of this species west of the river, although we did find *Rabdotus baileyi* (Dall, 1893) in both areas. To the north and south there is evidence of geologically recent volcanic activity in areas that seem to lack large land snails; these may be the factors that have isolated this species.

Dominant plants at the type locality include *Cassia biflora*, *Pachycereus pecten-aboriginum*, *Stenocereus thurberi*, *Ceiba acuminata*, *Sapium biloculare*, *Acacia cymbispina*, *Guaiaacum coulteri*, *Fouquieria macdougalii*, and *Bursera* sp.

Etymology: This species is named for Walter B. Miller, friend, mentor, and all around great camper and beer drinker, with whom I have enjoyed many trips into the field. He and his son originally found shells of this species and thought that it might be new. He also collected the

holotype and dissected out the reproductive anatomy, making both available for this study.

ACKNOWLEDGMENTS

I would like to thank Edna Naranjo-García and Jane E. Deisler, but especially Walter B. Miller, for help in the procurement of specimens of *Rabdotus milleri* for this study. In addition, I thank Carl C. Christensen and Richard L. Reeder for help and accompaniment on trips collecting *R. nigromontanus*.

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Figure 4

A and B. *Rabdotus nigromontanus*, W. B. Miller no. 7421, apertural and dorsal views. C and D. *Rabdotus milleri*, holotype, Santa Barbara Museum of Natural History no. 34490, apertural and dorsal views. All figures $\times 5.5$.

A New Species of *Drymaeus*
(Gastropoda: Pulmonata: Bulimulidae)
from Sonora and Sinaloa, Mexico

by

JAMES E. HOFFMAN

Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

Abstract. A new species, *Drymaeus reederi* Hoffman, is described from southern Sonora and Sinaloa, Mexico. A short discussion of other northwestern Mexico *Drymaeus* is included.

INTRODUCTION

DURING A TRIP to the Alamos area of Sonora, Mexico, over Christmas vacation in 1983, with Walter B. Miller, his wife Betty Sue, Edna Naranjo García, Jane E. Deisler, and Richard L. Reeder, I was surprised to find a population of *Drymaeus* living in trees along a remote canyon in southeastern Sonora. There has been no mention in the literature of *Drymaeus* occurring farther north than approximately Culiacan, Sinaloa. Subsequently, after she studied the land snail collection of the California Academy of Sciences, Jane Deisler informed me that it contained two lots of *Drymaeus* collected in Sonora by John T. Wright in 1931.

Taxonomic information about the Bulimulidae, and particularly *Drymaeus*, in Mexico is sparse, and in some cases inaccurate. The most recent attempts to bring order out of the chaos are by Breure and Eskens (BREURE, 1979; BREURE & ESKENS 1981). Breure and Eskens' work has helped greatly, but is only a start owing to the fact that many more collections must be made, and many more species compared.

SYSTEMATICS

Family BULIMULIDAE

Genus *Drymaeus* Albers, 1850

Subgenus *Mesembrinus* Albers, 1850

Drymaeus reederi Hoffman, sp. nov.

(Figures 1-3)

Diagnosis: A small *Drymaeus* with almost flat whorls and reproductive system characterized by the lack of an epiphallallic cecum.

Description of shell of holotype: Shell small, umbilicate, diameter about one-half height; all but embryonic and body whorls with three light brown spiral bands, broken into squarish spots on a white background over most of their lengths; body whorl displays lighter axial lines over a white background; embryonic whorls uniformly tan; entire shell glossy. Embryonic whorls, 1.8 in number, rounded with extremely fine, even spiral and radial threads, seeming to produce a very uniform field of square punctae. Post-embryonic whorls only slightly convex with irregularly spaced growth ribs and very shallow, closely spaced incised lines. Aperture subovate, its outer lip sharp, barely reflected, inner lip reflected around and almost effacing the rimate umbilicus. Maximum height 15.1 mm, diameter 7.3 mm; 5.6 whorls.

Reproductive anatomy of holotype: Diagnostic characters in penial complex. Penis 5.9 mm in length, partly covered by thick penial sheath 2.8 mm long; proximal 1.8 mm of penis contains highly convoluted glandular diverticuli. Epiphallus 3.5 mm long, its lumen lined by shallow longitudinal folds. Epiphallallic cecum lacking; short penial retractor muscle 0.2 mm long attached to apex of epiphallus. Vas deferens runs free from approximately its origin at base of prostate gland, along free oviduct and vagina, then turns distally and enters penial sheath 2.0 mm from genital orifice; it loops toward genital orifice, then continues proximally within the penial sheath, but externally to the penis, exiting the distal end of the sheath and running alongside the penis and epiphallus until its insertion at the end of the epiphallus.

Variations in paratypes: A total of seven adult entire shells and four immature or damaged shells was collected from the type locality. Of the undamaged adult shells, the

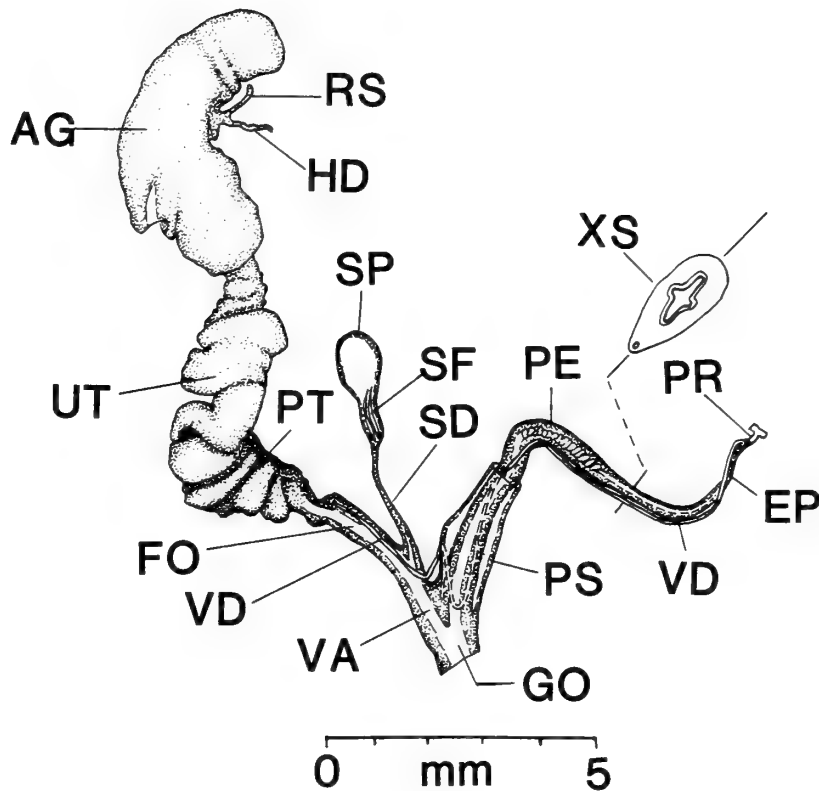


Figure 1

Genitalia of *Drymaeus reederi* sp. nov., holotype, J. E. Hoffman Collection no. 7. AG, albumen gland; EP, epiphallus; FO, free oviduct; GO, genital orifice; HD, hermaphroditic duct; PE, penis; PR, penial retractor muscle; PS, penial sheath; PT, prostate; RS, seminal receptacle; SD, spermathecal duct; SF, spermatophores; SP, spermatheca; UT, uterus; VA, vagina; VD, vas deferens; XS, cross section of epiphallus.

largest was 15.6 mm in height and 7.4 mm in diameter, and the smallest measured 13.0 mm in height and 6.4 mm in diameter; the mean height was 14.4 mm, and the mean diameter was 7.0 mm. The range of whorl counts was 5.6 to 6.0; the range of diameter-height ratios was 1.95 to 2.12. All specimens showed all of the characteristics of the holotype.

Disposition of types: Holotype: Santa Barbara Museum of Natural History no. 34664. Paratypes: Field Museum of Natural History no. 215221; R. L. Reeder Collection no. 698; W. B. Miller Collection no. 7344; J. E. Hoffman Collection no. 15.

Type locality: Sonora, Mexico; approximately 1 km east of Rancho Agua Salada, on the eastern slope of Arroyo el Taymuco in the Sierra San Ignacio. On the east slope of a canyon extending north from the road, on trees; 27°15.3'N, 108°46.5'W; elevation ca. 600 m.

Remarks: *Drymaeus reederi* is unusual, and probably unique, among *Drymaeus* in its lack of an epiphallallic cecum. Other members of this genus found nearby are universally larger and, where the genitalia are figured, have

an epiphallallic cecum. The species with which *D. reederi* would most likely be confused is *D. zieglerei* (Pfeiffer, 1846). However, *D. zieglerei* is larger (the shell of the holotype, according to the original species description, has a height of 29 mm and the specimen in the University of Arizona collection has a shell height of 23.0 mm, while the shell of the holotype of *D. reederi* is 15.1 mm high). Also, the whorls of *D. zieglerei* are more convex and the markings consist of radially arranged spiral bands that are not broken up into closely spaced spots as in *D. reederi*. The reproductive anatomy of *D. zieglerei* has never been described as such; however, I believe that it was described erroneously as *D. serperastrus* (Say, 1829) by BREURE & ESKENS (1981), whereas the correct reproductive anatomy of *D. serperastrus* is figured by SOLEM (1955). Whereas shells of *D. serperastrus* and *D. zieglerei* are similar, there are consistent differences (see PILSBRY 1899:39-40), and the former occurs only east of the central Mexican plateau while the latter occurs only west of it. Breure and Eskens did not illustrate their shell, but it was collected in Sinaloa, west of the Mexican plateau.

The size and shape of the shell of *Drymaeus reederi*, as well as the genitalia, are considerably different from

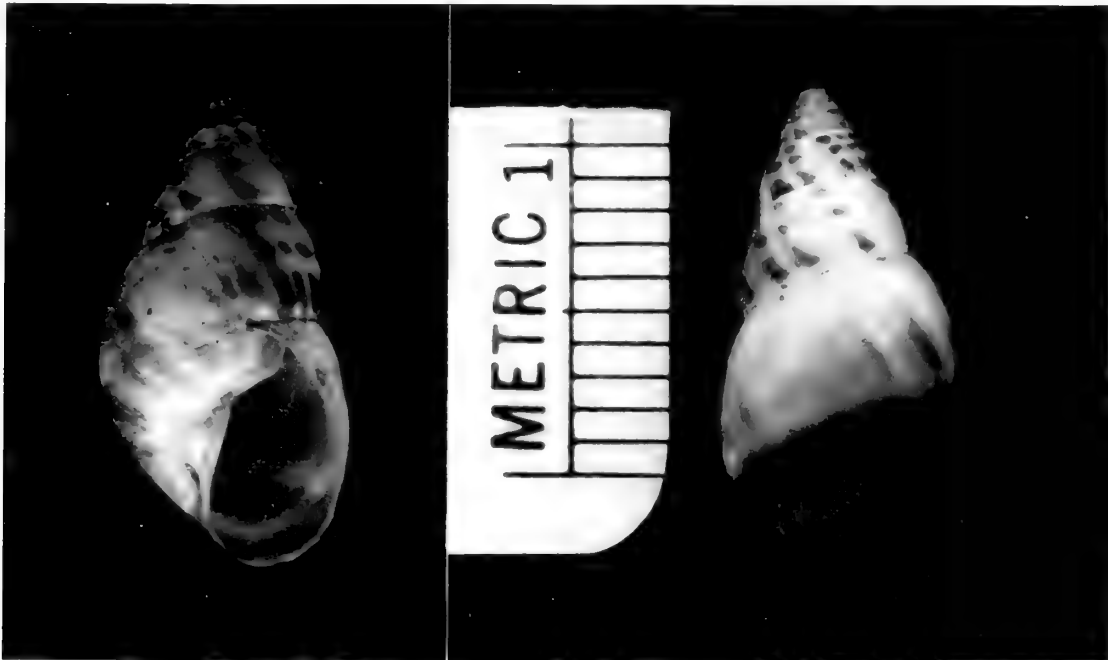


Figure 2

Drymaeus reederi, holotype, Santa Barbara Museum of Natural History no. 34664. Apertural and dorsal views. Scale = 1 mm.

those of any nearby *Drymaeus*, and its relationships to other snails in the genus are unclear.

The subgenus *Mesembrinus* Albers, 1850, was originally assigned to members of the genus *Drymaeus* that lacked an expanded or reflexed peristome (PILSBRY 1897–1898:194). BREURE (1979) and BREURE & ESKENS (1981) have modified this somewhat, adding such features as “mandibula with more than 20 plates, which are ca. 8 times as long as wide,” and V- to W-shaped transverse rows of teeth on the radula. In addition, BREURE & ESKENS (1981:97) state that members of *Mesembrinus* have a mean number of 116.92 squares per 0.1 mm² of the protoconch sculpture whereas those of *Drymaeus* s.s. have 51.79. I found only 49 squares/0.1 mm² for *D. serperastus*, as opposed to the 57 found by BREURE & ESKENS (1981), but counted 56 squares/0.1 mm² for *D. zieglerei*, further indicating that *D. zieglerei* was probably the snail that they observed. I counted 90 squares/0.1 mm² on the embryonic whorls of *D. reederi*. In addition, *D. reederi* has a mandible, or jaw, with 38 plates, but these are only ca. 5 times as long as wide (Figure 3), and it has moderately V-shaped transverse rows of radular teeth, although these rows are almost straight; the radular formula is (78–92)-1-(78–92); a rachidian, and a typical latero-marginal tooth are illustrated in Figure 3.

For the reasons enumerated above, I have tentatively placed *Drymaeus reederi* in the subgenus *Mesembrinus*.

Habitat and distribution: Shells of *Drymaeus reederi* have been collected in one locality in the Sierra San Ignacio in addition to the type locality. The second locality was ca. 5 km west of the type locality. Both of these localities are within the Sinaloan deciduous forest biome (GENTRY, 1982). In addition, shells of *D. reederi* have been found in diverse parts of Sonora and Sinaloa within the Sinaloan thornscrub biome (BROWN, 1982). In 1931, John T. Wright collected an adult and a juvenile shell at ca. 700 m (*sic*) elevation near Alamos, Sonora, and four juvenile shells at ca. 1000 m (*sic*) near Chinobampo, Sonora, approximately 37 km WSW of Alamos. These elevations seem erroneous because the elevation given for the Alamos collection is equal to the elevation of the highest peak in the area, while that given for the Chinobampo collection is higher than any elevation shown on topographic maps of the area. In December 1983, Jane E. Deisler collected an adult shell in river drift 17 km south of Alamos; and in January 1973, Walter B. Miller collected two adult and two juvenile shells in Sinaloa, along Hwy 15, 89 km north of Mazatlán.

The exact range limits and the limiting factors for *Drymaeus reederi* have yet to be elucidated; however, we can assume that it is limited to the Sinaloan biogeographic province. Its eastern limit is fairly definite, bounded by the steep rise into the Sierra Madre and the Madrean evergreen woodland biome; the northern limit within the

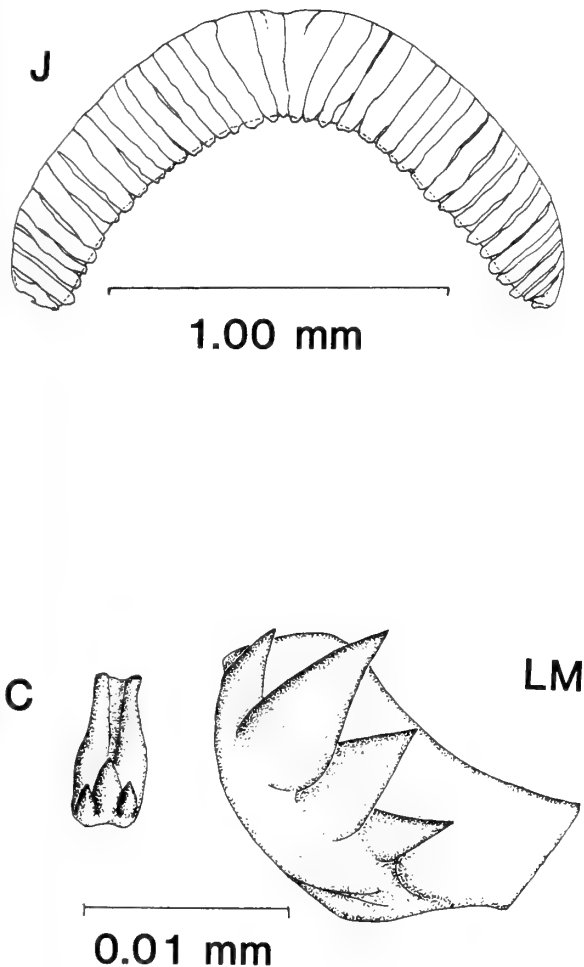


Figure 3

Jaw and radula of *Drymaeus reederi*, holotype, J. E. Hoffman Collection no. 7. J, jaw; C, rachidian tooth; LM, 13th latero-marginal tooth.

Sinaloan thornscrub biome will probably be found to be slightly north of Alamos because rainfall within this biome gradually decreases and becomes less regular toward the north; the western limit is probably caused by the reduction in elevation as the land approaches the Gulf of California; the southern limit can only be a source of conjecture. To the south, the rainfall increases, the forest becomes

thicker, and other arboreal species of *Drymaeus* begin to appear.

Dominant plants at the type locality include *Cassia emarginata*, *Pachycereus pecten-aboriginum*, *Stenocereus thurberi*, *Jatropha platanifolia*, and *Bursera* spp.

Etymology: This species is named for Richard L. Reeder, whose company I have enjoyed on this as well as several other expeditions into Mexico. It was his keen eyesight that enabled us to collect the holotype of this species.

ACKNOWLEDGMENTS

I would like to thank Edna Naranjo García, Jane E. Deisler, Walter B. Miller, and Richard L. Reeder for help in the procurement of specimens of *Drymaeus reederi* for this study. In addition, I thank Jane E. Deisler for suggesting that Breure and Eskens might be wrong in their descriptions of *D. serperastrus*, and for locating the specimens collected by John T. Wright in the California Academy of Sciences collection and apprising me of their existence and their collection numbers; in doing so, she has contributed greatly to the completeness of this manuscript. Additionally, I am very grateful to Carl C. Christensen for pointing out an error in my method of measuring the protoconch sculpture. I am also grateful to Robert Van Syoc and Tony Summers, both of the California Academy of Sciences, for the loan of material.

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A Comparative Study of Two Similar Panamic Cones: *Conus ximenes* and *Conus mahogani*

by

HENRY W. CHANEY¹

Center for Electron Microscopy, Department of Biological Sciences, University of Southern California,
Los Angeles, California 90089, U.S.A.

Abstract. Although often considered only a variant of *Conus ximenes*, *C. mahogani* differs from *C. ximenes* in characters of shell morphology, length of radula teeth, and male reproductive anatomy. The shell morphologies of both taxa were compared from specimens collected throughout the Panamic Province. Radulae and external anatomy were compared in populations of both species where they occur sympatrically. *Conus ximenes* lacks an operculum, a structure that is present in *C. mahogani*. It is concluded that these two taxa should be regarded as distinct, albeit closely related, species.

INTRODUCTION

THE SYSTEMATIC relationship of *Conus mahogani* Reeve, 1843, to *Conus ximenes* Gray, 1839, has been unsettled for much of the past 150 yr (REEVE, 1843; HANNA, 1963; KEEN, 1971; WALLS, 1979) with opinion divided over whether *C. mahogani* is a valid species. Both species are common in shallow water, having a mutual range extending throughout the Panamic Province from the northern Sea of Cortez (Gulf of California) to Ecuador and the Galápagos Islands.

The taxonomic history of both taxa has been previously discussed by HANNA (1963), who separated *Conus mahogani* from *C. ximenes* with some reservation. Both KEEN (1971) and WALLS (1979) figure *C. mahogani* as a variety of *C. ximenes*. The subspecific taxon *C. ximenes mahogani* was used earlier by KEEN (1958) and also appears occasionally in the popular shell collecting literature.

This study reconsiders the status of *Conus mahogani* in a comparison to *C. ximenes* based on characters of shell morphology, external anatomy, and radulae. Evidence is presented that clearly separates *C. mahogani* from *C. ximenes* and supports the contention that they are two closely related species, which share a similar habitat.

MATERIALS AND METHODS

This comparative study of *Conus ximenes* and *C. mahogani* was divided between a consideration of shell morphology and an examination of soft parts. Observations of shell morphology employed specimens from geographically diverse stations whereas external anatomy was based on freshly collected material from a single station in Baja California Sur.

Comparisons of shell morphology utilized selected specimens from the collections of the Los Angeles County Museum of Natural History (LACM), the Santa Barbara Museum of Natural History (SBM), Mrs. Helen DuShane (HD), and the author (HWC).

Not all the available materials from these sources were used. Three criteria were followed in choosing specimen lots for examination: (1) specimens were live collected and in good condition; (2) the selection of lots collectively represented the widest possible geographic distribution, and (3) where possible, juveniles and sub-adults were included. Duplicate lots from the same region or lots without replicates were not studied.

Because the results of a preliminary morphometric study comparing the length versus width of each species showed no significance, emphasis was directed to qualitative observations. The extent of intraspecific variation was recorded photographically.

Radulae and external anatomy of both species were

¹ Mail reprint requests to: 1633 Posilipo Lane, Santa Barbara, California 93108, U.S.A.

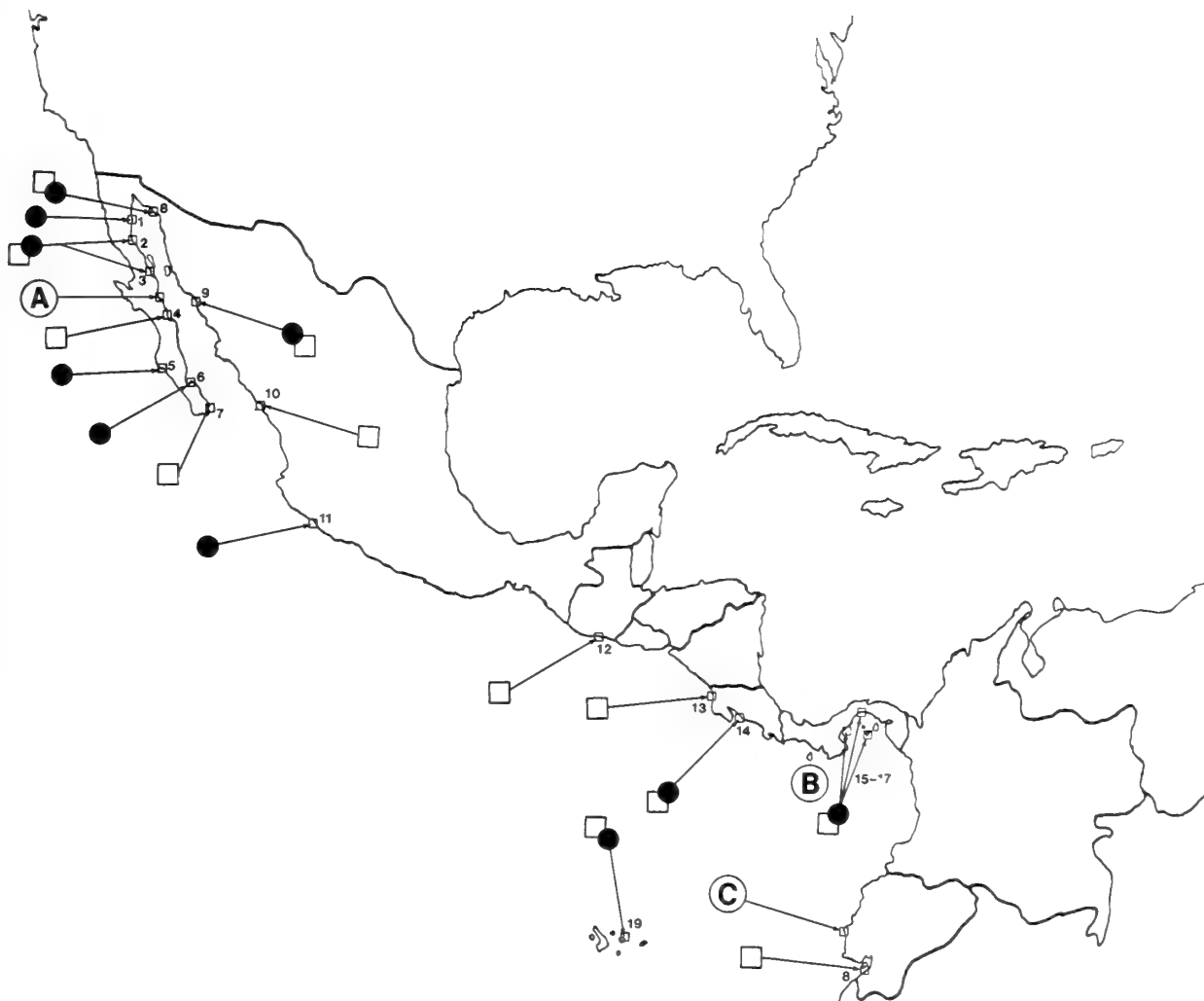


Figure 1

Geographic distributions of *Conus ximenes* (black circles) and *C. mahogani* (white squares) used in the study. Circled stations: **A** is Caleta San Lucas, Baja California Sur, a collecting station for both species (see text); **B** the type locality for *C. ximenes* is "Panama"; **C** the type locality for *C. mahogani* is "Salanga, West Columbia," now Salango, Ecuador. Numbered stations: Stations 1-11 are in western Mexico: 1, San Felipe, Baja California Norte; 2, Bahía San Luis Gonzaga, BCN; 3, Bahía de Los Angeles, BCN; 4, Punta Chivato, Baja California Sur; 5, Bahía Magdalena, BCS; 6, Isla Espiritu Santo, BCS; 7, Cabo Pulmo, BCS; 8, Puerto Penasco, Sonora; 9, Guaymas, Sonora; 10, Mazatlán, Sinaloa; 11, Manzanillo, Colima. 12, Puerto San Jose, Guatemala; 13, Bahía Salinas, Costa Rica; 14, Puntarenas, Costa Rica. Stations 15-17 are in Panama: 15, Bique (left arrow); 16, Far Fan (center arrow); 17, Isla Gibrleon, Perlas Islands (right arrow). 18, Posorje, Ecuador; 19, Isla San Salvador, Galápagos Islands.

examined using specimens personally collected from intermingled populations found on the exposed sand flats of Caleta San Lucas, Baja California Sur ($24^{\circ}12'N$, $112^{\circ}13'W$) during the minus tide on 5 March 1985. Specimens were collected at water's edge while they emerged vertically from sand, creating a distinct "bump," prior to moving actively on the surface. Both species become active at the turn of the low tide.

Animal colorations of the collected specimens were re-

corded prior to their narcotization in magnesium chloride and preservation in 70% ethanol. Subsequently, the bodies were removed from their shells, sexed, and preserved individually.

Radula sacs were dissected and the teeth were cleaned with a tissue solubilizer, 0.5 N quaternary ammonium hydroxide (Beckman BTS-450) using a method modified from BLEAKNEY (1982). Cleaned teeth were then counted and measured. Teeth from the short or "ready" sacs of

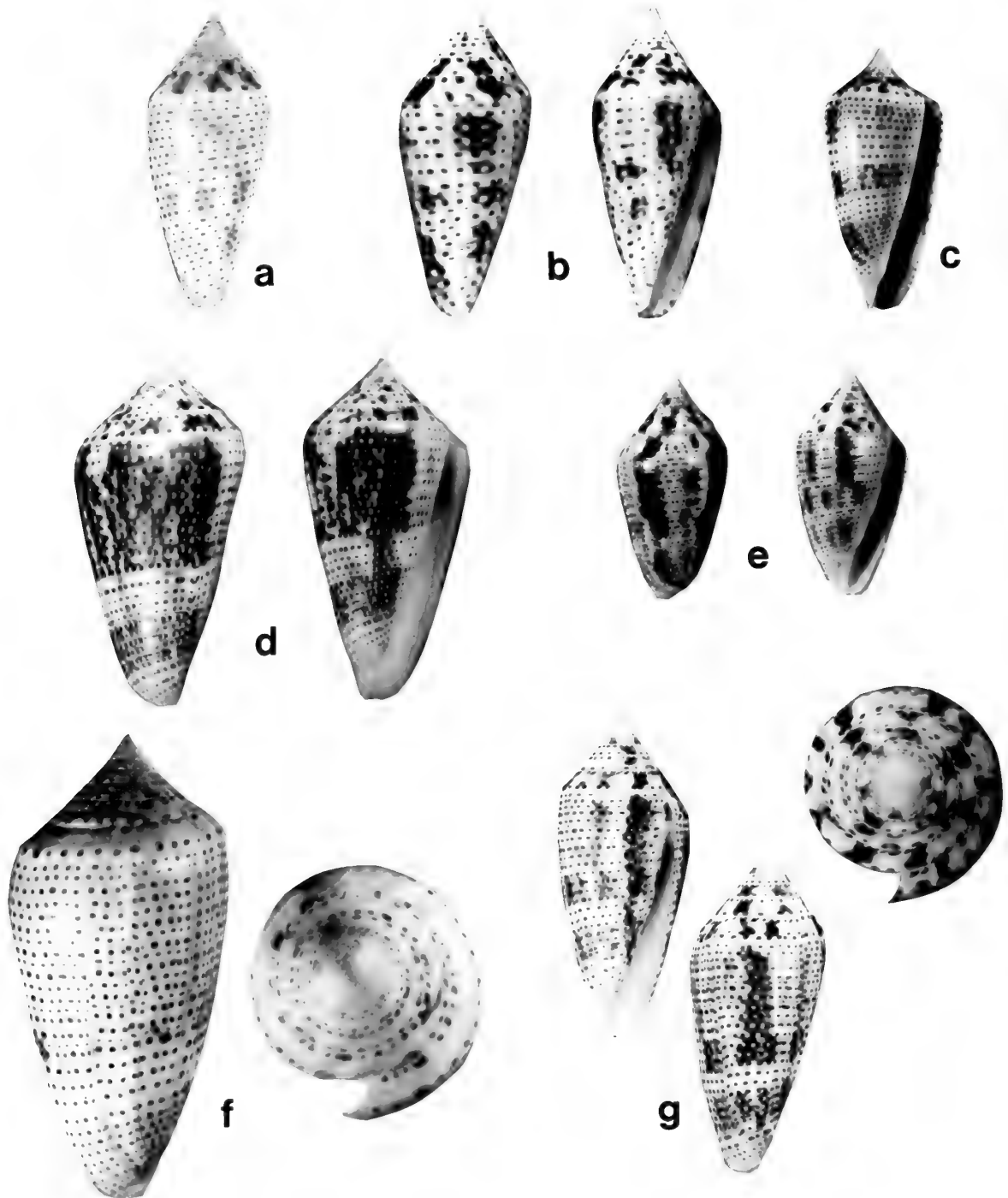


Figure 2

Adult and juvenile specimens of *Conus ximenes*, showing morphological variations. a, juvenile, Puerto Penasco, Sonora, Mexico, 25 mm long (LACM 610-37). b, juvenile, Las Perlas Islands, Panama, 31 mm (HD). c, sub-adult, Caleta San Lucas, Baja California Sur, 39 mm (HWC). d, adult, heavily flammulated, Puerto Penasco, 48 mm (LACM 120201). e, adult, reduced globose form, Manzanillo, Colima, Mexico, 33 mm (LACM 68-59). Form also noted from Bay of Panama. f, adult (enlarged, same length as 2g), with no flammules, Bahía de Los Angeles, Baja California Norte, 46 mm. Spire detail showing two rows of dots along suture, 20 mm wide (HWC). g, adult, Caleta San Lucas, 46 mm. Spire showing flammules on shoulder, 19 mm (HWC).

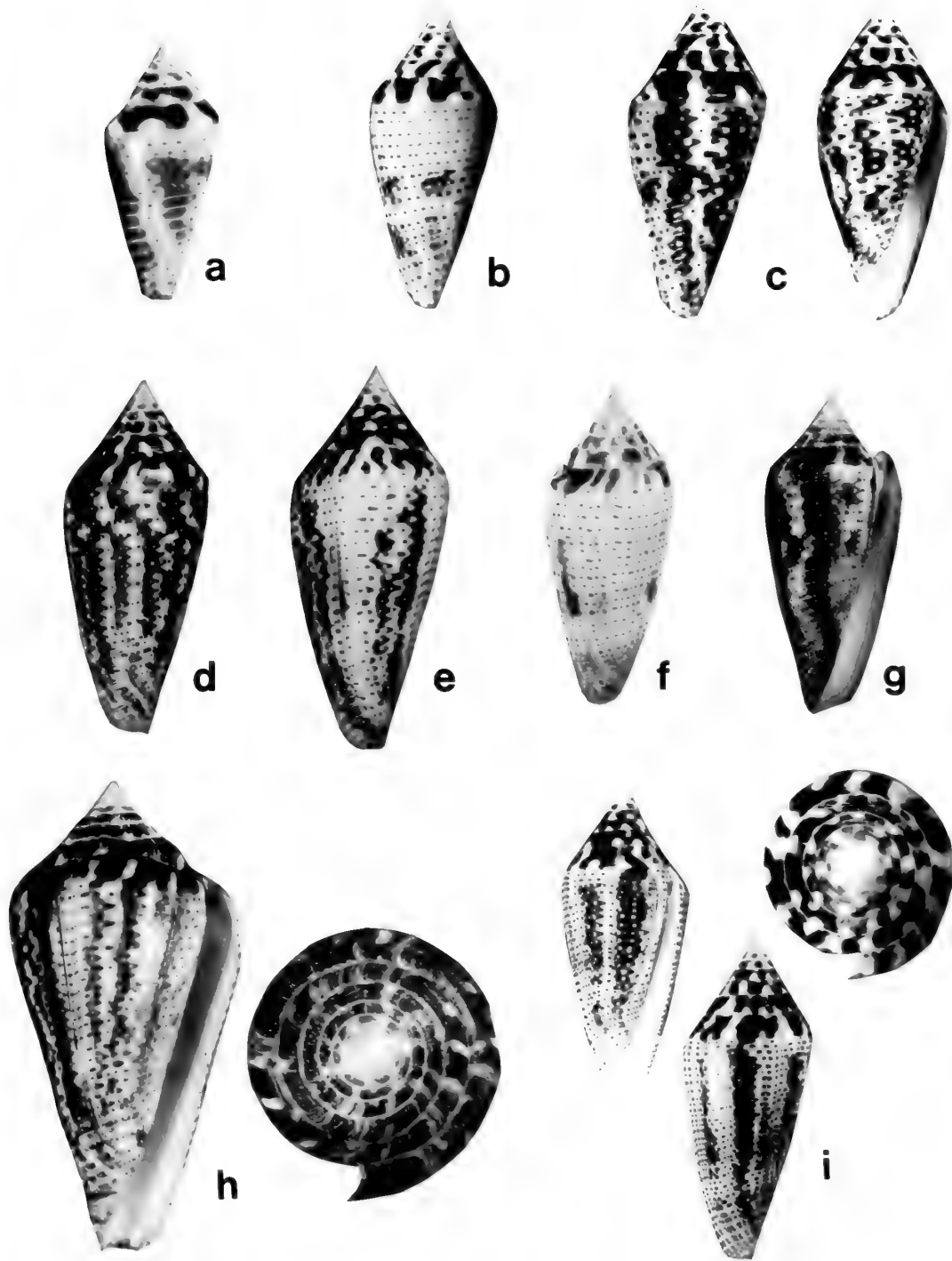


Figure 3

Adult and juvenile specimens of *Conus mahogani* showing morphological variations. a, juvenile, Las Perlas Islands, Panama, 13 mm long (LACM 66-65). b, juvenile, contrast spire detail with Figure 2b, Las Perlas Islands, 26 mm (HD). c, juvenile, with flammules, Las Perlas Islands, 30 mm (HD). d, adult, specimen similar to Reeve's original figure, Posorje, Ecuador, 40 mm (HWC). e, adult, with reduced flammules, Caleta San Lucas, 43 mm (HWC). f, adult, with flammules almost absent, Mulege, Baja California Sur, 37 mm (HWC). g, adult, with exaggerated shoulder, Venado Island, Panama, 38 mm (HD). h, adult (enlarged, same length as 3i), a "massive" form not observed from Gulf populations, 45 mm. Spire detail, note absence of dot pattern, 21 mm width, Bay of Panama (LACM 120200). i, adult, narrow form typical of Gulf specimens, 45 mm. Spire detail, compare with Figure 2g, 16 mm, Caleta San Lucas (HWC).

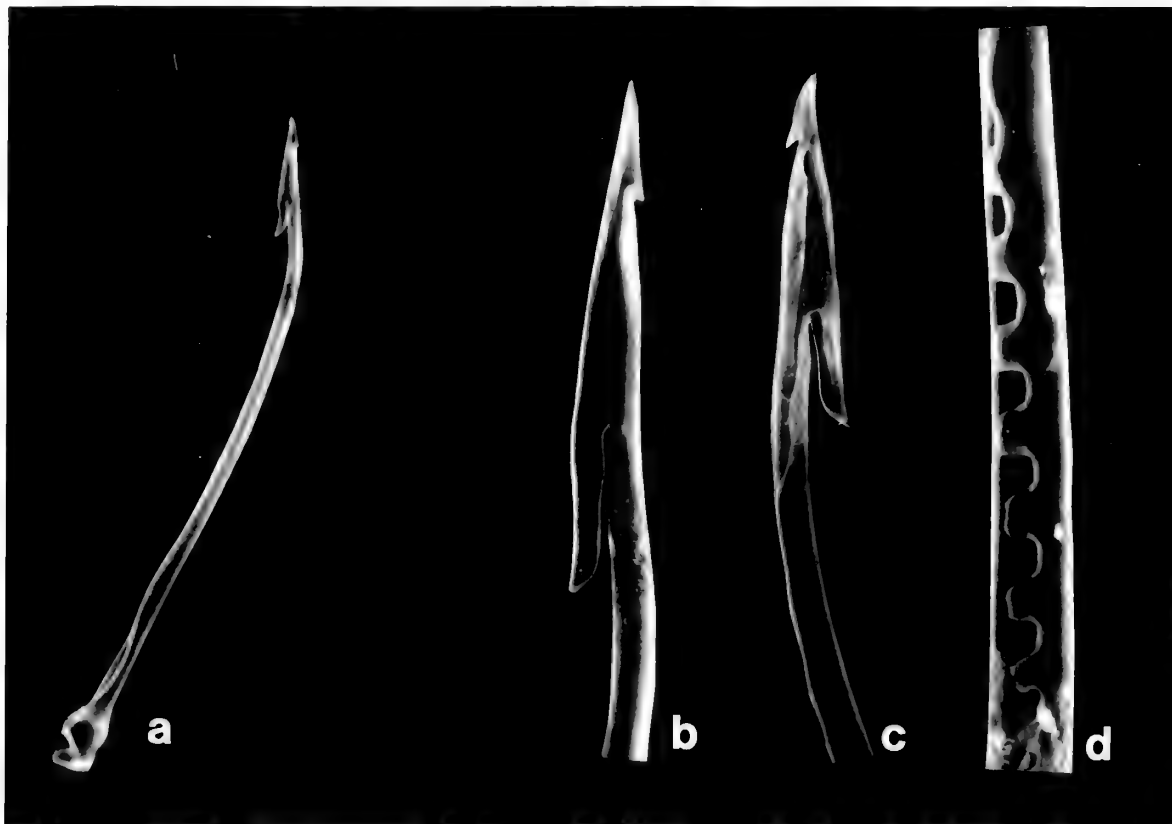


Figure 4

Radula tooth. *Conus ximenes* and *C. mahogani* have identical morphology. a, lateral view of complete tooth of *C. ximenes*, total length 1.10 mm. b, apical aspect of the tooth of *C. mahogani*, distal end, showing opposing barbs of the distal portion. c, adapical aspect of same tooth, showing light serrations barely visible along suture and hole for venom discharge near apex. d, mid-shaft region showing characteristic feature along margin, see text for discussion.

both species were prepared for scanning electron microscopy (SEM) using standard techniques.

The external anatomy was qualitatively observed and photographed.

RESULTS

Material Examined

Twenty-three lots of *Conus ximenes*, containing a total of 105 specimens, and 20 lots of *C. mahogani*, containing 101 specimens, were examined and measured. The material came from 21 localities as shown in Figure 1. Caleta San Lucas (A) and the type localities of *C. ximenes* (B) and *C. mahogani* (C) are also illustrated.

The majority of *Conus ximenes* available were collected from stations in western Mexico between Puerto Penasco, Sonora, and Manzanillo, Colima. An additional 32 specimens were taken from southern Panamic stations in Costa Rica, Panama, and the Galápagos Islands. Lots containing *C. mahogani* included 52 specimens from the Bay

of Panama and Costa Rica, with the remaining from the Sea of Cortez at Guaymas, Sonora, and Mulege, Baja California Sur. In total, 13 living *C. ximenes* and 9 *C. mahogani* were collected from Caleta San Lucas, Baja California Sur.

Shell Morphology

Variability in shell morphology, in both species, was noted in the material examined. *Conus ximenes* reached the greatest length and width in populations from the northern Gulf of California. Many of these larger shells were thicker and heavier than those from other localities (Figure 2f). Some specimens from southern Mexico and Panama were small and globose (Figure 2e) particularly in comparison to the more angular forms from the Sea of Cortez (Figures 2d, f, g). Body whorls of specimens had raised axial cords, a feature not consistent between shells even from the same station. The height of the spire also was variable.

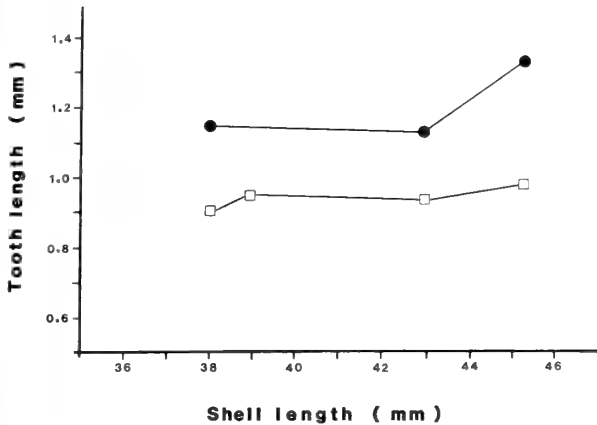


Figure 5

Comparison of radula tooth lengths versus total shell length between a size range of three *Conus ximenes* (black circles) and four *C. mahogani* (white squares). Each point is the mean length of 10 teeth removed from the short arm of the radula sac (SD: 0.005 mm).

Conus mahogani from the northern end of the range were consistently narrower (Figure 3i) when compared to the broad, massive specimens collected from the Bay of Panama (Figure 3h). Narrow specimens from Panama and Ecuador were also noted (Figures 3d, g).

The live-collected specimens from Caleta San Lucas showed that the females of both species were consistently larger than males (approximately 10% greater in shell length). Five male *Conus ximenes* and three male *C. mahogani* were collected.

Shell Pattern and Coloration

Three characters of shell markings were examined during the study: (1) axial patterns on the body whorl, (2) the pattern on the spire whorls, and (3) color within the aperture.

Color patterns on the body whorls of *Conus ximenes* were found to be highly variable even between specimens from the same station. Throughout the range, populations included individuals either very lightly marked with just rows of dots (Figure 2f) or ones with conspicuous axial flammules (Figures 2d, g). With *C. mahogani* the variability of these patterns was also apparent. Specimens from the southern part of the range tended to have heavy axial markings, in some cases darkening the entire shell (Figures 3d, g, h). The reverse was true with the Gulf populations examined in which axial flammules were reduced or nearly absent (Figures 3e, f).

The two contrasting character states of spire coloration were the presence or absence of dots and blotches, with each feature an extension of the axial flammules found on the body whorl.

Two rows of dots were found on the spire whorls of all

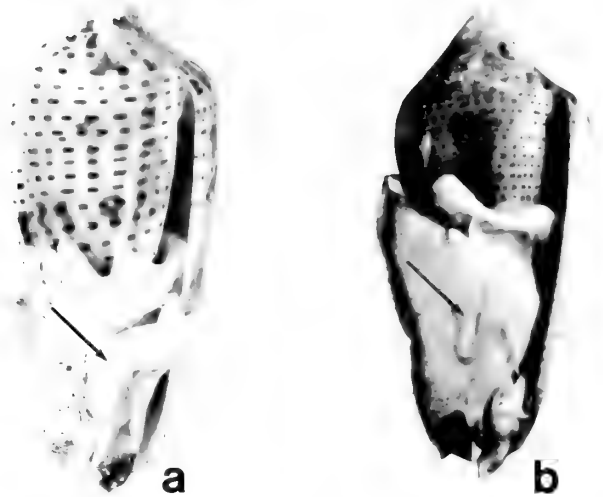


Figure 6

Male specimens of *Conus ximenes* and *C. mahogani* with animals partially extended. a, adult *C. ximenes* showing large verge (arrow). Mantle partially removed for clarity, penis positioned over lip of shell. b, adult *C. mahogani* showing much smaller penis (arrow), with mantle covering distal tip. Both shells are the same size, 2 \times .

the *Conus ximenes*, with each row bordering the suture (Figures 2f, g). On the final whorl the outer row of dots coincided with the shoulder. In some individuals with axial markings, the dotting pattern was partially obscured (Figure 2g). In contrast, the spire pattern of *C. mahogani* was dominated by wide, dark blotching, which in some parts of the spire may be reduced to the size of an isolated dot (Figures 3h, i). Unlike the continuous pattern of *C. ximenes*, the blotching pattern of the *C. mahogani* spire was often randomly arranged. The color patterns and markings of juvenile specimens were consistent with those of the adults (Figures 2a, b, 3a-c). Specimens of both species collected at Caleta San Lucas had similar axial markings (Figures 2g, 3i).

The apertures of all adult specimens of *Conus ximenes* were colored. Coloration ranged from dark violet to light pink in live-collected specimens but was absent in juveniles (Figures 2a, b), some sub-adults, and dead-collected specimens (which might otherwise be in good condition). In all specimens of *C. mahogani* the aperture was white.

The periostracum of both species, examined from the Caleta San Lucas specimens, was thin and without surface sculpture. The periostracum of living *Conus mahogani* gave the shell a rich golden color, a detail not as evident in the living *C. ximenes*.

Radula

Examination of the radulae of both species by SEM showed them to have morphologically identical shapes and

distal armatures (Figure 4). The teeth were narrow and flimsy, often curling when air dried from 100% ethanol. Better preparations were obtained after critical point drying in carbon dioxide.

The distal end of each tooth consisted of two opposing barbs, the smaller being nearest the tip (Figures 4b, c). The suture running up the length of the shaft terminated in a small hole below the tip which probably serves for venom discharge (Figure 4c). Very reduced serrations were visible along the suture between the opposing barbs (see adapical aspect).

The shaft of each tooth was ornamented by a series of squared projections, as opposed to serrations, that followed the margin of the rolled chitin sheet that formed the tooth (Figure 4d).

The one difference between the teeth of *Conus ximenes* and *C. mahogani* was in the overall length. Teeth from the short arm of the radular sac selected from a size range of three *C. ximenes* and four *C. mahogani* were measured and graphically arranged according to the overall length of the shells (Figure 5). Ten teeth from each specimen were measured, and their mean lengths represented by each data point.

In all respects the teeth from *Conus mahogani* were significantly shorter than those of *C. ximenes*, irrespective of shell length. There were no differences in either the number of rows or pairs of teeth produced by either species.

External Anatomy

Observations of the external gross anatomy of both species were limited to comparing animal coloration, external male genitalia, and opercula.

The coloration of the animals collected at Caleta San Lucas was identical, with no characters noted that could separate the two species. The basic color of the living animal was either pale yellow or white, with black mottling around the base of the foot, on the eyestalks, and the siphon. This mottling deteriorated soon after preservation. The outer margin of the mantle was highlighted by a single row of faint brown dots.

Male *Conus ximenes* could easily be distinguished from *C. mahogani* by comparing the cephalic penis (Figure 6). The penis, or verge, of *C. ximenes* is a large, flat structure with a small distal filament. The penis originated behind the right tentacle and extended over the dorsum of the animal underneath the mantle. Penis size was consistently massive in each of the five specimens examined, including one sub-adult (see Figure 2c).

The penis of *Conus mahogani* was a narrow, thin structure with two disparate lobes arranged distally, instead of a narrow filament. The penis of *C. mahogani* was only 20% the length of that of *C. ximenes* and was also greatly reduced in mass (Figure 6b).

No operculum, vestigial operculum, or opercular scar was found in any *Conus ximenes* collected from Caleta

San Lucas. All *C. mahogani* collected had a well developed operculum, similar to that of other *Conus* species.

DISCUSSION

The results of this study show that a variety of significant differences between *Conus ximenes* and *C. mahogani* allow specimens to be separated into two valid species which occur sympatrically throughout the Panamic Province.

Past attempts to distinguish these species morphologically have been hampered by a misplaced emphasis on body-whorl pattern as the primary descriptive character (WALLS, 1979). Coloration of the aperture was considered of secondary importance in the past, while the markings of the spire were rarely mentioned. In fact, this study shows that the importance of these three characters should be reversed, because body-whorl pattern is the most variable and spire markings the least.

When *Conus mahogani* was figured by REEVE (1843) he pictured a heavily flammulated, dark brown specimen and described its white aperture. A specimen from Ecuador, approximating the holotype in appearance and locality, is shown here in Figure 3d. Subsequent work continued to emphasize the axial pattern and the mahogany color as the decisive criteria (HANNA, 1963). In comparison, *C. ximenes* was considered lighter in color with greatly reduced markings and a purple interior.

For both species, these criteria as discussed by WALLS (1979) are incomplete. Because *Conus ximenes* also occurs as a heavily flammulated shell with a lightly colored aperture, Walls rightly questioned its separation from *C. mahogani*, thereby combining the two taxa as did KEEN (1971).

The present study showed that most *Conus mahogani* from Panama and Ecuador are dark colored and can be readily separated from the local *C. ximenes* on that basis alone (Figures 2c, 3b). However, shells collected from the Sea of Cortez possess a different set of characters. The body color of *C. ximenes* was highly variable within a single population. More importantly, all of the *C. mahogani* examined showed a reduction in axial markings. Aperture color for both species remained unchanged throughout the range.

Interestingly, what has not been discussed until recently is the third criterion of spire coloration (KEEN, 1971; WALLS, 1979). As shown in Figures 2f and g, *Conus ximenes* can readily be separated from *C. mahogani* by the presence of two rows of dots on the spire whorls. The occasional interruption by small blotches does not interfere with the basic integrity of this pattern. Rows of spire dots are not present in *C. mahogani*, in which the spire is covered with brown blotching, even in the Sea of Cortez populations where the axial markings are reduced.

Spiral dots were clearly figured by REEVE (1843) in his figure of *Conus interruptus* Broderip & Sowerby, 1829, and was also mentioned by HANNA (1963) in his discus-

sion of *C. ximenes* (a name which replaced the preoccupied *C. interruptus*).

The presence or absence of color in the aperture is also a reliable diagnostic feature. Its importance as a key feature seems to have been obscured by the importance placed on body-whorl coloration. *Conus mahogani* has a white aperture whereas the interior color of *C. ximenes* ranges from light pink to deep violet. The intensity of the color is dependent on the age of the specimen and its condition upon collection.

To summarize, the shells of these two species can be successfully distinguished by first examining the markings on the spire whorls, followed by noting the color within the aperture. The highly variable nature of the axial markings on the body whorl makes this criterion the least reliable.

The radulae of *Conus ximenes* and *C. mahogani* were studied by NYBAKKEN (1970) who noted their resemblance to each other and also distinguished them from those of all other Panamic species, including *C. tornatus* and *C. perplexus*, in which shell morphologies are superficially similar.

The evidence that the teeth of *Conus ximenes* are about 20% longer than those of *C. mahogani*, irrespective of shell size, may pertain to a role in prey selection. However, the morphological homologies between these teeth, including their high degree of flexibility, indicates a similar preference in diet.

Apart from radular studies on selected species of *Conus* (PIELE, 1939; NYBAKKEN, 1970; KOHN *et al.*, 1972; BANDEL & WILS, 1977; JAMES, 1980; BANDEL, 1984), there have been few published studies on other anatomical aspects of this genus (BERGH, 1895; SHAW, 1914). Although the use of reproductive structures as taxonomic characters is widespread in Mollusca (particularly in the opisthobranchs) it has not been used in *Conus* with the exception of BERGH (1895). In the present case, the disparity of penis size between *C. ximenes* and *C. mahogani* clearly indicates the value of characters of external anatomy.

The large, well developed verge of *Conus ximenes* was noted previously from two specimens examined by HANNA (1963) but no comparative material was available for *C. mahogani*. The fact that during the present study enough of both species were collected concurrently to allow for a replicated comparison leaves little doubt of their reproductive isolation from one another.

Although the use of the operculum as a taxonomic character in *Conus* has been discussed (ROCKEL *et al.*, 1980), particularly in the popular literature, its value is quite limited except in species in which there is a noticeable morphological feature like a heavily serrated margin (WALLS, 1979). In the present case, however, the absence of the operculum in *C. ximenes* in contrast to its obvious presence in *C. mahogani* is a dramatic difference.

To the best of my knowledge, the lack of an operculum in *Conus ximenes* is not only unique among the Panamic

cones but also may be unique in all *Conus*. Although the absence of this structure presents a mystery not easily explained, it may be a genetic clue toward understanding the evolutionary history of *C. ximenes*.

Unlike most other operculate prosobranchs, the operculum in *Conus* is vestigial, apparently no longer serving any purpose, such as aiding in defense, locomotion, or protection against desiccation. The fact that *C. ximenes* has entirely dispensed with this structure could be regarded either as a minor genetic variation (in comparison with the genus as a whole) or an evolutionary event in which a seemingly useless structure is beginning to be lost.

In spite of the differences between *Conus ximenes* and *C. mahogani* discussed above, the fact remains that these two species are closely related, especially in terms of general shell morphology, radula, and habitat. At present their population biology, diet, and reproductive habits are unknown. However, it seems plausible that these two species resulted from divergence from a common ancestor, perhaps due to a transitory isolating event in the past.

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Studies on Conidae (Mollusca: Gastropoda).

10. The Holotype and Identity of

Conus coffeae Gmelin

by

HENRY E. COOMANS

Zoological Museum, University of Amsterdam, P.O. Box 20125,
1000 HC Amsterdam, The Netherlands

AND

J. S. DE VISSER

Oranjestraat 2, 4361 EE Westkapelle, The Netherlands

Abstract. The holotype of *Conus coffeae* Gmelin, 1791, is traced in a private collection in The Netherlands, after being lost for two centuries. It is also the lectotype of *Cucullus caffer* Röding, 1798. The specimen is conspecific with the species generally identified as *Conus scabriusculus* Dillwyn, 1817, which is based on a doubtful type figure and erroneous locality. No longer being a *nomen dubium*, *C. coffeae* is recognized as the valid name for the species. The holotype is deposited in the Zoological Museum of Amsterdam.

INTRODUCTION

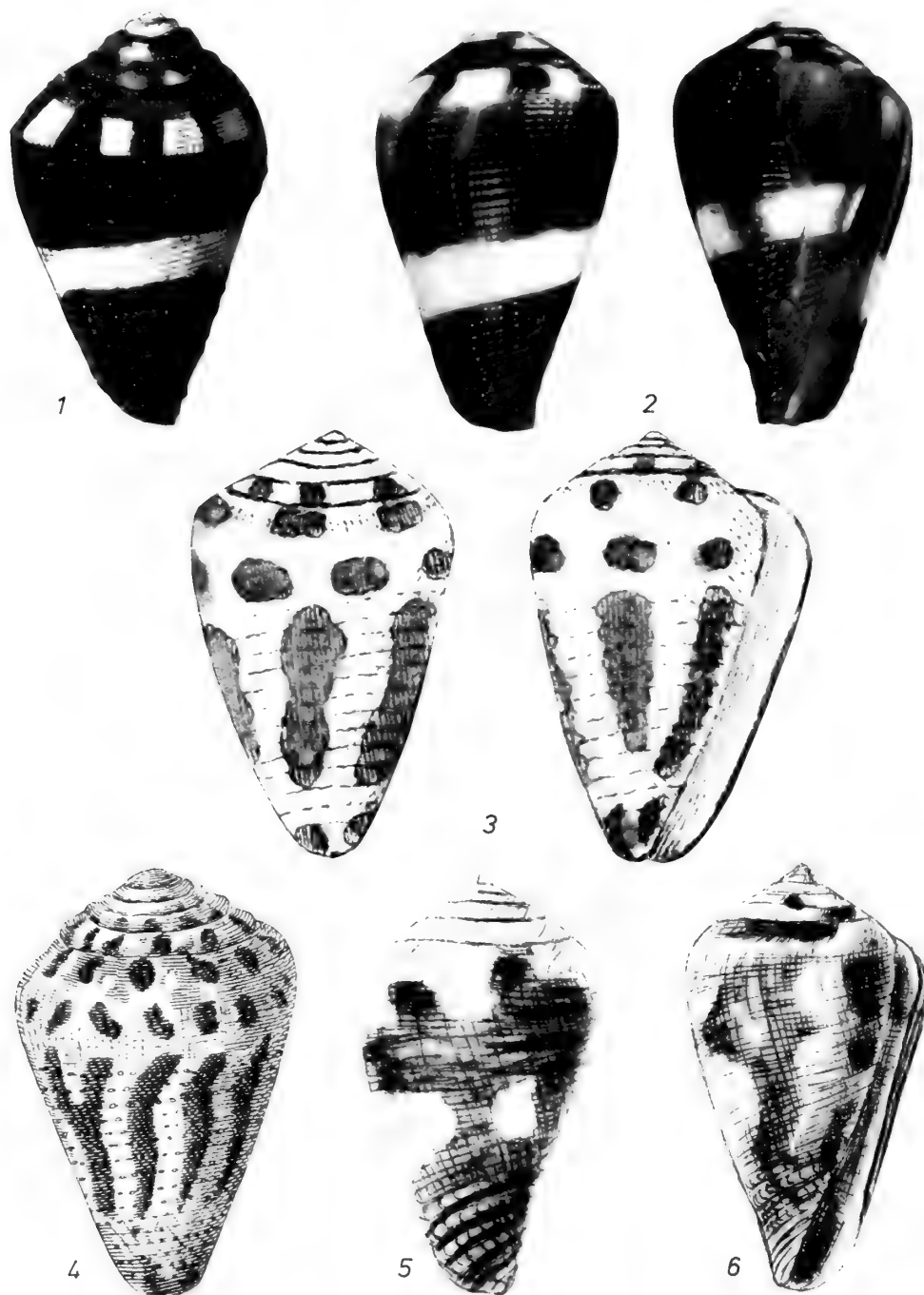
Conus coffeae was briefly described by GMELIN (1791:3388, no. 31) from a colored figure in MARTINI (vol. 2, 1773: pl. 56, fig. 618), a non-binominal work. Gmelin did not have a specimen available; thus the shell illustrated in Martini is the holotype. The specimen was at the time in the collection of MARTINI (1773:261), who described the coffee-brown shell as "Die Negerin mit weisser Stirnbinde" [the negro girl with a white forehead band]. The type figure is reproduced here (Figure 1). The locality of *C. coffeae* was not mentioned by either Martini or Gmelin. The specific epithet has often been misspelled by later authors as "coffea" or "coffaea."

During the 19th and 20th centuries the whereabouts of the type specimen of *Conus coffeae* was unknown; therefore, the identity of this nominal species was problematic (REEVE, 1849, Emendations:7). SOWERBY (1857:18, no. 141, pl. 8, figs. 173, 174) and others united it with *C. fumigatus* Hwass, 1792, a species from the Red Sea. However, the latter is larger, with a more triangular shape and a sharp shoulder; the body whorl is smooth instead of grooved, as in *C. coffeae*.

Japanese authors (HORIKOSHI *et al.*, 1963:83; AZUMA, 1973:16, pl. 1, fig. 3) mentioned "*Rhizoconus coffeae*" from their country, but this is a misidentification for *C. lischkeanus* Weinkauff, 1875 (COOMANS & FILMER, 1985:8).

KOHN (1966b:83) discussed *Conus coffeae* in his historical revision of the Conidae, and concluded that this taxon must be suppressed as a *nomen dubium*. A proposal to this effect was sent to the International Commission on Zoological Nomenclature (KOHN, 1966a:321-322), but as yet no action has been taken by the Commission.

WALLS (1979:967-968) believed that *Conus coffeae* was unrecognizable, and he designated its type figure as the lectotype of *Cucullus caffer* Röding, 1798. The type material of *Cucullus caffer* consisted of two specimens in the Bolten collection, which must be considered lost. In addition RÖDING (1798:48) mentioned two references in the literature: *Conus coffeae* in GMELIN (1791:spec. 31), and the illustration in MARTINI (1773:pl. 56, fig. 618). Röding gave only a vernacular name "Die zimmtbraune Tute" [the cinnamon-brown cone], without a description or locality. With Walls's lectotype designation, *Cucullus caffer* Röding is an objective secondary junior synonym of *Conus*



Explanation of Figures 1 to 6

Figure 1. Type figure of *Conus coffeae*, length 27 mm (after MARTINI, 1773).

Figure 2. Holotype of *Conus coffeae*, length 27.3 mm (coll. ZMA).

Figure 3. Type figure of *Conus scabriusculus*, length 19 mm, Sierra Leone (after CHEMNITZ, 1795).

Figure 4. Syntype figure of *Conus vermiculatus*, length 33 mm (after LAMARCK, 1816).

Figures 5 and 6. Syntype figures of *Conus fabula*, lengths respectively 21 and 26 mm (after SOWERBY, 1832-1841).

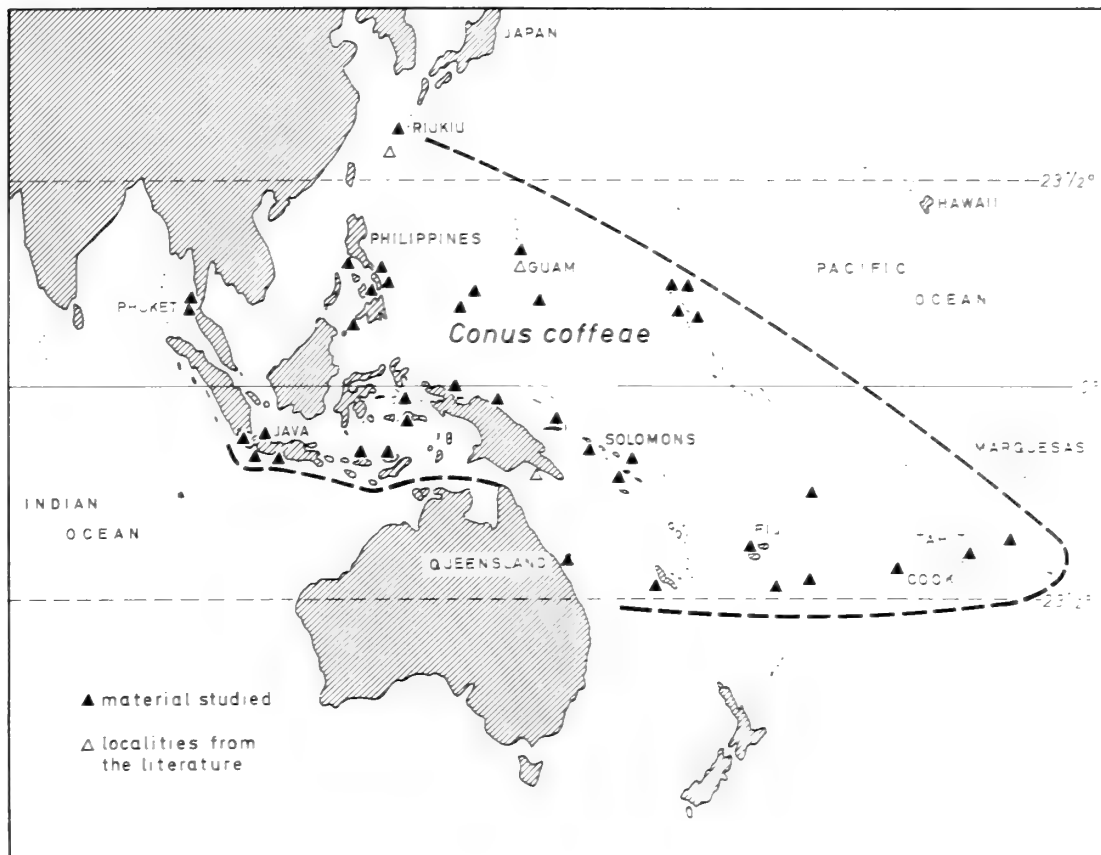


Figure 7

Distribution of *Conus coffeae*. The type locality is unknown.

coffeae Gmelin. *Conus caffer* (Röding) was also considered a *nomen dubium* by KOHN (1975:198).

COOMANS *et al.* (1983:70–73, fig. 314; 1985a:244) reproduced the type figure of *Conus coffeae* from Martini's work and agreed with Kohn in considering *C. coffeae* and *Cucullus caffer* Röding as *nomina dubia*.

TAXONOMY

The Type Specimen of *Conus coffeae*

In the collection of the late Leunis de Priester the second author has discovered a shell that looks identical to the type figure of *Conus coffeae*. After discussing the matter with R. G. Moolenbeek, the specimen together with the Notebook of de Priester were sent to the Zoological Museum in Amsterdam (ZMA) for further investigation.

The resemblance in shape and design is striking between the type figure of *Conus coffeae* (Figure 1) and this specimen (Figure 2). Also the measurements of the shell (27.3 × 16.1 mm) and the type figure (27 × 16½ mm) are alike. The specimen has the "Kaffeebraun" [coffee brown] color described and depicted by Martini, and the

position of two white spots on the post-nuclear whorls is the same. The only difference seems to be the number of white squares on the dorsal side of the shoulder; however, when the shell is viewed from a more apical direction, all four squares become visible, as in the type figure.

In de Priester's handwritten notebook, the "Catalog of his collection of Conidae," the following is stated on p. 71:

- "*Conus coffea* Gmelin = *fumigatus* Hw.
246a. 1 ex cotype, pl. LVI f. 618 Conch. Cab.
ex Zool. Mus. Berlin.
b. 1 patria ignota."

The label with the specimens bears the same information. Lot no. 246 contains two shells; the second specimen (b) is somewhat larger but conspecific. The remark "cotype" indicates that de Priester also related no. 246a to the specimen figured by Martini, especially as he referred to the plate and figure in the Conchylien-Cabinet. He had received this specimen on exchange from the Zoological Museum in Berlin before World War II. The holotype of *Conus coffeae* is now deposited in ZMA (no. 191001).

Leunis de Priester, 1880–1968, was a Dutch shell collector whose main interests were Conidae and Cypraeidae. His collection is presently under the care of Mrs. K. H. Roskam-de Priester of Flushing, The Netherlands. He exchanged specimens with his friend Philippe Dautzenberg in Paris, and with several museums. His correspondence contains letters from Dr. B. Rensch, at the time curator of the Zoological Museum in Berlin. De Priester was an Honorary Associate of the Zoological Museum in Amsterdam, and many of his duplicates were donated there (VAN BENTHEM JUTTING, 1939:180, 240). Except for co-editing DAUTZENBERG's posthumous work on Conidae (1937), de Priester did not publish on mollusks, but he kept notebooks for his collections of *Conus* and *Cypraea*. *Conus thalassiarachus* var. *depriesteri* Wils, 1972, was named after him (COOMANS *et al.*, 1985b:164, fig. 630).

The Identity of *Conus coffeae*

With the type specimen at hand we are now able to recognize this taxon, and it is no longer a *nomen dubium*. *Conus coffeae* is the first available name for what has generally been called *C. scabriusculus* Dillwyn, 1817. KOHN (1986:24, fig. 21) accepts *C. scabriusculus* as a valid species from the tropical western and central Pacific region. He refers to WALLS's redescription (1979:592, 841–842) and illustrations, which are conspecific with *C. coffeae*.

Conus scabriusculus is based on an illustration in CHEMNITZ (vol. 11, 1795:pl. 182, figs. 1768, 1769), a non-binominal work. It is a small specimen, 19 × 12 mm, reported by Chemnitz from Guinea, especially Sierra Leone. It is doubtful that the shell figured in Chemnitz (Figure 3) can be considered the "*C. scabriusculus*" of later authors. The type figure certainly is not convincing, and a west African type locality is in that case incorrect. The specimen of *C. scabriusculus* was at the time in Chemnitz's collection, but the present whereabouts are unknown. Chemnitz stated (1795:56–57) that the shell was covered with spiral cords, which were left out on the type figure. If the shell did originate from Sierra Leone, the only possibility is a juvenile specimen of *C. ermineus* Born, 1778. We also note that one of the syntypes (Figure 4) of *C. vermiculatus* Lamarck, 1810, figured in LAMARCK (1816: pl. 321, fig. 1), resembles the type figure of *C. scabriusculus*.

Nomenclatorial Discussion and Conclusion

We see three alternatives in this situation: (1) *Conus coffeae* Gmelin, 1791, is no longer a *nomen dubium*, and the name has not been suppressed by the ICZN. Because it is the oldest available one, it can be considered as a valid name. (2) Another possibility is to leave undisturbed the nomenclature and to maintain the long-accepted name of *C. scabriusculus* Dillwyn, 1817, considering *C. coffeae* an unused senior synonym (ICZN art. 23). However, there is a discrepancy between the generally accepted concept

of *C. scabriusculus*, compared to its doubtful type figure with a probably erroneous type locality. (3) The next available name for the taxon is *C. fabula* Sowerby, 1833 (Figures 5, 6). However, this nominal species is based solely on two (conspecific?) figures in SOWERBY (1832–1841:pt. 24, figs. 5, 5*); there is no description, the locality is unknown, and no type material is available.

Although a stable nomenclature is usually preferred by us, the reinstatement of *Conus coffeae* Gmelin, 1791, as the valid name for this taxon seems to be preferable. Of the three mentioned possibilities, *C. coffeae* is the oldest name, and also the only one based on an existing type specimen.

Synonymy and Distribution

The following synonyms for *Conus coffeae* are known:

- Conus coffeae* Gmelin, 1791, Syst. Nat., 13 ed., 1:3388, no. 31 (holotype in ZMA, no type locality).
- Cucullus caffer* Röding, 1798, Mus. Bolten. 2:48, no. 606/100 (lectotype = holotype of *Conus coffeae*). [Non *Conus caffer* Krauss, 1848, Südafr. Moll.:131, pl. 6, fig. 24; a junior secondary homonym, but not a synonym of *C. caffer* Röding.]
- ? *Conus scabriusculus* Dillwyn, 1817, Descr. Catal. Rec. Shells 1:406 (only type figure known, type locality the coasts of Guinea about Sierra Leone).
- Conus fabula* Sowerby, 1833 (in part), Conchol. Illustr., pt. 24, fig. 5 (only syntype figure known, not fig. 5*, no type locality).

The distribution of *Conus coffeae* covers the tropical western Pacific from the Riukiu Archipelago through Indonesia to Queensland, and including the island groups of the central Pacific, exclusive of Hawaii and the Marquesas. The species is also collected in the Andaman Sea on the coast of Thailand. Except for the southern coast of Java there are no records from localities in the Indian Ocean.

The distribution map (Figure 7) is based on material examined by the first author in the collections of the Academy of Natural Sciences in Philadelphia, the Delaware Museum of Natural History in Wilmington, the National Museum of Natural History in Washington, D.C., and the Zoological Museum of Amsterdam.

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The first author is thankful to his American colleagues for their hospitality and help during a recent visit to the U.S.A.: Ms. Diane Bohmhauser and Dr. R. Houbriek

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The Genus *Littoridinops* (Mesogastropoda: Hydrobiidae) in New England

by

DOUGLAS G. SMITH

Museum of Zoology, University of Massachusetts, Amherst, Massachusetts 01003, and
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

Abstract. The hydrobiid snail genus *Littoridinops* is represented in eastern North America by at least three species. One species, *Littoridinops tenuipes*, has been reported northward along the Atlantic coast to at least extreme southeastern New York. However, the taxonomic status of the northern populations of *L. tenuipes* remains unclear because of differences in the verge of New York specimens, and the generally accepted northern range limit of confidently identified specimens of *L. tenuipes* is Georgia. Snails identified as belonging to the genus *Littoridinops* were recently collected in coastal fresh and brackish waters in northeastern Massachusetts, thus extending the known range of the genus farther north. On the basis of shell characters and verge and radular morphology the populations are identical with *L. tenuipes*. The status of New York populations is still unclear due to the odd appearance of the verge, which may be either an artifact of preservation or representative of an as yet undescribed species.

INTRODUCTION

THE HYDROBIID genus *Littoridinops* Pilsbry, 1952, contains at least three species of fresh- and brackish-water inhabiting snails that live in subtropical and temperate regions of eastern North America (TAYLOR, 1966). Only one species, *Littoridinops tenuipes* (Couper, 1844), has a range that includes both climatic zones. However, the northern extent of the range of *L. tenuipes* has been in question since PILSBRY (1952) described the subgenus (now genus) *Littoridinops* to accommodate the distinctive *L. tenuipes*. PILSBRY (1952) gave the range of the species as including most of the Atlantic seaboard north to the Lower Hudson River system in New York, but in his description of *L. tenuipes* he included a figure of the verge that appears aberrant when compared to specimens of *L. tenuipes* from farther south along the coast. On the basis of this aberrancy, THOMPSON (1968) concluded that the material examined by PILSBRY (1952) belonged to an undescribed species. THOMPSON (1968, 1984) subsequently listed coastal Georgia as the northern range limit of populations that he could confidently identify as *L. tenuipes*. This decision has been adopted by BURCH (1982) as well. Nonetheless, JACOBSON (1953) recorded the species from

the Chesapeake Bay region and BEETLE (1973) listed the species as occurring in coastal Virginia. Recently, M. Mazurkiewicz (personal communication) has examined specimens of *L. tenuipes* collected in New Jersey.

RESULTS AND DISCUSSION

During the spring of 1986, specimens approaching the description of *Littoridinops tenuipes* were collected in two localities in the Parker River system in northeastern Massachusetts (Essex County). The two localities are (1) an open ditch just W of MA Rt. 1A, 0.3 km S of Newbury border, Rowley, and (2) a marsh off the Mill River just N of the Newbury-Rowley border and E of US Rt. 1, Newbury.

In the first locality, hundreds of specimens of *Littoridinops* were found associated with two other hydrobiid species, *Cincinnati winkleyi* (Pilsbry) and *Spurwinkia salsa* (Pilsbry), both of which were also abundant. No other mollusks were detected. The ditch contained cat-tails (*Typha* sp.) and unidentified rushes. The salinity level was 2.0‰ (oligohaline) as determined using a LaMotte Salinity Titration kit (Model POL-H). Elevation was about 3 m above sea level. The ditch drained an oak-alder-pine swamp on the E side of MA Rt. 1A.



Figure 1

Shell of *Littoridinops tenuipes* from the Parker River system in Massachusetts, $\times 15$.

At the second locality, mollusk species associated with *Littoridinops*, which was not common, were *Cincinnati winkleyi*, the freshwater pisidiid clam *Pisidium casertanum* (Poli), and pulmonate snails of the genus *Lymnaea* (species undetermined). The marsh was dominated by cat-tails (*Typha* sp.) and was, by its proximity to a tidal flat, undoubtedly affected by tidal water. At the time of collection the salinity measured 0.3‰ (freshwater).

All specimens collected alive were narcotized with menthol crystals and fixed in 10% formaldehyde. Specimens were subsequently stored in 50% isopropyl alcohol. With the exception of a small series of shells donated to the Museum of Comparative Zoology, Harvard University (MCZ296178), all specimens have been placed in the Invertebrate Division of the Museum of Zoology, University

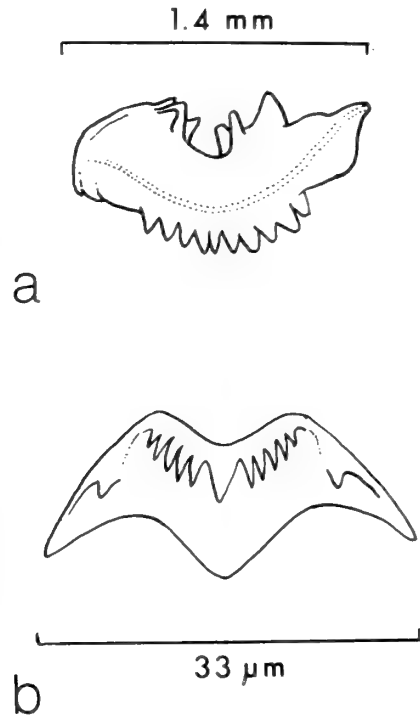


Figure 2

Morphology of the verge (a) and central tooth of the radula (b) of *Littoridinops tenuipes* from the Parker River system in Massachusetts.

of Massachusetts at Amherst (locality 1: UMA MO. 1593; locality 2: UMA MO. 1594).

Several morphological characters traditionally important in hydrobiid taxonomy were analyzed for purposes of comparison with the *Littoridinops* species described by PILSBRY (1952) and THOMPSON (1968). Shell measurements included shell length, shell diameter, aperture length, and aperture width (Table 1). The overall morphology of the shell (Figure 1) is distinctly littoridinine by nature of its relatively flat-sided whorls and shallow sutures (PILSBRY, 1952; THOMPSON, 1968, 1984). The operculum is paucispiral. The verge is also typical of *Littoridinops* in possessing a single lobe (penis) with a single duct (vas

Table 1

Shell and verge characteristics of Massachusetts populations of *Littoridinops*. R = range ; \bar{X} = mean; n = sample size.

	Shell dimensions				Verge papillae		
	Shell length	Shell diameter	Aperture length	Aperture width	Left side	Right side	Base
R	3.29-5.39	1.89-2.66	1.26-1.89	0.98-1.61	2-5	7-13	0-4
\bar{X}	3.82	2.14	1.54	1.23	3.4	8.7	1.33
n	20	20	20	20	15	15	15

deferens) extending to the distal tip, an absence of specialized glands, but with characteristic papillae present along each side and the base (Figure 2a). The number and arrangement of papillae on the verge are given in Table 1. Additionally, radula preparations of ten specimens revealed no dental characters unlike those described and figured by PILSBRY (1952) and THOMPSON (1968) for the genus.

An assessment of three characters described above indicates that the Massachusetts populations of *Littoridinops* are referable to *L. tenuipes*. Shell dimensions (see Table 1) compare favorably with data presented by THOMPSON (1968:61) for *L. tenuipes* from Florida and Georgia. The only difference noted was a slight increase in shell size in Massachusetts specimens. The shell length-diameter and shell length-aperture length ratios for Massachusetts specimens were 1.61–2.03 and 2.07–3.00, respectively, and these values are overlapped completely by those of *L. tenuipes* from Florida and Georgia (THOMPSON, 1968). The morphology of the verge, including the arrangement and number of papillae on the verge, is the single strongest indicator of the taxonomic affinity of the Massachusetts populations. Clearly, the presence of papillae on both sides and at the base of the verge (Figure 2a) and the number of papillae in each group (Table 1) show no difference from *L. tenuipes* from the southeastern Atlantic coast. In examined individuals the papillae along the right side were fairly uniform in size and formed a single row, although occasionally a few proximal papillae overlapped slightly. Left side papillae were less uniform in size and were bunched together (Figure 2a) or were scattered somewhat along the border. Basal papillae were present in all but one individual in a sample of 15 specimens (Table 1) and were usually of different size and arrangement.

The radular teeth exhibited the greatest variation among the characters examined. In 10 preparations the lateral teeth contained, in addition to a mesocone, from four to six ectocones and from four to six entocones, somewhat higher numbers than the total cusp count (including the mesocone) given by PILSBRY (1952) or individual counts in THOMPSON (1968). The central tooth in Massachusetts specimens (Figure 2b) also showed some variation in cusp count with formula variations ranging from $\frac{4-1-4}{1-1}$ to

$\frac{6-1-6}{2-2}$ (15 preparations). These formulae show no great deviation from those reported for *Littoridinops tenuipes* elsewhere.

Although it is evident that the Massachusetts populations examined in this study are identical with *Littoridinops tenuipes* when using traditional morphological characters, the question of the aberrant verge figured by PILSBRY (1952) for New York specimens is still unresolved. The specimens observed by PILSBRY (1952) may have been *L. tenuipes*, but the appearance of the figured verge may be the result of distortion due to preservation without prior relaxation. Alternatively, it could be argued that *L. tenuipes* occurs northward along the Atlantic coast to New England but that another undescribed species, with verge characters similar to those described by PILSBRY (1952), also exists in the region.

ACKNOWLEDGMENTS

I should like to thank Dr. Herb Hultin of the University of Massachusetts Marine Station at Gloucester for providing logistic support during this study and Dr. Mike Mazurkiewicz of the University of Southern Maine for helpful information. The study was sponsored by a grant from the Massachusetts Natural Heritage Program.

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NOTES, INFORMATION & NEWS

Concerning the Type Material of
Lasaea subviridis Dall, 1899

by

Eugene Coan

Research Associate,

Department of Invertebrate Zoology,

California Academy of Sciences,

Golden Gate Park,

San Francisco, California 94118, U.S.A.

In 1899, Dall made available a Carpenter manuscript name, *Lasaea rubra* "var." *subviridis*, in his review of the North American Leptonacea (DALL, 1899:881) for specimens from "Lower California" that were "pale greenish yellow." KEEN (1938:23, 24, 29-30, 32; pl. 2, figs. 1-3) designated a neotype for this species. It was Stanford University Paleontology Type Collection no. 6053 and is now at the California Academy of Sciences with the rest of the Stanford University collection.

This neotype designation is invalid because Dall's original material was never properly searched for. Paul Bartsch of the U.S. National Museum of Natural History looked on behalf of Dr. Keen only for Carpenter's original material (see footnote, KEEN, 1938:30). Because the name was made available by Dall, not by Carpenter, any material that Dall had in hand when he named the species would be available as type specimens.

According to the 1985 edition of the International Code of Zoological Nomenclature, a neotype designated before 1961 may be considered invalid (Art. 75g) if it does not meet the appropriate provisions of Art. 75, among them that the author publishes reasons for believing that the original material is lost or destroyed (Art. 75[d]3). Because it is clear that Bartsch and Keen did not establish that *Dall's* material was lost, the neotype designation does not stand.

I have set aside as syntypes a lot in the U.S. National Museum of Natural History that was in the collection before Dall worked on his paper and that was undoubtedly studied by him. It was numbered USNM 75032. Because this number does not correspond with the entry in the collection register with this number, it has been renumbered USNM 859071. It is from Bahía San Quintín, Baja California Norte, and was collected by Walter J. Fisher on 27 April 1876 among *Mytilus* on rocks. It contains 30 pairs and 6 valves.

I believe that the selection of lectotypes should be done by workers doing revisions of the particular groups involved. This ensures the selection of a specimen that may show particularly important characters not readily apparent to a non-expert. It is especially important that a lectotype designation of this species be made by someone knowledgeable about this genus, which is proving to be

more taxonomically complex than previously thought (D. Eernisse, *in litt.*, Nov. 1986).

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Important Notice:

Problems with Mailing of January Issue

Serious problems with the mailing of the January issue have been brought abundantly to our attention. Apparently, a new machine was used by the Printer to insert mailing labels into the plastic sleeve that encloses and protects your journal during postal delivery. Unfortunately, the machine malfunctioned, resulting on many occasions in more than one mailing label being inserted into the plastic sleeve, with one journal copy. If, for instance, three labels were accidentally inserted, only one subscriber received this journal issue on time, and two subscribers did not.

Although the California Malacozoological Society was in no way responsible for these errors, we apologize on behalf of the Printer for the inconvenience caused. We also sincerely thank those thoughtful subscribers who returned the additional mailing labels inserted with their journal copy. This allowed us to immediately send copies to many of those who were missed. We have received assurances that the mechanical problems have been corrected and should not reoccur.

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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.

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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*.

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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.

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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.

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Volumes 1 through 13, 24, 26, and 27 are out of print.

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International Commission on Zoological Nomenclature

The following applications have been received by the Commission and have been published in Vol. 43, Part 3, of the *Bulletin of Zoological Nomenclature* (6 October 1986). Comment or advice on them is welcomed and should be sent %The British Museum (Natural History), London, England. Comments will be published in the *Bulletin*.

Case No. 2512. *Megaloniaias* Utterback, 1915 (Mollusca, Bivalvia): proposed conservation by the suppression of *Magnoniaias* Utterback, 1915.

In addition, the following Opinions, rulings of the International Commission on Zoological Nomenclature, have been published in Vol. 43, Part 3, of the *Bulletin of Zoological Nomenclature* (6 October 1986):

Opinion No. 1410 (p. 249). *Williamia* Monterosato, 1884 (Mollusca, Gastropoda): conserved.

Opinion No. 1414 (p. 258). *Panopea* Ménéard de la Groye, 1807 (Mollusca, Bivalvia): conserved.

The Tenth International Malacological Congress

The tenth International Malacological Congress will be held from 27 August to 2 September 1989 in Tübingen, Germany. Papers dealing with any aspect of malacology are invited for oral or poster presentation. Malacologists wishing to attend should be prepared to submit provision-

al titles of papers, together with one or two sentences exposing the questions dealt with therein, before 30 September 1988 (not an abstract at this time).

Address inquiries to the current president of UNITAS MALACOLOGICA: Dr. Claus Meier-Brook, Tropenmed. Institut d. Univ., Wilhelmstr. 31, D-7400 Tübingen, Federal Republic of Germany.

The American Society of Zoologists
1987 Meeting

The 1987 meeting of the American Society of Zoologists will be held in New Orleans, Louisiana, from 27 to 30 December 1987. Meeting with the ASZ will be the Amer-

ican Microscopical Society, Animal Behavior Society, The Crustacean Society, International Association of Astacology, and Society of Systematic Zoology. Several symposia and workshops that are of potential interest to our readers are planned, among them "Adaptive sex ratios and sex ratio theories, kin recognition in animals, adaptive coloration in invertebrates, aquatic locomotion, vicariance biogeography, and science as a way of knowing—form and function."

The deadline for abstracts is 10 August.

For more information, contact: Mary Adams-Wiley, Executive Officer, American Society of Zoologists, Box 2739, California Lutheran University, Thousand Oaks, California 91360. Telephone: (805)492-3585.

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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.

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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.

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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.

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