

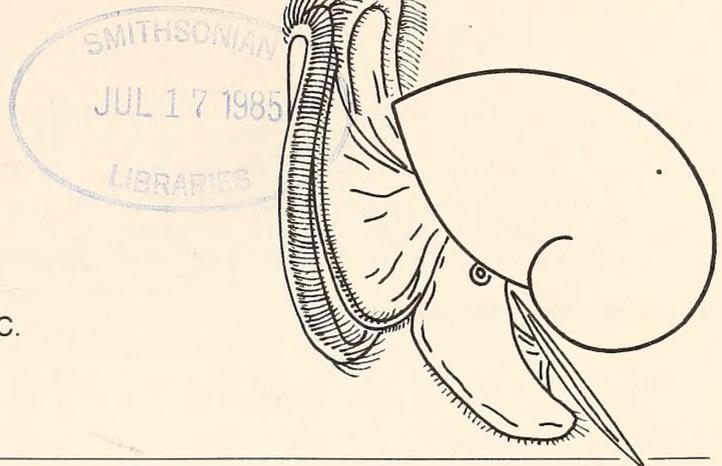




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Attack Mode in a Predatory Gastropod: Labial Spine Length and the Method of Prey Capture in *Acanthina angelica* Oldroyd

by

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Abstract. The function of the labial spine and the feeding behavior of the predatory gastropod *Acanthina angelica* were observed under controlled conditions. Long- and short-spined snails were presented three size classes of barnacle prey. The mode of attack was related to the length of the labial spine and the prey size. The spine was observed to function as a wedge to force apart the opercular valves of the prey (here termed wedging); drilling through the test or valves was an alternative mode of attack. As prey size increased, snails switched from wedging to drilling, with the short-spined snails switching at a smaller prey size than long-spined snails. The long-spined snails consumed medium-sized prey significantly sooner than short-spined snails. Short-spined snails are usually found in association with small barnacles, while long-spined snails predominate among larger barnacles. However, spine length is not fixed, and available evidence indicates that prey size controls spine length.

INTRODUCTION

MANY PREDATORY GASTROPODS attack barnacles, bivalves, and other gastropods by drilling through the shell of the prey (CARRIKER, 1961, 1981). "Wedging" is an alternative mode of attack in several of these species (PAINE, 1962; MACGINITIE & MACGINITIE, 1968); this entails the predator's forcing its shell margin between the valves of the prey (barnacle or bivalve) and, once access is gained, inserting the proboscis to consume the prey. Some members of the neogastropod family Thaididae, which includes the genus *Acanthina*, have apparently taken the wedging approach to attacking prey one step further. These species are characterized by an extension of the shell margin into a labial spine or "tooth."

A variety of functions has been attributed to the spine. HEWATT (1934) and MACGINITIE & MACGINITIE (1968) both observed several species of thaidids utilizing the spine as a "pry bar" or wedge to force apart and hold open barnacle valves. PAINE (1966) concluded that the spine of *Acanthina angelica* Oldroyd, 1918, is not used in this fashion, but rather it serves as a brace to afford a firm position on the substrate while drilling. MENGE (1974), working with *Acanthina punctulata* (Sowerby, 1825), arrived at a similar conclusion regarding use of the labial spine. SLEDER (1981), on the other hand, concluded that the spine

of *A. punctulata* helps the predator to apply a fast-acting toxin to its barnacle prey.

Acanthina angelica is endemic to the Gulf of California (KEEN, 1971), and is common in the rocky intertidal of the northern Gulf (TURK, 1981; HOUSTON, 1980). Adult snails attain a total shell length of 35-40 mm, and feed almost exclusively on barnacles (PAINE, 1966). The spine length of adult snails varies considerably among individuals; e.g., 30-mm snails have spines ranging from 2 to 7 mm in length (YENSEN, 1979). The intertidal distributions of the long-spined and short-spined snails are skewed in a manner that reflects the intertidal size distribution of the two dominant barnacle species upon which the snails prey (PAINE, 1966; YENSEN, 1979; TURK, 1981). Long-spined *A. angelica* are more common in the high intertidal zone characterized by the large barnacle *Tetraclita stalactifera* Lamarck, while short-spined snails are usually found in the lower intertidal in association with the small barnacle *Chthamalus anisopoma* Pilsbry. The correspondence between spine length and barnacle size suggests a functional relationship between the two. Both PAINE (1966) and YENSEN (1979) observed that snails with relatively long spines prey on *Tetraclita*, while short-spined snails feed primarily on *Chthamalus*. However, in contrast with Paine's suggestion that the snails only drilled, Yensen's

field observations and laboratory experiments strongly support the hypothesis that the labial spine is used directly in wedging apart the opercular valves of barnacles.

The purpose of this study was to elucidate the relationship between labial spine length, the size of the barnacle prey, and the mode of attack of *Acanthina angelica*. If the spine is used to wedge open the opercular valves of barnacles, and drilling is an alternative to wedging when the spine is too short to effectively reach the valves, then short-spined snails should switch to a drilling mode of attack at a smaller prey size than do long-spined snails. This is assuming that wedging would be quicker than drilling, and that the snails feed in the most efficient manner possible.

MATERIALS AND METHODS

A laboratory experiment was conducted to determine the foraging behavior of both long- and short-spined snails as they fed on three different size classes of barnacles. Specimens of *Acanthina angelica* were collected haphazardly during October of 1983 from the rocky intertidal near Puerto Penasco, Sonora, Mexico (31°18'N, 113°35'W) on the Gulf of California. The animals were brought to the University of Arizona where they were maintained without food in three 40-L aquaria for two weeks. Aquarium water temperature was approximately 22°C, comparable to that in the Gulf during October. Photoperiod was approximately 10 L, 14 D.

Two weeks after the snails were collected, barnacles were collected from the same area. To avoid the potentially confounding effects of using two species of barnacles for prey, as might arise from a species-specific mode of attack, I exclusively collected *Tetraclita stalactifera* over a range of sizes (2–40 mm basal diameter) for presentation as prey. Settlement of *Tetraclita* during the two months previous made it possible to collect adequate numbers of small individuals calculated to be of approximately the same size and body weight as the smaller barnacle species, *Chthamalus anisopoma* (MALUSA, 1983). The barnacles were brought to the University of Arizona and maintained in aquaria next to those harboring the snails.

Forty-five short-spined and 45 long-spined snails were chosen for the experiment on the basis of their spine length. Long-spined snails were defined as those having a labial spine measuring more than 4 mm from base to tip; short-spined snails were defined as those having a spine measuring less than 3.5 mm in length. No attempt was made to control for differences in shell length between the two groups. Long-spined snails were approximately 25–35 mm in length, while short-spined snails were approximately 20–35 mm.

The shells of all snails were numbered with a permanent felt tip marker to permit individual identification. Barnacles were sorted into three size classes based on the basal diameter along the rostral-carinal axis: less than 7 mm (small), 7–20 mm (medium), and greater than 20 mm

(large). Inappropriately sized individuals were removed from the pieces of the substrate bearing barnacles, leaving only the desired size class on each rock.

At the beginning of the experiment, each of the three aquaria received 15 long-spined snails, 15 short-spined snails, and 40 to 60 of one of the three size classes of barnacles. Within each aquarium the two groups of snails were separated by a plastic screen that allowed water passage. Approximately equal numbers of barnacles were made available on either side of the divider. The foraging activities of the snails were then observed continuously for the following 24 h, and thereafter two to three times daily for 26 days. I kept a record of (a) the mode of attack employed by each snail on its first successful feeding (wedging or drilling), and (b) the time from the start of the experiment until the first barnacle was successfully attacked and consumed (here termed the “consumption order”—see below).

The feeding behavior and the use of the spine could be observed closely in instances when the opercular valves of the barnacle were close to the opening of the shell, as is the case in small barnacles and those larger barnacles that happened to have badly eroded tests, permitting an adequate view. Observations of feeding behavior associated with wedging (a characteristic lunging movement described below) allowed me to infer wedging in cases where the snail's foot and mantle obscured direct observation of the spine. In addition, wedging attacks left scratch marks on the barnacle's valves. Drilling attacks could only be identified after the fact by the presence of a hole in the test or valves of the barnacle. I avoided handling the snails while drilling; thus, it was not possible to observe drilling directly. It is not known whether the relative hunger of *Acanthina angelica* modifies its foraging behavior, and consequently after any one snail had consumed a barnacle, both the predator and the remains of its prey were removed from the aquarium.

RESULTS

Close observation of feeding behavior established the following sequence of events. After encountering a barnacle the snail mounted it and brought the labial spine to the barnacle's opercular opening. The spine was then inserted into the opening, as if to “feel” for the opercular valves. The proximate stimulus for a wedging attack appears to be the contact of the spine with the opercular valves. Snails observed wedging kept the spine positioned in or above the opercular opening and, with the foot firmly attached to the barnacle, thrust the spine downward, apparently bringing the spine into forcible contact with the natural separation of the barnacle's opercular valves at a point on the scutum near its junction with the tergum. This “lunging” was repeated as often as five times per minute, until either gaining access to the mantle cavity of the barnacle, or giving up. Some snails maintained an attack for up to several hours, although with diminished frequency of

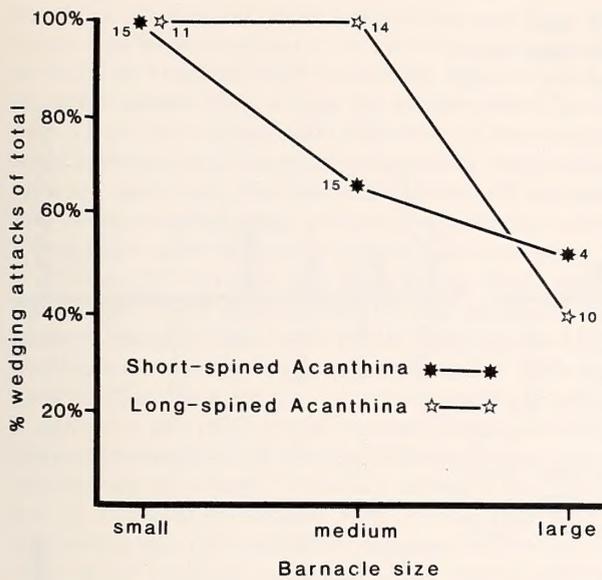


Figure 1

Results of the foraging experiment showing the variation in attack mode in *Acanthina angelica* relative to spine length and size of barnacle prey. Sample size is indicated.

lunging. These prolonged attacks resulted in an abraded elliptical depression where the barnacle's valves meet. This artifact of wedging could be mistaken for a drill hole, except it is not circular (as gastropod drill holes are), and it was associated only with lunging behavior. Interestingly, three snails that did drill failed because they entered the barnacle at a point above the opercular valves, and another snail completed a drill hole into an empty test. Most snails sequestered with the large barnacles either could not feed or chose not to feed during the entire 27 days of observation; these data were not included in the statistical analyses.

Relationships between attack mode, spine length, and the size of prey are shown in Figure 1. These data were analyzed with a G-test (Table 1). The mode of attack is clearly dependent on the barnacle size ($G = 20.995$, $df = 2$, $P < 0.001$). One hundred percent of the small barnacles were wedged open with the spine, as were 87% of the medium-sized barnacles, and only 43% of the large barnacles. Hence, successful use of the spine was dependent on barnacle size.

There is also a relationship between attack mode and spine length that varies according to barnacle size. Given small or large barnacles, short-spined and long-spined snails employed similar attack modes (*i.e.*, they both wedged small ones and drilled large ones with similar frequency; $P > 0.50$). However, for medium-sized barnacles, more short-spined snails drilled than did long-spined snails ($0.025 < P < 0.05$) (these tests represent partitioning of the G that is due to the spine length ×

attack mode and the spine length × attack mode × prey size interaction).

Figure 2 shows the time until the first barnacle was consumed for long and short-spined snails on all three size classes of barnacles. Note that this time interval includes the total time from the beginning of the experiment until the first barnacle was consumed, not simply the time from initiation of feeding to completion. Data were analyzed using a Mann-Whitney test for ordinal data by assigning rank values to the observations in each time interval (the "consumption order"). Pairwise comparisons of consumption order show that short-spined snails consumed small barnacles sooner than they did medium-sized barnacles ($P < 0.001$); the medium-sized barnacles were consumed, in turn, sooner than large barnacles ($P < 0.001$). Long-spined snails showed no significant difference in consumption order between small and medium-sized barnacles ($P > 0.20$). Large barnacles did take longer to consume than either small or medium-sized barnacles ($P < 0.001$).

Also using a Mann-Whitney test, I made comparisons between long- and short-spined snails on a given size class of barnacle. The results show no significant difference in consumption order between long- and short-spined snails when feeding on small barnacles ($0.1 > P > 0.05$), but that long-spined snails consumed medium-sized barnacles sooner than did short-spined snails ($P < 0.001$).

DISCUSSION

The results of the feeding experiment support the hypothesis that the labial spine of *Acanthina angelica* functions to force apart the opercular valves of its barnacle prey. Large barnacles were wedged significantly less frequently than either medium-sized or small barnacles, and short-spined snails switched to a drilling attack at a smaller prey size (medium-sized barnacles) than did long-spined snails. These results suggest a close relationship between spine length, barnacle size, and mode of attack.

As noted above, no attempt was made to control for differences in shell length between short- and long-spined

Table 1

Analysis of the relationship between spine length, barnacle size, and mode of attack (G-test, SOKAL & ROHLF, 1969).

Comparison	df	G
Spine length × barnacle size	2	3.294
Mode of attack × barnacle size	2	20.995*
Spine length × mode of attack (small)	1	0.000
Spine length × mode of attack (medium)	1	7.570**
Spine length × mode of attack (large)	1	0.116
Spine length × mode of attack × barnacle size	7	31.975*

* $P < 0.001$, ** $0.025 < P < 0.05$.

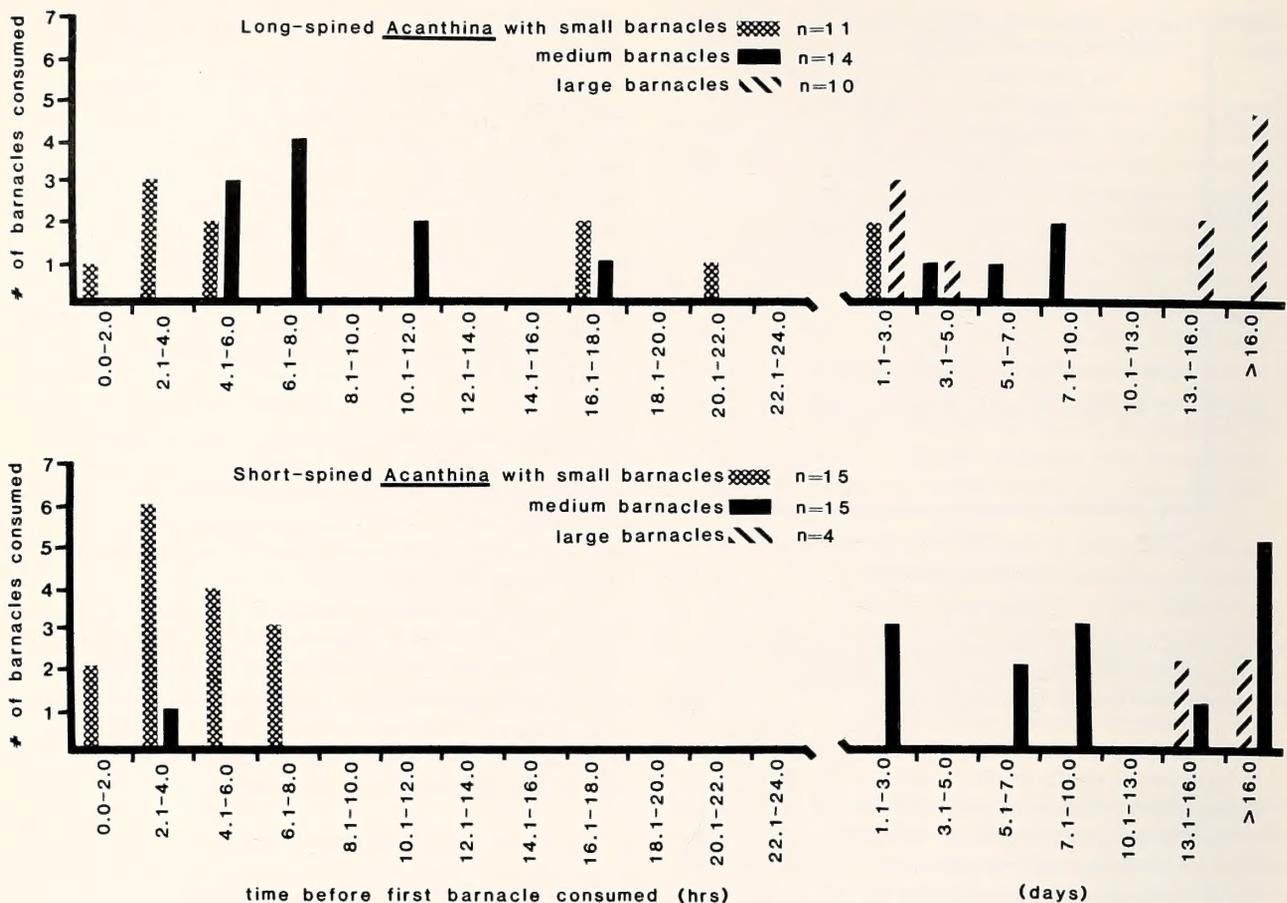


Figure 2

Consumption order of long- and short-spined *Acanthina angelica* feeding on three size classes of barnacles. Time is from the beginning of the experiment until the first barnacle was consumed.

snails used in the experiment. At Puerto Penasco, all *Acanthina angelica* less than 25 mm in length have a short spine (less than 3.5 mm), while larger *A. angelica* may have either a short or long spine (PAINE, 1966; YENSEN, 1979; and personal observations). It is, therefore, likely that in natural populations the mean size of a short-spined snail is less than that of a long-spined snail. The ontogeny of the feeding behavior of *A. angelica* remains to be investigated, but this study suggests that very small snails are probably restricted to drilling.

In general, the drilling of barnacles took considerably longer than wedging. The four failed drilling attempts, the increase in handling time, and the apparent reluctance to drill (judging from the paucity of attacks on the large barnacles during the experiment) indicate that drilling is a relatively inefficient mode of attack in *Acanthina angelica*. Very large barnacles may effectively have a size-escape from predation by *A. angelica*. DAYTON (1971) notes a similar size-escape from predatory thaidids by the barnacle *Balanus cariosus* (= *Semibalanus cariosus*).

Two of the barnacles that were successfully consumed

had holes drilled only partially through the test, near the base of the animal; they showed no evidence of other drilling or wedging attacks. PALMER (1982) reports similar incidents in the case of the *Thais* predation on four species of intertidal barnacles from the Pacific Northwest, and suggests (p. 35) that "because *Thais* are equipped with a powerful toxin (HUANG, 1971, 1972), they need only penetrate a barnacle far enough to reach a space that communicates with the rest of the body." Evidence for a toxin that paralyzes prey has also been found in *Acanthina punctulata* (SLEDER, 1981) and *A. spirata* (HEMINGWAY, 1978), indicating that the ability to produce and utilize a fast-acting toxin may be common within the Thaididae. That two incompletely drilled barnacles were nonetheless consumed during this experiment provides circumstantial evidence that *A. angelica* possesses a similar toxin.

The feeding experiment demonstrated that the short-spined snails consumed small barnacles significantly sooner than they consumed either medium-sized or large barnacles. Long-spined snails showed no significant difference in consumption order between small and medium-sized

barnacles. In addition, long-spined snails consumed medium-sized barnacles sooner than did short-spined snails, as might be expected when considering that one-third of the short-spined snails drilled the medium-sized barnacles. There was no significant difference in consumption order between long- and short-spined snails when feeding on small barnacles. This observation raises the question: how do short-spined snails persist in a population where a long spine allows a broader range of potential prey?

YENSEN (1979) found that short-spined snails gained significantly more weight when fed the small barnacle species *Chthamalus* than when fed the large species *Tetraclita* (and the converse for long-spined snails). This suggests that there is some cost, as well as benefit, to having a spine of a particular length. A spine length permitting efficient predation on one size class of barnacle may reduce efficiency on other sizes of barnacle, at least if one considers the extremes of barnacle sizes. In this regard, it is noteworthy that LEVITEN (1976) suggests that the radular tooth of the predatory gastropod *Conus* may be efficient over only a narrow range of prey sizes. A similar trade-off in *Acanthina angelica* would explain the predominance of short-spined snails among *Chthamalus*, and the association of the long-spined snails with *Tetraclita*. However, this experiment was not designed to test the snail's prey preference, as only one prey size was offered to each sample.

Furthermore, the labial spine of *Acanthina angelica* is not fixed in length. YENSEN (1979) has shown experimentally that spine length is controlled by barnacle prey size. Long-spined *A. angelica* offered only small barnacles had significantly shorter spines after three months, while short-spined snails grew longer spines when fed on large barnacles for three months. Controls did not change spine length significantly. Thus, barnacle size is determining labial spine length in a manner that maintains the "proper" relationship between the spine length and the size of the barnacle prey.

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LITERATURE CITED

- CARRIKER, M. R. 1961. Comparative functional morphology of boring mechanisms in gastropods. *Amer. Zool.* 1:263-266.
- CARRIKER, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* 20(2):403-422.
- DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monog.* 41: 351-389.
- HEMINGWAY, G. T. 1978. Evidence for a paralytic venom in the intertidal snail *Acanthina spirata* (Neogastropoda: Thaisidae). *Comp. Biochem. Physiol.* 60C:79-81.
- HEWATT, W. G. 1934. Ecological studies on selected marine intertidal communities of Monterey Bay. Doctoral Thesis, Stanford University. 150 pp.
- HOUSTON, R. S. 1980. Mollusca. Chap. 9. In: R. C. Brusca (ed.), *Common intertidal invertebrates of the Gulf of California*. The University of Arizona Press: Tucson, Arizona. 515 pp.
- HUANG, C. L. 1971. Pharmacological properties of the hypobranchial gland of *Thais haemastoma* (Clench). *J. Pharm. Sci.* 60:1842-1846.
- HUANG, C. L. 1972. Pharmacological investigations of the salivary gland of *Thais haemastoma* (Clench). *Toxicol.* 10:111-117.
- KEEN, A. M. 1971. *Sea shells of tropical west America*. 2nd ed. Stanford University Press: Stanford, Calif. 1064 pp.
- LEVITEN, P. J. 1976. The foraging strategy of vermivorous conid gastropods. *Ecol. Monog.* 46:157-178.
- MACGINITIE, G. & N. MACGINITIE. 1968. *Natural history of marine animals*. 2nd ed. McGraw-Hill: New York. 523 pp.
- MALUSA, J. R. 1983. The reproductive ecology of two species of rocky intertidal barnacle. Master's Thesis, University of California, San Diego, California. 98 pp.
- MENGE, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia* 17:293-316.
- PAINE, R. T. 1962. Ecological diversification in sympatric gastropods of the genus *Busycon*. *Evolution* 16:515-523.
- PAINE, R. T. 1966. Function of the labial spine, composition of diet, and size of certain marine gastropods. *Veliger* 9:17-24.
- PALMER, A. R. 1982. Predation and parallel evolution: recurrent parietal plate reduction in balanomorph barnacles. *Paleobiology* 8:31-44.
- SLEDER, J. 1981. *Acanthina punctulata* (Neogastropoda: Muricea): its distribution, activity, diet, and predatory behavior. *Veliger* 24:172-180.
- SOKAL, R. R. & F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Company: San Francisco.
- TURK, M. J. 1981. Intertidal migration and formation of breeding clusters of labial-spine morphs of the thaid gastropod, *Acanthina angelica*. Master's Thesis, University of Arizona, Tucson, Arizona. 66 pp.
- YENSEN, N. P. 1979. The function of the labial spine and the effect of prey size on "switching" polymorphs of *Acanthina angelica* (Gastropoda: Thaididae). Doctoral Thesis, University of Arizona, Tucson, Arizona. 62 pp.

Fluid-Dynamic Drag of Limpet Shells

by

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Abstract. This study examines the hydrodynamic significance of limpet shell morphology. An elongate shell and eccentric apex contribute to a streamlined form. The degree of apex eccentricity cannot, however, be explained solely as a consequence of drag reduction. Limpet shells are generally better streamlined than round protrusions. That there has been selective pressure for drag-reducing features is supported by the finding that those limpet species living in heavily wave-stressed environments experience a lower relative drag than their unstressed counterparts. Finally, relative projection of a shell into the boundary layer can strongly influence the dependence of drag upon free-stream velocity, a condition that may be of importance in the settlement and survival of those small, particularly larval forms in the intertidal zone.

INTRODUCTION

LIFE IN THE INTERTIDAL zone is characterized by exposure to significant forces of fluid drag and wave impact. The shell morphology of intertidal gastropods often incorporates drag-reducing features. It has been demonstrated that streamlining, as indicated by an anteriorly shifted apex, a large aperture relative to height, and a fineness ratio (length to width) significantly above unity, is generally characteristic for wave-exposed littorines (STRUHSAKER, 1968; HELLER, 1976), muricids (KITCHING & LOCKWOOD, 1974), and limpets (GRAHAM & FRETTER, 1947; DURRANT, 1975; LEWIS & BOWMAN, 1975; WARBURTON, 1976). Limpets are common intertidal gastropods whose depressed shells and noteworthy powers of tenacity seem particularly well-suited to conditions of heavy wave exposure. Surprisingly, only one attempt has been made to measure experimentally the drag forces on limpet shells. BRANCH & MARSH (1978) determined drag forces and coefficients of drag (C_D) for six species of *Patella* from South Africa. Their experimental design, however, lacked verisimilitude in that limpet shells were apparently placed in the free stream of flow, rather than as in the natural setting adjacent to a surface with a clearly defined boundary layer of fluid. Moreover, their data indicate a nearly inverse relationship between C_D and the Reynolds number ($C_D \propto Re^{-0.95}$). The Reynolds number for a particular situation of flow is defined as $Re = lU/\nu$, where l is some characteristic length of the object, U the

fluid velocity, and ν the kinematic viscosity of the fluid. As noted by VOGEL (1981), the only objects known that exhibit such an inverse relationship between C_D and Re are those that can reshape themselves with increasing velocities, such as trees. In this particular range of Reynolds number (10^3 to 10^5) $C_D \propto Re^0$, while for long flat plates parallel to flow, $C_D \propto Re^{-0.5}$ (HOERNER, 1965). The generally conical or ellipsoidal limpet shell in free-stream flow might well be expected to display a relationship more similar to that of a bluff body than that of a flat plate. The present study examines drag forces on limpet shells near a substratum. Drag is related to various morphological parameters, and the peculiar variation of C_D with Re for limpets within a relatively large boundary layer is noted.

MATERIALS AND METHODS

Drag forces on shells were measured in a continuously circulating flow tank (VOGEL & LABARBERA, 1978). Velocity was calibrated visually with ink at low velocities, and for higher velocities was derived from drag measurements of simple geometrical objects with known drag coefficients. Maximum tank velocity was 0.45 m/sec. In the working section of the tank (height 8.8 cm, width 10.4 cm), a thin plexiglas plate (20.3 by 8.7 by 0.2 cm, with a bevelled anterior edge) was fixed, parallel to flow, 4 cm below the water's surface (Figure 1). Limpet shells were filled with hard wax, and were positioned upside-down, 0.85 mm from the lower surface of the plexiglas plate. The center of each shell was 11 cm from the leading edge of the plate. A metal rod (1.5 mm in diameter) ran upwards from the center of the wax mass, through an open-

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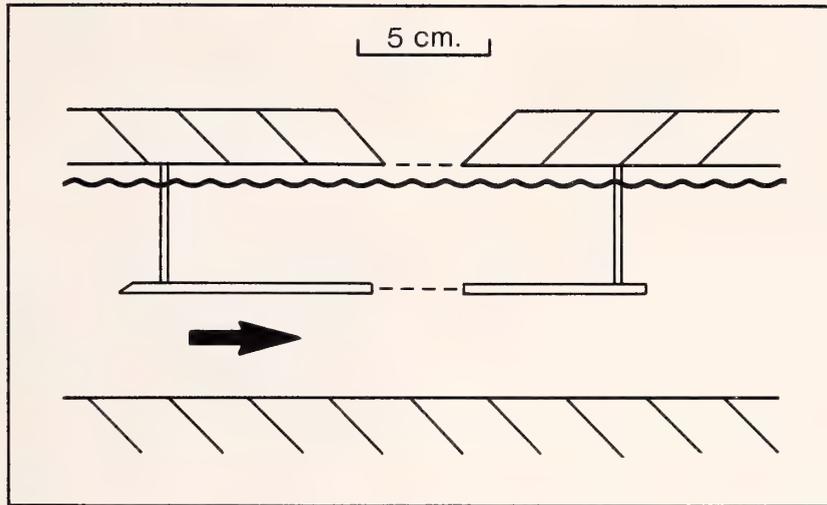


Figure 1

Lateral view of the working section of the flow tank.

ing in the plate (3 by 0.43 cm), to a thin metal strip (0.03 cm shim stock), in turn fixed firmly to the flow tank platform (Figure 2). A pair of strain gauges, attached to either side of the metal strip, were used as elements of a Wheatstone bridge, the output of which was amplified and displayed on a digital voltmeter. The voltage drop across the Wheatstone bridge was thus proportional to the drag force acting on the shell; the apparatus was calibrated by hanging weights from the end of the attachment rod, with the entire system held vertically. Reorientation of the shell with increased fluid velocity was observed to be minimal. For each shell, drag at a particular velocity was measured three times in each of three orientations: anterior end upstream, posterior end upstream, and shell lateral to flow. Drag measurements, with allowance taken for drag of the attachment rod, are estimated to be accurate to within 10%, and repeatable to within 5%.

The major and minor diameters, height from apex to base, and distances from the apex to the anterior and posterior shell margins were measured for 28 limpet shells with vernier calipers to within 0.05 mm. Perimeter measurements were taken from impressions in clay. The amount of water displaced by the shell and wax mass was taken as a measure of shell volume. Table 1 gives these data, along with geographical and ecological information for each limpet species. Also presented in Table 1 are the ratio X of the anterior to posterior distances from edge to apex (a measure of apex eccentricity), the fineness ratio R_F (major diameter/minor diameter, one possible measure of pressure-drag streamlining), and the relative shell height h_r , the ratio of the shell height to the geometrical mean of the major and minor diameters.

The drag of an object is related to the fluid velocity by the formula: $D = \frac{1}{2}C_D\rho SU^2$, where D is the drag, ρ the

fluid density, S a reference area of the object, U the fluid velocity, and C_D the aforementioned coefficient of drag, which for a given object and orientation is normally determined empirically. In practice, drag data are often reduced to a plot of C_D versus Re , with some reference cross-sectional or projected area taken for S . However, for a given object in a given medium, $C_D \propto D/U^2$ and $Re \propto U$. A plot of D/U^2 versus U will thus yield the same power dependence of C_D upon Re , the function being of the form $y = ax^b$. This latter approach is attractive in that any assumptions concerning the dimensions of often highly irregular biological objects are avoided. Volume to the

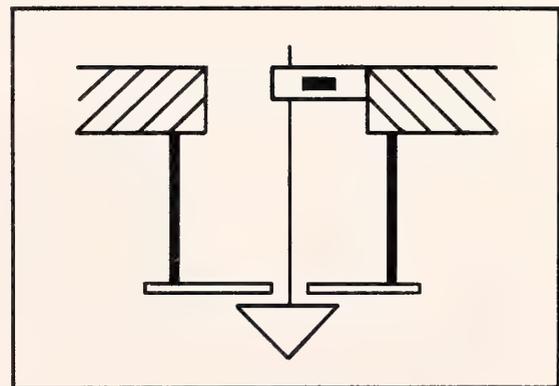


Figure 2

Details of the force transducer used in the drag measurements. Attached to one side of the shim stock is a strain gauge, given in black. The other strain gauge is hidden from view. Water flow is perpendicular to the plane of the diagram.

Table 1

Species identification, locale, habitat type, and morphological data for 28 limpet shells.

Shell no.	Species and locale	Habitat type
1	<i>Scurria scurra</i> (Lesson, 1830) Montemar, Chile	kelp stipes
2	<i>Scurria scurra</i> (Lesson, 1830) Montemar, Chile	
3	<i>Scurria scurra</i> (Lesson, 1830) Montemar, Chile	
4	<i>Patelloida saccharina</i> L. (1758) Ngeyanges, Palau	sheltered
5	<i>Patelloida saccharina</i> L. (1758) Ngeyanges, Palau	
6	<i>Patelloida saccharina</i> L. (1758) Ngeyanges, Palau	
7	<i>Patella flexuosa</i> (Quoy and Geimard, 1834) Salafai, Pagan	low intertidal, very heavily exposed
8	<i>Patella flexuosa</i> (Quoy and Geimard, 1834) Salafai, Pagan	
9	<i>Notoacmea inessa</i> (Hinds, 1842) Madison Port, Carmel, California	kelp stipes
10	<i>Notoacmea inessa</i> (Hinds, 1842) Madison Port, Carmel, California	
11	<i>Notoacmea inessa</i> (Hinds, 1842) Madison Port, Carmel, California	
12	<i>Collisella digitalis</i> (Rathke, 1833) Point Pinos, California	high intertidal and splash zones
13	<i>Collisella digitalis</i> (Rathke, 1833) Point Pinos, California	
14	<i>Siphonaria javanica</i> (Blainville, 1827) Rendrag, Palau	sheltered
15	<i>Siphonaria javanica</i> (Blainville, 1827) Rendrag, Palau	
16	<i>Siphonaria laciniosa</i> L. (1758) Rendrag, Palau	sheltered
17	<i>Siphonaria laciniosa</i> L. (1758) Rendrag, Palau	
18	<i>Fissurella nimbose</i> L. (1758) Rockoy, Guadeloupe	highly exposed, sand scour
19	<i>Fissurella nimbose</i> L. (1758) Rockoy, Guadeloupe	
20	<i>Fissurella nimbose</i> L. (1758) Rockoy, Guadeloupe	
21	<i>Fissurella nodosa</i> (Born, 1780) Fort Point, Jamaica	heavy exposure
22	<i>Fissurella nodosa</i> (Born, 1780) Fort Point, Jamaica	
23	<i>Nacella</i> sp. Tierra del Fuego	intertidal
24	<i>Nacella</i> sp. Tierra del Fuego	
25	<i>Nacella</i> sp. Tierra del Fuego	
26	<i>Patella vulgata</i> L. (1758) Cove, Scotland	moderate exposure

Table 1 (Continued)

Shell no.	Species and locale	Habitat type
27	<i>Patella vulgata</i> L. (1758) Cove, Scotland	
28	<i>Patella vulgata</i> L. (1758) Cove, Scotland	

The shell length l , width w , height h , volume V , perimeter p , fineness ratio R_F , eccentricity X , and the relative shell height h_r for 28 limpet shells. All lengths are given in millimeters, shell volume in milliliters.

Shell	l	w	h	V	p	R_F	X	h_r
1	27.2	23.5	18.1	4.1	79.7	1.15	0.98	0.72
2	21.7	19.4	11.5	2.0	65.0	1.12	0.83	0.56
3	17.5	15.4	8.4	1.0	52.5	1.14	0.85	0.51
4	23.2	19.4	11.5	1.3	70.1	1.19	0.89	0.42
5	21.3	18.5	7.2	1.1	66.1	1.15	0.83	0.36
6	17.5	13.5	5.4	0.4	48.3	1.30	0.89	0.35
7	41.5	29.6	9.2	3.3	118.9	1.40	0.73	0.26
8	34.5	26.5	6.5	2.9	97.9	1.30	0.71	0.22
9	16.2	10.2	9.5	0.9	42.5	1.59	0.82	0.74
10	15.5	9.4	8.5	0.5	40.0	1.64	0.79	0.70
11	14.4	9.7	8.0	0.3	39.1	1.49	0.71	0.67
12	20.4	16.6	8.6	1.8	57.3	1.23	0.46	0.47
13	21.0	21.0	7.8	1.1	74.8	1.00	0.38	0.37
14	22.6	19.2	11.6	1.2	65.8	1.17	0.94	0.56
15	21.6	15.1	9.2	0.9	55.8	1.43	0.82	0.51
16	25.2	22.5	6.7	1.0	75.4	1.12	0.90	0.28
17	21.6	19.6	6.5	0.9	66.9	1.10	0.88	0.31
18	36.2	24.1	12.3	3.9	94.9	1.50	0.79	0.42
19	27.6	19.5	8.3	1.7	72.8	1.41	0.80	0.36
20	17.4	10.3	6.3	0.6	45.8	1.68	0.83	0.47
21	32.9	21.4	17.8	4.8	90.2	1.54	0.96	0.67
22	21.0	18.3	12.8	2.6	71.4	1.15	0.92	0.65
23	48.2	40.0	24.7	24.0	137.8	1.20	0.80	0.56
24	32.0	25.5	20.7	7.5	90.5	1.25	0.90	0.73
25	61.4	42.4	12.3	22.0	164.8	1.45	0.55	0.24
26	41.8	34.6	17.4	10.0	121.9	1.20	0.85	0.46
27	35.0	29.2	13.3	4.9	102.5	1.21	0.83	0.42
28	29.7	24.7	13.1	4.0	84.8	1.21	0.73	0.48

power $\frac{2}{3}$ could well be the most biologically relevant reference area (VOGEL, 1981), but for craspedophilic organisms living in significant boundary layers it may not adequately reflect the relative importance of protrusion of the organism above the substrate. In the following analysis, the dependence of C_D upon Re will be determined from the equation $D/U^2 = aU^b$, but, for purposes of comparison with existing data, drag coefficients calculated on the basis of frontal (cross-sectional) area will also be presented.

RESULTS

A typical plot of drag versus velocity for shells in anterior, posterior, and transverse orientations is given in Figure 3.

After a logarithmic transformation of the quantities D/U^2 and U , linear regression ($\ln y = \ln a + b \ln x$) was used to determine a and b in the equation $D/U^2 = aU^b$. Correlation coefficients for this regression ranged from 0.91 to 0.99. From the two constants a and b , a "standard" drag for a particular orientation was calculated at a reference velocity of 0.3 m/sec from the formula $D = a(0.3)^{b+2}$. A mean drag, \bar{D} , was calculated for each shell from the formula $\bar{D} = (D_A + D_P + 2D_T)/4$, where D_A is the anterior drag, D_P the posterior drag, and D_T the transverse drag. The mean drag thus approximates from the experimental data the drag for a random orientation. Transverse drag was in all cases calculated only for the left side (with respect to the anterior-posterior) axis of the shell; limpets are generally, with the exception of the siphonarids, bilaterally symmetric, and for the sample of shells studied (excluding *Siphonaria laciniosa* and *S. javanica*) there was no significant difference in the shortest distance from the apex to the right and to the left side of the shell margin (χ^2 test, $P < 0.01$). From the anterior drag, a drag coefficient was calculated from the formula: $C_D = 2D/(\rho S U^2)$, where D and ρ are as previously given, U equals 0.3 m/sec, and S is the cross-sectional area normal to flow. Finally, considering each of the three orientations equally, a mean \bar{b} of the power b was calculated for each shell. Table 2 lists for each limpet shell D_A , D_P , D_T , \bar{D} , C_D , and \bar{b} .

Anterior drag was in most cases only slightly less than posterior drag. No correlation between the apex eccentricity and the ratio of anterior to posterior drag could be found. A low value of eccentricity is generally regarded as desirable for efficient streamlining (BAYLEY, 1958); velocity gradients at surface-fluid interfaces (to be discussed later) and forces of selection independent of drag minimization may well distort the predictive validity of such a result from main-stream fluid mechanics. In this context, it is interesting to note that limpets living on kelp stipes experience for the most part unidirectional flow, and might well be expected in the interests of streamlining to have an apex shifted far forward (low X). This is in fact observed in the kelp limpet *Helcion pellucida* (= *Patella pellucida*), with an apex eccentricity of 0.59 (WARBURTON, 1976). It should be mentioned that kelp limpets often possess a convex base corresponding to an excavated concavity in the kelp stipe. For those kelp limpets in the present study (*Scurria scurra* and *Notoacmea insessa*), vertical deviation of the base perimeter was less than 10% of the shell height, and was thus ignored. For a sample of three shells, apex eccentricity in *S. scurra* was not less than 0.83, while for *N. insessa* eccentricity was not less than 0.71. These values compare to an overall average (9 species, 28 shells in all) of 0.80. Those species with the lowest apex eccentricities were *Collisella digitalis*, a limpet found characteristically in the intertidal spray zone, and one of the particularly large *Nacella* shells. Neither species could reasonably be expected to experience only unidirectional flow. A further complication is the general trend towards

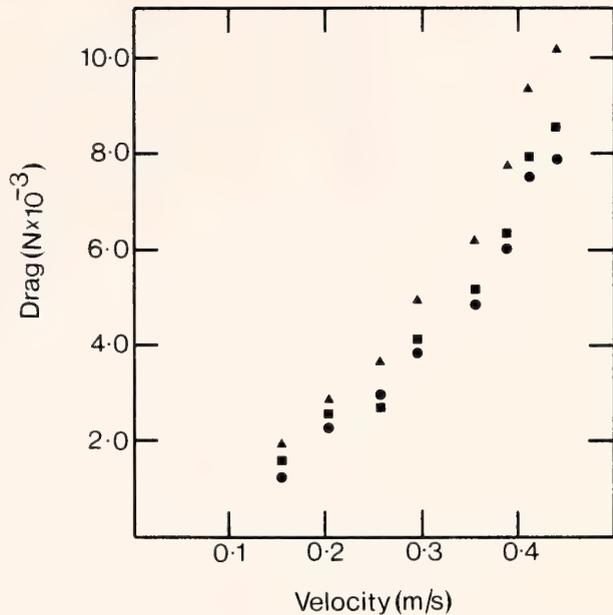


Figure 3

Variation of drag with water velocity for shell no. 25, in the anterior (●), posterior (■), and transverse (▲) orientations.

an anteriorly displaced apex among high-shore limpets with respect to their low-shore counterparts (VERMEIJ, 1978). It seems clear that apex eccentricity cannot be entirely explained as a consequence of a streamlined profile, and that other factors, such as predation (HOCKEY & BRANCH, 1983) and temperature and desiccation resistance, influence this aspect of shell form.

Transverse drag for all shells was greater than drag in a longitudinal orientation. Not surprisingly, the fineness ratio R_F is inversely correlated with the ratio of anterior and transverse drag (Figure 4). A relatively high R_F is clearly desirable in the event of unidirectional water flow, as the limpet can always preferentially orient in the current. The wave-swept intertidal zone, which can only be loosely described as a region of upward wave motion, is but vaguely reminiscent of a unidirectional current; a very high value of R_F could well be a liability under these circumstances. Given equal frontal area, the drag of bodies in free-stream flow is minimized when $R_F = 2$ (ALEXANDER, 1968). Values above two result in a higher total drag by virtue of an ever-increasing "friction drag" resulting from the forces of viscosity acting on the surface area of the body. For an object attached to a surface, the relevant value of R_F is not known, and may not be strictly comparable with the value of two given above. Nonetheless, of the 28 shells examined, the highest value of R_F was 1.68, with a mean of 1.27. Even for the stipe-dwelling limpets, minimization of drag along the anterior-posterior axis may not be the predominant factor determining the ratio of major to minor diameter.

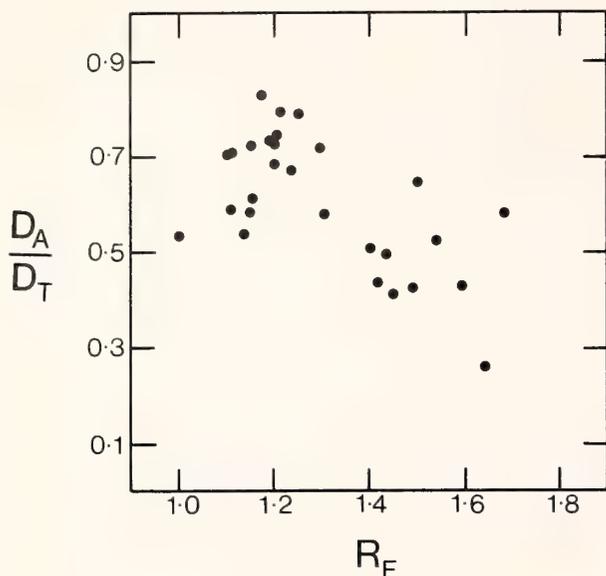


Figure 4

The ratio of anterior drag to transverse drag as a function of the fineness ratio R_F . The regression line is given by $Y = (-0.47)X + 1.21$, $r = -0.62$, $P < 0.05$.

Mean drag was found to be strongly correlated with shell length, height, and volume. The ratio of mean drag to $V^{2/3}$, where V equals shell volume, was chosen as a quantity indicative of the relative drag acting on a shell ($V^{2/3}$ being the biologically relevant reference area). This ratio increases only slightly with respect to relative shell height ($D/V^{2/3} \propto h_r^{0.32}$, $r = 0.41$, $P < 0.05$), and is not correlated with shell volume. There is admittedly considerable scatter in the data, but as a rough approximation the relative drag does not appear to increase with greater relative height or volume. Also of interest is the absence of correlation between relative drag and the ratio of the perimeter to the geometrical mean of the major and minor diameters. The latter is a dimensionless measure of the convolution of the shell's perimeter, and is thereby proportional to the amount of shell ribbing. BRANCH & MARSH (1978) reported that a slight roughening of the shell surface actually decreases the coefficient of drag (by inducing turbulent flow and thereby delaying flow separation), but that shells with pronounced radial striation experienced a higher relative drag (higher C_D). The present data, which again contain much scatter, cannot be sufficiently resolved so as to distinguish between the relative contributions of drag reduction by the induction of turbulence and the increase in drag brought on by an increase in cross-sectional area. The presence of ribbing and pronounced costae does not necessarily indicate a sheltered existence, as many wave-exposed species of limpets and other gastropods display strongly sculptured shells (VERMEIJ, 1978). Finally, the relative drag for those species generally living

in heavily wave-stressed environments (*Patella flexuosa*, *Fissurella nimbosa*, and *F. nodosa*) was significantly less than that of all other species considered (Mann-Whitney U test, $P < 0.05$). Although the sample size is small, it may not be incorrect to suggest that selection for drag-reducing features has been greater among wave-exposed species.

By virtue of viscosity, fluid velocity near a surface-fluid interface is less than the free-stream velocity. Directly at the interface there is no fluid movement. The thickness of the boundary layer is commonly defined as the distance from the surface at which fluid velocity is equal to 99% of the free-stream value. Assuming laminar flow, the boundary layer thickness δ for a flat plate parallel to flow is given by: $\delta = 5(x\mu/\rho U)^{1/2}$, where ρ and U are as defined previously, μ is the dynamic viscosity of the fluid, and x (11 cm) is the distance downstream from the leading edge of the plate (VOGEL, 1981). The assumption of laminar flow for the current situation is justified by the observation that the local Reynolds number (30,000), based upon 11 cm as the characteristic length, is less than the value generally associated with the transition to turbulent flow. Boundary layers in the present experimental arrangement, using for x the invariant distance from the leading edge of the plate to the center of the shell, ranged from 3.7 mm at $U = 0.2$ m/sec to 2.5 mm at $U = 0.45$ m/sec. These values are not insignificant when compared to the heights of particularly the smaller shells studied (Table 1). Drag of smaller shells should thus increase disproportionately with respect to larger shells as velocity is increased, because with the decrease in thickness of the boundary layer at higher velocities, a relatively greater shell area is exposed to the free-stream velocity. Figure 5 illustrates this inverse relationship between b ($C_D \propto Re^b$) and shell height. For taller limpets, C_D is roughly independent of Re ($C_D \propto Re^0$), while the very large values of b are reserved for very small shells. This finding is independently corroborated by the variation of b with shell orientation. The power b for shells in a transverse orientation was significantly less than that for shells in a longitudinal orientation (Mann-Whitney U test, $P < 0.05$). For higher absolute magnitudes of drag (transverse drag, for example, always being greater than anterior drag), the relative contribution of drag resulting from a smaller boundary layer is less. The value of b decreases correspondingly. The small values of b recorded for the larger shells may also indicate that the reported values ($b = -0.95$) of BRANCH & MARSH (1978) could be due to an error in calibration or in experimental design.

DISCUSSION

HOERNER (1965) presents coefficients of drag for protuberances within turbulent boundary layers. A round rivet head shows a $C_D = 0.32$, based on the maximum projected area (plan-form) of the head, while a highly streamlined protuberance has a C_D of 0.07. The drag coefficients for

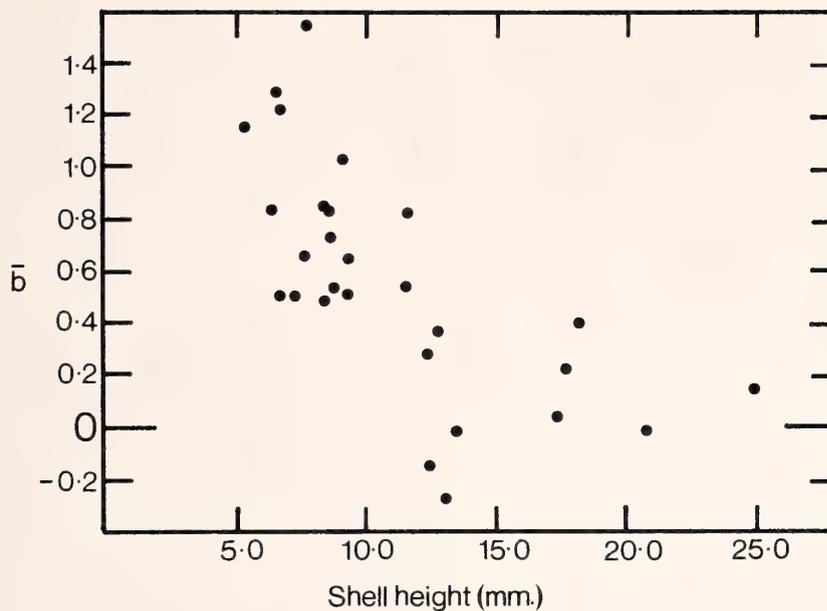


Figure 5

The variation of \bar{b} with shell height.

limpet shells (Table 2) are based on cross-sectional area, and reflect partial protrusion through a laminar boundary layer. Since in both cases the mean velocity experienced by the object is less than the free-stream velocity, drag coefficients calculated on the basis of the latter will be less than those calculated with some mean velocity. A drag coefficient could be calculated for smaller cross-sectional regions of the shell, using for U the velocity at the center of each region, and then the results summed over the entire cross-sectional area, but the significance of such a compound drag coefficient is not clear. Given the absence of a well-defined method of describing mean velocity relative to shell area, and lacking any data against which to compare drag coefficients calculated in such a manner, all drag coefficients in the present study were calculated with the free-stream velocity. It is nevertheless interesting that the values for limpet shells are generally between 0.07 and 0.32, suggesting that limpets have adopted, in comparison with a symmetrical round form, a better streamlined profile. As mentioned above, relative drag is less for those limpets living in wave-stressed environments, indicating that there may be selective pressure for the reduction of fluid-dynamic drag. There are two other forces generated by water movement that could potentially be of biological significance, namely shock pressures and acceleration forces. The former is a transient force corresponding to the establishment of flow in a temporarily stopped mass of fluid, while the latter is the force exerted on an object by the acceleration of the fluid displaced by the object (the so-called added mass). CARSTENS (1968) states

that, for continuous wave trains in shallow water, acceleration forces are likely to be negligible for bodies that are small in comparison to the wave height, and the shapes that minimize fluid-dynamic drag also minimize shock pressure, which in any event only rarely reaches extreme values, so that the concomitant drag associated with these forces is likely to be small for limpet shells (see however DENNY [1982] for description of a more complicated situation of flow). It should be noted that limpets are easily dislodged by wave surges if they have not anticipated, by means of clamping down in response to low velocity currents, a strong current flow (WARBURTON, 1976).

The hydrodynamic significance, if any, of shell sculpture remains unclear, given the absence of correlation between relative shell drag and convolution of the shell perimeter. Pronounced ribbing may of course have other roles. VERMEIJ (1973) noted the presence of increased shell sculpture among sun-exposed limpets, and JOHNSON (1975) demonstrated that shells of *Collisella digitalis* have slightly lower convective coefficients than shells of *C. scabra*, which are more ribbed and spinose. Strong shell sculpture reduces vulnerability to crushing predation in many gastropods (VERMEIJ, 1978), and in limpets has been specifically suggested as a deterrent to bird predation (GLYNN, 1965). The rough surfaces of many limpet shells may also be implicated in the reduction of the forces of shock pressure through the entrainment of air (CARSTENS, 1968), and in a redistribution of instantaneous drag forces. The expression of shell sculpture may thus be determined by a number of independent factors, and any explanation

Table 2

Drag forces in newtons ($\times 10^{-3}$) for anterior, posterior, and transverse orientations (D_A , D_P , D_T), mean drag \bar{D} , the coefficient of drag (C_D), and the mean power \bar{b} .

Shell	D_A	D_P	D_T	\bar{D}	C_D	\bar{b}
1	1.61	1.70	2.61	2.13	0.17	0.40
2	0.90	0.89	1.27	1.08	0.18	0.53
3	0.49	0.44	0.90	0.68	0.17	0.85
4	0.93	0.91	1.27	1.09	0.24	0.52
5	0.56	0.70	0.77	0.70	0.19	0.80
6	0.35	0.33	0.48	0.41	0.22	1.14
7	0.87	1.00	1.70	1.32	0.14	0.51
8	0.62	0.85	1.06	0.90	0.16	0.50
9	0.30	0.32	0.70	0.51	0.14	1.09
10	0.21	0.35	0.68	0.48	0.12	0.82
11	0.17	0.25	0.40	0.31	0.10	1.55
12	0.92	0.97	1.37	1.16	0.14	0.72
13	0.72	0.84	1.35	1.06	0.20	0.66
14	0.86	0.80	1.04	1.87	0.09	0.83
15	0.47	0.53	0.96	0.73	0.15	0.64
16	0.42	0.60	0.72	0.61	0.12	1.20
17	0.43	0.45	0.60	0.52	0.15	1.28
18	1.91	2.13	3.62	2.82	0.29	0.29
19	1.13	1.12	1.96	1.54	0.31	0.50
20	1.36	1.41	2.11	1.75	0.47	0.84
21	0.54	0.57	1.22	0.88	0.06	0.21
22	0.25	0.29	0.55	0.41	0.05	0.37
23	7.35	7.37	10.09	8.72	0.33	0.14
24	3.81	3.83	4.80	4.31	0.32	-0.01
25	3.68	3.77	8.88	6.30	0.32	-0.16
26	3.62	3.66	4.53	4.09	0.27	0.04
27	2.32	2.65	3.41	3.26	0.27	-0.03
28	2.09	2.12	2.82	2.46	0.29	-0.28

of the observed intraspecific, interspecific, and geographical variation in limpet shell sculpture that is solely concerned with fluid-dynamic drag seems at this time unwarranted.

In the present experimental design, the small gap between the limpet shell and the fixed surface (0.85 mm) precludes direct identification of measured drag forces with those likely to be encountered in the field. This small distance, however, is well within the boundary layer as calculated above, and there is no reason to suspect that the very low fluid velocities in this region will distort the validity of comparisons of drag forces on different shells. Velocities required for the dislodgement of living animals are substantially greater than those used in the present work (WARBURTON, 1976), and it is possible that drag coefficients at these velocities will differ from those reported herein. Boundary layers in the field, however ill-defined in the context of breaking waves and rock surfaces, may well be smaller than several millimeters. In this case, the variation of \bar{b} with height will be of relevance to yet smaller shells, and may only be of importance in larval settlement and survival, albeit at much lower Reynolds numbers. Intertidal boundary layers can also, under con-

ditions of turbulent flow and steady wave trains, be much larger than the shell heights considered here. The result that the relationship between C_D and Re can, in certain circumstances, vary according to the height of the object above the substrate has not been previously reported, and could represent an additional consideration in the adaptation of organisms to drag forces in the intertidal zone.

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LITERATURE CITED

- ALEXANDER, R. MCN. 1968. Animal mechanics. Sidgwick & Jackson: London. 346 pp.
- BAYLEY, F. J. 1958. An introduction to fluid mechanics. Allen & Unwin: London. 215 pp.
- BRANCH, G. M. & A. C. MARSH. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. J. Exp. Mar. Biol. Ecol. 34:111-130.
- CARSTENS, T. 1968. Wave forces on boundaries and submerged bodies. Sarsia 34:37-60.
- DENNY, M. W. 1982. Forces on intertidal organisms due to breaking ocean waves: design and application of a telemetry system. Limnol. Oceanogr. 27(1):178-183.
- DURRANT, P. M. 1975. An investigation into the effect of running water on shell dimension in *Ancylus fluviatilis* Muller. J. Conchol. 28:295-300.
- GLYNN, P. W. 1965. Community composition, structure, and interrelationships in the marine intertidal *Endocladia muricata*-*Balanus glandula* association in Monterey Bay, California. Beaufortia 12:1-198.
- GRAHAM, A. & V. FRETTER. 1947. The life history of *Patina pellucida* (L.). J. Mar. Biol. Assoc. U.K. 26:590-601.
- HELLER, J. 1976. The effects of exposure and predation on the shell of two British winkles. J. Zool. (Lond.) 179:201-213.
- HOCKEY, P. A. R. & G. M. BRANCH. 1983. Do oystercatchers influence shell shape? Veliger 26(2):139-141.
- HOERNER, S. F. 1965. Fluid-dynamic drag. S. F. Hoerner: 2 King Lane, Greenbriar, Bricktown, N.J.
- JOHNSON, S. E. 1975. Microclimate and energy flow in the marine rocky intertidal. In: D. M. Gates & R. B. Schmerl (eds.), Perspectives of biophysical ecology. Springer Verlag: New York.
- KITCHING, J. A. & J. LOCKWOOD. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. Mar. Biol. 28:131-144.
- LEWIS, J. R. & R. S. BOWMAN. 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. J. Exp. Mar. Biol. Ecol. 17:165-203.
- STRUHSAKER, J. W. 1968. Selection mechanisms associated with intraspecific shell variation in *Littorina picta* (Prosobranchia: Mesogastropoda). Evolution 22:459-480.
- VERMEIJ, G. J. 1973. Morphological patterns in high-inter-

- tidal gastropods and their limitations. *Mar. Biol.* 20:319-346.
- VERMEIJ, G. J. 1978. *Biogeography and adaptation: patterns of marine life*. Harvard University Press: Cambridge. 332 pp.
- VOGEL, S. 1981. *Life in moving fluids*. Willard Grant Press: Boston. 352 pp.
- VOGEL, S. & M. LABARBERA. 1978. Simple flow tanks for research and teaching. *BioScience* 28:638-643.
- WARBURTON, K. 1976. Shell form, behaviour, and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* 23:307-325.

The Effects of Aggregations on Water Loss in *Collisella digitalis*

by

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Abstract. Water loss rates were compared between isolated and aggregated *Collisella digitalis* of the same microhabitat. The solute concentration of the extra-corporeal water (ECW) was used as an indicator of water loss. Limpets within conspecific aggregations tended to have lower ECW solute concentrations than isolated limpets. Isolated limpets tended to orient with their head down on vertical surfaces, although this tendency was absent in the aggregations.

INTRODUCTION

HIGH-INTERTIDAL MARINE organisms are exposed to air with each tidal cycle. Prolonged calm periods and neap tides can increase the length of exposure, isolating some splash-zone animals in an essentially terrestrial environment for several days (WOLCOTT, 1973). While exposed, marine animals are vulnerable to evaporative water loss due to wind and solar radiation. Many animals subject to these conditions have physiological adaptations, such as high desiccation tolerance, that allow persistence in the intertidal. In addition, these animals may have behaviors that affect the physical parameters governing water loss, thereby reducing desiccation stress.

Collisella digitalis (Rathke, 1833), a high intertidal snail, demonstrates many behaviors that impede water loss when it is exposed to air. This acmaeid limpet occurs from the Aleutian Islands, Alaska, to the southern tip of Baja California (MORRIS *et al.*, 1980), predominately on vertical rock surfaces (HAVEN, 1971; COLLINS, 1976). Unlike the homing limpet *C. scabra*, *C. digitalis* does not fit exactly to the substrate. This leaves a gap between the shell and substrate through which water is lost. The mucous sheet formed by *C. digitalis*, and other limpets, significantly reduces this water loss, acting as a physical barrier to exchange (WOLCOTT, 1973). *Collisella digitalis* often aggregates in crevices and depressions during low tide (FRANK, 1965). Presumably the topographic relief provided by these sites reduces water loss rates, although this has yet to be demonstrated. *Collisella digitalis* also forms conspecific ag-

gregations on smooth rock surfaces which lack such topographic relief. HAVEN (1971) suggested that these aggregations reduce water loss from the animals but provided no supporting data.

In this study, I have examined the effects of clumping on water loss in *Collisella digitalis* by comparing solute concentrations of extra-corporeal water (ECW) between clumped and isolated limpets. The extra-corporeal water, held between the foot and shell, is the source of evaporative water loss from limpets (SEGAL, 1956). As freshwater is evaporated from the ECW, its solute concentration increases. Although ECW solute concentration is an indirect assessment of water loss, it is valuable in that data can be collected in the field.

MATERIALS AND METHODS

Specimens of *Collisella digitalis* were sampled during May, 1983, at three sites along the northern California coast: (a) Blind Beach, Sonoma County; (b) the Bodega Marine Laboratory, Sonoma County; and (c) Albion, Mendocino County. Most of the samples were taken from the smooth chert at Blind Beach. Individuals were sampled *in situ* at varying temperatures, wind conditions, and times of day. All samples were taken from smooth surfaces, well away from any crevices or depressions.

Freehand sketches of aggregations and nearby isolates served as permanent references of the position of each individual sampled. Usually eight limpets were sampled: four from within the aggregation, and four isolates from the surrounding area. For comparison, an isolate needed to be at least 4 cm from its nearest neighbor, but not more than 30 cm from the aggregation. This assured that the eight limpets, hereafter treated as a class, were from a similar microhabitat.

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Table 1

Solute concentration data for aggregated (Cl) and isolated (Is) individuals of *Collisella digitalis*.

Class ¹	Number of individuals		Average osmotic pressure (mOsm/kg)		Osmotic pressure difference	P ²	Relative change in concentration with time ³		
	Cl	Is	Cl	Is			Cl	Is	X ⁴
1	4	3	1362	1516	156	>0.20	245	399	0.385
2	5	3	1500	1723	223	<0.01	385	606	0.368
3	3	3	1420	1730	310	0.18	303	613	0.506
4	3	3	1180	1370	190	0.14	63	253	0.751
5	5	6	1041	1158	117	<0.01	—	—	—
6	6	5	1041	1118	77	0.02	—	—	—
7	3	3	986	966	-20	>0.20	—	—	—
8	3	3	1160	1176	16	>0.20	43	59	0.271
9	4	4	1187	1330	143	<0.01	70	213	0.671
10	4	3	1120	1243	123	<0.01	3	126	0.976
11	3	3	1126	1280	154	0.18	9	163	0.945
12	4	4	1215	1287	72	0.15	98	170	0.423
13	4	4	1135	1175	40	>0.20	18	58	0.690
14	5	4	1142	1205	63	0.17	25	88	0.716
15	4	4	1200	1375	175	>0.20	83	258	0.678
16	4	4	1230	1762	532	<0.01	113	645	0.825
17	4	4	1153	1460	307	0.09	36	343	0.895
18	4	4	1233	1355	222	<0.01	116	238	0.933
19	4	4	1206	1355	149	<0.01	89	238	0.626
20	4	4	1106	1147	41	<0.01	—	—	—
21	4	4	1092	1147	55	<0.01	—	—	—

¹ Clumped and isolated individuals occupying the same microhabitat.

² P-value for Student's *t*-test. Comparisons were between clumped and isolates' average osmotic pressure.

³ Derived by subtraction of estimated starting concentration (1117 ± 39 mOsm/kg) from average osmotic pressure.

⁴ Solute concentration ratio for Cl:Is as calculated using Equation 1 (see text).

Limpets were removed from the substrate with a narrow spatula. A 16- μ L sample of ECW was quickly removed from the posterior foot-shell margin with a microcapillary tube. The full tube was then capped with Seal Ease clay to inhibit further evaporation from the sample, and numbered to correspond with the sketch. The length of each individual was measured using calipers, after which the limpet was dipped in seawater and returned to the rock. The vapor pressure of each sample was measured in the laboratory using a Wescor Inc. 5130C Vapor Pressure Osmometer, which gave the ECW vapor pressure in milli-osmoles per kilogram (mOsm/kg). Vapor pressure of a sample is directly proportional to solute concentration.

All limpets on one rock ($n = 211$) were censused to determine their orientation. The direction of the anterior end of each limpet was scored according to an eight point

compass. An individual with its head straight up was scored as 1, straight down, as 5. One-way Chi-square tests were used for each group (clumped and isolates) to determine whether the orientation of individuals was random.

RESULTS

In all but one of the 21 classes sampled, the average ECW solute concentration of clumped limpets was lower than that of nearby isolates (Table 1). The range of differences between average solute concentrations was -20 to +532 mOsm/kg. In this pairwise comparison within classes, the size of the individuals was not considered. However, the volume of ECW determines the rate at which the concentration changes. To assess the role of size, an analysis of covariance was run using size as the covariate. Pooling the data in this way demonstrated that the ECW solute concentration of clumped limpets was lower than that of isolates ($F_{1,155} = 19.85$, $P < 0.01$). In addition, limpets in aggregations were arbitrarily ranked according to the degree to which they were surrounded. A completely surrounded individual was ranked 4, a limpet with no close neighbors was ranked 0. An analysis of covariance using the ranked positions as a covariate to solute concentration demonstrated that limpets with few close neighbors had higher solute concentrations than those that were completely surrounded. Consequently, those limpets at the periphery of the aggregation (usually rank 2) tended to have higher ECW solute concentrations than individuals in the interior ($F_{1,71} = 4.38$, $P < 0.05$) (Figure 1).

Due to the paired nature of the sampling procedure, relative rates of water loss between the two groups can be estimated. Fourteen limpets, eight of which were aggregating, were sampled to estimate the ECW concentration at the beginning of the dichotomy. The ECW solute concentration for these limpets was 1117 ± 39 mOsm/kg. The concentration change over the exposure period can thus be calculated by subtraction, and the values used to compare average concentration changes of the clumped and isolated limpets given by Equation 1 as

$$\frac{I - C}{I} = X$$

where C and I are the change in ECW solute concentration for the clumped and isolated limpets respectively. The average value for X was 0.67 ± 0.22 for all the classes used in the comparison (five were omitted because their final ECW solute concentrations were lower than the assumed starting value). Assuming that all animals in each class had been exposed for approximately the same period of time, the proportion X represents a difference in water loss rates. As such, the clumped limpets lost water 33% slower than isolates (Table 1).

Analysis of orientation on the substrate (Figure 2) revealed that neither the clumped nor the isolated limpets were randomly situated ($\chi^2 = 20.33$, $P < 0.05$ for clumped;

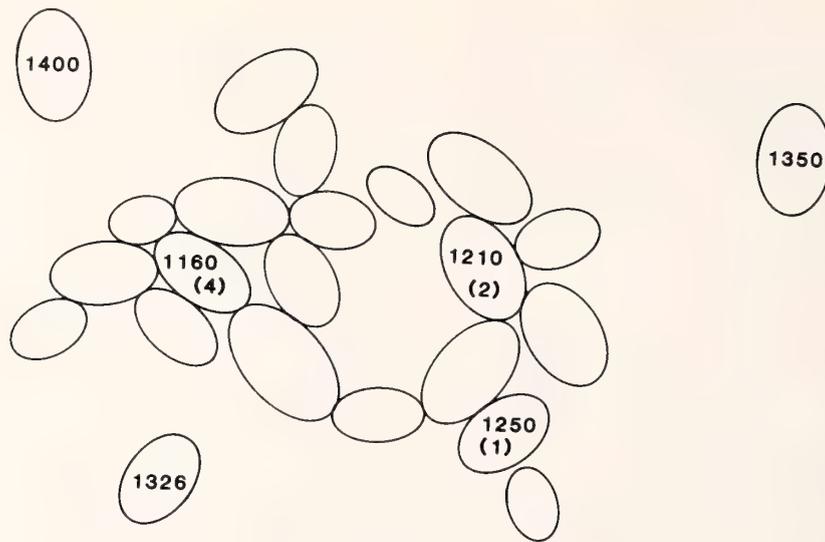


Figure 1

Diagram of a typical aggregation of *Collisella digitalis* and surrounding isolates. The ECW solute concentration (mOsm/kg) and rank (in parentheses) of some of the limpets from Class 19 are given. The positions of the isolated limpets have been changed to reduce the figure size.

$\chi^2 = 143.58$, $P < 0.01$ for isolates). The trend for the isolates was to orient with the head down. The trend for the clumped limpets was less obvious, but the most common orientation was with the head to the right.

DISCUSSION

Clumping has been shown to reduce water loss rates in both marine and terrestrial invertebrates. WARBURG (1968) and ALLEE (1926) showed that terrestrial isopods in ag-

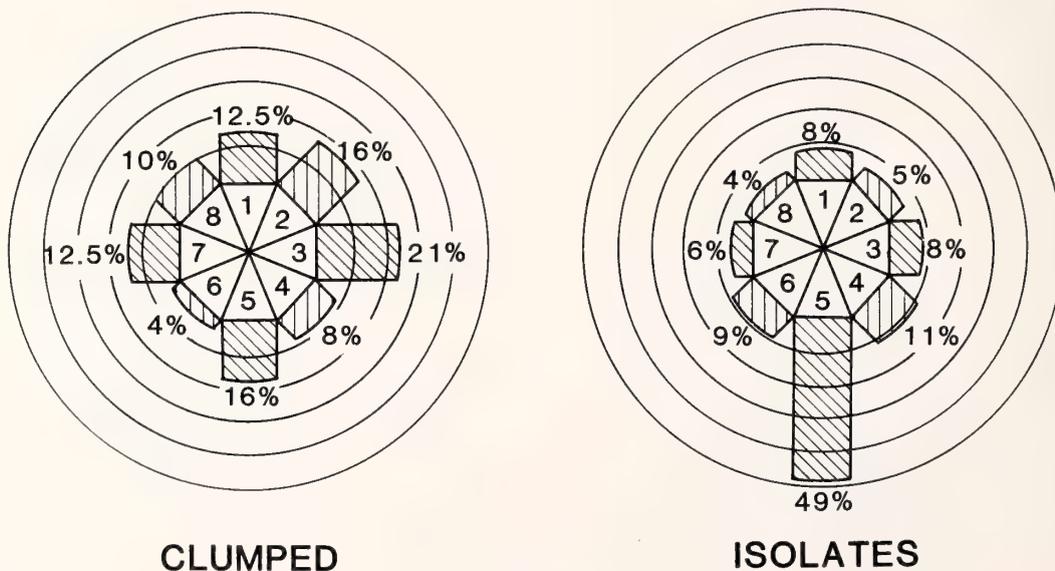


Figure 2

The orientation of *Collisella digitalis*, clumped or isolated, on vertical surfaces. The percentage figures are the relative frequency of each position with respect to vertical. The striped bar extends in the same direction as the anterior of the limpet. (n = 94 for aggregated, clumped, limpets; n = 117 for isolates.)

gregations lose water at one-half the rate of isolates. In addition, clumped hermit crabs survived longer under desiccating conditions than isolated crabs (SYNDER-CONN, 1981). The data presented in this paper clearly show a similar trend for *Collisella digitalis*: clumped limpets lost less water during the exposure period than isolated limpets. The reduction of water loss is most likely attributable to reduced wind velocities within the aggregation. Perimeter animals exposed to the wind would slow wind speed due to friction (drag). This notion is supported by the finding that perimeter animals (rank 2) have higher ECW solute concentrations than limpets within the aggregation. However, I did not resolve which solutes resulted in the ECW concentration changes. Thus, it is possible that the observed concentration differences are due to the addition of other solutes such as urine to the extracorporeal water. I have conducted preliminary studies on the biophysics of this system. The data gathered so far support the hypothesis that wind is the primary effector of water loss, and that wind velocities are lower within the aggregation.

There is indirect evidence that further supports the hypothesis that isolated limpets are under more extreme desiccation stress than clumped limpets. WOLCOTT (1973) reported that *Collisella digitalis* produces a mucous sheet that impedes water loss. I observed, but did not sample, several isolated limpets with mucous sheets, and I saw no clumped limpets with the barriers. Those isolates with the barriers had little extra-corporeal water, suggesting that the mucous sheets form as the ECW dries, preventing further water loss from the body tissues.

The orientation of isolated limpets may also indicate the severity of their condition. ABBOTT (1956) proposed that the head-down orientation observed in *Lottia gigantea* would ensure that the head and ctenidium would be the last to dry as the ECW volume decreased due to evaporative losses. The present work supports this hypothesis in that isolated limpets tended to orient with their head down on vertical surfaces (see also MILLER, 1968). In addition, some isolated limpets that had been subjected to acute dehydration, where almost all of the ECW was removed, were dried and discolored except in the head region. Interestingly, the tendency to orient head down is absent in clumped limpets, suggesting that the rigors of desiccation are reduced within an aggregation. Nevertheless, clumped limpets are subjected to evaporative water loss; however, position within the aggregation may be a more important factor governing their orientation.

The behavior of *Collisella digitalis* is consistent with the finding that the aggregations represent areas of reduced water loss. The crevices and depressions where the limpets often occur stay moist throughout the tidal cycle, limiting water loss because of moist air, cool temperature, and perhaps reduced wind speeds. ALLEE (1926) reported that isopods form aggregations when ordinary shelter is unavailable, thus satisfying the same tactile reaction. Simi-

larly, *C. digitalis* forms conspecific aggregations on smooth rock surfaces where no topographic shelter exists. This suggests that the aggregations are analogous to crevices with respect to shelter, and perhaps desiccation resistance.

The combination of aggregation, exploitation of crevices, and formation of mucous sheets, probably accounts for the persistence of *Collisella digitalis* in the high intertidal. The inability to fit exactly to the substrate renders the limpets vulnerable to environmental fluctuations. By forming aggregations, *C. digitalis* can effectively reduce the rates of evaporative water loss, thus reducing the degree of physiological stress normally imposed by its environment.

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I would like to thank Drs. Gary Adest and Val Conner for their advice on experimental design and Drs. Peter Frank, Ralph I. Smith, Victor Chow, E. Alison Kay, and Christopher Womersley for their careful readings of this manuscript. This research was conducted for Biology 100, a course offered by the University of California, Berkeley, through the Bodega Marine Laboratory. I am also indebted to all those involved in the course, students and faculty, for their support, particularly my friend Chad Hewitt.

LITERATURE CITED

- ABBOTT, D. P. 1956. Water circulation in the mantle cavity of the owl limpet, *Lottia gigantea* Gray. *Nautilus* 69(3):79-87.
- ALLEE, W. C. 1926. Studies in animal aggregation: causes and effects of bunching in land isopods. *J. Exp. Zool.* 45:255.
- COLLINS, L. S. 1976. Abundance, substrate angle and desiccation resistance in two sympatric species of limpets, *Collisella digitalis* and *Collisella scabra*. *Veliger* 19:199-203.
- FRANK, P. W. 1965. The biodemography of an intertidal snail population. *Ecology* 46:831-844.
- HAVEN, S. B. 1971. Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in central California. *Veliger* 13(3):231-248.
- MILLER, A. C. 1968. Orientation and movement of the limpet *Acmaea digitalis* on vertical rock surfaces. *Veliger* 11(suppl.): 30-44.
- MORRIS, R. H., D. P. ABBOTT & E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press: Stanford, Calif. 241 pp.
- RATHKE. 1833. *Acmaea*. In: Eschscholtz's "Zoologischer Atlas," Heft 5, pp. 16-21, 23-24.
- SEGAL, E. 1956. Adaptive differences in water holding capacity in an intertidal gastropod. *Ecology* 37:174.
- SYNDER-CONN, E. K. 1981. The adaptive significance of clustering in the hermit crab *Clibanarius digueti*. *Mar. Behav. Physiol.* 8:43.
- WARBURG, M. R. 1968. Behavioral adaptations of terrestrial isopods. *Amer. Zool.* 8:545.
- WOLCOTT, T. G. 1973. Physiological ecology and intertidal zonation in the limpets (*Acmaea*): a critical look at limiting factors. *Biol. Bull.* 145:389-422.

Relationship between Allometric Growth, with Respect to Shell Height, and Habitats for Two Patellid Limpets, *Nacella (Patinigera) macquariensis* Finlay, 1927, and *Cellana tramoserica* (Holten, 1802)

by

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Abstract. The relationship between allometric growth of the shell (with respect to height:length) and environmental influences of water turbulence and desiccation were examined in two patellid limpet species, *Nacella (Patinigera) macquariensis* Finlay, 1927, and *Cellana tramoserica* (Holten, 1802), from two widely different climatic regimes. The allometric intensity of increase of shell height in relation to length and increases in the relative shell heights (comparisons of height:length ratios in different allometric groupings) were found to be correlated with increasing water turbulence, especially in *N. (P.) macquariensis*. This contrasted with suggestions that the major environmental influence on the height of limpet shells is from desiccation. The results supported an existing hypothesis that the height:length ratio of the shells of limpets is influenced by the frequency with which a limpet is obliged to adhere strongly to the substrate. Other possible influences on the allometric growth, with respect to shell height, are discussed. Different shell forms in predation middens of Dominican gulls (*Larus dominicanus* Lichtenstein) were used to interpret the selection of limpets by the gulls.

INTRODUCTION

RELATIONSHIPS BETWEEN THE shell heights of intertidal limpets and their environment have been examined in a number of studies (RUSSELL, 1907; ORTON, 1932; EBLING *et al.*, 1962; BALAPARAMESWARA RAO & GANAPATI, 1971; WALKER, 1972; VERMEIJ, 1973, 1980; BRANCH, 1975; BANNISTER, 1975; WARBURTON, 1976; BRANCH & MARSH, 1978; LOWELL, 1984). In order to determine whether the shells of some limpets are relatively higher or lower than others, some form of standardization of the height is necessary. Usually shell height has been standardized against shell length, although other ratios have been employed, for example, shell height:geometrical mean of the major and minor diameters of the shell base (VERMEIJ, 1973). Early studies simply compared ratios of shell height:shell length over a range of lengths (RUSSELL, 1907; ORTON, 1932).

Limpets usually exhibit allometric growth, resulting in changing proportions between shell height and length; the height:length ratio increases with increasing size, al-

though an isometric pattern with increasing size has been recorded in some species (BRANCH, 1975). Consequently, in later studies, more complete comparisons between groups of limpets employ comparisons between regressions of shell height versus shell length over a range of limpet sizes.

Different methods, objectives, and descriptive terms used in previous studies can lead to confusion in comparisons across them. Consequently, I will use the following terms: (1) *allometric intensity* of shell-height increase—the continuum of shell height regressed against shell length for a range of lengths (*i.e.*, the slope of a regression equation), (2) *relative shell height*—height:length proportions of shells in comparisons between allometric continuums, (3) *height ratio* of shells—height:length proportions of shells where allometry has not been considered.

In previous studies, comparisons between limpets using the above criteria have attributed larger height ratios and relative shell heights to stress from desiccation (ORTON, 1932; DAVIES, 1969; BALAPARAMESWARA RAO & GANAPATI, 1971; VERMEIJ, 1973, 1978; BANNISTER, 1975; BRANCH, 1975), increased water turbulence (EBLING *et*

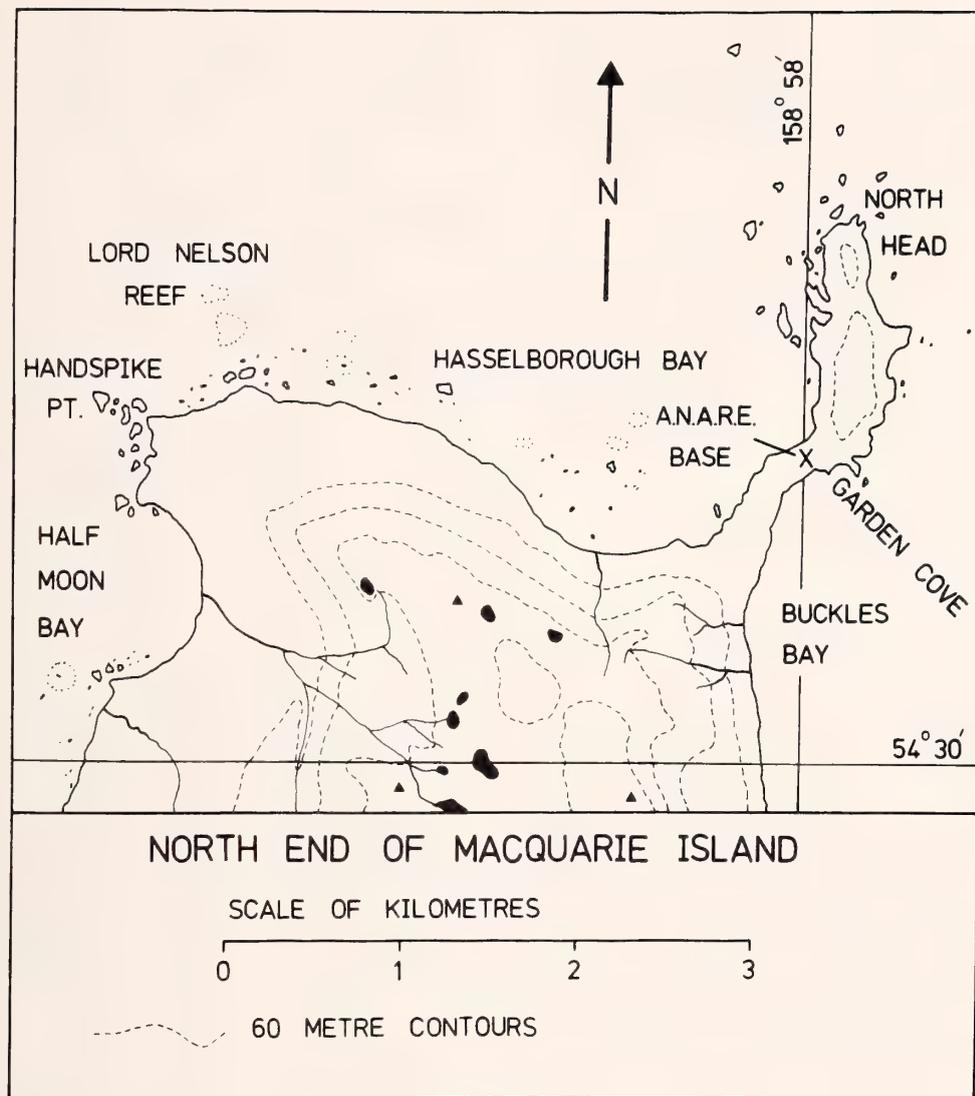


Figure 1

North end of Macquarie Island. Collections of *Nacella (P.) macquariensis* were made in the vicinity of the ANARE base.

al., 1962; WALKER, 1972), and slower growth rates (VERMEIJ, 1980).

The aim of the present study was to investigate the associations of desiccation and water turbulence with the allometric growth of shell height of limpets from two widely separated localities in different climatic regimes. On sub-Antarctic Macquarie Island (54°38'S, 158°53'E) *Nacella (Patinigera) macquariensis* Finlay, 1927, was the study animal. Variations in the height ratios of shells of *N. (P.) macquariensis* were noted in previous collections examined by DELL (1964). The other species, *Cellana tramoserica* (Holten, 1802), was collected at Arrawarra, northern New South Wales (30°3'S, 153°12'E).

The heavy predation on *Nacella (P.) macquariensis* by

Dominican gulls (*Larus dominicanus* Lichtenstein) and the resultant availability of shells from gull middens, nest sites, and roosts gave rise to a connected, subsidiary aim to the study. If limpet shell shape proved to be correlated with habitat, then shell characters of a predation sample could indicate that part of the limpet population particularly susceptible to predation by the gulls.

SITES, MATERIALS, AND METHODS

Specimens of *Nacella (P.) macquariensis* were collected from six habitats in the region of the isthmus at the northern end of Macquarie Island (Figure 1): (1) rock surfaces in the eulittoral zone on the west coast exposed to the

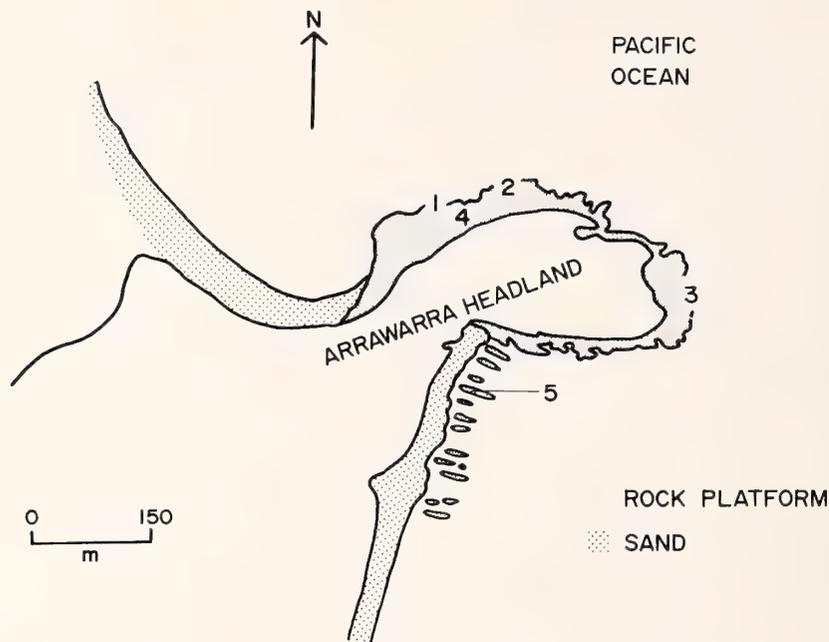


Figure 2

Arrawarra Headland. The numbers on the figure correspond to the collection localities for *Cellana tramoserica*, outlined in the text.

open sea; (2) rock surfaces in the eulittoral zone on the east coast exposed to the open sea; (3) rock surfaces at the top of the sublittoral zone on the east coast exposed to the open sea; (4) deep rock pools in the eulittoral zone on the east coast; (5) high rock pools situated approximately 3.5 m above the waterline on the east coast; (6) at a depth of 6 m on the east coast ("diving station"). Shells of limpets preyed upon by Dominican gulls (*Larus dominicanus*) were collected and divided into two categories: (a) shells from Dominican gull feeding sites where the gulls pecked out the flesh and left the shell behind and (b) shells from nest sites and roosting areas where the gulls regurgitated the remains, having swallowed the limpets whole. Two feeding sites were sampled in the "pecked out" predation category.

Limpets in habitats (1) and (2) were exposed to a high degree of turbulence from breaking waves and were subjected to potential desiccation only during emersion in windy and/or sunny conditions, the latter condition being very rare on Macquarie Island (the prevailing winds are from the west and, consequently, wave action is usually more severe on the west coast; however, for some months the turbulence on the east coast, estimated by a combination of wave height and wave frequency, is comparable to that of the west coast [SIMPSON, 1976]). Limpets in habitat (3) were also exposed to a high degree of turbulence both from breaking waves and water flow; stress from desiccation was virtually nonexistent. Habitats (4), (5), and (6) presented no desiccation problems for limpets.

At habitat (6) water currents could be strong, but the forces would be much less than that of wave action in the littoral zone. Habitat (4) was subjected to very little water movement, from flow into the pools at high water. The pools from habitat (5) represented a rare situation and, hence, provided limited data. These pools were located high on a steeply sloping face that received wave splash during moderate to heavy seas. The steep aspect prevented fouling by deposited kelp or from seals, as was the case for high rock pools (in which no limpets were found) on more gently sloping rock platforms. The effect of turbulence in these latter two habitats was negligible.

The headland from where *Cellana tramoserica* was collected is shown in Figure 2. The prevailing seas are from the southeast, causing the eastern and southern side of the headland to be exposed to heavier wave action than the northern side. There were five collection sites: (1) the bottom of the range of the limpets (lower part of the eulittoral zone) on the northern shore of the headland in an area partly sheltered by a fringing reef; (2) rock surfaces exposed to heavy wave action in the barnacle zone (*Tessieropora rosea* [Krauss]) on the northern shores of the headland; (3) rock surfaces in the barnacle (*T. rosea*) zone on the eastern point of the headland; (4) a gently sloping rock platform in the upper eulittoral zone on the northern shore of the headland; and (5) rock outcrops in the upper eulittoral zone on the beach immediately south of the headland. The above habitats were classed as follows: (1) little influence from either desiccation or wave action, (2)

moderate influence from desiccation and subjected to heavy wave action, (3) moderate influence from desiccation and heavier wave action than for (2), (4) frequently subjected to air exposure and desiccation with only moderate wave action, and (5) subjected to both desiccation and very heavy wave action.

If limpets regularly moved from one habitat type to another, possible effects on shell form from particular environmental factors of any one habitat would be masked. Consequently, specimens of both *Nacella (P.) macquariensis* and *Cellana tramoserica* were marked to record the amount of movement between habitats.

RESULTS

The movement of marked specimens in different habitats over a one year study period showed that *Nacella (P.) macquariensis* tends to live in fixed areas. In the eulittoral zone, individuals mostly remained in a small area (<1 m²); movements greater than 3 m were rare, usually being horizontal movements within the zone. Limpets in rock pools in the eulittoral zone showed a very high constancy of location. Limpets at the top of the sublittoral zone showed the greatest amount of movement. They were always in the same general area, but individuals sometimes moved into the eulittoral zone above the region of *Durvillea antarctica* (Chamisso) Hariot holdfasts, which represents a sublittoral fringe. Transect counts over one year showed seasonal variations in numbers, but there were no seasonal migrations of populations between eulittoral and sublittoral zones, such as shown by WALKER (1972) for the Antarctic limpet *Nacella (Patinigera) concinna* (Strebels) where migration down the shore was correlated with low temperatures and the formation of an ice film on the shore.

Specimens of *Nacella (P.) macquariensis* at diving stations were not marked for studies of movement. However, the heavy and normal encrustation of coralline algae on specimens indicated that they had been continuously submerged at the depth of collection. Limpets from the top of the sublittoral zone had a sparser covering of coralline algae, and limpets from the eulittoral zone either had no, a poor, or (when in shallow pools) a gnarled growth of coralline algae on the shells. The only coralline algal cover on the shells, similar to that for diving station limpets, was found on specimens from deep pools in the lower littoral and sublittoral zones. Encrustations of the tube-worm *Spirorbis aggregatus* Caullery & Mesnil were frequently but not always found on limpets in eulittoral rock pools, and provided some indication of type of habitat. The constancy of location exhibited by *N. (P.) macquariensis* was sufficient to ensure that the samples represented populations from the selected sites.

For *Cellana tramoserica*, marked specimens were found to remain within the habitat areas selected over a period of nine months. In addition, the encrustations of living algae and living barnacles indicated that the limpets were

Table 1

Regression analysis of shell height (y) on shell length (x) for *Nacella (P.) macquariensis* from all categories.

Category	Size range (lengths, mm)	n	Regression equation (log y = log a + b log x)	
			log a	b
High rock pools	17.9-47.2	16	-0.771	1.063
Predation (regurgitated)	16.2-47.5	126	-0.720	1.128
Diving station	18.0-45.1	131	-0.807	1.166
Deep rock pools	29.1-42.0	34	-0.933	1.194
Eulittoral, east coast	20.2-49.0	102	-0.974	1.322
Predation (pecked out #1)	18.5-44.8	58	-1.039	1.336
Predation (pecked out #2)	25.7-49.5	95	-1.039	1.371
Top of sublittoral, east coast	22.6-42.1	41	-1.369	1.541
Eulittoral, west coast	20.6-60.7	66	-1.430	1.583

long-term inhabitants of the lower littoral and the barnacle zones, respectively. Conversely, limpets from the upper eulittoral zone had no encrustations, indicating that at least they had not recently come from the other two habitats. In studies of *C. tramoserica* near Sydney over a period of 20 months, FLETCHER (1984) also found that marked limpets had not moved between four shore subdivisions: high, mid, and low intertidal and subtidal (there were no subtidal populations at the headland in the present study). As well, MACKAY & UNDERWOOD (1977) have shown that a proportion of *C. tramoserica* populations exhibits homing behavior.

Two models of the allometric relationship between shell height (y) and shell length (x) were fitted for all sets of data using the Minitab statistical package (RYAN *et al.*, 1981): (1) a linear regression model ($y = a + bx$) and (2) the linear regression form ($\log_{10}y = \log_{10}a + b \log_{10}x$) of the power relationship $y = ax^b$. For both species and all sites, the power relationship proved to be a better fit to the data, where b = slope and $\log_{10}a$ = intercept for each line.

For each species, particular models, ranging from a single regression for all data to separate regressions for each habitat/category, were fitted using the generalized linear interactive model computer program, GLIM (BAKER & NELDER, 1978). Mean deviances were compared to test the fit of particular models. Variance ratios were determined as (difference of deviances)/(mean deviance of the fuller model) on m:(n - m - 1) degrees of freedom, with m being the number of coefficients (slopes and intercepts) in the model and n being the total number of data considered.

For the nine sites from which *Nacella (P.) macquariensis* was collected, the relationships between shell height and shell length are given by the regressions in Table 1. To determine the most appropriate combination of regressions, the following models were tested:

Table 2

Combination of categories of *Nacella (P.) macquariensis* into separate groups on the basis of slope.

Group	Intercepts (log a)	Common slope (b)
(1) High rock pools	-0.885	1.139
Deep rock pools	-0.848	
Diving station	-0.767	
Predation (regurgitated)	-0.737	
(2) Predation (pecked out #1 + pecked out #2)	-1.049	1.344
Eulittoral, east coast	-1.008	
(3) Eulittoral, west coast + top of sublittoral, east coast	-1.430	1.582

Model I: 1 slope, 1 intercept (a single regression);

Model II: 1 slope, 9 intercepts;

Model III: 9 slopes, 1 intercept;

Model IV: 3 slopes, 9 intercepts;

Model V: 9 slopes, 9 intercepts.

Model II was found to be a more appropriate model than Model I ($F = 49.33$ on 8,659 d.f.; $P < 0.001$). Model IV was found to be more appropriate than both Model II ($F = 24.05$ on 2,657 d.f.; $P < 0.001$) and Model III ($F = 21.40$ on 2,657 d.f.; $P < 0.001$). The fullest model, Model V, was found not to be more appropriate than Model IV ($F = 0.20$ on 6,651 d.f.; $P > 0.50$).

Model IV separated out three groups on the basis of significantly different slopes. Within two of these groups two data sets could be combined in terms of no significant difference between intercepts, resulting in Model VI (3 slopes and 7 intercepts). Model VI was tested against Model IV and it was found that the fuller model, Model IV, did not give a significant reduction in mean deviance and was, therefore, not more appropriate than Model VI ($F = 0.20$ on 2,257 d.f.; $P > 0.50$). Hence, the most appropriate combination of regressions was that represented by Model VI, and this is shown in Table 2 and Figure 3.

The total variability in shell height attributable to the dependence of shell height on shell length in a particular model is given by the unbiased estimator $\hat{\rho}^2$, the adjusted coefficient of variation (ZAR, 1974). For Model VI, $\hat{\rho}^2$ was 0.88.

In group 1 (Table 2, Figure 3), all the limpets came from continuously submersed habitats except for one set—the predation (regurgitated) category. Group 2 included limpets from the east coast—from eulittoral rock surfaces and from both the predation (pecked out) categories. Group 3 was made up of limpets from the eulittoral zone on the west coast and from the top of the sublittoral zone on the east coast. In group 2, the height:length proportions of the shells at both the predation (pecked out) sites were

not significantly different in terms of either slope or intercept and, hence, could be combined. The shells of limpets from the top of the sublittoral zone on the east coast were not significantly different, in terms of either slope or intercept, from those of the west coast eulittoral zone. These were combined in group 3.

For the five sites from which *Cellana tramoserica* was collected, the relationships between shell height and shell length are given in Table 3. In determining the most appropriate combinations of linear regressions in this case, the following models were tested:

Model I: 1 slope, 1 intercept;

Model II: 1 slope, 5 intercepts;

Model III: 5 slopes, 1 intercept;

Model IV: 2 slopes, 5 intercepts;

Model V: 5 slopes, 5 intercepts.

Model II was found to be more appropriate than Model I ($F = 57.46$ on 4,390 d.f.; $P < 0.001$). Model IV was found to be more appropriate than both Model II ($F = 10.97$ on 1,389 d.f.; $P < 0.01$) and Model III ($F = 10.86$ on 1,389 d.f.; $P < 0.01$). The fullest model, Model V, was

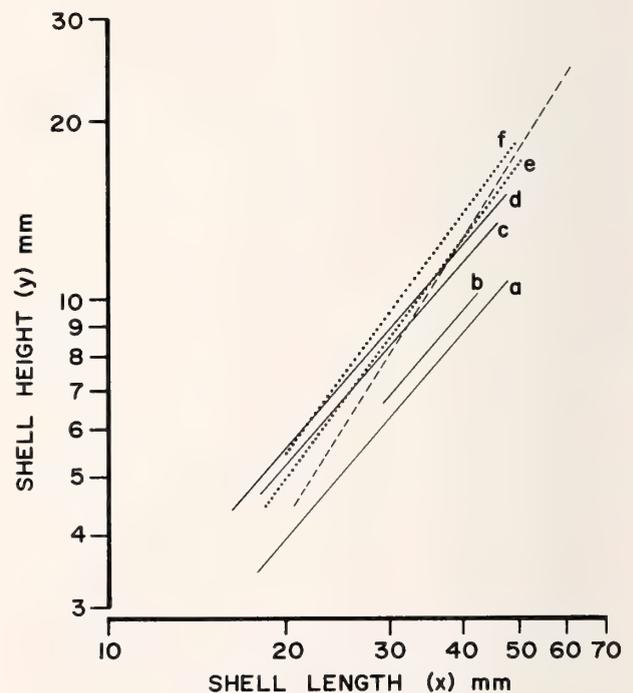


Figure 3

Regressions of height on length of categories within groups of *Nacella (P.) macquariensis*, plotted on log axes. Solid lines = group 1 where a = "high rock pools," b = "deep rock pools," c = "diving station," and d = "predation regurgitated." Dotted lines = group 2 where e = "predation (pecked out #1 + pecked out #2)" and f = "eulittoral, east coast." Dashed line = group 3 ("eulittoral, west coast" + "top of sublittoral, east coast").

Table 3

Regression analysis of shell height (y) on shell length (x) for *Cellana tramoserica* from all categories.

Category	Size range (lengths, mm)	n	Regression equation ($\log y = \log a + b \log x$)	
			log a	b
Upper eulittoral zone	15.6–42.4	81	–1.110	1.429
Barnacle zone, northern side	17.2–42.0	93	–1.101	1.435
Lower eulittoral zone	15.7–44.6	98	–1.181	1.435
Barnacle zone, eastern side	16.1–38.4	71	–1.106	1.443
Upper eulittoral, southern rocks	15.0–52.7	53	–1.377	1.615

found not to be more appropriate than Model IV ($F = 0.05$ on 3,386 d.f.; $P > 0.50$).

Model IV separated out two groups on the basis of significantly different slopes. Within one of these groups two data sets could be combined in terms of no significant difference between intercepts, resulting in Model VI (2 slopes, 4 intercepts). Model VI was tested against Model IV, and it was found that the fuller model, Model IV, did not give a significant reduction in mean deviance and was, therefore, not more appropriate than Model VI ($F = 0.25$ on 4,386 d.f.; $P > 0.50$). The most appropriate combination of regressions is that represented by Model VI and shown in Table 4 and Figure 4. For Model VI, the adjusted coefficient of variation, $\hat{\rho}^2$, was 0.93.

Group 1 (Table 4, Figure 4) included limpets from both the upper and lower eulittoral zone on the northern side of the headland, and the limpets from the barnacle zone areas. Both sets of limpets from the two barnacle-zone areas could be combined, as there was no significant difference between the intercepts. The limpets comprising group 2 (upper eulittoral, southern rocks) were significantly different from the others on the basis of slope of the regression.

There are two components to the allometric growth of the limpet shells of *Nacella (P.) macquariensis* and *Cellana tramoserica*, as shown by the regressions of height on length—slopes and intercepts. The slopes show the rate of increase of height with increasing length. When the slopes are significantly different, there is a difference in allometric intensity of height increase in relation to length during growth. If possible influence from some environmental factor during the growth of the limpet shell through adulthood is being examined, then consideration of slopes is the prime concern. Within a group having nonsignificantly different slopes, significantly different intercepts indicate differences in relative shell heights; that is, limpets from different sites had different “starts” to their relative shell heights, and maintained the same allometric inten-

sity of height increase throughout growth. Comparing relative shell heights between groups with significantly different slopes will give different answers depending on the selected value of length. This emphasizes the futility of comparing shell heights among groups of limpets for some standard length of shell, if allometric growth is not considered.

DISCUSSION

The climate of Macquarie Island (with precipitation occurring over approximately 330 days in each year, a mean relative humidity of 88%, and persistent cloud cover—see SIMPSON [1976]) poses very few desiccation problems for intertidal limpets. Desiccation stress would be encountered by intertidal animals only on the occasional sunny day in summer with calm seas. COURTNEY (1972) identified wind as a desiccating factor for intertidal mollusks, but the persistent precipitation, high humidity, and heavy seas would greatly reduce any desiccating effect of the wind on Macquarie Island shores. Thus, with minimal influence from desiccation, the habitats selected on Macquarie Island shores effectively represent a gradation of water turbulence.

A number of authors have suggested that water turbulence has either a negligible or no effect on increasing the height of limpet shells (ORTON, 1932; BALAPARAMESWARA RAO & GANAPATI, 1971; BERRY & RUDGE, 1973; BRANCH & MARSH, 1978). Further, it could be argued from the equations of drag forces on limpet shell shape (WARBURTON, 1976; BRANCH & MARSH, 1978) that a lower-spined shell should reduce drag and, hence, be more favorable for an environment with a high degree of water movement. If the above were generally true, shells of *Nacella (P.) macquariensis* could be expected to show either no difference in allometric growth with respect to shell height or even a decrease in height across a gradient of increasing water turbulence.

For *Nacella (P.) macquariensis* there were three groupings on the basis of allometric intensity of height increase. These groups had significantly different slopes to their combined regressions, in ascending order from group 1

Table 4

Combination of categories of *Cellana tramoserica* into separate groups on the basis of slope.

Group	Intercepts (log a)	Common slope (b)
(1) Lower eulittoral zone	–1.178	1.433
Upper eulittoral zone	–1.116	
Barnacle zone (northern + eastern sides)	–1.095	
(2) Upper eulittoral, southern rocks	–1.377	1.615

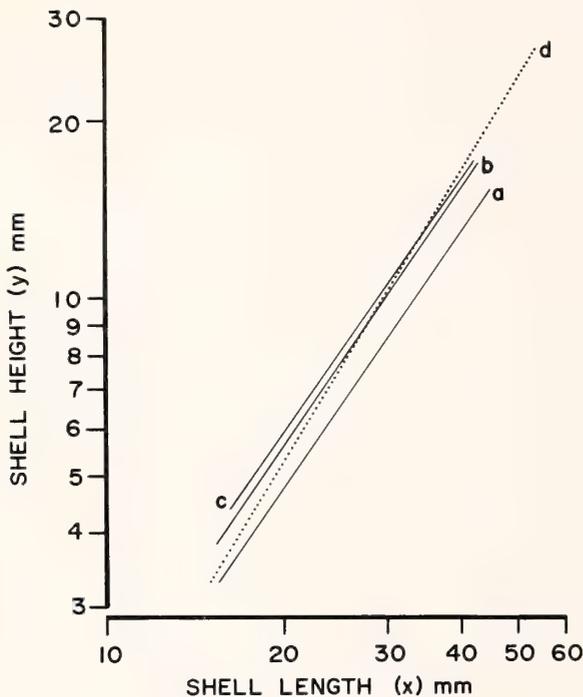


Figure 4

Regressions of height on length of categories within groups of *Cellana tramoserica*, plotted on log axes. Solid lines = group 1 where a = "lower eu littoral zone," b = "upper eu littoral zone," and c = "barnacle zone (northern and eastern sides)." Dotted lines (d) = group 2 ("upper eu littoral, southern rocks").

through group 3 (Table 2, Figure 3). This order matched the increasing degree of water turbulence impinging on the habitat categories within the groups, with the apparent exception of the "top of the sublittoral, east coast" category which was combined with the category subjected to the heaviest wave action of all ("eu littoral, west coast") in group 3. However, the longer period of lower intensity wave action at the top of the sublittoral zone on the east coast may have the same degree of impact as a shorter period of higher intensity wave action in the eu littoral zone on the west coast.

For *Cellana tramoserica*, collections from four sites were combined on the basis of no significant difference between slopes of their regressions (group 1). Thus, in group 1 the differential effects from either wave action or desiccation could not be identified as influencing the allometric intensity of height increase. Group 1 limpets had a significantly lower slope for the combined regression than that of group 2 (Table 4, Figure 4). The limpets in group 2 were subject to stress from both heavy wave action and desiccation. Further, parts of the rocks in the group 2 habitat were occasionally covered by shifting sands that could encroach on the areas occupied by the limpets, thus presenting a further stress.

For both species, there were significant differences in intercepts among categories comprising some of the groups. That is, although some categories showed the same allometric intensity of shell height increase, there were significant differences in relative shell heights for limpets from different habitats. In group 1 for *Nacella (P.) macquariensis*, limpets in high rock pools had the lowest relative shell height followed by, in ascending order, limpets from deep rock pools, diving station, and predation (re-gurgitated). The increase in relative shell height of the three habitat categories followed a sequence of increasing water turbulence. For *Cellana tramoserica*, the significantly different intercepts for limpet populations in group 1 followed a sequence that could be associated with both increasing desiccation stress and water turbulence, with the relatively highest shells occurring in the area of greatest wave action.

Thus, for *Nacella (P.) macquariensis* the allometric intensity of shell-height increase and the increase in relative shell heights were clearly correlated with increasing water turbulence. For *Cellana tramoserica* allometric intensity of shell-height increase was greater only where wave action was constant and very strong. Desiccation stress was not correlated with allometric intensity of shell-height increase. Both increasing water turbulence and desiccation stress were correlated with an increase in relative shell heights, with evidence of the most effect being associated with increasing water turbulence.

The data for both species showed that, if there is a significantly greater slope for a group, then members of that group will eventually reach a greater relative shell height (Figures 3, 4). What is curious is that in those groups that have the significantly greatest slopes, the smaller (by length) shells should have such low relative shell heights, i.e., group 3 for *Nacella (P.) macquariensis* (Figure 3) and group 2 for *Cellana tramoserica* (Figure 4). Perhaps the smaller limpets in such areas of greater environmental stress occupy some form of protected microhabitat and move out onto more open rock surfaces as they grow.

A number of factors have been previously suggested as influencing the shell height of limpets and these require examination here.

Variation in shell-height ratios of *Patella vulgata* Linnaeus on English shores formed the basis of the earliest studies on this topic in intertidal limpets. RUSSELL (1907) observed that specimens from localities that were exposed to heavy wave action were lower-spined than those from sheltered localities. ORTON (1932) found that the shells of adult limpets living on the upper shore were taller than those of individuals near the low water level or in rock pools. Orton correlated higher shell types with desiccation. He suggested that limpets inhabiting higher levels would hold their shells closer to the substrate to prevent drying out. The consequently strong grip would pull in the mantle margin, the site of secretion of new shell. Hence, a smaller peripheral increment of growth would be made

and continued growth would result in a steeper shell. ORTON (1932) further suggested that wave action would have a negligible influence on shell shape of *P. vulgata*, although he recognized that wave action would also cause a limpet to adhere more firmly. MOORE (1934) found that specimens of *P. vulgata*, with large height ratios, developed a shelf of flatter shell growth when transferred from the shore into a fish-hatching pond. Moore attributed this to the removal of desiccation stress, but the experimental design could not entirely discount decrease in water turbulence as an effect. Curiously, nearly all the "shelved" limpets returned to the initial angle of shell growth while still in the pond.

EBLING *et al.* (1962), working on *Patella* species in Ireland, found significantly greater relative shell heights for *P. aspersa* Röding where they were permanently submerged and subjected to strong currents. Ebling *et al.* suggested that water turbulence could also cause greater relative shell heights by obliging the limpets to adhere firmly. In a study on the tropical limpet *Cellana radiata radiata* (Born), taken from different habitats and zonal levels, BALAPARAMESWARA RAO & GANAPATI (1971) concluded that desiccation was more important than wave action in influencing shell characters.

From shell measurements of a number of limpet species, VERMEIJ (1973, 1978) found that the shell-height ratio increased in an upshore direction and suggested that this was an adaptation to desiccation stress. VERMEIJ (1973) argued that a taller shell would increase the water reservoir and decrease the region of water loss, *i.e.*, the area and perimeter of the base. BANNISTER (1975) recorded greater desiccation tolerance in the taller-shelled *Patella lusitanica* (Gmelin) of the upper eulittoral zone to that of the lower-shelled *Patella caerulea* (Linnaeus) of the lower eulittoral zone of Mediterranean shores. In comparisons across seven species of *Patella* on South African shores, BRANCH (1975) found a strong correlation between zonal position on the shore and tolerance to water loss; however, there was no close correlation between zonation and relative shell heights.

In a review of limpet biology, BRANCH (1981) noted that many authors have recorded greater height ratios and relative shell heights in drier habitats for a number of species. Also, BRANCH (1981) observed that an intraspecific increase in relative shell height usually occurs in limpets from higher on the shore but the same pattern is not always true when different species are compared. Results from interspecific comparisons will always embody wide genotypic options for morphological strategies. Consequently, it is perhaps not surprising that general hypotheses will be confounded when pooling results from a number of species.

On the coasts of North America, there have been a number of studies on the possible effects of desiccation on the morphology of acmaeid limpets. On the east coast, WALLACE (1972) found that, in *Acmaea testudinalis* (Müller), tolerance of desiccation was related to size and that

limpets in a habitat with increased desiccation stress (intertidal rock face versus tide pools and subtidal area) did not have greater shell height ratios. On the west coast, WOLCOTT (1973) reported no correlation between either size or shell shape and desiccation rates or tolerances in interspecific comparisons among five species of limpets (although no quantitative details of shell shape were presented). Wolcott determined that the ability to form a mucus sheet between the shell margin and the substrate was the most important adaptation to desiccation. Aware that interspecific comparisons may confuse the issue, LOWELL (1984) undertook intraspecific investigations for four species of acmaeid limpets. Lowell determined that increasing size significantly reduced water loss but that variation in shell shape (as measured by volume/circumference) had no effect on water loss. Lowell suggested that variation in shell shape might be partially or primarily due to factors other than resistance to desiccation.

In Britain, DAVIES (1969) recorded a greater desiccation tolerance in specimens of *Patella vulgata* from high levels of the shore compared to that of specimens from low levels. While Davies speculated that this may be partly attributable to shell shape, his results primarily showed that desiccation tolerance was inversely related to body size.

As shown here for *Nacella (P.) macquariensis*, one factor associated with allometric intensity of shell-height increase and greater relative shell heights is an increase in water turbulence. As previously mentioned, some authors have discounted wave action as having an influence on the shell height of limpets. However, EBLING *et al.* (1962) and WALKER (1972) found associations between increased water turbulence and relative shell height. DURRANT (1975) found significantly different height:width ratios in the freshwater limpet *Ancylus fluviatilis* Müller from river and lake populations, where there was no exposure to desiccation. The river populations (with greater water flow) had taller shells. BRANCH (1981) has noted the contrasting arguments for influences on shell height in areas of strong water movement: (a) flatter shells are adaptive where wave action is strong because they cause less drag, versus (b) strong water currents cause a limpet to clamp down tightly and thereby deposit shell in a tall conical form—in the manner as postulated by ORTON (1932). Further, BRANCH (1975) and BRANCH & MARSH (1978) have reasoned that higher-domed shells will allow greater muscle development and insertion that, in turn, would strengthen tenacity.

GRENON & WALKER (1981) found no significant differences between the tenacity of low and high shore level *Patella vulgata* on both exposed and sheltered shores. Thus, the taller-shelled populations (from the upper shore) did not display a greater tenacity. BRANCH & MARSH (1978) reported that relative shell height was not correlated with tenacity in six *Patella* species. However, in the two species with strong allometric intensity of height increase against length (*P. argenvillei* Krauss and *P. granatina* Linnaeus),

relative shell height was significantly correlated with tenacity per unit area of the foot.

VERMEIJ (1978) noted that a pattern in allometric growth intensity of mollusks for different parts of the shore may be a function of an adaptive trend or a by-product of variation in growth rate. VERMEIJ (1980) went on to state "Various lines of evidence have led me to believe that many instances of gradual changes in shell allometry (especially doming) are geometrically tied to growth rate." In experimental manipulations of *Collisella* limpets in California, HAVEN (1973) noted that rapid growth in *C. scabra* resulted in new shell being deposited at a flatter angle. Growth rates of intertidal limpets have often been found to decline in an upshore direction (BRANCH, 1974; LEWIS & BOWMAN, 1975; PHILLIPS, 1981) and this corresponds with the previously mentioned trend for relative shell heights of limpets to increase in an upshore direction. Presumably, the slower growth rates are related to lesser abundance of food or time available for grazing. LEWIS & BOWMAN (1975) showed that *Patella vulgata* had different growth rates in different habitats. Growth rates were higher at low tidal levels compared to high tidal levels, and superimposed on this was the biological influence of growth rates being lower in sites inhabited by barnacles and/or mussels, whose presence reduced the surface area that could be easily grazed. In five of these habitats, Lewis & Bowman recorded a matching sequence between decrease in growth rate and increasing allometric intensity of shell-height increase. This presents strong evidence for shell allometry being a function of growth rate. THOMPSON (1980) also found growth rates of *P. vulgata* to be highest on bare rock and lowest on areas with a dense population of barnacles.

Of particular relevance to the present study, FLETCHER (1984) found that a mid-tidal population of *Cellana tramoserica* had a lower growth rate, a higher density, and a significantly greater allometric intensity of shell-height increase than that for a subtidal population. However, the correlation with growth rate did not hold true for all of the study sites investigated by Fletcher (high, mid-, and low intertidal and subtidal). The order of allometric intensity of shell height increase across the four populations was "high" = "mid-" > "low" > "sub," while that for the growth rates was "mid-" < "high" = "low" < "sub." A reverse trend of higher growth rates at upper levels has been found where densities of limpets at higher levels are lower, which would result in more food being available (SUTHERLAND, 1970; CREESE, 1980). Unfortunately, there are no corresponding data on shell heights in these cases.

Water turbulence and desiccation could be acting with different emphases upon intertidal limpets in different climatic regions and different parts of the shore. The data from the present study and the mixed findings from other works show that no one environmental factor has a universal relationship with allometric growth of shell height. If, as ORTON (1932) suggests, an obligation to adhere

firmly increases the steepness of shell formation, then any factor (*e.g.*, water turbulence or desiccation) that causes a limpet to clamp down frequently enough will have such an ultimate effect. Although alternative explanations have been put forward in seeking relationships between relative shell height and tenacity (BRANCH, 1975; BRANCH & MARSH, 1978), Orton's argument would apply, whatever the tenacity capability of a species. The assigning of adaptive trends to allometric growth in limpets relies almost entirely on correlative evidence. Indeed, correlations between such features as allometric intensity of shell-height increase and degree of stress from water turbulence and desiccation may simply be because such stresses reduce growth rates rather than because of any adaptive advantage. Experimental proof for time-related features such as shell growth is difficult to obtain. Field manipulation of animals, for example, between habitats of differing intensities of desiccation and water turbulence would also have to account for possible differences in food availability, grazing capabilities, or densities, which, in turn, would affect growth rates. A useful addition to the present data would be to apply an immediate aging technique (*i.e.*, from shell growth lines) to limpets from several habitats, and this will form the subject of further studies.

The predation categories of *Nacella (P.) macquariensis* present an interesting result, subsidiary to the central aim of the study. The similarity in the shells of limpets from the two predation (pecked out) sites on the east coast showed that gulls feeding in this way were selectively taking limpets with respect to shell shape in terms of height: length proportion. The similarity in slope to that for limpets in the eulittoral zone indicated that the gulls were taking the limpets from that region, but they were selecting limpets that had lower relative shell heights, as indicated by the significantly different lower intercept for the predation category. Limpets taken by gulls and later regurgitated were combined with limpets from pools and the diving station into the one group, on the basis of slope. This implies that the gulls took limpets that they could swallow from pools. As they floated among intertidal rocks during calm seas, Dominican gulls were observed diving their heads under water to pick off limpets. A similar situation was reported for Dominican gulls feeding on *Nacella (P.) delesserti* (Philippi) on Marion Island by BLANKLEY (1981). However, in regard to rock pools at Macquarie Island, Dominican gulls were observed taking limpets only from the edges of pools. Also, it is highly unlikely that pool populations could supply the number of limpets swallowed whole by gulls—not only in the area covered in this study but also for the whole island. It is more likely that the inclusion of the predation (regurgitated) category in group 1 is an artifact from the gulls' selection of limpets. That is, their selection of smaller limpets for swallowing (the majority of the limpets in this category were in the lower end of the length range) biased the result, placing these limpets in with group 1.

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LITERATURE CITED

- BAKER, R. J. & J. A. NELDER. 1978. The GLIM system manual, release 3. Numerical Algorithms Group: Oxford.
- BALAPARAMESWARA RAO, M. & P. N. GANAPATI. 1971. Ecological studies on a tropical limpet, *Cellana radiata*. Structural variation in the shell in relation to distribution. *Mar. Biol.* 10:236-243.
- BANNISTER, J. V. 1975. Shell parameters in relation to zonation in Mediterranean limpets. *Mar. Biol.* 31:63-67.
- BERRY, R. J. & P. J. RUDGE. 1973. Natural selection in Antarctic limpets. *Br. Antarc. Surv. Bull.*, No. 35:73-81.
- BLANKLEY, W. O. 1981. Marine food of Kelp Gulls, Lesser Shearwaters and Imperial Cormorants at Marion Island (Subantarctic). *Cormorant* 9:77-84.
- BRANCH, G. M. 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 3. Growth-rates. *Trans. Roy. Soc. S. Afr.* 41:161-193.
- BRANCH, G. M. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. *Mar. Biol.* 32:179-188.
- BRANCH, G. M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanogr. Mar. Biol. Ann. Rev.* 19:235-280.
- BRANCH, G. M. & A. C. MARSH. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. *J. Exp. Mar. Biol. Ecol.* 34:111-130.
- COURTNEY, W. A. M. 1972. The effect of wind on shore gastropods. *J. Zool. (Lond.)* 166:133-139.
- CREESE, R. G. 1980. An analysis of distribution and abundance of populations of the high-shore limpet *Notoacmea petterdi* (Tenison-Woods). *Oecologia* 45:212-260.
- DAVIES, P. S. 1969. Physiological ecology of *Patella*. III. Desiccation effects. *J. Mar. Biol. Assoc. U.K.* 49:291-304.
- DELL, R. K. 1964. Marine Mollusca from Macquarie and Heard Islands. *Rec. Dom. Mus., Wellington, N.Z.* 4:267-301.
- DURRANT, P. M. 1975. An investigation into the effect of running water on shell dimensions in *Ancylus fluviatilis* Müller. *J. Conchol.* 28:295-300.
- EBLING, F. J., J. E. SLOANE, J. A. KITCHING & H. M. DAVIES. 1962. The ecology of Lough Ine XII. The distribution and characteristics of *Patella* species. *J. Anim. Ecol.* 31:457-470.
- FLETCHER, W. J. 1984. Intraspecific variation in the population dynamics and growth of the limpet, *Cellana tramoserica*. *Oecologia* 63:110-121.
- GRONON, J.-F. & G. WALKER. 1981. The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *J. Exp. Mar. Biol. Ecol.* 54:277-308.
- HAVEN, S. B. 1973. Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. *Ecology* 54:143-151.
- LEWIS, J. R. & R. S. BOWMAN. 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *J. Exp. Mar. Biol. Ecol.* 17:165-203.
- LOWELL, R. B. 1984. Desiccation of intertidal limpets: effects of shell size, fit to substratum and shape. *J. Exp. Mar. Biol. Ecol.* 77:197-207.
- MACKAY, D. A. & A. J. UNDERWOOD. 1977. Experimental studies on homing in the intertidal patellid limpet *Cellana tramoserica* (Sowerby). *Oecologia* 30:215-257.
- MOORE, H. B. 1934. The relation of shell growth to environment in *Patella vulgata*. *Proc. Malacol. Soc. Lond.* 21:217-222.
- ORTON, J. H. 1932. Studies on the relation between organism and environment. *Proc. Liverpool Biol. Soc.* 46:1-16.
- PHILLIPS, D. W. 1981. Life-history features of the marine intertidal limpet *Notoacmea scutum* (Gastropoda) in central California. *Mar. Biol.* 64:95-103.
- RUSSELL, E. S. 1907. Environmental studies on the limpet. *Proc. Zool. Soc. Lond.* 11:856-870.
- RYAN, T. A., JR., B. L. JOINER & B. F. RYAN. 1981. Minitab Reference Manual. Duxbury Press: Boston. 154 pp.
- SIMPSON, R. D. 1976. The shore environment of Macquarie Island. ANARE Rep. Ser. B1, No. 125:1-41.
- SUTHERLAND, J. P. 1970. Dynamics of high and low populations of the limpet *Acmaea scabra* (Gould). *Ecol. Monogr.* 40:169-188.
- THOMPSON, G. B. 1980. Distribution and population dynamics of the limpet *Patella vulgata* L. in Bantry Bay. *J. Exp. Mar. Biol. Ecol.* 45:173-217.
- VERMEIJ, G. J. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Mar. Biol.* 20:319-346.
- VERMEIJ, G. J. 1978. Biogeography and adaptation. Patterns of marine life. Harvard University Press: Cambridge, Mass. 352 pp.
- VERMEIJ, G. J. 1980. Gastropod shell growth rate, allometry, and adult size: environmental implications. Pp. 379-394. *In*: D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms. Plenum: New York.
- WALKER, A. J. M. 1972. Introduction to the ecology of the Antarctic limpet *Patinigera polaris* (Hombron and Jacquinot) at Signy Island, South Orkney Islands. *Br. Antarc. Surv. Bull.*, No. 28:49-69.
- WALLACE, L. R. 1972. Some factors affecting vertical distribution and resistance to desiccation in the limpet, *Acmaea testudinialis* (Müller). *Biol. Bull.* 142:186-193.
- WARBURTON, K. 1976. Shell form, behaviour and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* 23:307-325.
- WOLCOTT, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors." *Biol. Bull.* 145:389-422.
- ZAR, J. J. 1974. Biostatistical analysis. Prentice-Hall Inc.: New Jersey. 620 pp.

Spatial and Temporal Distribution and Overlap of Three Species of *Bullia* (Gastropoda, Nassariidae) on Exposed Sandy Beaches

by

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Abstract. Three species of plough shell, *Bullia rhodostoma*, *B. digitalis* and *B. pura*, coexist on dynamic sandy beaches in the Eastern Cape, South Africa. The robust *B. rhodostoma* is most abundant in the zone of swash and backwash, and exhibits great efficiency in foraging behavior, feeding on carrion stranded on the shore. The entire life cycle of this species is spent intertidally, while only adults of *B. digitalis* and *B. pura* appear on the beach, where they prefer a more subtidal habitat. The latter species exploit their surfing ability in the quest to capture food on its path shorewards and to migrate offshore during winter probably to spawn their eggs in deeper water. All three *Bullia* species move horizontally with the tides, a behavior facilitating continuous access to food. Although zonation is evident among the three whelk species, some spatial overlap exists. *Bullia rhodostoma* is the most widely distributed while *B. digitalis* shows the greatest overlap with the other two species.

INTRODUCTION

THE EXPOSED SANDY BEACH, despite little spatial heterogeneity and much physical instability, harbors a marine fauna of some ecological diversity. Eighteen species have been recorded in the Eastern Cape, South Africa, with four mainly intertidal forms constituting 99.5% of the biomass. The plough shell *Bullia rhodostoma* Reeve, 1847, makes up 1.7%, while the other two species, *B. digitalis* (Dillwyn, 1787) and *B. pura* Melvill, 1885, account for only 0.4% of the total biomass. The large white sand mussel *Donax serra* Botten, 1848, dominates the macrofauna comprising 97.3%, while the smaller mussel *D. sordidus* Hanley, 1845, contributes only 0.1% of the biomass (MC GWYNNE, 1980; MC LACHLAN *et al.*, 1981).

Although their contribution to the macrofaunal biomass is small, the ecological importance of *Bullia* is indicated by their abundance (particularly *B. rhodostoma*) and their position in the food chain (BROWN, 1964, 1971). Snails of *B. rhodostoma* with shell lengths ranging from 3 to 52 mm have been recorded (MC LACHLAN *et al.*, 1979a) while a much narrower size range has been encountered in both *B. pura* (11-29 mm) and *B. digitalis* (22-42 mm) (MC GWYNNE, 1980). The snails function as predator/scavengers, feeding on a wide range of organisms stranded in

the swash. The most important predator of *Bullia* is the swimming crab *Ovalipes* (DU PREEZ, 1981). The holoccephalan *Callorhynchus*, elasmobranch *Rhinobatus*, and teleosts *Coracinus*, *Lithognathus* and *Rhabdosargus* prey on the plough shells during high tide. The sanderling *Crocebia* feeds on *Bullia* while they are exposed at low tide (MC LACHLAN *et al.*, 1981; BROWN, 1982).

Brown described the mode of life of *Bullia* on beaches in the Western Cape and conducted extensive research into their ecophysiology. Recently, BROWN (1982) reviewed the existing knowledge on the biology of *Bullia* in South Africa. In the Eastern Cape, the general ecology of *B. rhodostoma* has been described (MC LACHLAN *et al.*, 1979a, 1979b) and aspects of the physiology of the genus recorded (ANSELL & MC LACHLAN, 1980; DYE & MC GWYNNE, 1980; MC GWYNNE, 1980; MC LACHLAN & YOUNG, 1982).

On beaches in the Eastern Cape, *Bullia rhodostoma*, *B. digitalis*, and *B. pura* appear to coexist in a relatively unstructured habitat where little niche differentiation is evident. The aim of this paper is to describe aspects of the ecology of only the latter two species, such as distribution and abundance, and to determine how the three whelk species apparently coexist successfully in the "uniform" environment of the sandy beach.

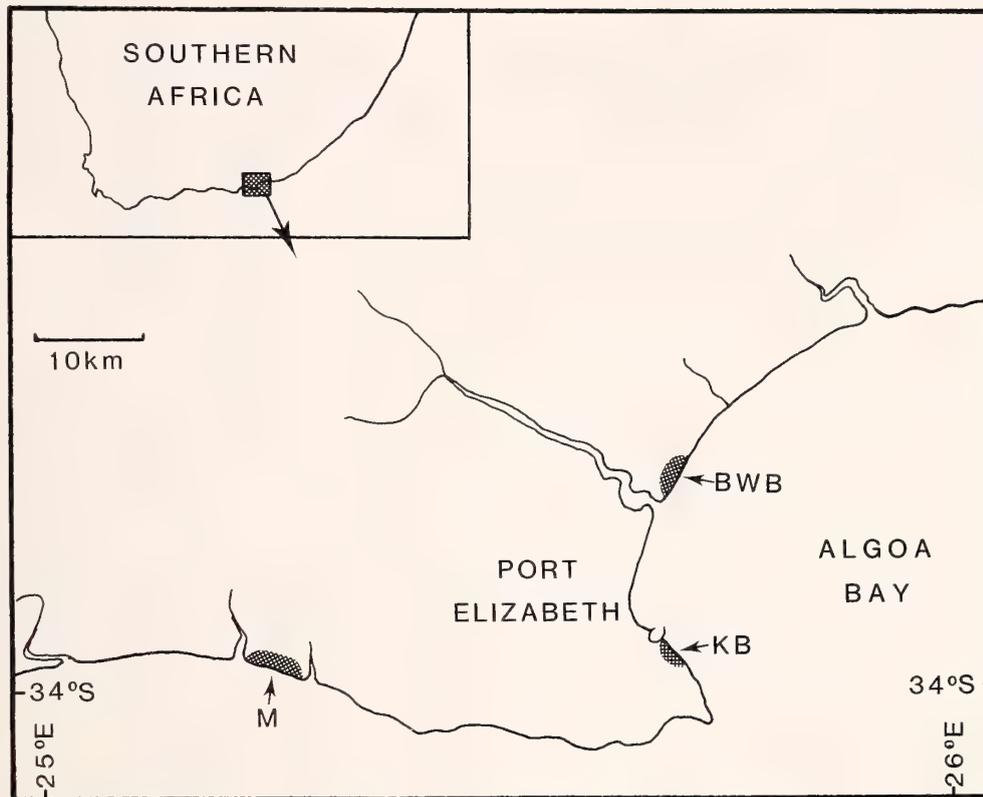


Figure 1

Map of Southern Africa, showing the locations of the three study beaches: Maitlands (M), Kings (KB) and Bluewaterbay (BWB).

THE STUDY AREA

Three beaches were selected as study sites (Figure 1). Maitlands beach is a southfacing beach lying 30 km west of Port Elizabeth; Kings beach and Bluewaterbay beach face northeast and east, respectively, into Algoa Bay. The main features characterizing the three beaches have already been described by MC LACHLAN (1977, 1979) and are summarized in Table 1. These represent average conditions, which may differ markedly during extreme calm or storms.

Maitlands beach supports a high macrofaunal biomass. The total ash-free dry biomass approaches 7 kg/m of shoreline (MC LACHLAN *et al.*, 1981), the major contributor being the large white sand mussel *Donax serra*. Less common inhabitants of the beach zone include the swimming crab *Ovalipes*, sand-burrowing mysid *Gastrosaccus*, and isopods, chiefly *Eurydice*. *Donax serra* is absent on Kings beach and present in low numbers on Bluewaterbay beach. Populations of beach macrofauna on the latter two beaches are much smaller than on the high energy beach at Maitlands.

METHODS

Distribution and Abundance

Sampling of *Bullia digitalis* and *B. pura* was conducted approximately every six weeks from January 1978, to December 1979, on Maitlands beach, and from January to December 1979, on Kings and Bluewaterbay beaches. A dredge (0.5 m wide with 1.5-mm mesh) was used to complete a series of five hauls for each sample. Each haul was 10 m long and cut 5 cm into the sand; thus, a 25-m² area was sampled. The hauls were continuous, with no overlap between each haul. The sampling procedure covered a 50-m line from a point 5 m below LWS (low water springs) to just above the mean tide level. This was essential as *B. digitalis* and *B. pura* inhabit deeper water than the intertidal resident, *B. rhodostoma*.

The appearance of *Bullia rhodostoma* in dredged samples was ignored, as its distribution and abundance has already been described (MC LACHLAN *et al.*, 1979a). The occurrence of this species was, however, noted in five samples taken from Maitlands beach from April to October 1979, to measure the degree of overlap in the distribution

Table 1

Characteristic features of the three East Cape beaches, Maitlands (M), Kings (KB), and Bluewaterbay (BWB).

Feature	Maitlands	Kings	Bluewaterbay
Average slope of beach	gentle $\frac{1}{33}$ concave	moderate $\frac{1}{25}$ concave	steep $\frac{1}{20}$ concave
Average width of intertidal	100 m	50 m	40 m
Width of surf zone	150–400 m	30–120 m	50–200 m
Swash periods	20–30 sec	10–23 sec	12–20 sec
Wave periods	14 sec	10 sec	10 sec
Volume of seawater filtered through interstices (m ³ /m/day)	9	7	12
Grade of sand	very well-sorted medium quartz particles	clean fine well-sorted quartz	well-sorted fine to medium quartz sand with large shell fragments and pebbles around LWS
Particle size range (median diameters)	268–308 μm	200–220 μm	variable size, median 250 μm
General appearance	Gentle sloping beach backed by extensive dune system. Strong wave action.	Berm present 2 m above LWS, dunes poorly developed. Moderate wave action.	Berm 1.25 m above MTL, dunes poor. Wave action moderate to strong.

of the three beach populations. All animals collected were measured to 1 mm greatest shell length using vernier calipers.

Due to the absence of juvenile snails of both *Bullia digitalis* and *B. pura* from the beach zone, sampling was extended into the offshore region beyond the breakers. A dredge 0.33 m wide with a mesh size of 4 mm was dragged by a motorboat and guided by a diver using SCUBA. The series of hauls was approximately 10 m in length and in water depths ranging from 3 to 8 m.

Tidal Migrations

The tidal movements of *Bullia digitalis* and *B. pura* were monitored during spring tides in March and again in November 1979. MC LACHLAN *et al.* (1979b) recorded the tidal migrations of macrofauna resident in the intertidal zone just below ELWS to EHWS (extreme low water springs, extreme high water springs). Preliminary observations showed *B. digitalis* and *B. pura* to prefer a more subtidal habitat than the intertidally dominant *B. rhodostoma*. During March of this study, the sampling zone was extended from ELWS seawards to the line of breakers initiating the dynamic surf zone. In November, the first line of breakers marked the seaward extent of the sampling procedure. Steel rods, at 20 m intervals, marked each sampling site. A second series of rods, 10 m from and parallel to the first, marked the length of each strip of beach to be dredged. Samples were taken every 3 h for 12 h over two tidal cycles using the smaller 4-mm mesh size dredge. No area was sampled more than once in 6 h. The dredge proved to be efficient on dry sand and at water depths to approximately 4 m.

Niche Breadth and Overlap

In terms of the spatial model of the niche by HUTCHINSON (1958), niche breadth is the "distance through" the niche along some particular line in niche space. The distribution of whelks on the beach was taken to represent this line, and its vertical range and evenness of spread were calculated using an index of niche breadth, *B*. We used data collected at Maitlands beach over five months (from April to October 1979) when all three species were sampled through a series of five tidal levels. Numbers collected in 5-m² dredged samples at each level were used to calculate the following quantity:

$$B = \frac{1}{\sum_{i=1}^n P_i^2}$$

where *B* is the niche breadth of a species, *P_i* is its proportion (in numbers) in the *i*th habitat unit of the environment, and *n* is the number of units. The sandy beach was the habitat and the series of five dredges taken each month made up the units. The index was calculated for each species for every month over the five-month period. The theoretical maximum niche-breadth value was estimated by assuming an even distribution of the three species over the five units.

Niche overlap is simply the joint use of a resource by two or more species. As in niche breadth, the resource is space. Niche overlap is calculated as:

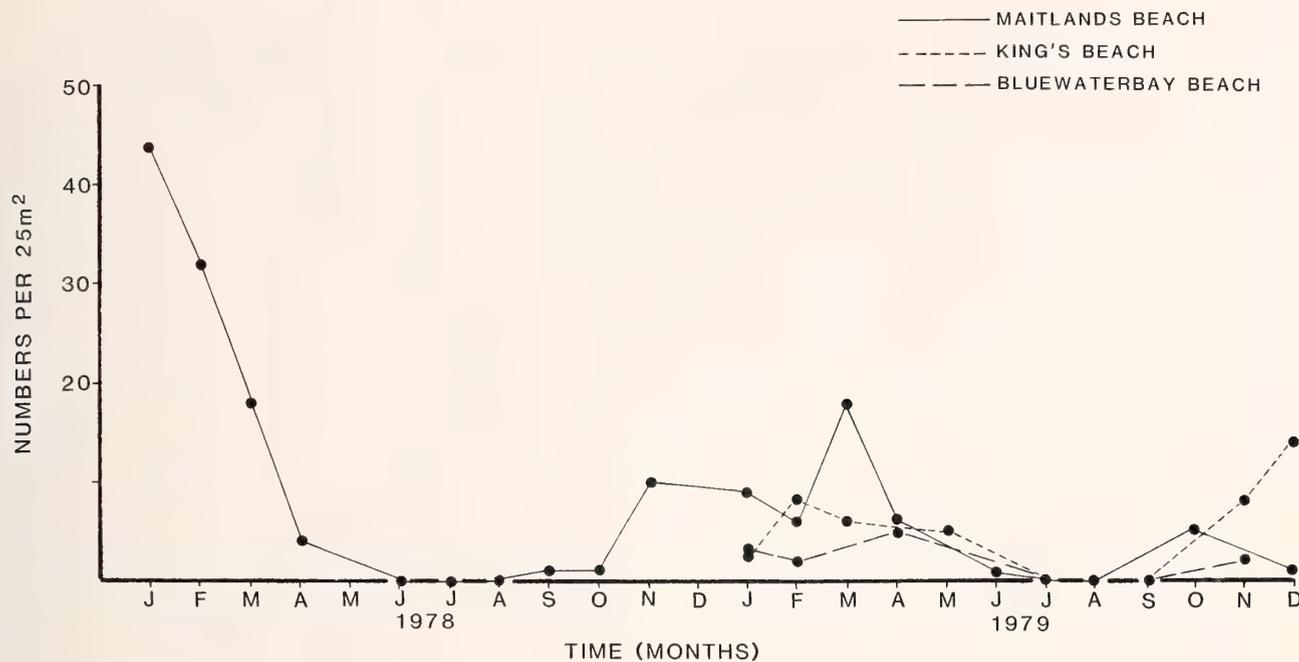


Figure 2

Temporal abundance of *Bullia digitalis* on three beaches in the Eastern Cape, South Africa.

$$\alpha = \frac{\sum_h P_{jh} P_{kh}}{\sum_h P_{jh}^2}$$

where α is the niche overlap or probability of species k overlapping species j , and P_{jh} and P_{kh} are the proportions of species j and k respectively in the h th unit of the habitat. If the distribution for the two species is identical (*i.e.*, complete overlap), $\alpha = 1$ (LEVINS, 1968). Interspecific niche overlaps were calculated monthly and estimated for the overall sampling period.

RESULTS

Temporal Abundance and Distribution

Two peaks of abundance were evident for both *Bullia digitalis* and *B. pura* on all three beaches (Figures 2, 3). Maximum densities of *B. digitalis* occurred during mid-summer (November to January) with a smaller peak in and around March. *Bullia pura* was most numerous in December and January, and then again during March and April. Numbers of both species were low, reflecting the absence of juvenile snails. No distinct year classes were discernible. Snails appeared to be patchily distributed in groups. The sampling procedure, and probable inefficiency of the dredge, did not always reflect the true distribution and abundance patterns on the beach.

The samples containing *Bullia rhodostoma* show this

population to occur intertidally and higher on the shore than *B. digitalis* and *B. pura*, which were confined to lower tidal levels and deeper waters.

The offshore hauls located juvenile snails of both *Bullia pura* and *B. digitalis* coexisting with juveniles of four other *Bullia* species, namely *B. callosa* Wood, 1828, *B. annulata* (Lamarck, 1816), *B. laevissima* (Gmelin, 1791), and *B. tenuis* Gray, 1839. Notable differences in shell morphologies eliminated confusion over their taxonomic identity. A *t*-test indicated a significant difference in the mean shell lengths between the beach and offshore populations of *B. digitalis* ($P < 0.005$) and *B. pura* ($P < 0.005$). Two other gastropods, *Ancilla albozonata* Smith, 1904, and *Melapium lineatum* (Lamarck, 1822), were also found in the deep-water samples.

Tidal Migrations

Figures 4 and 5 show the profile of Kings beach along with the pattern of tidal migration undertaken by the whelks during both monitoring sessions. Only the spatial ranges and not changes in abundance of the snails are shown. One snail in a dredged sample was taken as representative of the presence of a species at a particular location and time. Despite low numbers, migration patterns on both occasions revealed similar trends. All three species showed distinct movements with the tides. *Bullia rhodostoma* kept abreast and sometimes slightly ahead of the incoming swash, while *B. pura* and *B. digitalis* failed to penetrate the swash, always remaining in deeper water.

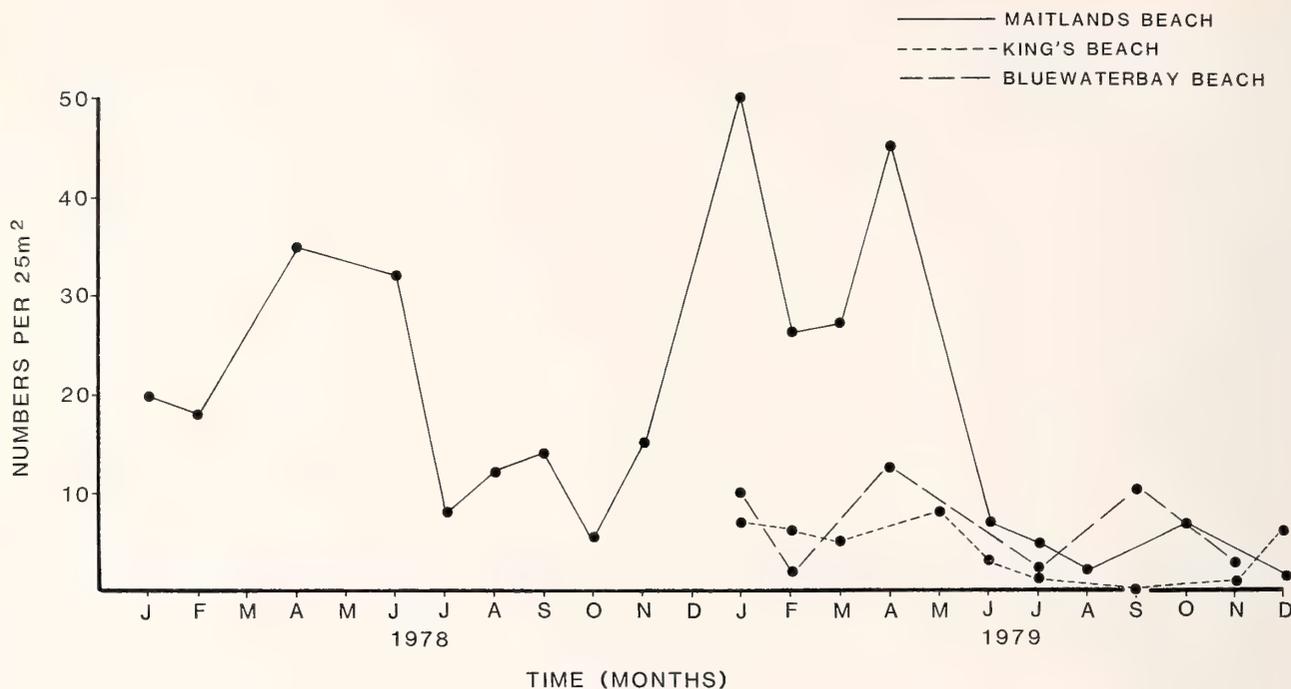


Figure 3
Temporal abundance of *Bullia pura* on the three South African East Cape beaches.

Bullia pura, however, extended into shallower water than *B. digitalis*.

Niche Breadth and Overlap

Numbers of *Bullia digitalis* and *B. pura* collected were generally low and fluctuated over the sampling period (Table 2), while numbers of *B. rhodostoma* increased steadily towards October. *Bullia digitalis* was absent during mid-winter (July–August) and numbers of *B. pura* declined over this period. B values were all under 5, the theoretical maximum that would indicate a uniform distribution of snails throughout the study area. The greatest niche breadth was recorded in *B. rhodostoma* for October, the value reaching 78% of the maximum. Niche breadths of *B. digitalis* and *B. pura* proved variable, ranging from 0 to 3.5. Calculation of the overall B for each species showed *B. rhodostoma* to be the most widespread population, with *B. pura* confined to the narrowest zone. Interspecific zonation is suggested by the average B values (Table 3), as these never reach 60% of the value indicative of an even distribution.

The greatest species overlap occurred between *Bullia rhodostoma* and *B. pura* (Table 4) particularly during April and October. Overlap between each of the former species and *B. digitalis* was negligible, except for October when the overlap proved noteworthy. *Bullia digitalis* and *B. pura* populations overlapped markedly when both species were present on the shore.

DISCUSSION

Distribution

The same basic pattern of distribution appeared on all three sandy beaches. *Bullia rhodostoma* occupied a broad band of the intertidal, whereas the adults of *B. digitalis* and *B. pura* restricted themselves to the subtidal, the juveniles remaining offshore beyond the breakers. MC LACHLAN *et al.* (1979a) recorded a size-based zonation at low tide, with the smaller snails situated uppermost on the shore. The effect of shell length on distribution patterns was not measured in this study.

On Muizenberg beach in the Western Cape, BROWN (1971) found snails of *Bullia rhodostoma* and *B. digitalis* occurring in well-defined groups of a single species within a narrow size range. No vertical pattern of zonation was noted. He attributed this distribution to a sorting process promoted by wave action. MC GWYNNE (1980) demonstrated that *B. rhodostoma*, aided by a large foot and a light shell, surfed at a faster rate than the other two species. Both *B. digitalis* and *B. pura* have smaller feet and heavier shells, which enable them to withstand current surges more effectively than *B. rhodostoma* and, thus, maintain their subtidal position on the shore. The physical characteristics of *B. rhodostoma* also promote speed and efficiency in crawling on wet sand, essential attributes for this species to reach carrion stranded in the swash. *Bullia digitalis* and *B. pura* are not equipped to compete with *B. rhodostoma*

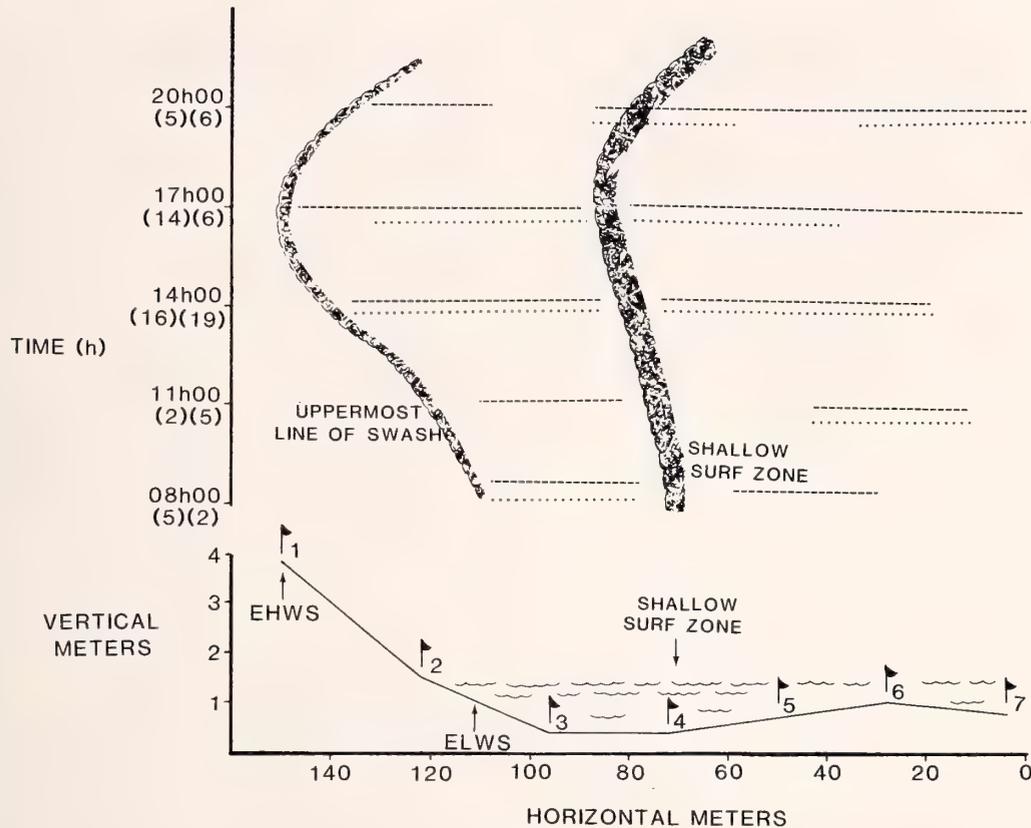


Figure 4

The migration patterns of beach populations of *Bullia pura* (---) and *B. digitalis* (····) during a spring tidal cycle in March 1979. Actual numbers of each species caught in the dredge at each sampling time are shown in parentheses below the time scale on the vertical axis. The profile of Kings beach is also shown.

in this pursuit and probably exploit different feeding strategies subtidally in their quest for food and, therefore, survival.

In experiments correlating the distribution of *Bullia digitalis* with the grade of sand on west coast beaches, BROWN (1961) and BALLY (1981) showed this species to prefer no particular sediment. At Bluewaterbay beach in Algoa Bay, a series of dredge hauls from the beach towards and along the mouth region of the Swartkops River indicated the presence of *Bullia* until a point where the ripple effect of waves became negligible. This coincided with an increase in the slope of the river bank. During the hauls, there was no marked change in either sediment grade or salinity of seawater. A combination of the effects of wave action, water currents, and beach slope could act as factors limiting the distribution of the snails.

Abundance

The absence of juveniles of both *Bullia digitalis* and *B. pura* from the beach and their appearance in offshore dredged samples suggest that the egg-laying females mi-

grate to deeper, less turbulent waters to deposit their egg capsules. This presumed offshore migration could account for the decrease in the beach populations of *B. pura* during January and February and *B. digitalis* from February to April. Eggs of *B. rhodostoma* are spawned in mid-summer (December/January) (MC LACHLAN *et al.*, 1979a) at the same time as those of *B. pura*, but slightly before *B. digitalis* (MC GWYNNE, 1980).

The entire population of *Bullia digitalis* moves offshore during the winter, while snails of *B. pura*, although few in number, are always found on the beach. This may be related to the apparently seasonal occurrence of carrion (MC GWYNNE, 1980) and the possible presence of a more constant food supply in deeper waters in winter. *Bullia digitalis* has been found at depths exceeding 20 m (BROWN, 1982) along the west coast, particularly off exposed beaches with steep slopes.

Snails of both species return in late spring to early summer to the shallows. Copulation takes place then, with the males exploiting the mobility of the swash to find mates. Females remain on the beach for about two to three

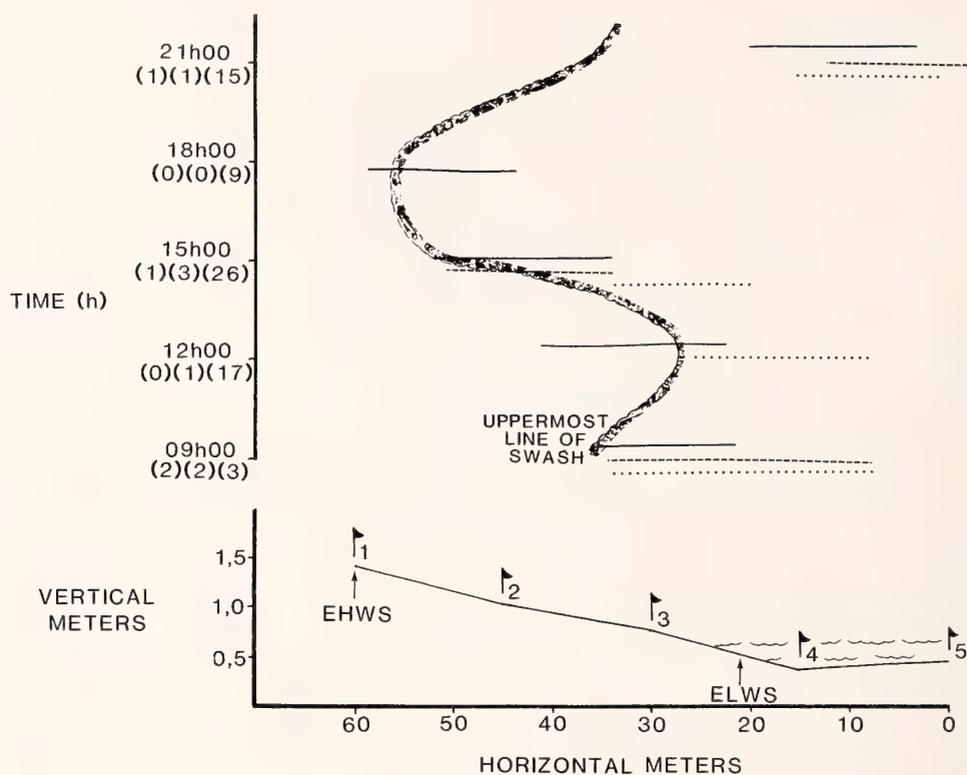


Figure 5

Migrations undertaken by beach populations of *Bullia pura* (---), *B. digitalis* (.....), and *B. rhodostoma* (—) during a spring tidal cycle in November 1979. Actual numbers of each species caught in the dredge at each sampling time are shown in parentheses below the time scale on the vertical axis. The profile of Kings beach is also shown.

months after copulation, with the sperm presumably stored. The second peak of abundance of *Bullia digitalis* and *B. pura*, in March and April, respectively, could indicate the return of the females to the beach after depositing their egg capsules offshore.

Tidal Migrations

All three *Bullia* species migrate with the tides, differing in the extent of their vertical penetration. *Bullia rhodostoma*, located higher on the shore than *B. digitalis* and *B. pura*, is carried with the swash and often stranded above

Table 2

Numbers of *Bullia rhodostoma* (Br), *B. digitalis* (Bd), and *B. pura* (Bp) at five beach sites, each 4 m², from the swash (site no. 1) to water of approximately 1 m deep (site no. 5). B = niche breadth.

Site no.	April			June			July			August			October		
	Br	Bd	Bp	Br	Bd	Bp	Br	Bd	Bp	Br	Bd	Bp	Br	Bd	Bp
5	0	1	1	2	1	0	6	0	1	1	0	1	0	2	0
4	0	3	1	0	1	2	3	0	0	9	0	1	32	2	0
3	0	2	11	4	0	2	2	0	3	3	0	1	24	1	3
2	5	1	13	10	0	3	17	0	0	2	0	0	41	0	0
1	12	0	20	19	0	1	22	0	1	50	0	0	40	0	4
Total	17	7	46	35	2	8	50	0	5	65	0	3	137	5	7
B	1.7	3.2	3.1	2.5	2.0	3.5	3.0	0.0	2.7	1.6	0.0	3.1	3.9	2.7	1.9

Table 3

Niche breadth values, B, calculated for each species.

Species of <i>Bullia</i>	Total B over all months	Average B	% B of theoretical maximum
<i>B. rhodostoma</i>	0.46	2.5	50
<i>B. digitalis</i>	0.87	1.6	32
<i>B. pura</i>	0.53	2.9	58

the tide, where it forages in search of stranded carrion. The latter two species are carried up the beach with waves on the incoming tide, and burrow rapidly into the sand as the velocity of the incoming wave diminishes.

ANSELL & TREVALLION (1969), working on *Bullia* species on the Indian coastline, found the changing velocity of the backwash of the ebbing tide to be the critical factor in the emergence and subsequent movement back to deeper water of these snails.

Bullia digitalis and *B. rhodostoma* on west coast beaches occupy the same intertidal position (BROWN, 1971). Here, they kept pace with the tides during low and mid-water, emerging occasionally in the saturated foreshore to feed; they always remained buried at high water. On east coast beaches, *B. digitalis* (and *B. pura*) maintains a subtidal position, probably feeding on dead-animal remains washing back and forth in the waves. It has not been seen foraging in the manner of the west coast species (MC GWYNNE, 1980). The movements of the plough shells over a large part of the intertidal zone give them access to food in a wider area than if they remained fixed at one tidal level.

Niche Breadth and Overlap

Niche breadth indices suggest some spatial partitioning between the three *Bullia* species on the shore. Dredging

Table 4

Niche overlap (α) between each of the three intertidal *Bullia* species over the period from April to June 1979.

Br = *B. rhodostoma*. Bd = *B. digitalis*. Bp = *B. pura*.

Species overlapping/ species overlapped	Niche overlap (α) ^a					
	April	June	July	August	October	Overall
Br/Bd	0.14	0.06	0.00	0.00	0.35	0.17
Bd/Br	0.07	0.08	0.00	0.00	0.49	0.09
Br/Bp	1.20	0.72	0.36	0.20	0.46	0.54
Bp/Br	0.65	0.53	0.41	0.11	0.92	0.47
Bd/Bp	0.37	0.43	0.00	0.00	0.16	0.17
Bp/Bd	0.38	0.25	0.00	0.00	0.23	0.28

^a The values indicate the probability of one species overlapping the other with the species being overlapped read as the denominator.

covered only an area from the swash line to a water depth of approximately 1 m. The niche breadth and overlap analyses, therefore, only indicate spatial niches in the shallow zone of swash sampled, and do not reveal the total dominance of the upper intertidal by *B. rhodostoma* or the absence of this species from deeper waters. The niche indices also give no indication of the competitive interactions involved in the partitioning of food between the three whelk species, the access to which is vital for their survival on the beach.

The offshore migrations presumably undertaken by *Bullia digitalis* and *B. pura* would obviously reduce spatial overlap between all three species and increase their niche breadths. The species diversity and population dynamics of deep-water macrofauna have not been measured. The area beyond the breakers remains relatively unexplored.

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LITERATURE CITED

- ANSELL, A. D. & A. MC LACHLAN. 1980. Upper temperature tolerances of three molluscs from a South African sandy beach. *J. Exp. Mar. Biol. Ecol.* 48:243-251.
- ANSELL, A. D. & A. TREVALLION. 1969. Behavioural adaptations of intertidal molluscs from a tropical sandy beach. *J. Exp. Mar. Biol.* 4:9-35.
- BALLY, R. 1981. The ecology of three sandy beaches on the west coast of South Africa. Doctoral Thesis, University of Cape Town.
- BROWN, A. C. 1961. Physiological-ecological studies on two sandy beach Gastropoda from South Africa: *Bullia digitalis* Meuschen and *Bullia laevissima* Gmelin. *Z. Morph. Okol. Tiere.* 49:629-657.
- BROWN, A. C. 1964. Food relationships on the intertidal sandy beaches of the Cape Peninsula. *S. Afr. J. Sci.* 60(2):35-41.
- BROWN, A. C. 1971. The ecology of the sandy beaches of the Cape Peninsula, South Africa. Part 2. The mode of life of *Bullia* (Gastropoda: Prosobranchiata) *Trans. Roy. Soc. S. Afr.* 39:281-319.
- BROWN, A. C. 1982. The biology of sandy beach whelks of the genus *Bullia* (Nassariidae). *Oceanogr. Mar. Biol. Ann. Rev.* 20:309-361.
- DU PREEZ, H. H. 1981. The biology of the three-spotted swimming crab, *Ovalipes punctatus* (de Haan) (Brachyura: Portunidae) with special reference to feeding. Master's Thesis, University of Port Elizabeth.
- DYE, A. H. & L. E. MC GWYNNE. 1980. The effect of temperature and season on the respiratory rates of three psammolittoral gastropods. *Comp. Biochem. Physiol.* 66A:107-111.
- HUTCHINSON, G. E. 1958. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415-427.

- LEVINS, R. 1968. Evolution in changing environments. Princeton University Press: Princeton, N.J.
- MC GWYNNE, L. E. 1980. A comparative ecophysiological study of three sandy beach gastropods in the Eastern Cape. Master's Thesis, University of Port Elizabeth. 144 pp.
- MC LACHLAN, A. 1977. Studies on the psammolittoral meiofauna of Algoa Bay, South Africa. I. Physical and chemical evaluation of the beaches. *Zool. Afr.* 12:15-32.
- MC LACHLAN, A. 1978. A temporal study of niche breadth and overlap in two sympatric species of Mystacocarida (Crustacea). *Zool. Afr.* 13(2):351-357.
- MC LACHLAN, A. 1979. Volumes of sea water filtered through East Cape sandy beaches. *S. Afr. J. Sci.* 75:75-79.
- MC LACHLAN, A. 1980. The definition of sandy beaches in relation to exposure: a simple rating system. *S. Afr. J. Sci.* 76:137-138.
- MC LACHLAN, A., C. COOPER & G. VAN DER HORST. 1979a. Growth and production of *Bullia rhodostoma* on an open sandy beach in Algoa Bay. *S. Afr. J. Zool.* 14(1):49-53.
- MC LACHLAN, A., T. ERASMUS, A. H. DYE, T. WOOLDRIDGE, G. VAN DER HORST, G. ROSSOUW, T. A. LASIAK & L. E. MC GWYNNE. 1981. Sand beach energetics: an ecosystem approach towards a high energy interface. *Estuarine, Coastal and Shelf Science* 13:11-25.
- MC LACHLAN, A., T. WOOLDRIDGE & G. VAN DER HORST. 1979b. Tidal movements of the macrofauna on an exposed sandy beach in South Africa. *J. Zool. (Lond.)* 188:433-442.
- MC LACHLAN, A. & N. YOUNG. 1982. Effects of low temperature on the burrowing rates of four sandy beach molluscs. *J. Exp. Mar. Biol. Ecol.* 65:275-284.

Aspects of Reproduction, Larval Development, and Morphometrics in the Pyramidellid *Boonea impressa* (= *Odostomia impressa*) (Gastropoda: Opisthobranchia)

by

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Abstract. *Boonea impressa* is an important ectoparasite of the American oyster, *Crassostrea virginica*. Here, the reproductive and larval life history, intraspecific variation in certain shell characters, and the internal anatomy of the feeding apparatus are described for populations of *B. impressa* from the western Gulf of Mexico (Texas) and, for the latter two subjects, the western Atlantic (North Carolina). Larval development in the Pyramidellidae is reviewed. The life-span of *B. impressa* was approximately one year. Reproduction occurred throughout the year, but peaked in mid-summer. Eggs (182–238 μm diameter) were deposited in numbers of 20–250 per egg mass. Larval development from oviposition to hatched veliger required 3.3–4.8 days. Two days after hatching, the veligers became negatively phototactic. Metamorphosis occurred within one week of hatching. The developmental mode of *B. impressa* fits that designated as Type II-lecithotrophic, and agrees with that expected for an opisthobranch with a stable food source. The short pelagic life-span may facilitate dispersal for a species with a non-mobile, but patchy host. Recently metamorphosed *B. impressa* often attached near the aperture of an adult. This behavior may protect the young snail from predation and increase access to its food supply. The internal anatomy of the feeding apparatus differed from European odostomians in the absence of a well developed first buccal pump. Shell sculpture (number of cords per whorl) was most dependent on the length of the whorl. Adult snail size, whorl length, whorl width, and the number of spiral cords varied significantly between populations collected from Texas and from North Carolina. Egg size, size of the components of the feeding apparatus, whorl length-width ratio, and protoconch size differed less. These latter characters might be employed advantageously in the study of interspecific differences among odostomians where, heretofore, characters with greater intraspecific variability typically were used.

INTRODUCTION

PYRAMIDELLID GASTROPODS ARE important components of many shallow-water benthic communities (SANDERS, 1958; WELLS *et al.*, 1961; FRANZ, 1976). Presumably, all are parasitic (FRETTER & GRAHAM, 1949). As such, their impact on host population dynamics and subsequent changes in community structure may be important. Little is known, however, about pyramidellid life histories or their impact on host populations.

The pyramidellid *Boonea impressa* (= *Odostomia impressa*) is a frequent component of oyster reef communities on the east and Gulf coasts of the United States. ROBERTSON & MAU-LASTOVICKA (1979) found that *B. impressa* can feed on 36 different gastropod and bivalve species. The predominant host, however, was the oyster *Crassostrea virginica*. WHITE *et al.* (1984) showed that the growth rate of juvenile oysters was reduced significantly at a parasite level of 10 *Boonea impressa* per oyster. Numbers as high as 100 per oyster occurred on the Texas Coast (WHITE *et al.*, 1984). WHITE *et al.* (1984) concluded that *B. impressa* may have a significant impact on oyster populations and oyster population dynamics.

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ROBERTSON (1978) found that *Boonea impressa*, like all other American odostomians* studied, utilize spermatophores for sperm transfer, whereas European species use penial copulation (FRETTER, 1951, 1953; MAAS, 1964). Data of WELLS (1959), ROBERTSON (1978), and WHITE *et al.* (1984) indicated that reproduction occurs throughout the year, but peaks during early summer. ROBERTSON (1978) also noted that spermatophores are larger in Texas populations of *B. impressa* than in North Carolina populations. Additional morphometric data for North Carolina populations were reported by PORTER (1976) and PORTER *et al.* (1979).

In view of the potential impact of *Boonea impressa* parasitism on oyster populations and the limited data available on the reproductive life history of *B. impressa*, we undertook a study of its reproductive cycle and larval life history. In addition, we review the available data on other pyramidellids to elucidate whether the general trends in larval development described for other opisthobranchs are also applicable to the ectoparasitic Pyramidellidae.

Taxonomic and ecologic studies on the Pyramidellidae have been hindered by a poor understanding of intraspecific variation within the group. Species distinctions and species descriptions tend to rely on highly variable characters. Species identifications often are difficult. ROBERTSON'S (1978) work is notable for the use of anatomical criteria beyond shell characters to confirm taxonomic distinctions. Intraspecific variability in anatomical characters still is documented poorly in the Pyramidellidae, however. The degree of variability in shell characters between populations also is little known. POWELL (1981) found whorl width to be highly variable between populations in some *Turbonilla*, for example, thus limiting its taxonomic usefulness. Here, we also report data on some aspects of morphometrics, both of shell characters and internal anatomy, in North Carolina and Texas populations of *B. impressa* with particular emphasis on a comparison of the variability present in the internal anatomy of the feeding apparatus vis-à-vis that observed in shell morphology.

MATERIALS AND METHODS

Oyster clumps were collected from Big Slough on Harbor Island near Port Aransas, Texas, and kept in a running seawater system with adult *Boonea impressa*. Approximately every 3 or 4 days, these clumps were examined for the presence of egg masses. Egg masses were removed with forceps and placed in small dishes of filtered seawater (24–26°C) to which penicillin G and streptomycin sulfate were added to control bacterial growth (BONAR & HAD-

FIELD, 1974). Development from oviposition through metamorphosis was studied by examining these egg masses under a microscope at hourly intervals. Additionally, daily observations were made of oyster clumps with attached egg masses that were kept in large bowls under the same conditions.

Specimens of *Boonea impressa* were collected every other month from a relatively undisturbed reef located off the south side of Mud Island near Port Aransas, Texas. Clumps of oysters were shaken vigorously in a bucket of seawater to remove all *B. impressa*. A careful visual check was done and the process repeated until no more snails were found. Snails were separated from debris by using a 500- μ m sieve and preserved in formalin. For shell morphometrics, the following measurements were taken using an ocular micrometer: shell length, shell width, number of whorls, length, width and number of cords of the second and sixth whorl, and the width of the larval shell. Shell length was determined by measuring the length from the apex to the abapical end of the shell. Only those shells with an intact protoconch were used. Shell width was determined by measuring the width of the largest whorl with the aperture facing upwards. These measurements also were recorded for specimens of *B. impressa* from North Carolina generously loaned by H. Porter. Collections were made at Virginia Creek near Topsail Sound and at Williston Creek. PORTER (1976) and PORTER *et al.* (1979) gave additional information on these specimens.

Specimens from Big Slough (Texas) and from North Carolina were dissected while living. The feeding apparatus including the proboscis, stylet apparatus, buccal pump, and salivary glands were removed and measured. Occasional staining with 0.5% toluidine blue or methylene blue during the dissection proved to be efficacious (DAVIS, 1967). The longest dimension of eggs taken from egg masses laid by both groups of snails also was measured.

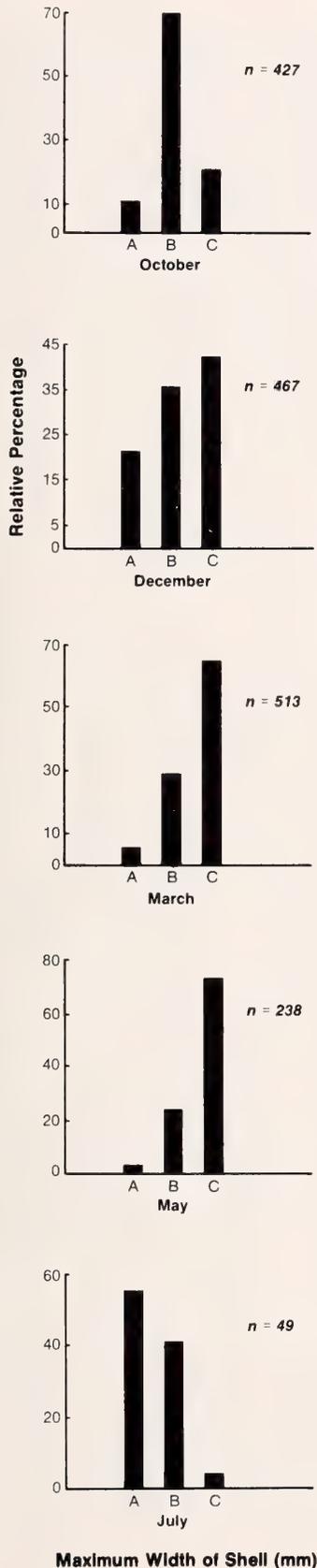
Boonea impressa specimens from each sample taken at Mud Island were decalcified using 0.5 M EDTA (ethylene diamine tetraacetic acid) and subsequently embedded in a paraffin medium and sectioned at 6 μ m. Sections were stained for one hour with toluidine blue (method of PREECE, 1972, modified by using colloidization during the rehydration step to ensure further that sections would remain on the slides). The sections were examined for the presence of sperm, as well as the number and size of the oocytes.

RESULTS

Larval Development and Population Dynamics

The mean size of *Boonea impressa* in the population from Mud Island increased from October to May (Figure 1). The population's size-frequency distribution changed significantly (Chi-square test, $P < 0.05$) between all sampling periods except March and May ($P < 0.10$ for the latter two).

* The term odostomian is used here for species usually referred to the genus *Odostomia* prior to ROBERTSON (1978) (e.g., ABBOTT, 1974; DALL & BARTSCH, 1909).



Recruits (specimens 0.5–1.00 mm in width) were observed in all samples, but recruitment in December (22% of the population sampled were new recruits) was noticeably higher than in October (10%), March (5%), or May (3%). The largest recruitment of juvenile snails was in July (55% of the population sampled were new recruits). Just prior to the July sampling, an extremely low tide and high temperature caused extensive mortality among the intertidal oysters. Although the population of *B. impressa* sampled was subtidal, the population structure for July may not be indicative of the normal summer condition.

Mean oocyte size did not differ significantly among the October, March, and May collections (Duncan's multiple range test, $P < 0.05$) (oocyte diameters in μm for October, March, and May were 17 ± 2 , 15 ± 4 and 17 ± 3 respectively). Significantly more oocytes were found in the snails collected in May than in those collected in either March or October (Kruskal-Wallis test, $P < 0.05$) (Table 1). The latter two months' collections were not significantly different. No oocytes were found in any specimen collected in December, and oocytes were found in only a single specimen collected in July. Sperm were present in most or all specimens examined in every collection period.

The eggs (Figure 2a) of *Boonea impressa* were laid in clear, irregular, gelatinous masses (Figure 3a) often deposited in crevices near the edge of the oyster shell. The number of eggs in an egg mass varied from approximately 20 to 250 under laboratory conditions. Egg diameter (maximum dimension) ranged from 182 to 238 μm . Significant differences were present in mean egg size between egg masses (Table 2). The range in egg size within an egg mass was always less than the range in egg size among all the egg masses measured. Eggs in a single egg mass tended to be of similar size so that some egg masses consisted almost exclusively of small eggs, whereas others consisted almost exclusively of large eggs. No difference was apparent, however, between the North Carolina and Texas populations.

The early embryological development of *Boonea impressa* followed the typical pattern for opisthobranch mollusks by exhibiting spiral cleavage and asynchronous cell division (RAVEN, 1958, 1964). Total developmental time required from oviposition to hatched veliger was 80–114 h (Table 3). The first cleavage of eggs occurred 2 h after oviposition, the second and third divisions (8 cells) after 4–6 h (Figure 2b). After 26–30 h, a gastrula had formed (Figures 2c–e).

Further development was divided into three stages: ear-

Figure 1

Size-frequency distributions for the *Boonea impressa* population at the Mud Island reef during Fall 1981 to Summer 1982. Shell widths of A, B, and C are 0.50–1.00 mm, 1.01–1.66 mm, ≥ 1.67 mm respectively.

Table 1

The mean, standard deviation, and range of the number of oocytes observed in the stained sections of *Boonea impressa* gonad. The snails were collected from the Mud Island reef.

Sampling period	Mean \pm SD	Range
October	53.25 \pm 5.38	48–60
December	0	0
March	50.25 \pm 20.02	33–75
May	140.00 \pm 27.12	102–160
July	2.25 \pm 4.5	0–9

ly-, mid- and late-veliger. The early-veliger stage, reached 32–36 h after oviposition, was characterized by the first noticeable movement of the embryo and the beginnings of velum development; however, neither shell nor statocysts were present and a bipartite velum was not observed. The mid-veliger stage, reached 50–54 h after oviposition, was characterized by the presence of statocysts, a bipartite velum, and a partially developed shell. The shell, however, did not extend down to the level of the statocysts, but covered only the upper part of the visceral mass (Figure 2f). The capability of retraction into the shell was not present nor was the velum completely developed. In particular, although the velum was ciliated, the long cilia characteristic of the velum of the hatched veliger were not present. Movement within the egg was most rapid at this stage and slowed noticeably thereafter. Between this stage and the late-veliger stage, reached 56–60 h after oviposition, the embryo grew rapidly from a size roughly one-half of the egg volume to a size nearly filling the entire egg volume. Prior to this, development had not markedly increased embryo size. The late-veliger stage was characterized by a fully developed velum and a completely developed shell extending down below the level of the statocysts. The long cilia characteristic of the velum of a planktonic larva were fully formed only at this stage. Additionally, the embryo first showed the capability of retraction into the shell at this stage.

Hatching occurred 80–114 h after oviposition (Figure 3b). After hatching, veligers frequently were caught at the air-water interface by surface tension. Strands, probably the remnants of the "mucus string" that bound the eggs together (RASMUSSEN, 1944), often connected as many as 20 floating larvae together. Trapped veligers did not seem to be capable of submerging and subsequently died at the

surface, unless the surface water was actively disturbed. Submerged veligers immediately demonstrated rapid movement both horizontally and vertically. During the first two days, movement was positively phototactic and rapid. Afterwards, the veligers became negatively phototactic and movement slowed considerably. For lengthy periods of greater than 1 h, the veligers often remained retracted into the shell or were stationary on algae or the bottom.

Many larvae metamorphosed in the large bowls in which oyster clumps were present; however, only a single individual was observed to metamorphose under the microscope. This occurred seven days after hatching. In an attempt to get more larvae to metamorphose, various possible metamorphosis inducing factors such as oyster shells, living oysters, algae typically found on oyster shells, and adult *Boonea impressa* were placed separately in bowls with apparently competent larvae (in the sense of CHIA, 1978), but without success. Larvae probably were competent to metamorphose, however, when negative phototaxis was observed, about two days post-hatching. Thus, seven days is probably an overestimate of the average larval life span in this species.

Newly metamorphosed snails were observed crawling freely, but most often they attached just outside the aperture on the outer lip of an adult *Boonea impressa* (Figures 3c, d). Juvenile *B. impressa* up to two teleoconch whorls frequently were observed demonstrating this behavior.

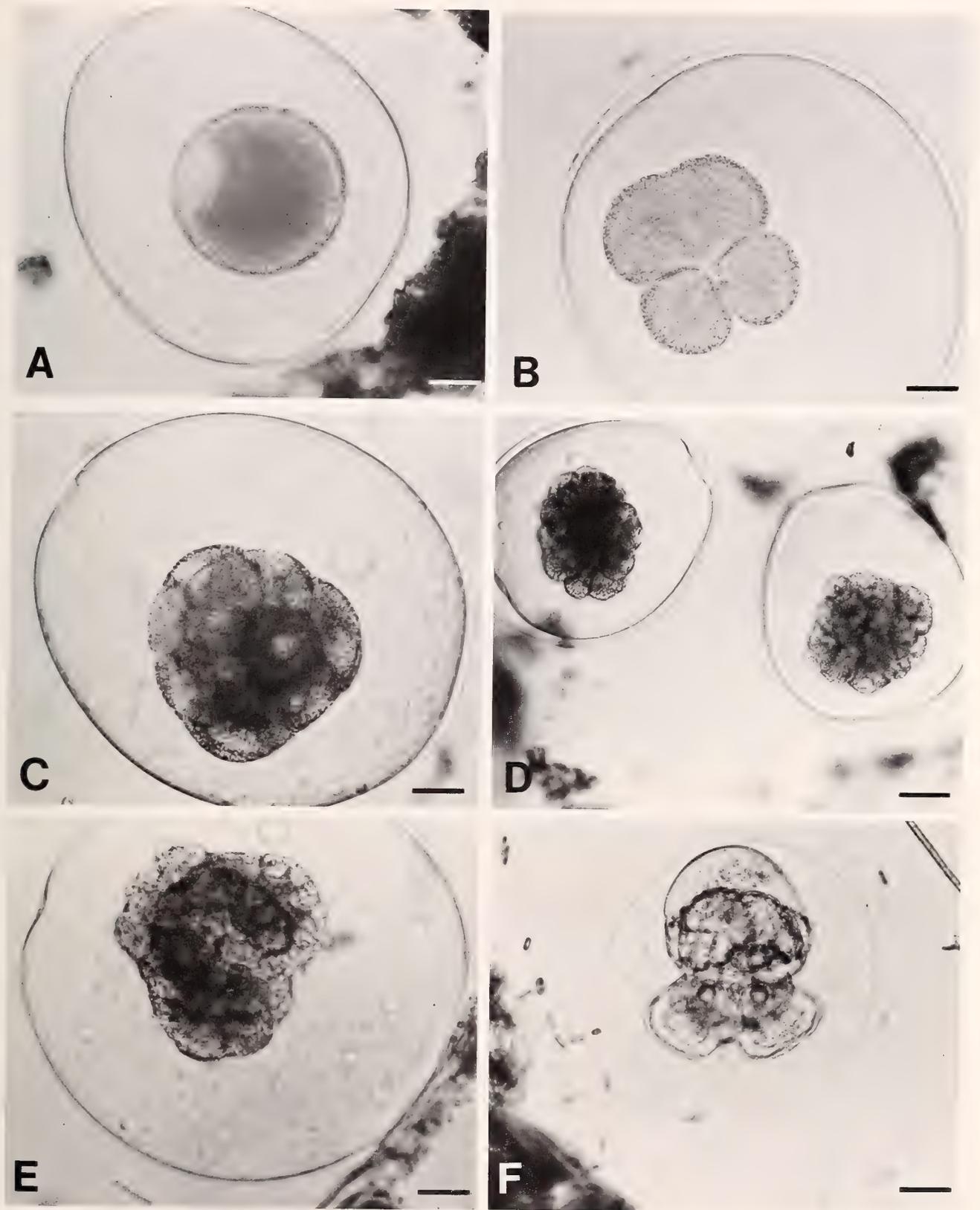
Shell Morphometrics

The mean length, width, and length-width ratio of whorls 2 and 6 of snails from Mud Island, Texas, were similar in each of the five collecting periods (Table 4). The number of spiral cords in whorl 2 was not significantly different for any of these samples (Duncan's multiple range test) either, averaging about three. The number of spiral cords in whorl 6 varied considerably more. Snails collected in May had significantly fewer cords than in any other month but October (Duncan's multiple range test, $P < 0.05$). The October, December, March, and July samples did not differ significantly, nor did October samples differ significantly from May ($P > 0.05$). The width of the protoconch varied only slightly, ranging from 234 to 240 μm . This variation was considerably less than noted for egg size.

The two populations of North Carolina snails were not significantly different except for the number of spiral cords and length of whorl 6; thus, they were treated as one

Figure 2

Developmental stages of *Boonea impressa* from the Mud Island reef, Texas. A, egg. B, 4-celled stage. C, multi-celled stage. D, blastula. E, gastrula. F, mid-veliger stage. Scale bars: A, 40 μm ; B, 24 μm ; C, 23.6 μm ; D, 57.5 μm ; E, 21.5 μm ; F, 38.8 μm .



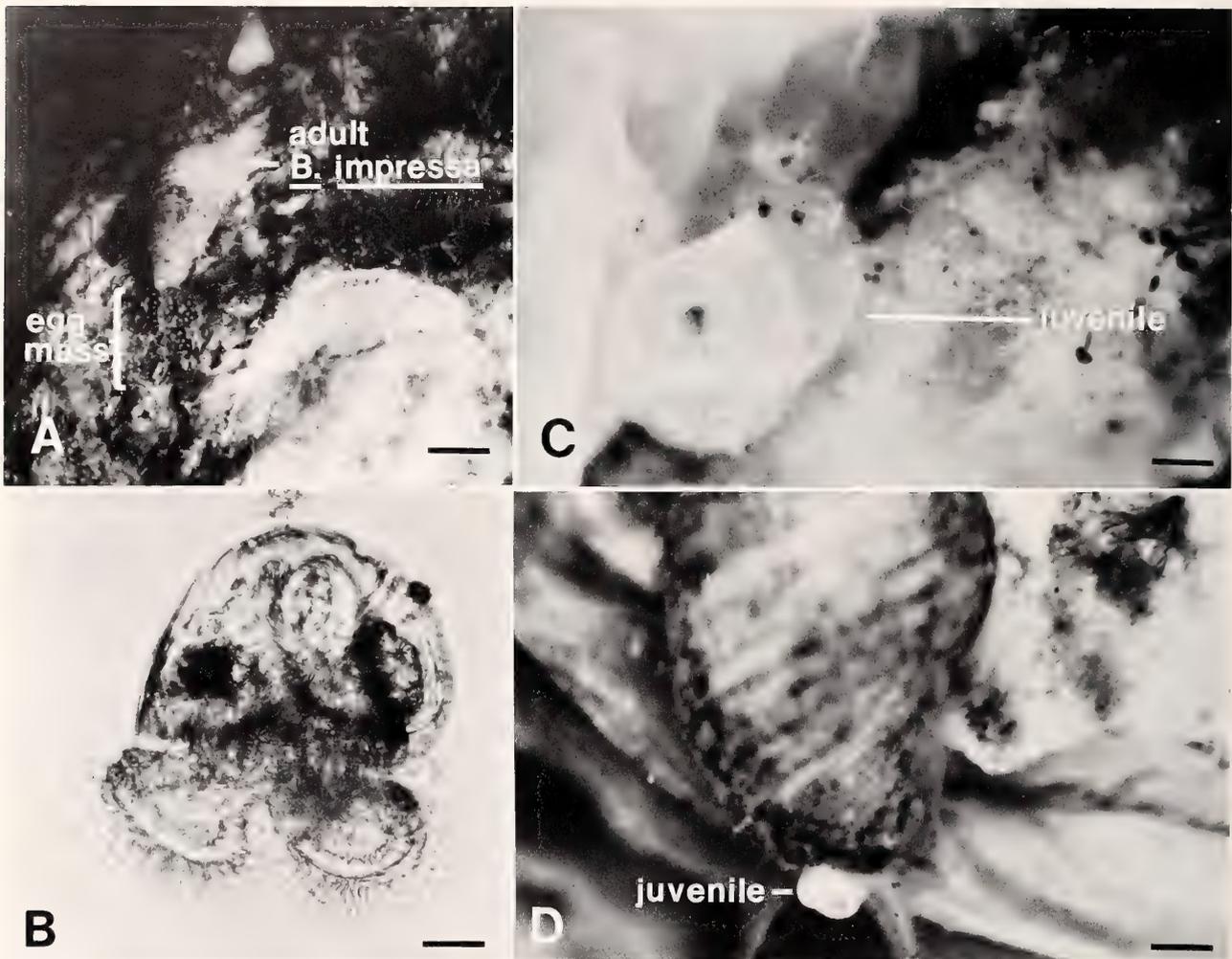


Figure 3

Larval and juvenile stages of *Boonea impressa* collected from the Mud Island reef, Texas. A, adult *B. impressa* and egg mass. B, hatched veliger. C and D, juvenile on adult aperture. Scale bars: A, 2 mm; B, 48 μm ; C, 68.5 μm ; D, 240 μm .

sample (Table 5). Overall, North Carolina snails were larger. The width of whorl 6, for example, was significantly larger (Duncan's multiple range test, $P < 0.05$) than in any of the Texas samples, except May. The length of whorl 6 was also larger than in any of the Texas samples, but the difference was significant only for the December and October samples (Duncan's multiple range test, $P < 0.05$). The number of spiral cords in whorl 6 in the North Carolina snails was significantly higher than in any of the Texas samples (Duncan's multiple range test, $P < 0.05$). In contrast, protoconch size and the length-width ratio of whorl 6 differed little between the two populations. Mean egg size also was very similar (Table 2).

A Pearson product-moment correlation test based on all

shell measurements was conducted on the Texas samples (Table 6). The shell length, width, and number of whorls all were significantly correlated with each other for every month. In most samples, the whorl width and length for whorl 6 were correlated with both the total shell width and total shell length. This was not true for whorl 2. The width of whorl 2 was correlated with the width of whorl 6, but the lengths were not consistently correlated. Thus, the rate of whorl expansion was more constant than the rate of whorl translation. Consequently, although the length and width of whorl 6 were correlated in most samples, the correlation coefficients were low. The length of whorl 6 and the number of spiral cords in whorl 6 were also correlated in most samples, but width of whorl 6 was correlated less well with spiral cord number than was the

Table 2

Mean and range of the sizes of eggs in each *Boonea impressa* mass. Seven egg masses were measured: five from snails collected at Big Slough, Texas (No. 1, 2, 3, 4, 7) and two from North Carolina (No. 5, 6). n is the number of eggs measured. A, B, and C indicate results of Duncan's multiple range tests ($\alpha = 0.05$) where mean egg size for egg masses with the same letter are not significantly different.

Egg mass	Mean (μm)	Range (μm)	n	Significance ($\alpha = 0.05$)
1	218	214-238	8	A
2	209	198-222	15	B
3	207	198-222	9	B
4	205	214-222	12	B
5	205	190-222	12	B
6	192	190-206	12	C
7	189	182-190	10	C

length. The number of spiral cords in whorl 2 was poorly correlated with any other shell feature. Larval shell width was poorly correlated with any other character except the width of whorl 2.

In order to determine whether the number of cords in whorl 6 was influenced by any other shell feature besides whorl length, a stepwise regression test (maximum R^2 improvement) was conducted. This procedure (for all samples—Texas and North Carolina) showed that the length of whorl 6 was the best one-variable model for

Table 3

Development time for the embryonic stages of *Boonea impressa*.

Larval stage	Time from oviposition to when stage was first observed
Two cells	2 h
Four cells	4-6 h
Gastrula	26-30 h
Early-veliger	32-36 h
Mid-veliger	50-54 h
Late-veliger	56-60 h
Hatched veliger	80-114 h
Veliger negatively phototactic	~ 6 day (2 day post-hatch)
Metamorphosis	~11 day (7 day post-hatch*)

* Probably a maximum.

determining the cords in whorl 6. The R^2 values, however, were only 0.04, 0.13, 0.18, 0.18, and 0.24 (October, December, March, May, and North Carolina respectively). For the Texas populations, addition of shell width, width of whorl 6, and the number of whorls improved the correlation only marginally (corresponding $R^2 = 0.05, 0.19, 0.25, 0.20$). In contrast, the same procedures improved the correlation considerably for the North Carolina population. By adding the width of whorl 6, R^2 increased from 0.24 to 0.45, and then to 0.54, by adding the number of whorls and shell width.

Table 4

Mean and standard deviation of shell characters (in mm) of the samples of *Boonea impressa* from the Mud Island, Texas reef. Number measured is in parentheses.

Sample	Shell length	Shell width	Number of whorls	Length-width				Length-width				Width larval shell
				Length—whorl 6	Width—whorl 6	ratio—whorl 6	Cords—whorl 6	Length—whorl 2	Width—whorl 2	ratio—whorl 2	Cords—whorl 2	
October	3.44 ± 0.96 (293)	1.47 ± 0.27 (400)	5.99 ± 1.15 (293)	0.71 ± 0.05 (231)	1.43 ± 0.09 (231)	0.50	3.92 ± 0.34 (231)	0.23 ± 0.02 (293)	0.48 ± 0.03 (293)	0.48	3.00 ± 0.03 (293)	0.234 ± 0.01 (293)
December	2.97 ± 1.40 (331)	1.42 ± 0.41 (462)	5.53 ± 1.52 (331)	0.74 ± 0.07 (143)	1.42 ± 0.09 (143)	0.52	3.99 ± 0.43 (143)	0.23 ± 0.01 (331)	0.48 ± 0.02 (331)	0.48	2.99 ± 0.08 (331)	0.236 ± 0.02 (331)
March	3.75 ± 1.35 (280)	1.65 ± 0.32 (537)	6.20 ± 1.31 (280)	0.77 ± 0.07 (170)	1.48 ± 0.12 (170)	0.52	4.09 ± 0.49 (170)	0.24 ± 0.01 (280)	0.49 ± 0.03 (280)	0.49	3.01 ± 0.18 (280)	0.238 ± 0.01 (280)
May	4.05 ± 1.23 (133)	1.78 ± 0.33 (237)	6.39 ± 1.22 (133)	0.76 ± 0.07 (104)	1.51 ± 0.13 (104)	0.50	3.76 ± 0.51 (104)	0.24 ± 0.01 (133)	0.49 ± 0.03 (133)	0.49	3.00 ± 0.00 (133)	0.239 ± 0.01 (133)
July	2.06 ± 0.94 (49)	1.03 ± 0.31 (49)	4.14 ± 1.27 (49)	0.76 ± 0.07 (8)	1.44 ± 0.14 (8)	0.53	4.00 ± 0.00 (8)	0.24 ± 0.02 (49)	0.50 ± 0.04 (49)	0.48	3.00 ± 0.00 (49)	0.240 ± 0.00 (49)

Table 5

Mean and standard deviation of shell characters (in mm) of samples of *Boonea impressa* from North Carolina.

Character	Williston Creek (n = 22)	Virginia Creek (n = 9)	Combined
Number of whorls	6.98 ± 0.32	7.00 ± 0.65	6.99 ± 0.43
Width of shell	1.73 ± 0.11	1.75 ± 0.16	1.74 ± 0.12
Length—whorl 6	0.80 ± 0.05	0.75 ± 0.03	0.79 ± 0.05
Width—whorl 6	1.56 ± 0.10	1.51 ± 0.09	1.55 ± 0.10
Cords—whorl 6	4.55 ± 0.65	4.06 ± 0.17	4.40 ± 0.60
Width—larval shell	0.24	0.24	0.24
Length-width ratio— whorl 6	0.51	0.50	0.51

Feeding Apparatus

The proboscis and associated feeding structures of *Boonea impressa* were similar to other odostomians described by MAAS (1965). Here, we use the terminology of FRETTER & GRAHAM (1949) and cross-reference it to that of MAAS (1965) as much as possible. Rather than repeating the detailed descriptions of MAAS (1965), we emphasize only the differences observed. The feeding apparatus of *B. impressa* consisted of a buccal pump (*Pumpbulbus II* of MAAS, 1965) to which the esophagus and salivary glands attached at its proximal end, a long tubular structure homologous to the first buccal pump (*Pumpbulbus I*) described by MAAS (1965), the stylet and associated structures, and the proboscis (Figure 4). The first buccal pump, well developed in the European odostomians described by MAAS (1965), ANKEL (1949a, b), and FRETTER & GRAHAM (1949), was poorly developed. In its place was a long tubular structure connecting the buccal pump to the stylet tube. This long tube thickened gradually but noticeably over the last 25% or so of its length at the end where it connected with the buccal pump. Possibly this thicker portion functions as the first buccal pump does in European odostomians.

The salivary glands consisted of four sections: a proximal section containing about 2 or 3 small linearly arranged, circular rings of cells; a larger, wider middle section with 5 or 6 linearly arranged, circular groups of cells; a second but usually narrower middle section with 15–17 circular groups of small cells; and a very narrow distal region that might function as a storage compartment for the salivary cells' products (FRETTER & GRAHAM, 1949; MAAS, 1965). Serial sections were not studied; cell numbers were determined by staining during dissection. Thus, the variability in the number of cells observed within each group might be an artifact of preparation rather than true variability. Considerable variation was present in the width of the salivary glands so that, on occasion, the salivary glands were nearly cylindrical in shape, as opposed to the

more common appearance depicted in Figure 4. Even when cylindrical, however, the four groups of cells were readily distinguishable. The salivary glands closely resembled those described by MAAS (1965) and ANKEL (1949b) from *Odostomia plicata* and by FRETTER & GRAHAM (1949) from *O. unidentata*, except that the proximal group of small cells is absent in *O. plicata*. Differences in shape observed by MAAS (1965) for *O. eulimoides*, however, which are similar to differences described above for *Boonea impressa*, and the hypothesized cell cycle whereby new cells originate near the middle of the gland and move proximally as they grow (ANKEL, 1949b; FRETTER & GRAHAM, 1949) suggest that salivary gland morphology may be variable from snail to snail. Thus, the significance of the similarities and differences noted by MAAS (1965) and us as taxonomic criteria remains unclear.

Approximate sizes for the various components of the feeding apparatus are given in Table 7. Except for the two cuticularized structures, the stylet (*Stachel* of MAAS, 1965) and the stylet tooth (*Stempel* of MAAS, 1965), the sizes varied considerably in different preparations due to relaxation or contraction and should be considered as rough estimates only. No significant difference in the sizes of any component was found between the North Carolina and Texas populations.

DISCUSSION

Reproduction and Growth

Our results agree with those of WELLS (1959) from North Carolina that the life-span of *Boonea impressa* is approximately one year and that reproduction and recruitment to the population occurs more or less continuously. Reproduction and recruitment rates are not constant, however. Although sperm were present in all adult specimens in all months sampled, marked differences in oocyte numbers were found. In May, approximately 38% more oocytes were found than during any other sampling period. No oocytes were found in December; this could possibly be correlated with the cold water temperatures encountered at that time. WELLS & WELLS (1961) suggested that reproduction in *B. seminuda* was directly related to water temperature. The absence of oocytes in most of the specimens in July probably was due to the young age of the majority of the specimens collected.

Growth rates also were comparable between the Texas population studied here and the North Carolina population examined by WELLS (1959). In both populations, the large summer set reached adult size in early spring of the following calendar year. Both populations consisted of predominately juvenile individuals in mid-summer and predominately adult individuals in late spring. Thus, reproduction and recruitment, although continuous, are markedly higher in early summer (May–July). This more or less coincides with the peak period of oyster reproduction in the study area (GUNTER, 1941; COPELAND & HOESE, 1966). Adults of *Boonea impressa* were most abun-

Table 6

Shell sculpture characters of *Boonea impressa* which were correlated significantly ($\alpha = 0.05$). Numbers 1, 2, 3, 4, and 5 represent samples from October, December, March, May, and July respectively. Correlation coefficients for significant correlations are given in the mirror image left and below of the diagonal midline. For example, width of whorl 6 was significantly correlated with shell lengths in months 1, 2, 3, 4 with $r = 0.62, 0.46, 0.37,$ and 0.29 respectively.

	Shell length	Shell width	Number of whorls	Length—whorl 2	Width—whorl 2	Cords—whorl 2	Length—whorl 6	Width—whorl 6	Cords—whorl 6	Width larval shell
Shell length	*	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3	2, 3	1	1, 2, 3, 4	1, 2, 3, 4	2, 3, 4	—
Shell width	0.96, 0.93, 0.95, 0.96, 0.97	*	1, 2, 3, 4, 5	1, 2, 3	2, 3	1	1, 2, 3, 4	1, 2, 3, 4, 5	3, 4	—
Number of whorls	0.96, 0.97, 0.96, 0.93, 0.97	0.92, 0.92, 0.94, 0.92, 0.94	*	1, 2	2	1	2, 3, 4	1, 2, 3	2, 3, 4	—
Length—whorl 2	0.23, 0.18, 0.18	0.22, 0.17, 0.16	0.15, 0.16	*	1, 3, 5	2	1, 3	1	3	1
Width—whorl 2	0.17, 0.12	0.11, 0.16	0.12	0.28, 0.19, 0.75	*	—	1, 2, 3	1, 2, 3, 4	1, 2	1, 2, 4
Cords—whorl 2	0.13	0.13	0.13	0.12	—	*	—	—	—	—
Length—whorl 6	0.54, 0.50, 0.61, 0.67	0.57, 0.22, 0.48, 0.67	0.33, 0.40, 0.38	0.46, 0.28	0.28, 0.25, 0.31	—	*	2, 3, 4	1, 2, 3, 4	1
Width—whorl 6	0.62, 0.46, 0.37, 0.29	0.77, 0.32, 0.60, 0.47, 0.80	0.23, 0.28, 0.24	0.34	0.27, 0.43, 0.39, 0.39	—	0.33, 0.34, 0.38	*	2, 3, 4	1
Cords—whorl 6	0.39, 0.42, 0.28	0.31, 0.25	0.29, 0.39, 0.23	0.19	0.17, 0.17	—	0.13, 0.36, 0.42, 0.42	0.27, 0.22, 0.19	*	—
Width larval shell	—	—	—	0.22	0.23, 0.13, 0.17	—	0.23	0.29	—	*

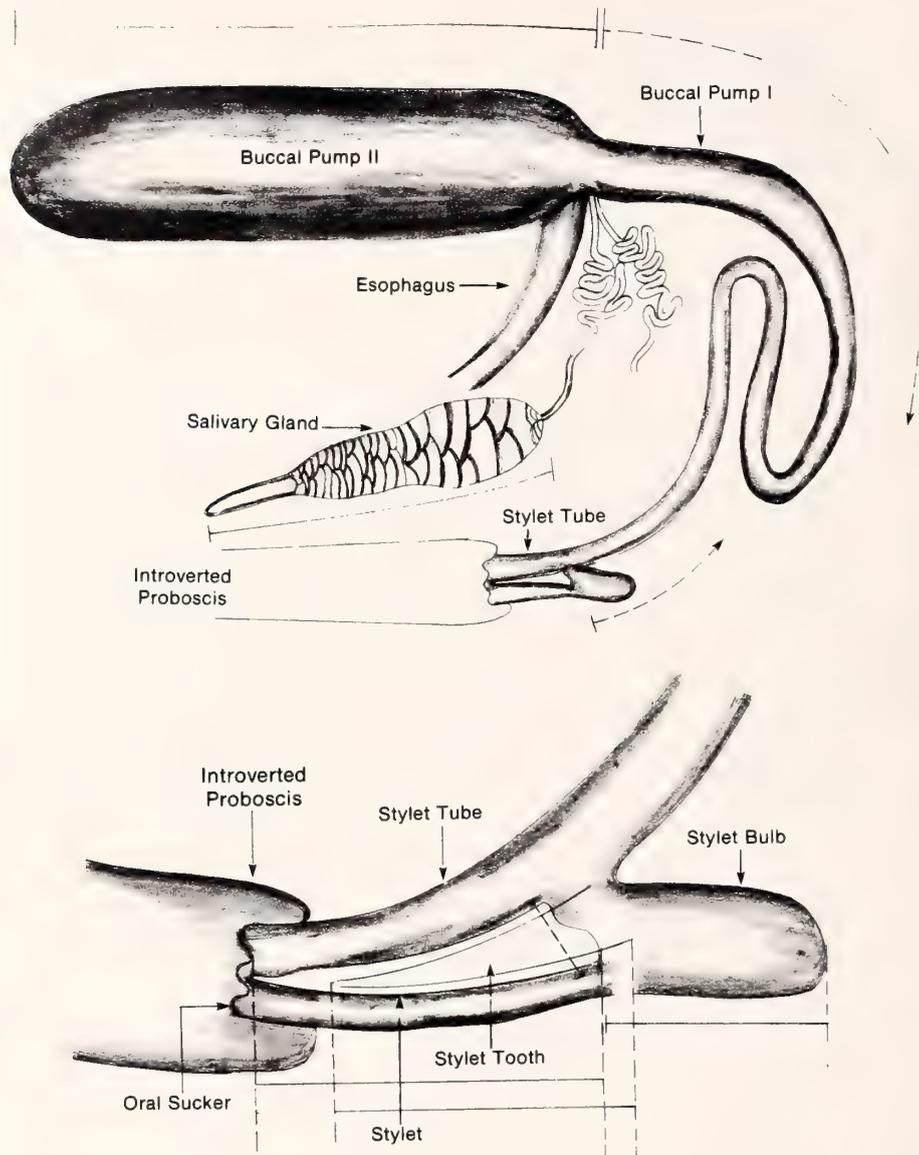


Figure 4

The internal anatomy of the feeding apparatus. Bars indicate the method of measurement for dimensions reported in Table 7. Above, the entire feeding apparatus excluding the proximal portion of the proboscis. Below, an enlargement of the stylet tube.

dant during the spring when oyster gonadal development and spawning occurred, and juveniles of *B. impressa* were most abundant in the summer and fall when oyster spat were also most common.

Larval Development—*Boonea impressa*

THOMPSON (1967) classified the larval development of opisthobranchs into three categories: Type I-planktotrophic larvae with small ova (40–170 μm), a short embryonic period (2–28 days), and a free-swimming veliger stage usually of >3 days duration; Type II-lecithotrophic

larvae with larger eggs (110–250 μm), a longer embryonic development (4–42 days), and a free-swimming veliger stage usually of <3 days duration; and Type III-direct development with even larger ova (205–400 μm), an even longer embryonic period (13–50 days), and hatching at the post-larval stage. Type II includes THORSON'S (1950) planktonic larvae with a short pelagic life-span. Development in pyramidellids fits more or less into THOMPSON'S (1967) scheme. In Table 8, we compare our data on *Boonea impressa* with other data available on pyramidellids where both egg size and embryonic development time are

Table 7

Measurements of components of the feeding apparatus of *Boonea impressa*. Terminology of MAAS (1965) appears in parentheses. Measurements were made as shown by the bars in Figure 2.

Structure	Population	Mean (μm)	Range (μm)	n	Mean ($\mu\text{m}/\mu\text{m}$)	Range ($\mu\text{m}/\mu\text{m}$)
Maximum width of shell	NC	1920	1840-2000	6		
	TX	1856	1760-1920	5		
Buccal pump, length (<i>Pumpbulbus</i> II)	NC	1497	1310-1736	6	0.781	0.616-0.904
	TX	1616	1499-1767	5	0.873	0.781-0.960
Buccal pump connecting tube, length (<i>Pumpbulbus</i> I)	NC	3834	2761-4418	5	1.990	1.381-2.301
	TX	3676	3077-4181	5	1.984	1.603-2.186
Salivary glands, length	NC	861	757-994	9	0.447	0.395-0.540
	TX	921	742-1136	8	0.500	0.386-0.617
Stylet bulb, length (blind sack)	NC	152	136-174	3	0.077	0.068-0.091
	TX	131	124-143	4	0.070	0.067-0.074
Stylet length (<i>Stachel</i>)	NC	218	202-233	5	0.113	0.101-0.127
	TX	207	182-225	5	0.112	0.095-0.128
Stylet width	NC	45	39-47	4	0.023	0.020-0.024
	TX	44	39-47	5	0.023	0.022-0.026
Stylet tooth, length (<i>Stempel</i>)	NC	199	174-221	5	0.103	0.087-0.120
	TX	196	174-233	5	0.106	0.091-0.132
Stylet opening, length (<i>Stachelöffnung</i>)	NC	47	39-54	5	0.024	0.020-0.029
	TX	40	39-43	4	0.022	0.020-0.023

known. *Boonea impressa* is Type II. Egg size and development time from oviposition to hatching are well within the range suggested by Thompson. Larval life-span is somewhat longer than Thompson's range for other Type II larvae; however, if the advent of negative phototactic behavior marks the initial competence for metamorphosis, then the minimum planktonic life-span would be about 3 days rather than 7. This is close to THOMPSON'S (1967) range for Type II life-spans. Furthermore, *B. impressa* does not show significant growth during the planktonic

phase. Egg size and hatched veliger size are no less than 80% of size at metamorphosis. Egg sizes range up to 238 μm and protoconch size as measured on the adult was also in this range. Thus, feeding, if it occurs, probably is relatively unimportant in the planktonic stage.

Overall, development in *Boonea impressa* most closely resembles that described for the form of *Brachystomia rissoides* with a planktonic larva (RASMUSSEN, 1944) and *Odostomia eulimoides* (FRETTER & GRAHAM, 1949), both of which also are Type II. Egg size is similar, as are de-

Table 8

Comparison of egg size, development time, and larval life-span in the Pyramidellidae.

Species	Egg size	Development time: oviposition to hatching	Larval life-span	Authority
<i>Boonea impressa</i>	182-238 μm	>3 to <5 days	7 days (probably 3-7)	our data
<i>Brachystomia rissoides</i>	300-650 μm	25 days	none	RASMUSSEN (1951)
<i>Brachystomia rissoides</i>	~200 μm	6.5 days	?	RASMUSSEN (1944, 1951) THORSON (1946)
<i>Eulimella nitidissima</i>	~100 μm	5 days	long	RASMUSSEN (1944)
<i>Odostomia eulimoides</i>	~160 μm	10-12 days	3-4 days	FRETTER & GRAHAM (1949) LEBOUR (1932)
<i>Chrysalida cincta</i>	300-340 μm	22-27 days	none	LAFOLLETTE (1977, 1979)
<i>Odostomia omaensis</i>	120-150 μm	8 days	?	AMIO (1963)
<i>Odostomia desimana</i>	130-160 μm	14 days	?	AMIO (1963)

velopment time and larval life-span (Table 8). The longer development times for *O. eulimoides* and *Brachystomia rissoides* probably are due to a lower temperature regime (see SPIGHT, 1975). On the other hand, RASMUSSEN (1944) found that the shell and statocysts of *Brachystomia rissoides* with a planktonic larva developed prior to formation of a bipartite velum, and observed first movement only after 100 h. In *Boonea impressa*, the statocysts and a bipartite velum were present prior to complete formation of the shell. First movement was observed at 32–36 h, prior to shell formation or the development of a bipartite velum. In fact, in this regard, *Boonea impressa* more closely resembles *Eulimella nitidissima* for which movement was observed at 53 h, prior to the development of a bipartite velum or statocysts (RASMUSSEN, 1944). Additionally, the 75 h embryo is similar to our mid-veliger stage reached at 50–54 h in that shell formation is incomplete: the shell covers only the visceral mass somewhat above the level of the statocysts. *Eulimella nitidissima*, however, has a Type I-planktotrophic larva. Egg size is considerably smaller than in *Boonea impressa* and the larva more than triples in size during the planktonic phase (RASMUSSEN, 1944). Thus, although the larval development of *Boonea impressa* is best described as Type II overall, certain aspects of its embryonic development more closely resemble that of *E. nitidissima* which results in a Type I larva.

Larval Development—Pyramidellidae

Some information is available for a number of other pyramidellid species. *Parthenia decussata*, which grows considerably during its planktonic life-span and has a small egg size (90–120 μm) (LEBOUR, 1936), also can be considered Type I. At the other extreme, *Chrysallida cincta* and one form of *Brachystomia rissoides* have direct development (Type III of THOMPSON, 1967) (RASMUSSEN, 1951; LAFOLLETTE, 1977, 1979). ROBERTSON & ORR (1961) suggested that *Odostomia chitonicola* also may have direct development. AMIO (1963) discussed two additional *Odostomia* species with egg sizes and development similar to *Boonea impressa*. Thus, all three types of larval development described by THOMPSON (1967) are present in pyramidellids, with each larval type represented by at least two of the seven species for which some data are currently available.

Apparently, ectoparasitism has produced no obvious universal modification to the opisthobranch developmental plan. This suggests that factors determining developmental mode in opisthobranchs generally might apply to the Pyramidellidae also. CLARK & GOETZFRIED (1978) suggested that trophic stability was an important factor. Direct development would be favored when the food source was stable or predictable, a planktonic larva when the food source was unstable or unpredictable. The pyramidellid species listed in Table 8 having either direct development (Type III) or a lecithotrophic larva (Type II) usually parasitize organisms with long life-spans or or-

ganisms that are components of persistent (in the sense of BOESCH *et al.*, 1976) communities. *Chrysallida cincta* has direct development and parasitizes gastropods such as *Haliotis corrugata* and *Tegula eiseni* whose life-spans probably exceed 10 yr (LAFOLLETTE, 1977). Similarly, hosts for *Brachystomia rissoides* and *Odostomia eulimoides* live 10–20 yr (FRETTER & GRAHAM, 1949; COMFORT, 1957; ANKEL & CHRISTENSEN, 1963). The host of *Boonea impressa* is the keystone species of a particularly persistent community, the oyster reef, so that food supply and location is dependable year to year. In contrast, although the host of *Eulimella nitidissima* is unknown, the planktotrophic larva of *E. nitidissima* suggests that the host's population will be temporally less stable than in the above species.

Although adult snails frequently move from one host to another (ANKEL & CHRISTENSEN, 1963; WHITE *et al.*, 1984), movement by adults between host populations probably is rare. A short pelagic life-span of the type demonstrated by *Boonea impressa* might be expected, particularly when the host species is immobile, even though trophic stability might favor direct development. Both gene flow and dispersal between host populations would be facilitated. Of the three species with uniformly only Type II or Type III development, both species (*B. impressa* and *Odostomia eulimoides*) which primarily parasitize immobile hosts (bivalves in these cases) have larvae with a short pelagic phase. In contrast, the one species with only direct development, *Chrysallida cincta*, parasitizes gastropods, all of which have at least some mobility that might facilitate adult dispersal.

The few data available suggest that development time increases with increasing egg size in pyramidellids, as was suggested for other gastropods (*e.g.*, SPIGHT, 1975; STRATHMANN, 1977). The shorter time for *Boonea impressa* relative to other species of the same egg size probably can be attributed to the higher temperature regime of Texas bay waters. There appears to be little relationship between development mode and taxonomic status. Disparate modes are found in one species, *Brachystomia rissoides*, and very similar modes in clearly distinct genera (*e.g.*, *Boonea* and European *Odostomia*).

Juvenile Behavior

The behavior of the young *Boonea impressa* veligers was positively phototactic the first two days but then became negatively phototactic. THORSON (1950) suggested that positive phototaxis allowed young larvae to stay near the surface where currents might aid their dispersal, whereas negative phototaxis in older larvae that were ready to metamorphose increased the time spent near the bottom and, thus, increased their chances of finding a suitable substrate for settlement.

The frequent observations of juvenile *Boonea impressa* attached near or at the aperture on the outer lip of the shell of adult *B. impressa* are too frequent to be simply

accidental, but suggest a behavioral mode that might increase juvenile survival. Several advantages are possible. (1) Predation might be decreased, particularly by predators that are too small to attack an adult snail. Small predators, such as polychaetes and juvenile crabs, are common on oyster reefs. Movement over the host might be accomplished more safely by hitching a ride because fewer potential predators would be encountered. (2) Small *B. impressa* may be unable to approach the oyster's mantle closely enough for feeding or to maintain a stable foothold on the oyster shell because the proboscis and foot are small and the edge of the oyster shell tends to be ragged. Adult *B. impressa* may provide a more stable substrate. (3) In fact, one cannot rule out the possibility that juveniles actually might feed on the adults for a short time until a size is reached that allows feeding on the oyster host. It seems unlikely that the outer mantle fold of the oyster can be fed upon because newly formed periostracum would interfere (see GALTISOFF, 1964; WALLER, 1980), and the remainder of the mantle might be difficult to reach with the short proboscis of a juvenile. Juvenile gastropods frequently utilize food resources not used by adults (KITTING, 1984). *Boonea impressa* certainly is capable of feeding on a variety of species, some of which may be more easily utilized by juveniles than are oysters.

Morphometrics—Shell Characters

LOPES (1958), WHARTON (1976), PORTER (1976), PORTER *et al.* (1979), POWELL (1981), and others discussed the intraspecific variability in certain shell characters often used for taxonomic identification in pyramidellids. Some, such as axial rib number and spiral cord number, are particularly variable. The North Carolina and Texas populations differed considerably in some respects. Snails from the North Carolina population were larger, and they had a greater width and length at whorl 6 than the Texas snails. Mean width of whorl 6, for example, ranged from 1.42 to 1.51 mm among the Texas samples, but was 1.55 mm in the North Carolina snails. In addition, the number of cords in whorl 6 was significantly greater in the North Carolina specimens than in any sample from the Texas population. The number of populations sampled was too few to suggest a regional difference in size or cord number. The data do indicate, however, that significant inter-population differences are present in shell sculpture and size. POWELL (1981), PORTER (1976), and PORTER *et al.* (1979) described similar variability in other pyramidellid species. Unfortunately, both shell sculpture and size are often used as taxonomic characters for identification.

In *Boonea impressa*, certain characters are much less variable. North Carolina and Texas specimens had very similar length-width ratios at whorl 6. Egg size and protoconch size were nearly identical. The size and shape of the feeding apparatus, including stylet, buccal pump and salivary glands, also were very similar. POWELL (1981) found that both length-width ratios and protoconch size

were less variable between populations of several *Turbonilla* (*Pyrgiscus*) species than other shell characters, and suggested their taxonomic usefulness in the Pyramidellidae. Our data support this conclusion.

The number of cords at whorl 6 was more closely correlated to whorl 6 length than any other parameter. Certainly, the larger lengths of whorl 6 in the North Carolina snails explain the larger number of cords observed. Whorl 6 length alone, however, cannot explain all of the variation observed. The significant differences in cord number for whorl 6 between some collections from the Texas population (*e.g.*, the May and March collections), for example, cannot be explained easily by differences in whorl 6 length or in any other shell character measured. Thus, seasonal or other environmental changes also may influence cord number.

The size of the protoconch was correlated with only one other shell feature, the width of whorl 2. Interestingly, the widths of whorls 2 and 6 were correlated much better than the lengths of the same two whorls. POWELL (1981) pointed out that the length-width ratio and the sculpture of early whorls frequently differ considerably from those of the later adult whorls in pyramidellids. That is, both shell sculpture and growth form often change dramatically with age (see also LAWS, 1937). Increased variability with age is an important taxonomic problem in the Pyramidellidae where species frequently are described from juvenile individuals. Our data suggest that, for *Boonea impressa*, whorl width and the rate of whorl expansion are determined to a larger extent by factors also determining protoconch size than are the whorl length and the rate of whorl translation. Additionally, the number of cords in whorl 2 was not correlated with any other shell feature, unlike whorl 6 where a good correlation with whorl length was present. In fact, there was almost no variability in cord number in whorl 2, and this number was less than that typically given in descriptions of the species (*i.e.*, three rather than four cords).

Morphometrics—Feeding Apparatus

ROBERTSON (1978) distinguished American and European odostomians based on several features including the method of sperm transfer. European odostomians used penial copulation, whereas spermatophores were present in American species. The feeding apparatus of *Boonea impressa* exhibits another striking difference between *Boonea* and European odostomians. In all European odostomians studied, the first buccal pump is well developed (MAAS, 1965; FRETTER & GRAHAM, 1949) and attaches closely to the stylet tube. In *B. impressa*, the first buccal pump is very poorly developed and attaches by way of a long tube (over twice as long as the second buccal pump) to the stylet tube. This reinforces ROBERTSON's (1978) suggestion that American odostomians are deserving of a separate generic status from their European counterparts

and suggests that anatomical studies may provide important information for species and generic determinations.

Descriptions by FRETTER & GRAHAM (1949), FRETTER (1953), and MAAS (1965) all suggest that stylet length and size of the salivary glands and buccal pump may be good taxonomic characters, but measurements relative to shell size for comparison to *Boonea impressa* are unavailable. Nevertheless, the similarity between populations in the feeding apparatus (and in the size of the larval shell) sharply contrast to the differences present in many shell characters normally used for species distinctions. Characters with limited inter-population variability should be highly useful taxonomic characters when species specific differences are present. The evidence suggests that detailed studies of the feeding apparatus in the Pyramidellidae may provide useful comparative data when shell morphological criteria are too variable to provide unambiguous results, just as internal anatomical characteristics have in other groups of small, taxonomically abstruse groups of snails (DAVIS, 1967; DAVIS & CARNEY, 1973).

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LITERATURE CITED

- ABBOTT, R. T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold Co.: New York.
- AMIO, M. 1963. A comparative embryology of marine gastropods, with ecological considerations. Shimomoseki Univ. Fisheries J. 12:15-144.
- ANKEL, F. & A. M. CHRISTENSEN. 1963. Non-specificity in host selection by *Odostomia scalaris* Macgillivray. Vidensk. Medd. Dansk. Naturh. Foren. 125:321-325.
- ANKEL, W. E. 1949a. Die Mundbewaffnung der Pyramidelliden. Arch. Molluskenk. 77:79-82.
- ANKEL, W. E. 1949b. Die Nahrungsaufnahme der Pyramidelliden. Verh. Dtsch. Zool. Ges. Kiel 1949:478-484.
- BOESCH, D. F., M. L. WASS & R. W. VIRSTEIN. 1976. The dynamics of estuarine benthic communities. Pp. 177-196. In: M. L. Wiley (ed.), Estuarine processes, Vol. 1. Uses, stresses, and adaptation to the estuary. Academic Press, Inc.: New York.
- BONAR, D. B. & M. G. HADFIELD. 1974. Metamorphosis of the marine gastropod *Phestilla sibogae* Bergh (Nudibranchia: Aeolidacea). I. Light and electron microscope analysis of larval and metamorphic stages. J. Exp. Mar. Biol. Ecol. 16: 227-255.
- CHIA, F. S. 1978. Perspectives: settlement and metamorphosis of marine invertebrate larvae. Pp. 283-285. In: F. S. Chia & M. E. Rice (eds.), Settlement and metamorphosis of marine invertebrate larvae. Elsevier: New York.
- CLARK, K. B. & A. GOETZFRIED. 1978. Zoogeographic influence on development patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion on factors affecting egg size and number. J. Moll. Stud. 44:283-294.
- COMFORT, A. 1957. The duration of life in molluscs. Proc. Malacol. Soc. Lond. 32:219-241.
- COPELAND, B. & H. HOESE. 1966. Growth and mortality of the American oyster, *Crassostrea virginica*, in high salinity shallow bays in central Texas. Publ. Inst. Mar. Sci. Univ. Tex. 11:140-158.
- DALL, W. H. & P. BARTSCH. 1909. A monograph of west American pyramidellid mollusks. Bull. U.S. Natl. Mus. 68: 1-258.
- DAVIS, G. M. 1967. The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana* (Prosobranchia: Hydrobiidae). Malacologia 6:1-143.
- DAVIS, G. M. & W. P. CARNEY. 1973. Description of *Oncomelania hupensis lindoensis*, first intermediate host of *Schistosoma japonicum* in Sulawesi (Celebes). Proc. Acad. Natur. Sci. Philadelphia 125:1-34.
- FRANZ, D. 1976. Benthic molluscan assemblages in relation to sediment gradients in northeastern Long Island Sound, Connecticut. Malacologia 15:377-399.
- FRETTER, V. 1951. *Turbonilla elegantissima* (Montagu), a parasitic opisthobranch. J. Mar. Biol. Assoc. U.K. 30:37-47.
- FRETTER, V. 1953. The transference of sperm from male to female prosobranchs with reference, also, to the pyramidellids. Proc. Linn. Soc. Lond. 164:217-224.
- FRETTER, V. & A. GRAHAM. 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. J. Mar. Biol. Assoc. U.K. 28:493-532.
- GALTSOFF, P. 1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Fish. Wildl. Serv. Fish. Bull. 64:1-480.
- GUNTER, G. 1941. Seasonal condition of Texas oysters. Tex. Acad. Sci. Proc. Trans. 25:89-93.
- HOPKINS, S. 1956. *Odostomia impressa* parasitizing southern oysters. Science 124:628-629.
- KITTING, C. L. 1984. Selectivity by dense populations of small invertebrates foraging on seagrass blade surfaces. Estuaries 7:276-288.
- LAFOLLETTE, P. I. 1977. Inbreeding and intraspecific variation in *Chrysallida* Carpenter, 1857 (Gastropoda: Pyramidellidae). Western Soc. Malacol. Ann. Rep. 10:18-23.
- LAFOLLETTE, P. I. 1979. Observations on the larval development and behavior of *Chrysallida cincta* Carpenter, 1864 (Gastropoda: Pyramidellidae). Western Soc. Malacol. Ann. Rep. 11:31-34.
- LAWS, C. R. 1937. Review of the Tertiary and Recent Neozelanic pyramidellid molluscs No. 1—The genus *Turbonilla*. Trans. Proc. Roy. Soc. N.Z. 66:402-422.
- LEBOUR, M. V. 1932. The eggs and early larvae of two commensal gastropods, *Stilifer stylifer* and *Odostomia eulimoides*. J. Mar. Biol. Assoc. U.K. 18:117-119.
- LEBOUR, M. V. 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. J. Mar. Biol. Assoc. U.K. 20:547-565.
- LOPES, H. DE S. 1958. Sobre "*Turbonilla* (*Pyrgiscus*) *dispar*" Pilsbry, 1897 (Gastropoda, Pyramidellidae). Rev. Bras. Biol. 18:17-21.
- MAAS, D. 1964. Über Cuticularbildungen am Penis von Pyramidelliden. Zool. Anz. 173:137-148.

- MAAS, D. 1965. Anatomische und histologische Untersuchungen am Mundapparat der Pyramidelliden. *Z. Morphol. Oekol. Tiere* 54:566-642.
- PORTER, H. J. 1976. Spiral cord variation of *Odostomia impressa* (Say) and *O. seminuda* (C. B. Adams) family Pyramidellidae. *Bull. Amer. Malacol. Union* for 1976:38-41.
- PORTER, H. J., L. A. HOWIE & R. B. DERISO. 1979. Morphometric character variation in *Boonea impressa* (Say) and *B. seminuda* (C. B. Adams)—family Pyramidellidae. *Bull. Amer. Malacol. Union* for 1979:43-48.
- POWELL, E. N. 1981. Three *Turbonilla* (Pyramidellidae, Gastropoda) of North Carolina, with comments on pyramidellid systematics. *J. Elisha Mitchell Sci. Soc.* 97:37-54.
- PREECE, A. 1972. A manual for histologic technicians. Little, Brown & Company: Boston. 428 pp.
- RASMUSSEN, E. 1944. Faunistic and biological notes on marine invertebrates I. The eggs and larvae of *Brachystomia rissoides* (Harl.), *Eulimella nitidissima* (Mont.), *Retusa truncatula* (Brug.) and *Embletonia pallida* (Alder & Hancock), (Gastropoda marina). *Vidd. Medd. Dansk. Naturh. Foren.* 107: 207-233.
- RASMUSSEN, E. 1951. Faunistic and biological notes on marine invertebrates II. The eggs and larvae of some Danish marine gastropods. *Vidd. Medd. Dansk. Naturh. Foren.* 113: 201-249.
- RAVEN, C. P. 1958. Morphogenesis: the analysis of molluscan development. Pergamon Press: New York. 311 pp.
- RAVEN, C. P. 1964. Development. Pp. 165-195. In: K. M. Wilbur & C. M. Yonge (eds.), *Physiology of the Mollusca*. Vol. I. Academic Press: New York.
- ROBERTSON, R. 1978. Spermatophores of six eastern North American pyramidellid gastropods and their systematic significance (with the new genus *Boonea*). *Biol. Bull.* 155:360-382.
- ROBERTSON, R. & T. MAU-LASTOVICKA. 1979. The ectoparasitism of *Boonea* and *Fargoa* (Gastropoda: Pyramidellidae). *Biol. Bull.* 157:320-333.
- ROBERTSON, R. & V. ORR. 1961. Review of pyramidellid hosts, with notes on an *Odostomia* parasitic on a chiton. *Nautilus* 74:85-91.
- SANDERS, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.* 3:245-258.
- SPIGHT, T. M. 1975. Factors extending gastropod embryonic development and their selective cost. *Oecologia* 21:1-16.
- STRATHMANN, R. R. 1977. Egg size, larval development, and juvenile size in benthic marine invertebrates. *Amer. Natur.* 111:373-376.
- THOMPSON, T. E. 1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *J. Mar. Biol. Assoc. U.K.* 47:1-22.
- THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the Sound (Oresund). *Danmarks Fiskeri. og. Havundersogelser, Medd. fra. Komm. ser: Plankton* 4:1-523.
- THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev. Camb. Philos. Soc.* 25:1-45.
- WALLER, T. R. 1980. Scanning electron microscopy of shell and mantle in the order Arcoida (Mollusca: Bivalvia). *Smithsonian Contrib. Zool.* 313:1-58.
- WELLS, H. 1959. Notes on *Odostomia impressa* (Say). *Nautilus* 72:140-144.
- WELLS, H. & M. WELLS. 1961. Three species of *Odostomia* from North Carolina, with description of new species. *Nautilus* 74:149-157.
- WELLS, H. W., M. J. WELLS & I. E. GRAY. 1961. Food of the sea-star *Astropecten articulatus*. *Biol. Bull.* 120:265-271.
- WHARTON, R. A. 1976. Variation in the New England pyramidellid gastropod, *Turbonilla nivea* (Stimpson). *Nautilus* 90:11-13.
- WHITE, M. E., E. N. POWELL & C. L. KITTING. 1984. The ectoparasitic gastropod *Boonea* (= *Odostomia*) *impressa*: population ecology and the influence of parasitism on oyster growth rates. *P.S.Z.N.I.: Mar. Ecol.* 5:283-299.

On the Anatomy and Fine-Structure of a Peculiar Sense Organ in *Nucula* (Bivalvia, Protobranchia)

by

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Abstract. A peculiar, tubelike sense organ, called Stempel's Organ (StO) is found in the protobranch genus *Nucula* immediately dorsal to the anterior adductor muscle. The single organ forms a closed tube which is cerebrally innervated. So-called collar receptors present in the sensory portion of the StO indicate a mechanoreceptive function of the organ. Three special muscles are attached to the StO: two of them (m2 and m3) stabilize the tube, the third (m1), whose contractions are detected by the organ, is used in connection with the special mode of feeding (by palps, palp proboscides, and ctenidia) found in the Nuculidae. Comparison is made between the StO and other molluscan sense organs, likewise having collar receptors.

INTRODUCTION

AT THE END OF THE last century, STEPELL (1898) described a peculiar, tubelike organ in *Nucula nucleus*, located dorsally to the anterior adductor muscle. Although he investigated its histology in some detail, the author could not trace any special function of the suggested sense organ. Later on, this organ was noticed by DREW (1901) in his admirable paper on the ontogeny of *Nucula delphinodonta*. According to the author this "organ of unknown function" appears during embryogenesis together with the first anlage of the ctenidium, a short time after the test of the embryo is shed. Since that time this peculiar sense organ has not been reported by scientists.

In honor of its discoverer I shall call this structure Stempel's Organ (StO). In this paper a detailed description of the anatomy and the fine-structure of the StO will be presented with a discussion on its presumed function.

MATERIAL AND METHODS

Nucula nucleus (Linné, 1758) and *Nucula sulcata* (Bronn, 1831), both from the Atlantic (Bergen, Norway), were histologically and fine-structurally investigated with respect to the StO.

For histological investigations serial sections were used, stained with Heidenhain's Azan.

For ultrastructural research entire specimens (3-5 mm) of *Nucula nucleus* were fixed in phosphate-buffered glutaraldehyde (2.5%) and osmium (2%), decalcified with ascorbic acid (1%) after DIETRICH & FONTAINE (1975), and embedded in an epon-araldite mixture (MOLLENHAUER, 1964). Semithin sections were stained with 0.1% toluidine-

blue, while ultrathin sections, made with a diamond knife, were stained with uranyl acetate and lead citrate. For observation a Zeiss EM9/S2 was used.

RESULTS

Anatomical Context of Stempel's Organ

Position and innervation: The StO is located dorsal to the anterior adductor (Figures 1, 2). There is some variation with respect to the position of the posterior end of the StO, which may reach the first tooth of the hinge or a little into the dorsal mantle process. The organ forms a narrow, elongate tube nearly as long as the anterior adductor in adult specimens 700-800 μm , closed at both ends. Its diameter varies between 30 and 60 μm , depending on the state of contraction of the attached muscles (see below). The anterior end of the StO is always expanded and forms a bulb (see DREW, 1901, and Figure 1b).

Innervation is from the pair of anterior pallial nerves which emerge from the outside of the most dorsal/anterior parts of the cerebral ganglia (Figure 1b).¹ Each nerve runs

¹ In this respect it should be stressed that the pleural ganglia of *Nucula* (*N. nucleus*, *N. sulcata* investigated here, *N. delphinodonta* after DREW, 1901) are not separated as described by PEL-SENEER (1891), but are fused as in all other bivalves. In addition, the visceral loop is not a nerve, but a neural cord over its whole length, as known from the primitive cephalopod *Nautilus*. Since neural cords in primitive gastropods are pedal ones, evolution of ganglia in higher conchiferous groups is clearly due to convergence, contradicting a (monophyletic) taxon "Ganglioneura" (LAUTERBACH, 1984).

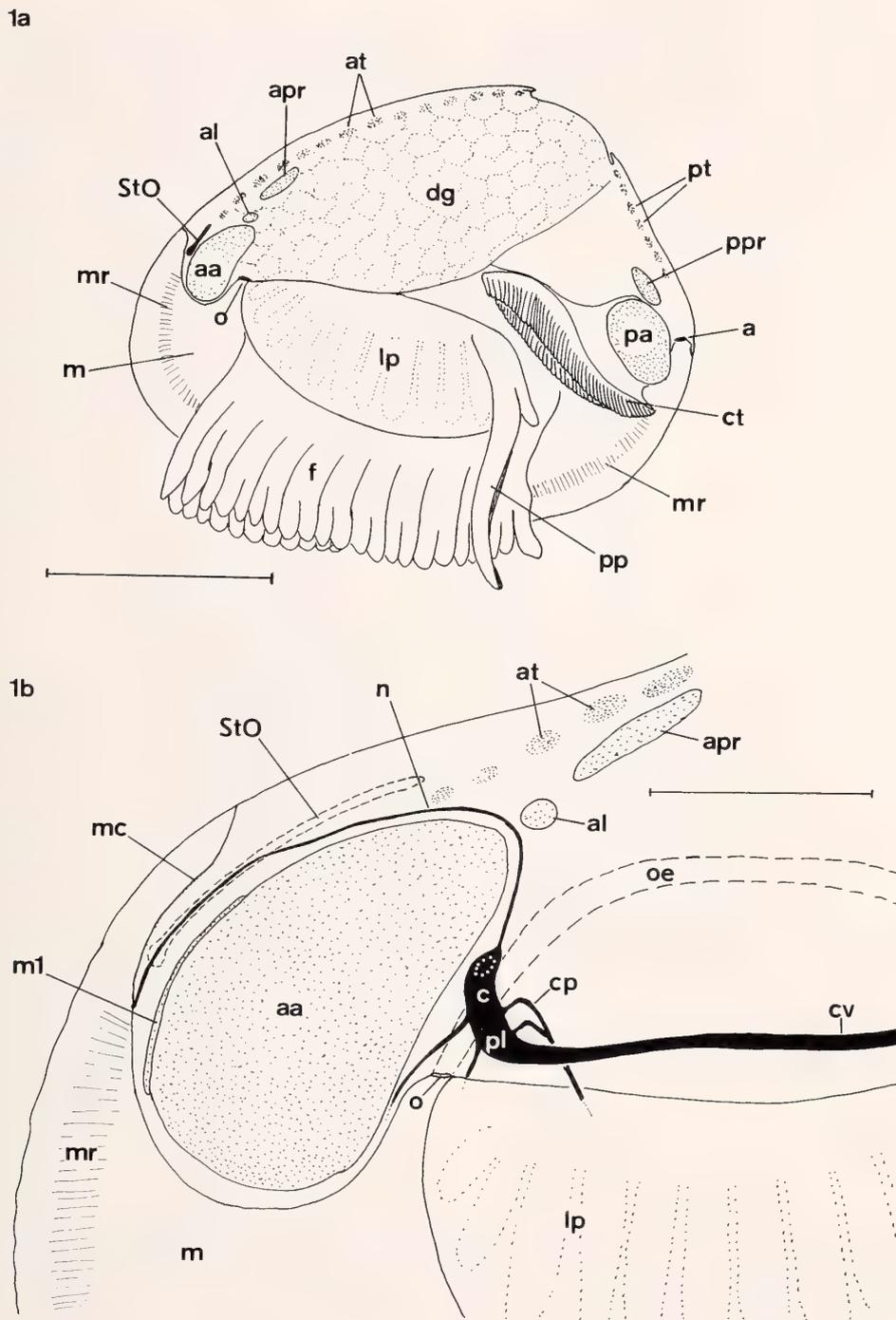


Figure 1

Nucula sulcata. Position and innervation of Stempell's Organ (StO). Figure 1a, lateral view of the left side (left mantle omitted). Figure 1b, detail view to show innervation of the StO (all tissues are shown transparent). a, anus; aa, anterior adductor; al, anterior retractor of labial palp; apr, anterior pedal retractor; at, anterior teeth of hinge; c, cerebral ganglion; cp, cerebropedal connective; ct, ctenidium; cv, cerebrovisceral connective; dg, digestive gland; f, foot; lp, labial palp; m, mantle; m1, attachment zone of muscle m1; mc, central cleft of mantle margin; mr, mantle retractors; n, nerve of StO; o, oral opening; oe, eosophagus; pa, posterior adductor; pl, pleural ganglion; pp, palp proboscides; ppr, posterior pedal retractor; pt, posterior teeth of hinge; StO, Stempell's Organ. Scale bars: 1a, 5 mm; 1b, 1 mm.

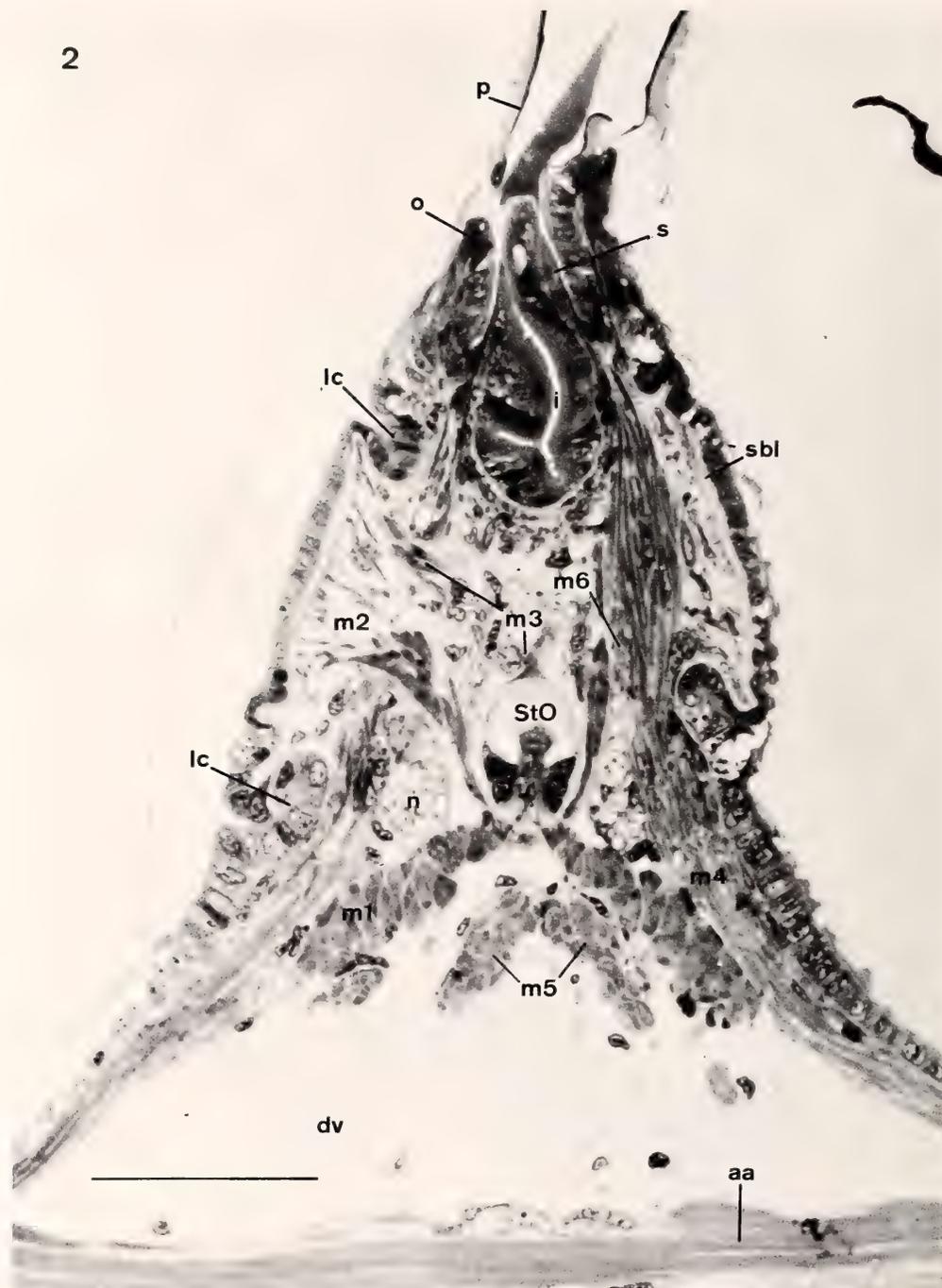


Figure 2

Nucula nucleus. Cross section of the dorsal mantle at middle zone of Stempel's Organ. aa, anterior adductor; dv, dorsal blood vessel; i, inner fold of mantle margin; lc, longitudinal clefts; m1, 2, 3, 4, 5, 6—muscles m1, m2, m3, m4, m5, m6; n, nerve of StO; o, outer fold of mantle margin; p, periostacum; s, sensory fold of mantle margin; sbl, specialized basal lamina (attachment zone of m2 and m3); StO, Stempel's Organ. Scale bar: 50 μ m.

between the anterior adductor and the first pedal retractor, and then forward beneath the StO dorsal to the anterior adductor (Figures 1b, 2). The nerve supplies the organ, especially in the anterior region, by several very thin neural fibers passing laterally through the basal lamina into the epithelium (Figure 4). After passing the anterior end of the StO the nerve runs into the anterior mantle margin.

Mantle epithelium: Three folds of the mantle margin can be distinguished in the region of the StO (Figures 2, 8): The inner fold (i) forms a cleft anteriorly, but changes gradually into a strong central fold at the middle region of the StO; the sensory fold (s) is very small and there are no special sensory elements in this region; the outer fold (o) produces the periostracum at its inner side.

Laterally in the mantle epithelium there appear two longitudinal clefts (lc) limiting the insertions of muscles m2 and m3 (see below). Ventral to this zone there are no special features until the attachment area of the anterior adductor begins.

Muscle system: Several special muscles are found near the StO and three of them (paired) are attached to its basal lamina:

The thickest of these muscles (m1) is attached to the StO at its ventral side. The muscle runs obliquely forward and is attached to the shell immediately anterodorsally to the anterior adductor (Figure 1b). The attachment epithelium consists of very flat (1–2 μm high) cells containing many bundles of microfilaments. It is similar to the attachment epithelium of the anterior adductor, which is higher (2–3 μm), but nearly lacks nuclei (Figure 16).

A second pair of muscles (m2) is attached to the StO immediately dorsal to m1. The muscles m2 turn dorsally and laterally and are attached to the epithelium of the mantle (Figure 2). The attachment epithelium of these muscles (m2) is characterized by an extremely thick (2.5–3 μm) basal lamina that is divided by a very thin electron-dense membrane into two layers (Figure 17). The muscle fibers penetrate the lower layer only and are attached by an electron-dense vesicle. The epithelium itself consists of two cell types, one with electron-dense cytoplasm and few microfilaments (x), the other with a more electron-lucent cytoplasm (y).

The third pair of muscles (m3) is attached dorsally to the StO. The muscles m3 cross each other (Figures 2, 3, 5) and run sideways to reach the mantle epithelium immediately dorsal to muscle m2. Their attachment epithelium is elaborated in the same way as described above for muscle m2 (Figure 17).

Along the whole length of the StO, the mantle is coated on the inside by a substantial muscle (m4), extending from the outside of the inner cleft (i) of the mantle margin ventrally (Figures 2, 9). It is attached to the shell dorsal to muscle m1 (or dorsal to the anterior adductor in the posterior region). The attachment epithelium of this muscle looks like that of muscle m1.

Two pairs of longitudinal muscles (m5 and m6) are found near the StO, reaching into the dorsal mantle process up to the hinge, where they are fused and attached to the shell. The larger pair (m5) is located ventral to muscle m1; the smaller pair (m6) is found lateral to the StO, immediately above the nerve (n) (Figures 2, 3, 8).

Structure of Stempell's Organ

General organization: Stempell's Organ forms a narrow tube that is closed at both ends and thus lacks direct contact with the external water. In general the lumen of the organ is not placed centrally, but is shifted dorsally by a thickened ventral epithelium. The lumen is additionally narrowed by a high, longitudinal, ventral crest whose cilia fill it almost entirely.

In the following, the structure of the StO as a whole is described at five positions (a–e) from the anterior to the posterior end (Figures 4–8). All measurements are for adult specimens.

(a) A short distance behind the anterior end a cross section of the StO is circular, with a diameter of 60 μm . The dorsal epithelium is very flat (1–2 μm), extending 15 μm ventrally, and the crest is 25 μm high (Figure 4). A special central zone is not elaborated, but most of the innervation is in this region.

(b) From a short distance behind the anterior bulb to the posterior quarter the StO has the following organization. The diameter is smaller (50 \times 30 μm), and the extremely flat dorsal epithelium lacks nuclei. A special tissue, forming "longitudinal septa" (see below), separates a central zone below the crest which is narrower in this region (Figures 2, 3, 5).

(c) In the last quarter of the StO its diameter increases, the dorsal epithelium is thickened to 8 μm , and it contains nuclei (Figure 6).

(d) The crest flattens toward the end of the organ, then disappears together with the central zone (Figure 7).

(e) Finally the lumen disappears. There is no posterior bulb in *Nucula nucleus* and *N. sulcata* as figured by DREW (1901) for *N. delphinodonta* (Figure 8).

Structure of the non-specialized epithelium: Although the height of the epithelium lining the lumen of the StO varies greatly, its structure does not change. All cells have more or less round nuclei and bear a microvillous border, but otherwise there are no special features. Anteriorly some nervous tissue is found at the bases of the cells, running from the place of innervation (always lateral) downward into the central zone, penetrating the "longitudinal septa."

The basal lamina of the StO is thick (2–3 μm). This seems to be necessary for the attachment of the muscles, which are fixed to the lamina by prominent toothlike projections (especially m1, see Figure 3). Laterally the basal lamina is penetrated by the thin neural fibers emerging from the laterally placed nerves (Figure 4).

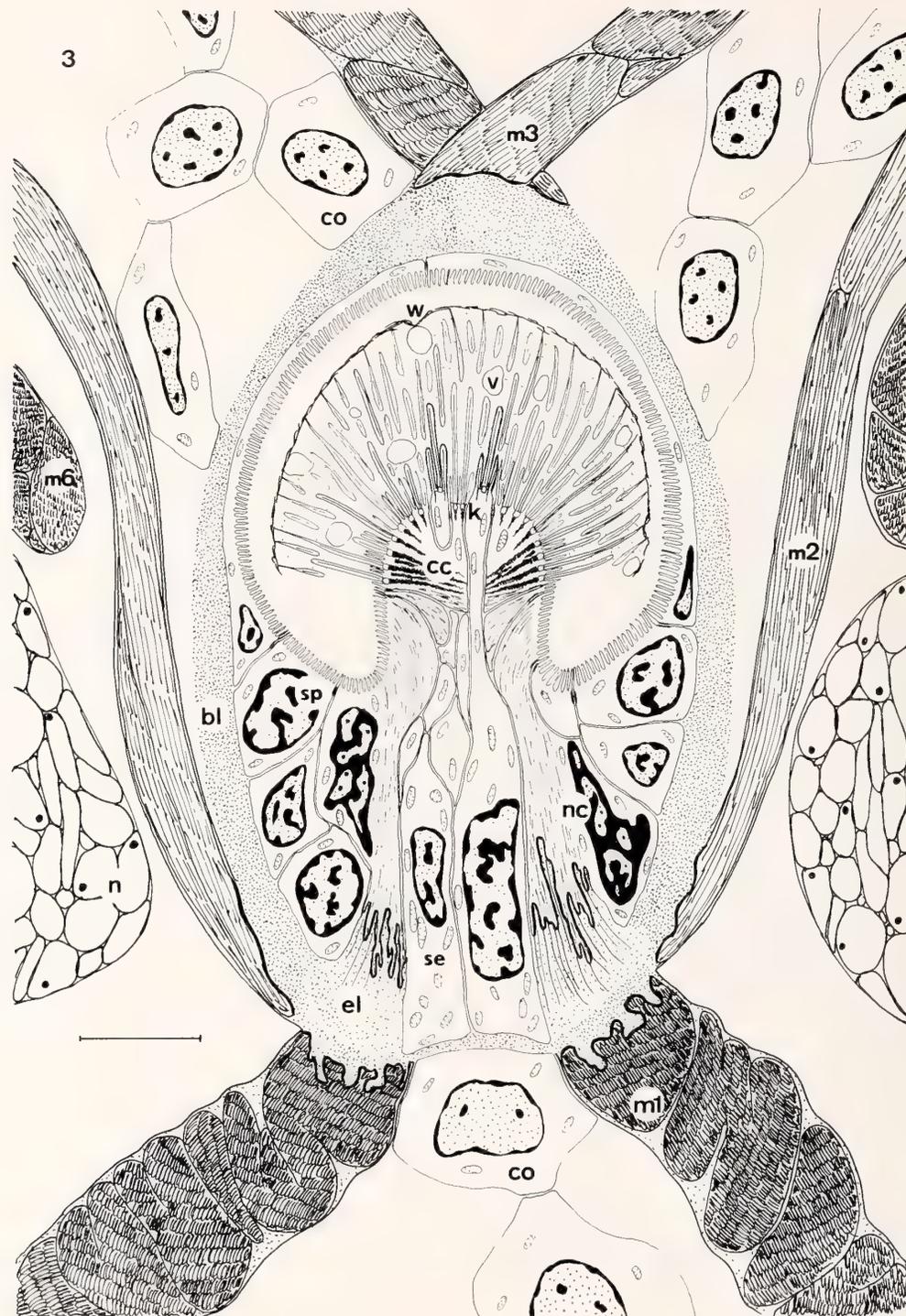


Figure 3

Nucula nucleus. Cross section of middle zone of Stempell's Organ (semischematic). bl, basal lamina; cc, ciliated cell; co, connective tissue; el, elastic layer (a specialized portion of the basal lamina); k, sensory knob; m1, 2, 3, 6—muscle m1, m2, m3, m6; n, nerve of StO; se, sensory cell; sp, supporting cell; nc, neighboring cell (with a specialized portion); v, vesicle; w, wrapper. Scale bar: 5 μ m.

Structure of the "longitudinal septa": The symmetrically placed longitudinal septa separate a central zone in the ventral area of the lining epithelium. These septa are located exactly above the place of attachment of the thick oblique muscle m1. They consist of two portions (Figures 3, 15): (a) Ventrally a specialized region (el) of the basal lamina, conical in cross section, contains numerous thin microfilaments. (b) This region is continued upward by muscular portions of the laterally adjacent cells (nc) entering the crest and forming its lateral basis. The attachment to the lower portion of the longitudinal septa is by numerous rootlike projections which are invested with electron-dense material. The nuclei of the adjacent cells are slightly different from those of the non-specialized epithelium, having a more oval shape and bigger granules (150–200 nm) within their reduced euchromatin.

Structure of the central zone and of the crest: The central zone consists of large cells with oval nuclei. The cytoplasm of these cells is granular and more electron-lucent than that of the supporting cells (Figures 3, 15). They project slender (1 μm) processes up to the median surface of the crest. There, these processes form a kind of knob (2–3 μm), being somewhat higher than the surrounding ciliated cells (cc). The processes are arranged in transverse rows (Figure 14). At the anterior end of the StO up to seven processes are found within a row; going backward this number is gradually reduced to two. Each of the knobs bears a so-called collar receptor, consisting

of a specialized cilium that is surrounded by nine specialized microvilli (= "stereo-cilia" of many authors) (Figure 12). These cilia lack striped roots, have an thickened outer membrane, and are somewhat stouter (280–300 nm) than the cilia of the ciliated cells (200–230 nm). The structure of the collar cilia is likewise distinctive, showing a 9×3 pattern of outer microtubules and an electron-dense circle around the central tubules up to their tips (Figure 12). The basal body of the cilium forms a starlike plate from which several rootlets (not striped) run downward (Figure 13). The microvilli are triangularly shaped in cross section with amplified tips toward the central cilium. They are connected by a dense glycocalyx forming a kind of fence around the central cilium.

Between the rows of processes and surrounding them, ciliated cells (cc) form the bulk of the crest. The whole breadth of the crest is always occupied by a single ciliated cell which obviously lacks a nucleus. The ciliated cells bear many cilia, but only few mitochondria are found. Whereas the more dorsally placed cilia have short roots, those of the more laterally placed cilia are very long and cross each other at the center of the crest (Figures 3, 14). Since these roots are alternately arranged with the rows of processes, a striped pattern is found in oblique sections of the crest (Figures 4, 14). The cilia of the ciliated cells are connected one to another by a net of glycocalyx (Figures 3, 10, 11, 14) and so form a kind of matrix. In contrast to the shafts of the cilia, which are of normal structure, the microtubule pattern is progressively dis-

Explanation of Figures 4 to 13

Nucula nucleus. Figures 4 to 7. Cross sections of Stempell's Organ at different zones of the organ. Scale bars: 10 μm .

Figure 4. Immediately behind the anterior end (arrow: innervation).

Figure 5. Middle zone (for details see Figure 3).

Figure 6. Posterior quarter.

Figure 7. Near the posterior end.

Figure 8. Cross section of the dorsal mantle process at the first anterior hinge-tooth (immediately before the posterior end of Stempell's Organ). Scale bar: 50 μm .

Figure 9. Detail of Figure 2 to demonstrate the secretion of hypostracum material (decalcified). Scale bar: 10 μm .

Figures 10 to 13. Specialized cilia of Stempell's Organ; all cross sections are slightly oblique and are centripetally arranged. Scale bars: 200 nm.

Figure 10. Spearlike tips of supporting cilia together with the netlike wrapper.

Figure 11. Supporting cilia connected by glycocalyx.

Figure 12. Typical collar receptors.

Figure 13. Bases of collar receptors.

h, hypostracum; i, inner fold of mantle margin; lc, longitudinal cleft; m(5+6), fused muscles m5 and m6; o, outer fold of mantle margin; p, periostracum; s, sensory fold of mantle margin; StO, Stempell's Organ.

Explanation of Figures 14 to 17

Nucula nucleus. Figure 14. Oblique section of the crest of Stempell's Organ immediately behind the anterior end.

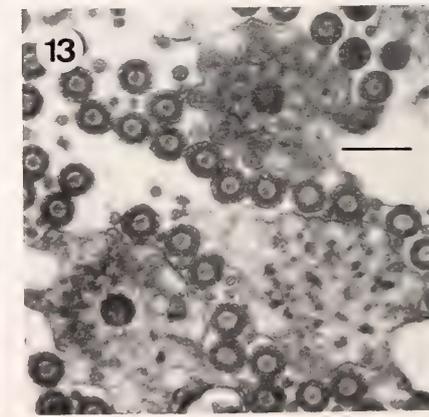
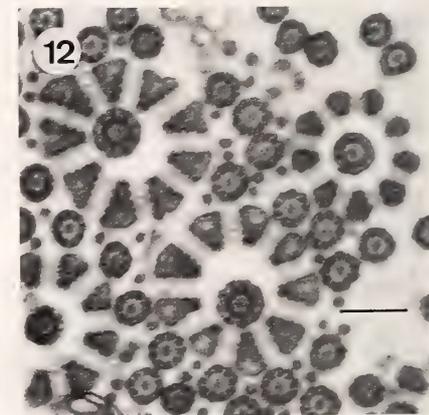
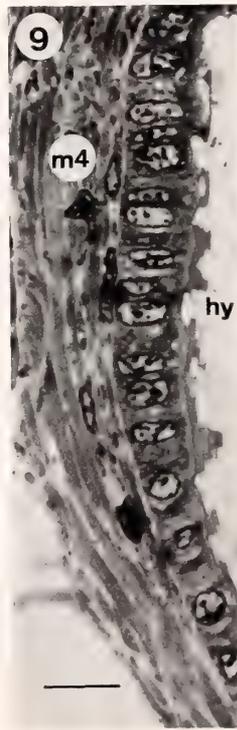
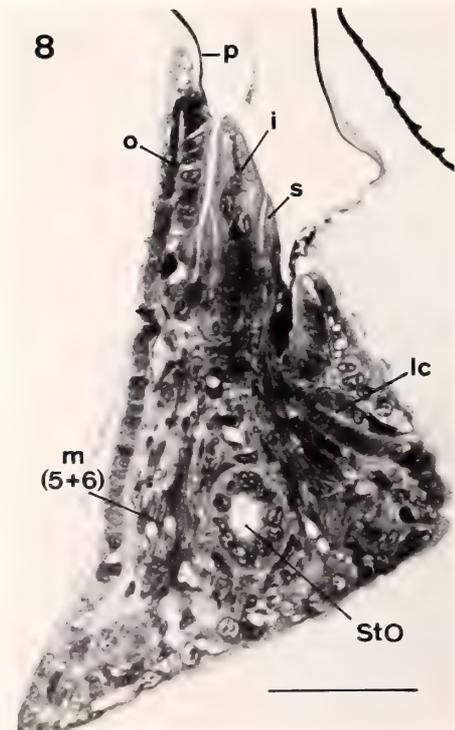
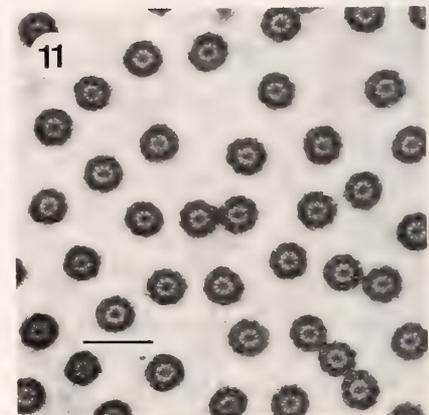
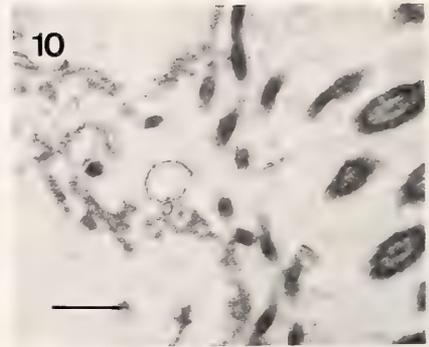
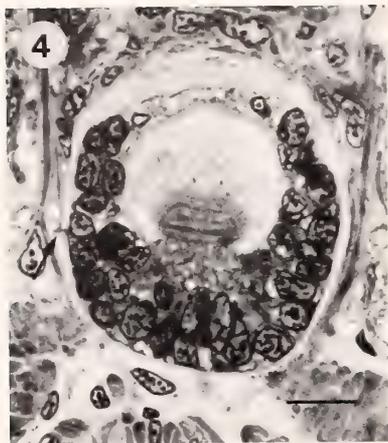
Figure 15. Cross section of the central zone and the longitudinal septa of Stempell's Organ near middle zone (see also Figure 3).

Figure 16. Attachment epithelium of the anterior adductor.

Figure 17. Attachment epithelium of muscle m2.

at, adhesive tissue; bl, basal lamina; cc, ciliated cell; cr, collar

receptor; ct, connective tissue; el, elastic layer (a specialized portion of the basal lamina); ibl, inner layer of basal lamina; hy, hypostracum; k, sensory knob; mf, muscle fibrils; nc, neighboring cell; obl, outer layer of basal lamina; se, sensory cell; sp, supporting cell; v, vesicle; w, wrapper; x and y, cell types x and y (see text). All scale bars: 2 μm .



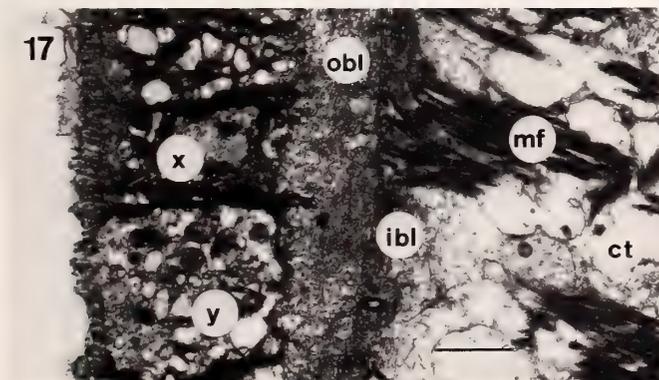
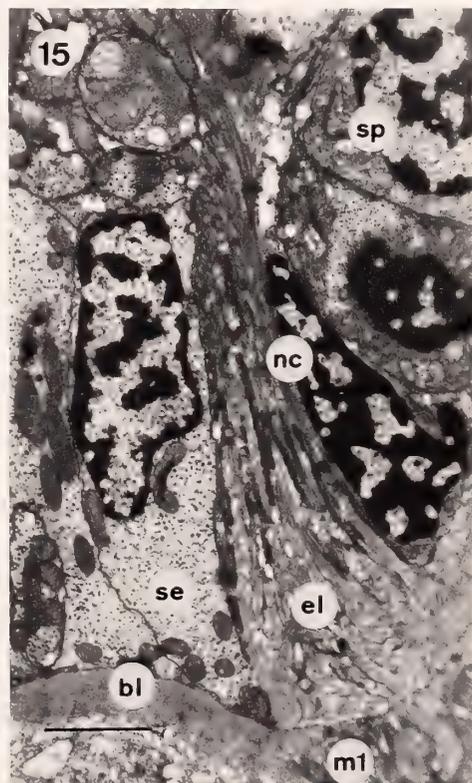
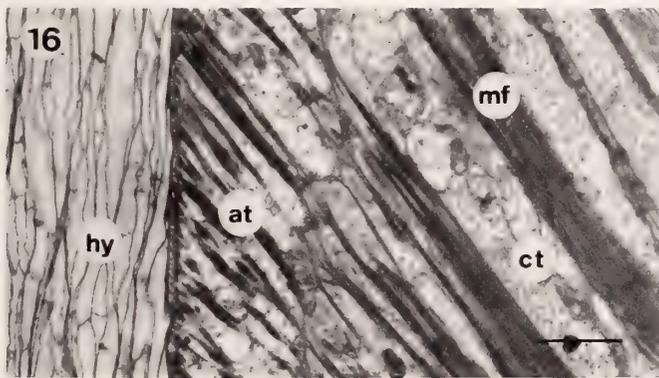
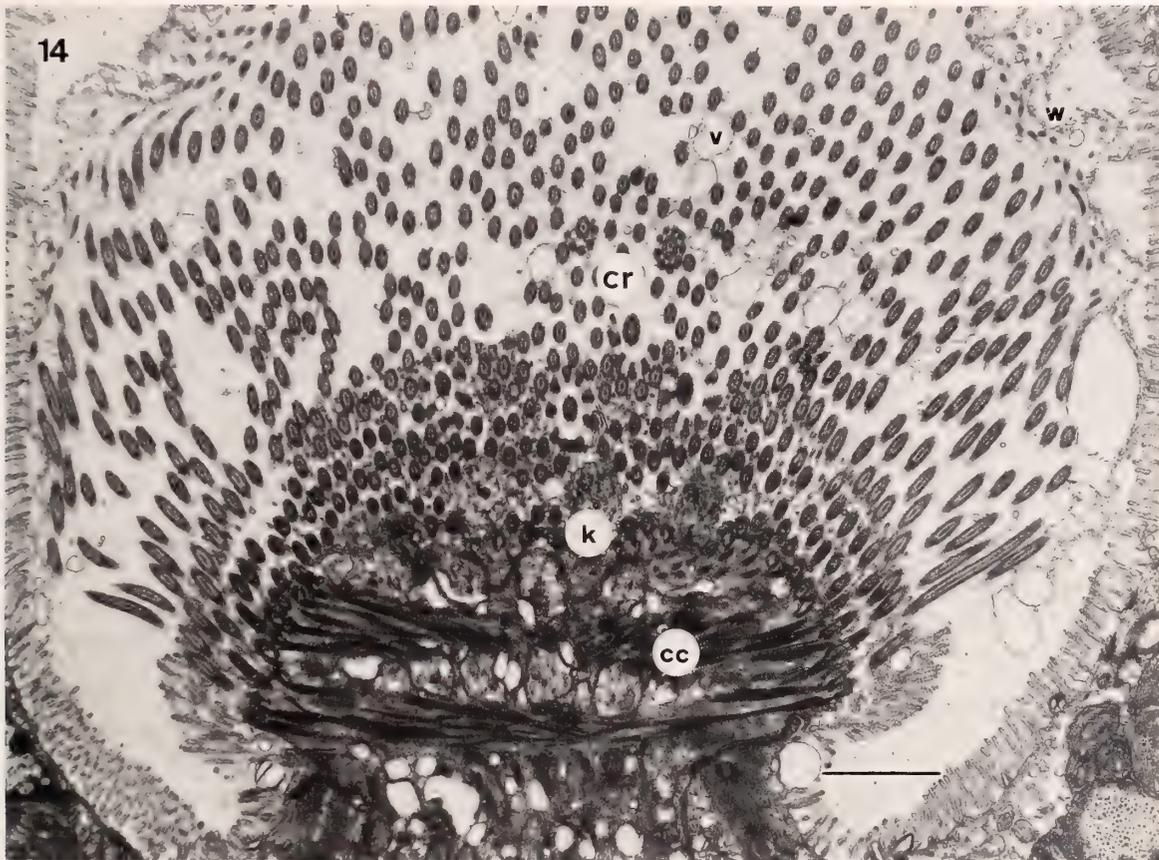


Table 1
Comparison of well investigated molluscan sense organs with collar receptors.

Organ	Stempell's organ	Abdominal sense organ	Long mantle tentacles	Epipodial sense organ	Subpallial sensory strip
Found in	<i>Nacula</i> (Nuculidae?)	Pteriomorpha and <i>Neotrigonia</i>	<i>Placopecten</i> (Pectinoidae?)	Vetigastropoda ¹	Docoglossa
Number per specimen	one	one or two	numerous	two to numerous	two
Position	dorsal to the anterior adductor	ventral to the posterior adductor (inside or outside of ctenidia)	mantle margin	ventral bases of epipodial tentacles	around the anterior edge of the shell muscles, subpallial
Innervation	cerebral	visceral	visceral	pedal	pleural (and osphradial?)
Contact with medium	no contact (closed tube)	contact with water of the mantle cavity	contact with external water	contact with external water	contact with water of the subpallial cavity
Basis of collar receptor	slightly higher than adjacent cells	same height as adjacent cells	forming a papilla together with adjacent cells	deeper than adjacent cells	slightly higher than adjacent cells
Central cilium of collar receptor	short (up to 5 μm); lacking roots and basal foot specialized structure	very long (up to 500 μm); with long roots and basal foot; normal structure; sometimes swollen membranes	short (up to 5 μm); with long roots and basal foot; normal structure	variable (4 to 80 μm); lacking root and basal foot; less specialized structure; accessory centriole	variable (2 to 15 μm); with root and basal foot; normal structure
Specialized microvilli ("stereo-cilia")	nine; triangular in cross section; lacking rootlets	nine; round in cross section; with rootlets	eight (?); round in cross section; lacking rootlets	eight or nine; triangular in cross section; lacking rootlets	nine; round in cross section; with rootlets
Suggested primary function	mechanoreceptor	mechanoreceptor	mechanoreceptor	mechanoreceptor	mechanoreceptor
Suggested secondary function	reception of muscle contractions to regulate water currents and feeding movements	reception of pallial water currents to regulate them	reception of touch	reception of touch stimuli from the bottom (in connection with epipodial tentacles)	water currents to regulate them
References	this paper	MOIR, 1977a; ZHADAN & SEMEN'KOV, 1982; HASZPRUNAR, 1985	MOIR, 1977b	MACDONALD & MAINO, 1964; CRISP, 1981; Haszprunar unpubl.	STÜTZEL, 1984; HASZPRUNAR, 1984

¹ According to SALVINI-PLAWEN (1980): zeugobranchs and trochoids.

solved near the tip of the cilium. The tip itself is spearlike and contains a single tubule only. Since the tips are found bent (Figure 10, 14), they appear to be flexible. Between the cilia, vesicles (v) of various diameters (0.5–2 μm) are found that are probably transported up to the tips of the cilia. There the vesicles form a netlike wrapper enveloping the whole crest complex (Figures 3, 10, 14).

DISCUSSION

On the Structure of the Receptor Elements

There can be little doubt that the so-called collar receptors found in the crest are sensory structures. This is shown not only by their specialized structure, but also by the fact that the presumed sensory cells, which bear these receptors, are in synaptic contact with the fine nervous fibers emerging from the lateral nerve.

Such collar receptors are found in many invertebrate groups, but appear to be often confused by authors with the so-called choanocyte-like cells (*e.g.*, CRISP, 1981). Choanocyte-like cells are not sensory and lack the special features of the central cilium as well as of the surrounding microvilli. Within the Turbellaria collar receptors are found in the integument of nearly all groups, and structural differences are used for phylogenetic suggestions (*e.g.*, EHLERS, 1977; EHLERS & EHLERS, 1977; SOPOTT-EHLERS, 1984).

Within the Mollusca, collar receptors are found so far in very different organs: they occur (a) in the subpallial sensory stripe of the Docoglossa (STÜTZEL, 1984; HASZPRUNAR, 1984); (b) in the epipodial sense organs of Vetigastropoda² (CRISP, 1981; Haszprunar, unpublished); (c) at the mantle slit (or siphon) of fissurellids (Herbert, personal communication); (d) at the ventral mantle margin of the pteropod *Creseis virgula* (Haszprunar, unpublished); (e) in the abdominal sense organs of Pteriomorpha (MOIR, 1977a; HASZPRUNAR, 1985); (f) at the long mantle tentacles of the scallop *Placopecten magellanicus* (MOIR, 1977b); and (g) in Stempell's Organ of *Nucula* (this paper).

Although the organs of the various classes and tribes, where collar receptors occur, are certainly not homologous, it seems hardly likely that such a complex structure would have evolved independently in each case. However, as outlined in the cases within the Mollusca, which have been investigated in detail, there are several differences in the detailed structure of the collar receptors of the respective organs (Table 1). Thus, two possibilities remain: (i) the collar receptors of different organs are the products of convergence, independently developed from a choanocyte-like cell, or (ii) there is a common basal genetic information to develop an archetype of these receptors, which have been secondarily specialized for the special function of the particular sense organ. This view is the theoretical

basis of all phylogenetic implications based on the structure of collar receptors within the Turbellaria (EHLERS, 1977). This would be a special kind of "normative" homology (*e.g.*, RIEDL, 1975) which is normally restricted to single organelles only (*e.g.*, mitochondria, cilia), or known as "serial" homology with respect to organs (*e.g.*, ROTH, 1984).

In any case this type of receptor appears to be typical for mechanoreceptors (although there are many mechanoreceptors, such as statocysts, lacking collar receptors). In the case of the abdominal sense organ its suggested mechanoreceptive function (regulating water currents, see THIELE [1889], HASZPRUNAR [1985]) has been recently confirmed by electrophysiological results (ZHADAN & SEMEN'KOV, 1982). Further, a chemo- or osmosensitive StO is very improbable, since the organ has no contact with external water, being closed.

Therefore, it is very probable that the StO is a mechanoreceptor.

On the Structure of the Supporting Elements

The well-developed roots found in the ciliary cells indicate a high mechanical stress on their cilia (especially the laterally located ones). In contrast, several structural facts indicate that these cilia do not move, but form a kind of elastic matrix covered by the netlike wrapper: (i) the presence of few mitochondria in the ciliated cells (Figure 14); (ii) the connection of the cilia among each other by a glycoaxial (Figure 11); (iii) the spearlike tips of the cilia which appear to be flexible (Figures 10, 14). It follows that there is a passive mechanical stress on these cilia.

In fact, a highly developed structure to transmit mechanical forces from outside to the crest is found in the paired longitudinal septa, immediately situated above the place of attachment of muscle m1. Any contraction of this muscle is transmitted via the specialized basal lamina and via the muscular portion of the adjacent cell to the lateral basis of the crest (Figures 3, 15).

Comparing the three muscles attached to the StO, the following main differences between muscles m2 and m3 and muscle m1 are found. The former muscles are symmetrically arranged with respect to the longitudinal axis of the StO. Their mode of attachment at the lateral mantle epithelium by a thickened basal lamina (Figure 17) does not allow extreme mechanical stress. In addition, there are no special structures to transmit contractions of these muscles into the StO, and their attachment zone on the StO is not toothlike (as for muscle m1), likewise indicating a low degree of mechanical stress. Thus, it is probable that the muscles m2 and m3 are necessary for the stability of the StO, but do not act in the reception process. In contrast, muscle m1, which is the thickest, runs obliquely forward and this appears to be correlated (a) with the presence of the majority of the collar receptors at the anterior end of the StO, and (b) with the fact that penetrating neural fibers likewise are found only in the anterior

² After SALVINI-PLAWEN (1980): zeugobranchs and trochoids.

third of the organ. In addition, the muscle is directly attached to the shell via a special attachment tissue similar to that of the adductor muscle (Figure 16), and its contractions can be transmitted by the longitudinal septum.

On the Function of the StO

Summing up the considerations presented so far, it can be concluded that the StO is a mechanoreceptor, detecting contractions of muscle m1.

To date, a StO has been found only within the genus *Nucula*, but is likely present also in other genera of the Nuculidae (Nuculoidea). Because the discoverer of the StO did not describe a similar structure in any of the members of the Nuculanoidea and Solemyoidea he investigated (STEMPELL, 1898, 1899; DREW, 1899), the StO appears to be restricted to the Nuculidae.

The Nuculidae is the sole family among all Bivalvia which has retained an anterior-posterior water current (similar conditions found in the Lucinoidea are accepted by most authors to be secondary, see *e.g.*, ALLEN [1958], MORTON [1979]). STASEK (1961) stated that feeding in nuculids is done (a) by the palp proboscides (as in all protobranchs), (b) by the outer palp lamellae (only nuculids in such a degree), and (c) by the ctenidia (less important in nuculids). Thus, the incoming water is used not only for respiration, but also for feeding. Reflecting that the adhesive zone of muscle m1 is located immediately dorsal to the anterior adductor and thus exactly beside the inhalant opening of the water current (Figure 1b), it appears probable that the StO detects movements (also longitudinal) of this important region, where disturbances are essential for two main life processes.

Therefore, the presence of the StO within the Nuculidae is additional evidence for the ideas of STASEK (1961) that nuculids are not direct forerunners of higher Bivalvia. They represent an early offshoot of the bivalve stock, specialized in a considerable degree. The StO represents one example of this specialization.

ACKNOWLEDGMENTS

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LITERATURE CITED

- ALLEN, J. A. 1958. On the basic form and adaptations to habitat in the Lucinoidea (Eulamellibranchia). *Phil. Trans. Roy. Soc. Lond. B* 241:421-484.
- CRISP, M. 1981. Epithelial sensory structures of trocnids. *J. Mar. Biol. Assoc. U.K.* 61:95-106.
- DIETRICH, H. F. & A. R. FONTAINE. 1975. A decalcification method for ultrastructure of echinoderm tissue. *Stain Technol.* 50: 351-354.
- DREW, G. A. 1899. The anatomy, habits and embryology of *Yoldia limulata* Say. *Johns Hopkins Univ. Mem. Biol. Lab.* 4(3):1-37.
- DREW, G. A. 1901. The life history of *Nucula delphinodonta* (Mighels). *Quart. J. Micr. Sci.* 44:313-391.
- EHLERS, U. 1977. Vergleichende Untersuchungen über Collar-Rezeptoren bei Turbellarien. *Acta Zool. Fennica* 154: 137-148.
- EHLERS, U. & B. EHLERS. 1977. Monociliary receptors in interstitial Proseriata and Neorhabdocoela (Turbellaria, Neophora). *Zoomorphology* 86:197-222.
- HASZPRUNAR, G. 1984. The fine morphology of the osphradial sense organs of the Mollusca. I. Gastropoda, Prosobranchia. *Phil. Trans. Roy. Soc. Lond. B* 307:457-496.
- HASZPRUNAR, G. 1985. The fine-structure of the abdominal sense organs of Pteriomorpha (Mollusca, Bivalvia). *J. Moll. Stud.* (in press).
- LAUTERBACH, K.-E. 1984. Das phylogenetische System der Mollusca. *Mitt. Dtsch. Malak. Ges. (Frankfurt A.M.)* 37: 66-81.
- MACDONALD, J. & C. B. MAINO. 1964. Observations on the epipodium, digestive tract, coelomic derivatives, and nervous system of the trochid gastropod *Tegula funebris*. *Veliger* 6(Suppl.):50-55.
- MOIR, A. J. G. 1977a. On the ultrastructure of the abdominal sense organ of the giant scallop *Placopecten magellanicus* (Gmelin). *Cell. Tiss. Res.* 184:359-366.
- MOIR, A. J. G. 1977b. Ultrastructural studies on the ciliated receptors of the long tentacles of the giant scallop *Placopecten magellanicus* (Gmelin). *Cell. Tiss. Res.* 184:367-380.
- MORTON, B. 1979. The biology and functional morphology of the coral-sand bivalve *Fimbria fimbriata* (Linnaeus, 1758). *Rec. Austral. Mus.* 32(11):371-387.
- MOLLENHAUER, H. H. 1964. Plastic embedding mixtures for use in electron microscopy. *Stain Technol.* 39:111.
- PELSENEER, P. 1891. Contribution à l'étude des Lamellibranches. *Arch. Biol.* 11:147-312.
- RIEDL, R. 1975. Die Ordnung des Lebendigen. Parey Verlag: Hamburg. 372 pp.
- ROTH, L. V. 1984. On homology. *Biol. J. Linn. Soc.* 22:13-29.
- SALVINI-PLAWEN, L. V. 1980. A reconsideration of systematics in th the Mollusca (phylogeny and higher classification). *Malacologia* 19:249-278.
- SOPOTT-EHLERS, B. 1984. Epidermale Collar-Rezeptoren der Nematoplanidae und Polystyliphoridae (Plathelminthes, Unguiphora). *Zoomorphology* 104:226-230.
- STASEK, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae), with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. *Proc. Zool. Soc. Lond.* 137:511-538.
- STEMPELL, W. 1898. Beiträge zur Kenntnis der Nuculiden. *Zool. Jb. Suppl.* 4:339-430.
- STEMPELL, W. 1899. Zur Anatomie von *Solemya togata* Poli. *Zool. Jb. Syst.* 13:89-170.
- STÜTZEL, R. 1984. Anatomische und ultrastrukturelle Untersuchungen an der Napfschnecke *Patella* L. unter besonderer Berücksichtigung der Anpassung an den Lebensraum. *Zoologica (Stuttgart)* 135:1-54, 36 pl.
- THIELE, J. 1889. Die abdominalen Sinnesorgane der Lamellibranchiaten. *Z. Wiss. Zool.* 48:47-59.
- ZHADAN, P. M. & P. G. SEMEN'KOV. 1982. Function of the abdominal organ in *Patinopecten yessoensis*. *Dokl. Biol. Sci.* 262(1-6):87-90.

The Anatomy and Histology of *Phyllidia pulitzeri* Pruvot-Fol, 1962, with Remarks on the Three Mediterranean Species of *Phyllidia* (Nudibranchia, Doridacea)

by

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Abstract. In this study is given the first extensive examination of the anatomy and the histology of the organ systems of a phyllidiid: the Mediterranean species *Phyllidia pulitzeri* Pruvot-Fol, 1962.

The digestive tract of *Phyllidia pulitzeri* differs from that of other species of the genus by the lack of the typical oral glands lying on the outside of the oral tube. Oral glands can be found only at the inside wall of the oral tube. The genital system corresponds to the triaulic scheme of all other Doridacea. The penis has no armament. Gastro-esophageal ganglia, as described by other authors, are not present. Special features of the excretory system are the very long renopericardial duct and a glandular mass that lies in the posterior part of the nephridium and continues in the ureter. Basophilic subepithelial glands that are scattered over the mantle, foot, and gills seem to be responsible for the intensive secretion of mucus.

A comparison of the three Mediterranean species of *Phyllidia* (*P. rolandiae*, *P. aurata*, and *P. pulitzeri*) led to the conclusion that *P. rolandiae* is a *nomen dubium*, because its description does not allow a clear distinction from the two other species.

INTRODUCTION

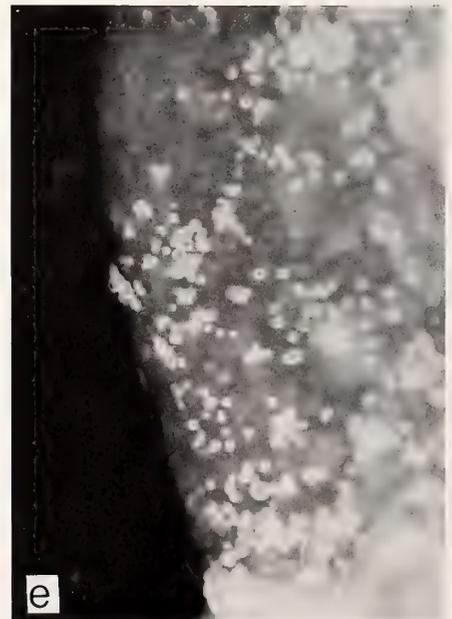
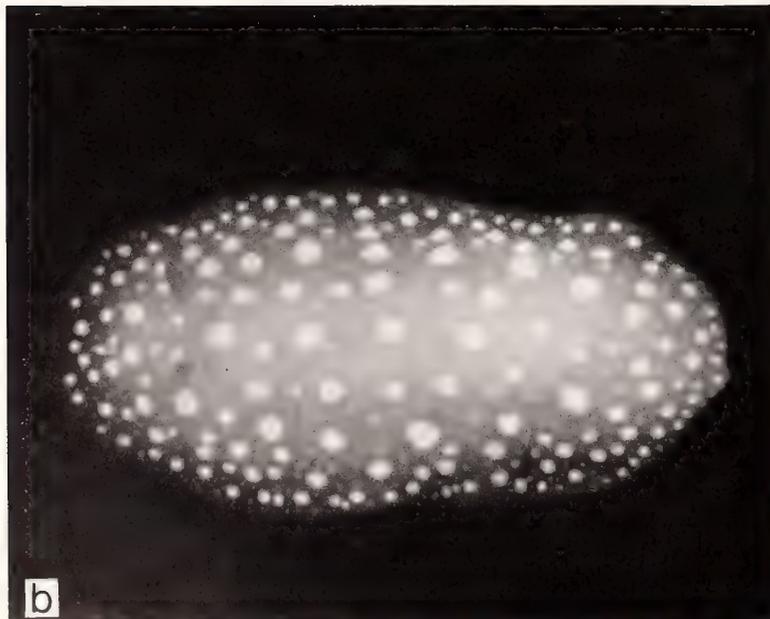
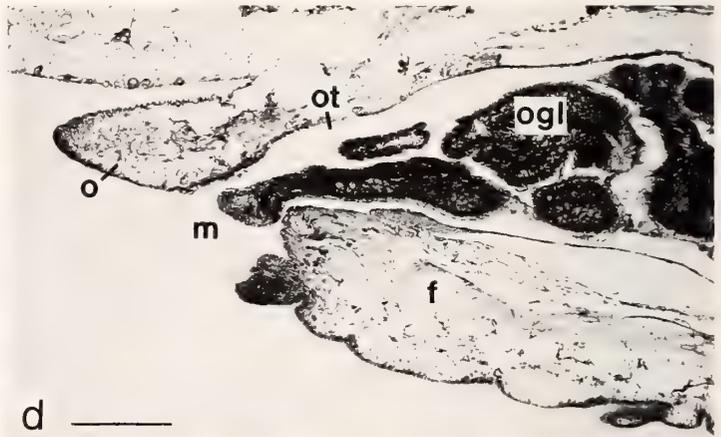
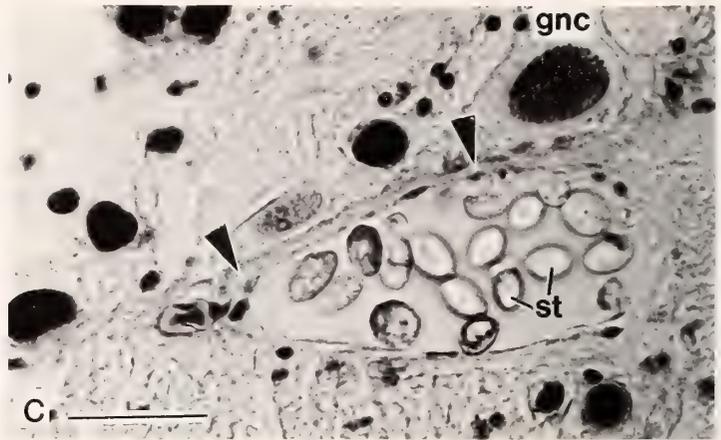
"THE PHYLLIDIIDAE ARE the longest known of all nudibranchs (Bergh, 1876) and were figured as early as 1735" (MARCUS, 1962:477). Nevertheless, little is known about their anatomy and even less about the phylogeny of this family or the life histories of its species. It is occasionally maintained in the literature that dissection of phyllidian species is unnecessary for identification (*e.g.*, PRUVOT-FOL, 1962). Therefore, several species are known only by their external features. That dissection is an absolute necessity is demonstrated by several studies (EALES, 1938; ELIOT, 1903, 1904; MARCUS, 1962) which show that there are both interspecific and intraspecific differences.

The phyllidiids have an oval, flat form similar to the cryptobranchiate Doridacea, but they can be easily distinguished from those by their gills lying ventrally between the notum and foot, being interrupted only by the mouth and the genital papilla. The anus lies dorso-median (*Phyl-*

lidia, *Phyllidiella*, *Phyllidiopsis*, *Ceratophyllidia*) or ventro-median between the gill leaflets (*Fryeria*). The phyllidiids have no radula or mandible, a feature that they have in common with the Dendrodorididae and on which was based their association with the latter family into the group Porostomata (BERGH, 1876, after BERGH, 1889).

The most important anatomical feature for systematics is the foregut, as it distinguishes the two genera *Phyllidia* and *Phyllidiopsis*. Yet, the first description of *Phyllidia pulitzeri* Pruvot-Fol, 1962, is based on a single specimen only, and its internal anatomy is completely unknown. As a consequence its generic status is not certain. Does it belong to the genus *Phyllidia* or to *Phyllidiopsis*?

Having a few specimens in well-fixed condition at my disposal, I have been able to answer this question and to give a detailed description of the anatomy and the histology of some of the organs. Moreover, this examination is regarded as a first step toward a complete systematic re-



vision of the family Phyllidiidae and toward a determination of its correct phylogenetic position.

MATERIAL AND METHODS

In September 1980, four specimens of *Phyllidia pulitzeri* were collected by SCUBA diving in Khalkidhiki (Northern Aegean Sea/Greece). The animals were found on a sponge of the genus *Axinella* in depths between 10 and 20 m (Figure 1a). In May 1983, additional specimens were discovered in Gozo/Malta in depths between 5 and 30 m. They were collected from crevices, and a group of five animals was found on rock material at the back of a large cave.

The material from Greece (length of specimens: 22–32 mm; breadth: 12–22 mm) was fixed in 4% formaldehyde/seawater, that from Malta (length: 12.5–22 mm; breadth: 6–13 mm) in Bouin's fluid. Previous narcosis with MS 222 prevented deformation of the animals during fixation.

For anatomical and histological examinations, three specimens were embedded in paraplast. Serial longitudinal sections (8 μm) were made of two small animals (specimen L1: 12.5 mm; specimen L2: 22 mm) and serial cross sections (8 μm) of a larger specimen (C1: 31 mm). Staining of the sections was carried out according to ROMEIS (1968) with May-Grünwald/Giemsa or trichrome (azan or hemalaun/lightgreen). Four specimens were dissected under the stereomicroscope.

As the fixatives did not penetrate the digestive gland, histological examination of this organ was not possible.

The following descriptions apply to all specimens examined, except where special reference is made to particular specimens.

One specimen is deposited as a neotypus in the Muséum National d'Histoire Naturelle, Paris.

RESULTS

External Morphology

In the living animal the notum above the visceral hump is covered with white tubercles arranged in five longitudinal lines. Between them are smaller, orange-colored tubercles. On the margin of the notum the white and orange-colored warts are scattered irregularly (Figure 1b). Immediately behind the yellow rhinophores a small white tubercle is located on each rhinophore sheath (Figure 2a:

rhst), the so-called "Rhinophorenscheidentuberkel" (SCHMEKEL & PORTMANN, 1982:140).

Fixed animals are ivory-colored and the arrangement of the white tubercles in longitudinal lines is hardly visible. The tubercles of different animals vary in size and form. In some they are higher than broad and stand close together (Figure 2d). In others the warts are flat, widely separate, and protrude only slightly. This great variability in the form of the tubercles is due to fixation, because it was not observed in living animals.

The rhinophores, each with approximately 12–14 lamellae, are situated in the anterior $\frac{1}{4}$ to $\frac{1}{5}$ of the body (Figure 1b). The rhinophore sheaths are very small. The anal papilla lies in an anal tubercle of varying size located medio-dorsally in the posterior $\frac{1}{5}$ of the body (Figure 2b).

The ventral side of the living animal is uniformly gold to light yellow in color. The margin of the notum is slightly transparent and the radial and net-shaped arrangement of the spiculae is visible. Beneath the slitlike oral aperture, which is surrounded by two short, triangular, marginally grooved, oral tentacles, the foot has a short, longitudinal notch (Figure 2e). The 100–130 gill leaflets, lying in a groove between the foot and mantle margin, are triangular-shaped and are fused to the ventral notum along their broad base. Large and small gill leaflets alternate more or less regularly (Figure 2c).

The genital papilla lies on the right side in the anterior third of the body between the gill leaflets. The vestibulum (v), with vagina and vas deferens, opens on the distal part of the papilla and the oviduct (ov, Figure 2c) opens on the proximal part.

All the specimens fixed in formaldehyde are covered with small crystalline globules (Figure 1e). Some of them could easily be detached, but the greater part of them could not be removed without the surrounding tissue.

Digestive Tract

Anatomy: The general anatomical outline can be seen in Figure 2f. The vertical slit of the oral aperture leads into a vestibulum, from where the oral tube rises. After entering the perivisceral cavity (pc) the oral tube widens into a club-shaped chamber; the highly folded walls of this chamber consist of a glandular epithelium (ogl). There are no glands on the outside of the oral tube.

Two thick retractor muscles arise laterally, one on each

Figure 1

a. Living animal in natural surrounding, on a sponge of the genus *Axinella*. Photograph was taken in Corfou/Greece in August 1974. Specimen was not collected; depth 10 m. b. Living animal from Gozo/Malta; note the transparency of the mantle margin. c. Longitudinal section through statocyst; arrows, neurilemma; May-Grünwald/Giemsa; scale 10 μm . d. Longitudinal section of the anterior digestive tract; note the protruding parts of the oral gland; azan; scale 50 μm . e. "Crystallized" mucus on the ventral side of the mantle margin; scale 10 μm . Key: f, foot; gnc, giant nerve cell; m, mouth; o, oral tentacle; ogl, "oral gland"; ot, oral tube; st, statolith.

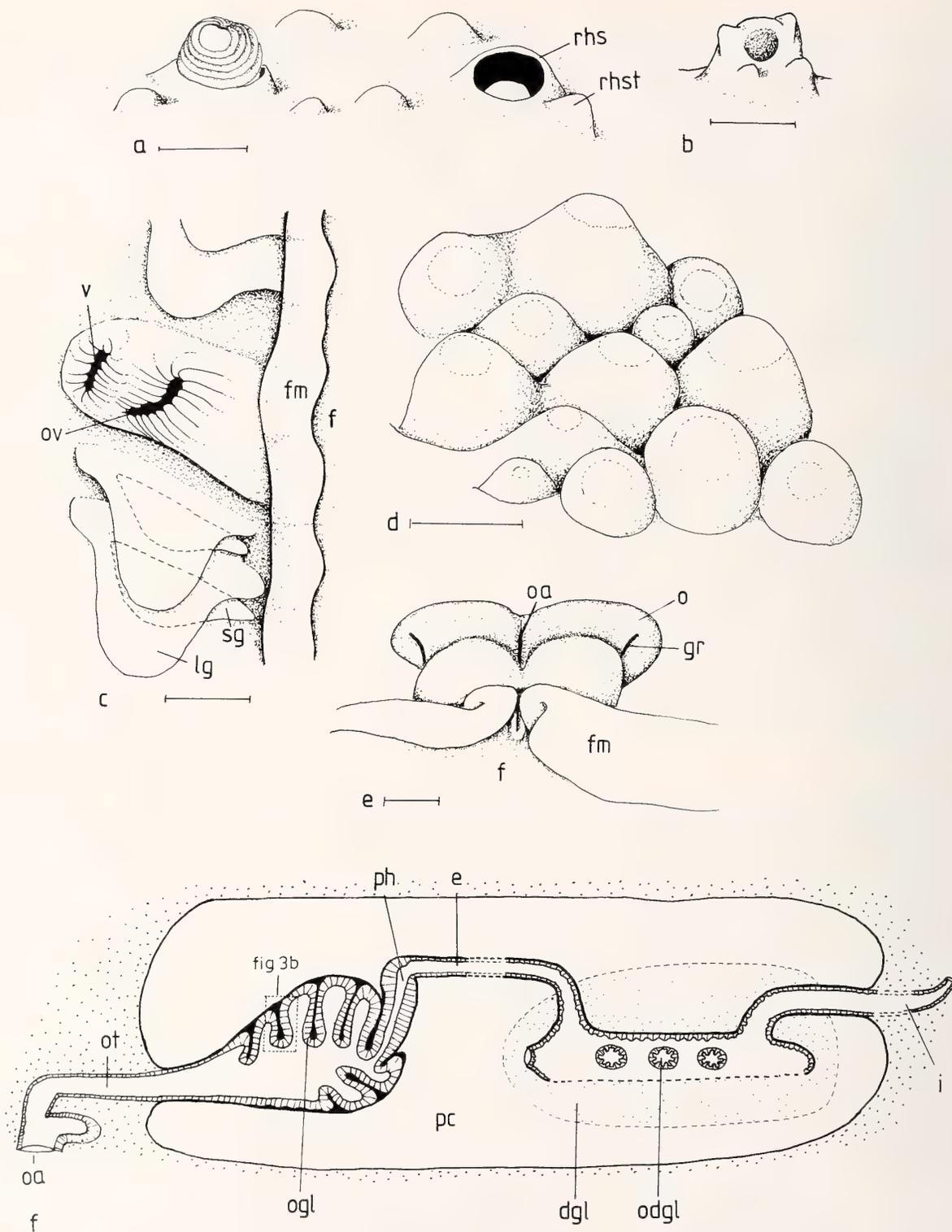


Figure 2

a-e. External morphology, details; scales 1 mm. a. Openings of the rhinophoral cavities. b. Anal papilla. c. Ventral side; genital papilla and gill leaflets (after WÄGELE, 1984). d. Tubercles of the fixed animal; they are high and stand very close together. e. Ventral side; oral tentacles (o). f. General outline of the digestive tract, longitudinal

side of the oral tube. The muscles run caudo-medially, inserting in the dorsal body wall. The pharynx arises between these two retractor muscles, narrows after two small bends into the esophagus and then passes through the central nerve ring.

The esophagus leads directly backward and opens into the stomach (Figure 3a).

A distinct separation between the stomach and a central lumen of the digestive gland is not present: several tubes of the digestive gland open laterally into a central cavity of the digestive tract (Figure 2f: odgl), where also the esophagus ends and the intestine starts dorsally.

The digestive gland occupies nearly $\frac{2}{3}$ of the whole visceral hump. The ventral side is covered with a wide-spread network of vessels, which open into four visceral sinuses (see WÄGELE, 1984).

The intestine originates in the posterior third of the stomach, runs forward, and turns to the left, making an arch in front of the heart (Figure 3a: i). It then runs posteriorly on the right side under the pericardium and ends in the anal papilla.

Histology: Around the vestibulum and along the sides of the mouth lies a thick glandular mass; these glands open into the vestibulum or externally at the base of the oral tentacles.

The anterior oral tube is surrounded by connective tissue containing longitudinal muscular fibers laterally, and mainly transverse muscular fibers dorsally and ventrally. Cilia could not be detected by light microscopy. Goblet cells filled with basophilic grana are interspersed between the epithelial cells. The anterior oral tube seems to be very distensible: in one specimen, the oral glandular folds of the posterior oral tube (see below) were protruded out of the mouth, and the anterior oral tube was several times wider than in other specimens (Figure 1d).

The oral glands are situated inside of the posterior, club-shaped part of the oral tube (Figure 2f), the ectodermal epithelium of which projects inward, forming the folded and finger-shaped glands. The glandular folds (Figure 3b) contain, in particular, transversal and longitudinal muscle fibers. The ectodermal epithelium consists mainly of tall columnar cells, with the nuclei lying basally. Goblet cells similar to those of the oral tube are interspersed between them. Toward the apex of the glandular folds these mucus-secreting cells replace the epithelial cells. Subepithelial basophilic glands (bsgl) were recognized along the ectodermal epithelium. In the apex, additional granular glands with acidophilic contents (agl) could be seen in the connective tissue. However, it was not possible

to decide whether these glands were single glandular cells or multicellular glands.

Most fibers of each of the great retractor muscles insert in one glandular septum of the corresponding side. Other branches envelop the posterior part of the oral tube and the anterior part of the pharynx. The pharynx consists (from outside to inside) of a thin layer of connective tissue (ct), a thin layer of circular muscles (cm), a layer of fewer radial muscle fibers (rm), and a thin layer of longitudinal muscle fibers (lm). An apocrine-secreting epithelium lines the pharyngeal lumen, which in cross section has the shape of a triangle. The inner layer of longitudinal muscle fibers is well developed along the sides of the triangle (Figure 3c).

The transition into the esophagus is abrupt. The esophagus is enclosed by a thin outer layer of connective tissue, followed by a layer of circular and a thick layer of longitudinal muscle fibers. The lumen is lined by smooth columnar epithelium (Figure 3d). Cilia could not be found by light microscopy. In the layer of circular muscles two nerves were observed (Figure 3d: nv).

The entrance of the esophagus into the stomach is characterized by regular folds of the, here, ciliated cuboidal epithelium. These folds continue in the dorsal wall of the stomach. Glandular cells were not detected. Ciliated epithelial linings exist only in dorsal areas around the openings of the esophagus and intestine, and sometimes around the large entrances into the digestive gland. The ventral epithelium is similar to that of the digestive gland.

The intestine is characterized by a cuboidal ciliated epithelium (Figure 7c), which in the proximal part is highly folded and invested by muscle fibers.

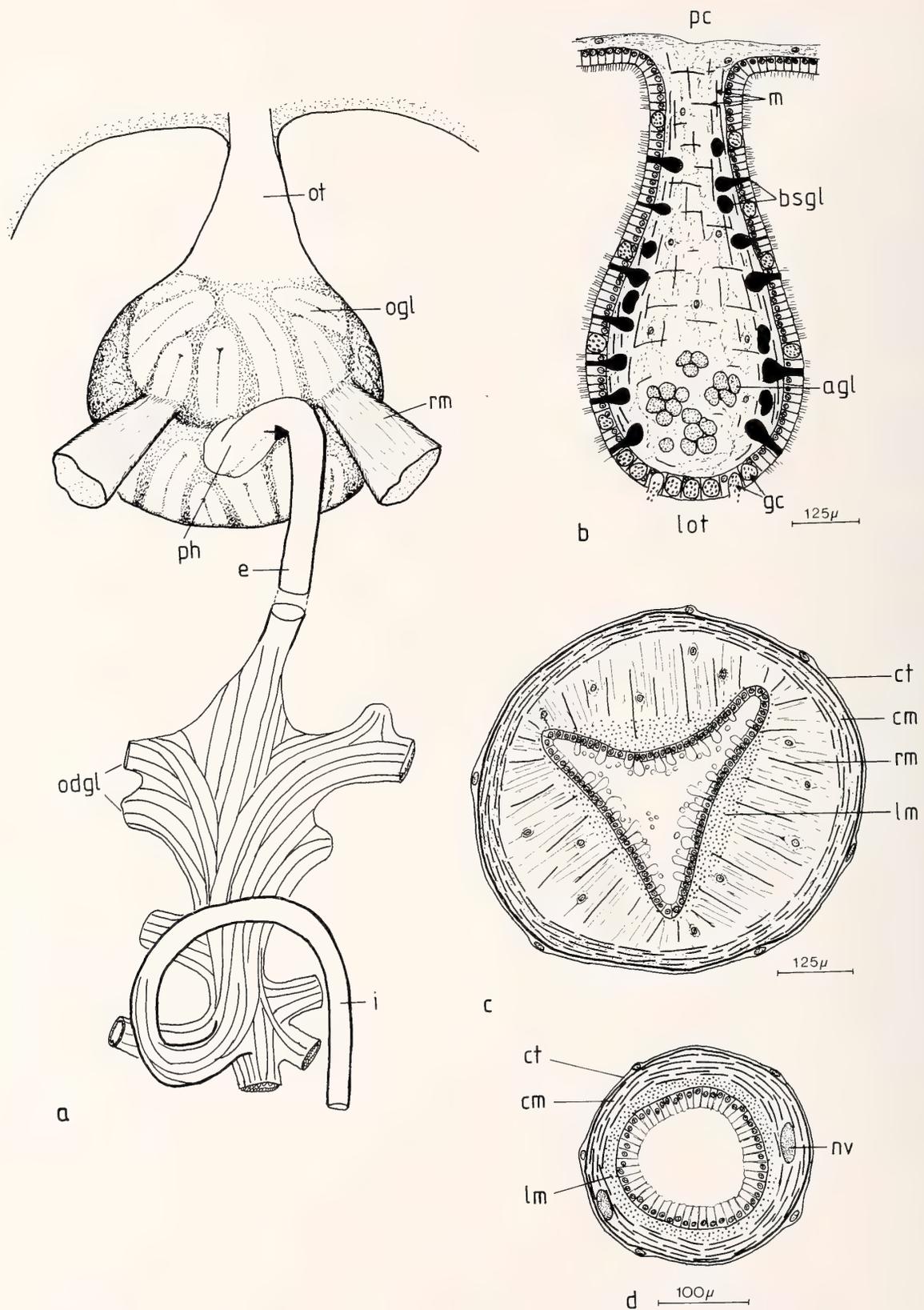
Genital Apparatus

Anatomy: The structure of the genital system of *Phyllidia pulitzeri* corresponds to that of all Doridacea: it is triauletic and bears two vesicles (bursa copulatrix and receptaculum seminis) on the vaginal duct (Figure 4a).

The hermaphroditic gonad is a more or less flat organ surrounded by the kidney dorsally and laterally and the digestive gland ventrally. Running initially for a short distance along the esophagus, the hermaphroditic duct (gonoduct gd) opens into a yellow-whitish oval ampulla (Figures 4b, c: a). The postampullar gonoduct (pogd) leads ventrally along the female gland, then divides into the vas deferens and oviduct.

After a short distance the vas deferens enlarges into the brownish prostate (pr) which, after a few bends, leads above the female gland directly to the right side of the

← section: dgl, digestive gland; e, esophagus; f, foot; fm, foot margin; gr, groove of oral tentacle (o); i, intestine; lg/sg, large/small gill leaflets; oa, oral aperture; odgl, opening into the digestive gland; ogl, oral gland; ot, oral tube; ov, oviduct; pc, perivisceral cavity; ph, pharynx; rhs, rhinophore sheath; rhst, "Rhinophorenscheidetuberkel"; v, vestibulum with vagina and vas deferens.



body. Shortly before entering the thick notum tissue, the prostate narrows and forms the ductus ejaculatorius (dej), then passes into the penis (p) without being separated from it. The penis is not armed, and accessory glands were not observed. The vas deferens opens into the vestibulum (Figures 4a, b).

The middle-sized proximal oviduct (Figure 4b: prov) leads ventrally of the female gland to the right side, where it disappears into the gland. Therefore, the bifurcation of the proximal oviduct into the glandular oviduct and the vaginal duct could not be observed macroscopically.

The vaginal duct with its two vesicles lies dorsal to the female gland. The white, oval receptaculum seminis (r) and the yellow-brownish, round bursa copulatrix (b) are both stalked. In the smaller specimens the receptacula were smaller than the bursae. From the bursa the vaginal duct leads directly into the vestibulum, thus having a common opening with the vas deferens (Figure 4a).

Histology: In specimen C1, the largest of the three histologically examined animals, the oocytes of the gonad were in the final stage of development. They measured 85 μm in diameter and were full of granular yolk. The nutritional cells were deformed by the large oocytes into elongate structures. The few regions of sperm development were at the margin of the gonad.

The epithelium of the thin preampullar gonoduct (gd) consists of cuboidal cells. Sometimes sperm were found in the lumen of the duct.

The ampulla is coated with a pavement epithelium, except near the openings of the pre- and postampullar duct, where cuboidal cells predominate. The ampullae of all examined specimens were filled with autosperm, which were distributed irregularly, not lined up (Figure 5d).

The muscular postampullar duct (pogd) is lined with a cuboidal epithelium with long cilia. The duct arises at the distal end of the ampulla and is separated from it by a small septum. At the bifurcation into the vas deferens and proximal oviduct there is a chamberlike enlargement, which is characterized by folds with long cilia.

At the beginning of the vas deferens of C1, some sperm were observed in the lumen. The transition of the proximal vas deferens (which is lined by cuboidal ciliated cells) into the glandular prostate is abrupt. The glandular cells of the prostate are high and rather slender. They are full of acidophilic grana (azan: red). Small apical nuclei in-

dicating that there are supporting cells between the secretory cells (according to SCHMEKEL, 1971). Toward the distal end of the prostate the secretory cells become smaller and disappear at the transition into the ductus ejaculatorius, where cuboidal ciliated cells, thickly underlaid by muscle fibers, dominate.

The penis is a thin, muscular tube forming the end of the ductus ejaculatorius.

The proximal oviduct and its bifurcation in the glandular oviduct and vaginal duct are lined by a cuboidal ciliated epithelium. In the proximal oviduct, spermatozoa were found, single or arranged in groups (Figure 5b: arrows).

The high columnar secretory cells of the membrane gland are densely filled with grana, whereas the contents of the columnar cells of the ripe mucous gland stain homogeneously. The distal part of the mucous gland is formed by a highly folded epithelium of lower, columnar cells, with basophilic granular contents. This seems to be the "adhesive region." In specimen C1, an area was observed with cells that had large, optically empty vacuoles within the cytoplasm (Figure 5a). These seem to be "old" mucous cells that had secreted their contents, indicating that the animal must have had an oviposition.

The vaginal duct is coated with a cuboidal, ciliated epithelium and covered with a layer of muscle fibers at the distal part in particular.

The receptaculum is filled with sperm, the heads of which face the coating epithelium. The tails of the sperm are arranged in lines toward the stalk of the receptaculum (Figure 5e).

The coating of the bursa copulatrix in specimen C1 is a pavement epithelium with large but flat nuclei. Only around the stalk does the epithelium consist of cuboidal cells, which still might have secretory function (see SCHMEKEL, 1971). The lumen is filled with aggregates of more or less dissolved sperm and prostatic secretion granula (Figure 5g). Occasionally oocyte-like cells were found (Figure 5f).

The vestibulum is lined with a columnar ciliated epithelium with mucus-secreting goblet cells between them. The surrounding tissue is interwoven with transverse and longitudinal muscle fibers.

Only spermiogenesis could be observed in the smaller specimens. The development of the prostate secretion was not so advanced as in specimen C1: in smaller specimens,

Figure 3

Anatomy and histology of the digestive tract. a. Digestive tract seen from the dorsal side; arrow, position of the central nerve ring; the internal septa of the oral glands are indicated. b. Cross section of a septum of the oral gland; position of the section see Figure 2f. c. Cross section of the pharynx. d. Cross section of the esophagus. Key: agl, acidophilic glands; bsgl, basophilic subepithelial glands; gc, goblet cells; ct, connective tissue; e, esophagus; i, intestine; lot, lumen of oral tube; (c,l,r)m, (circular, longitudinal, radial) muscle fibers; nv, nerve; odgl, opening of the digestive gland; ogl, "oral gland"; ot, oral tube; pc, perivisceral cavity; ph, pharynx; rm, retractor muscle.

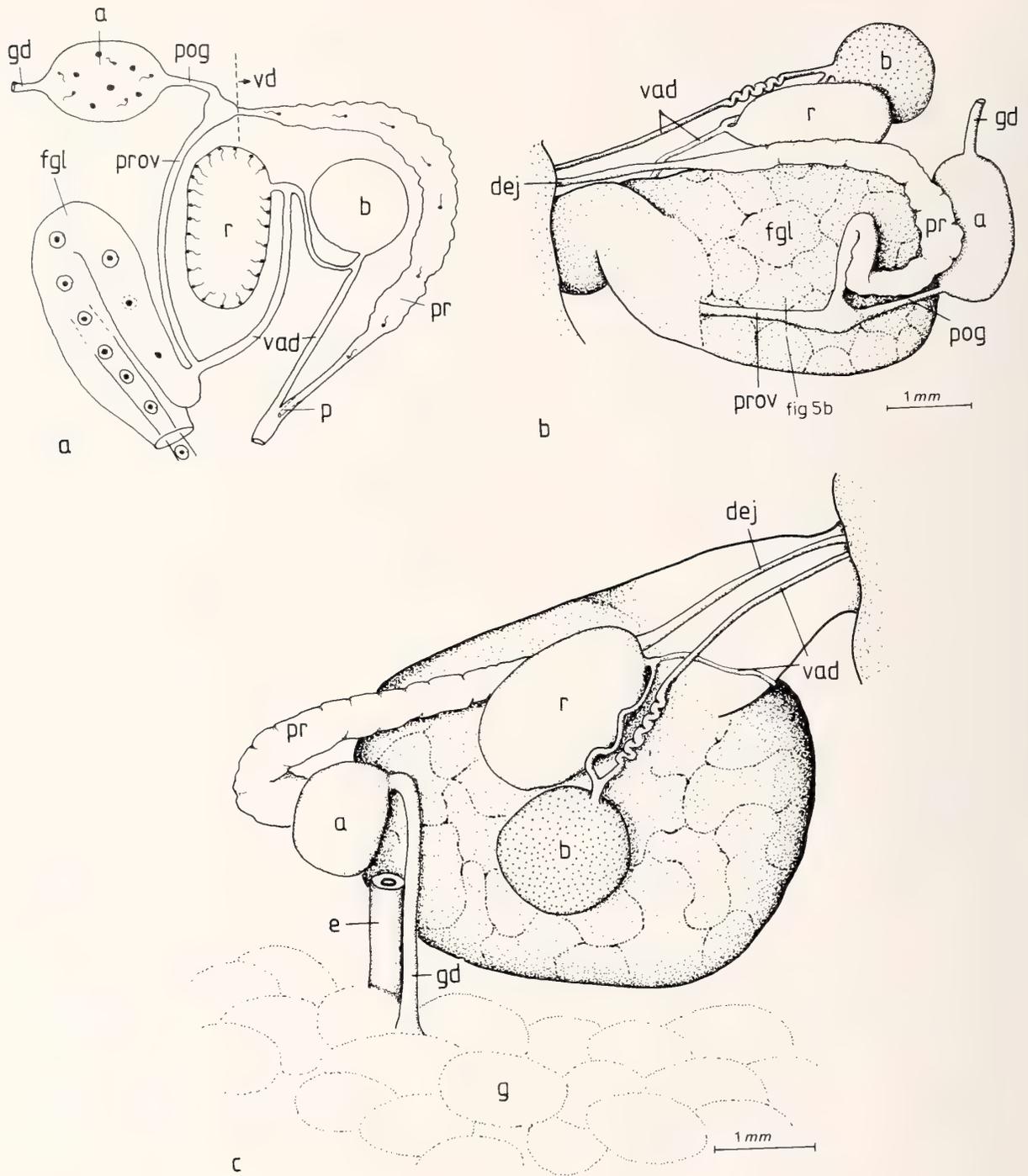


Figure 4

External morphology of genital system. a. General outline. b. *In situ*, seen from the front. c. Same as Figure 4b, dorsal side. Key: a, ampulla; b, bursa copulatrix; dej, ductus ejaculatorius; e, esophagus; fgl, female gland; g, gonad; gd, gonoduct; p, penis; pogd, postampullar gonoduct; pr, prostate; prov, proximal oviduct; r, receptaculum seminis; vad, vaginal duct; vd, vas deferens.

the contents of the cells did not stain red, but instead a bluish-gray. Also, no spermatozoa were found in the proximal oviduct.

Contrary to that of the large specimen C1, the mucous gland in the small specimens contained a great number of immature mucous cells, their contents not being of homogeneous but of granular consistency. No sperm were found in the receptacula seminis. The epithelium of the bursa consisted mainly of apocrine secretory cells (Figure 5c). A pavement epithelium, as found in C1, was not seen; this feature probably depends on the functional phase of the bursa.

Nervous System and Sensory Organs

Morphology: The central nerve ring is placed at the proximal part of the esophagus (Figures 3a: arrow; 6a). The cerebropleural ganglia are close to each other dorsally and connect by the visceral loop (vl) ventrally. All ganglia of this visceral loop are fused with the brain.

The pedal ganglia are placed close to the cerebropleural complex. The thick pedal commissure (pc) lies between the buccal commissure (bc) and the visceral loop.

The two buccal ganglia are placed slightly asymmetrically at the left side of the buccal commissure, which is as short as the other commissures.

In the following list, all nerves originating from the cerebropleural complex are designated with a C, those originating from the pedal ganglia with a P and those branching from the visceral loop with a V. Nerves lying symmetrically on both sides and innervating the same organs are marked by a +.

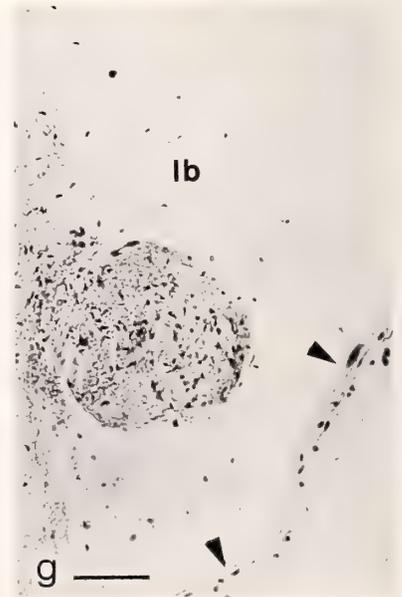
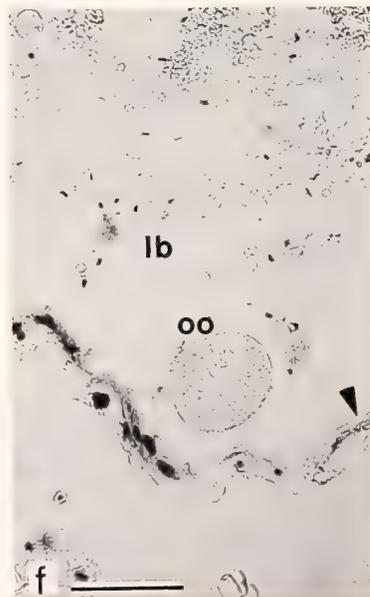
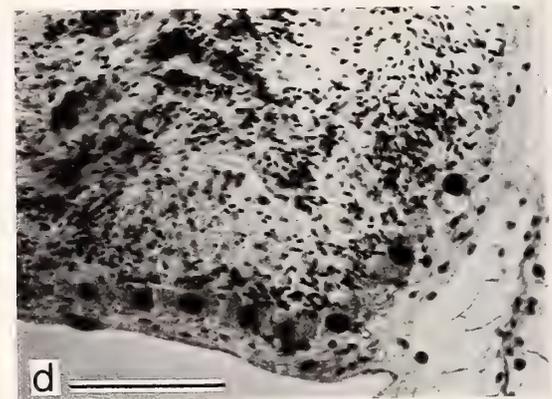
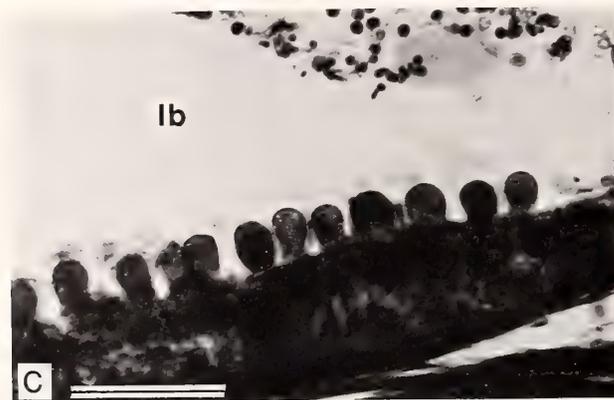
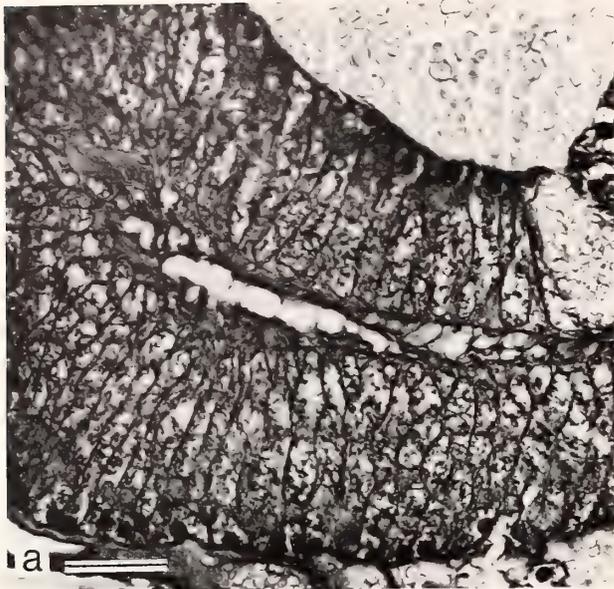
- C1+ Rhinophoral nerve; the proximal part of it forms the bulbous rhinophoral ganglion.
- C2+ This nerve runs along the oral tube to the oral tentacles.
- C3+ Optic nerve; it is very thin and shows no sign of pigmentation in *Phyllidia pulitzeri*.
- C4+ This nerve runs to the rhinophores, and branches several times in the notum; it possibly innervates the rhinophore sheaths and the anterior dorsal part of the notum.
- C5 This branch of the right C4 runs ventrally into the notum and could not further be observed.
- C6+ This stout nerve leads into the retractor muscles, ramifies, and among other organs innervates the muscle fibers of the oral gland.
- C7+ Nervus pallialis posterior (HOFFMANN, 1939); it runs backward along the lateral side of the mantle, occasionally giving off nerves leading to the kidney and heart.
- C8 This thin, unpaired nerve lies in the connective tissue of the kidney, innervating the latter and leading to the genital apparatus.
- C9 This nerve leads ventrally under the oral glandular mass and disappears into the foot.
- P1+ This single pedal nerve is very thick, runs along the posterior part of the club-shaped oral tube to the ventral side, and leads caudally under the visceral mass. It disappears into the tight tissue of the foot in the posterior third of the body.
- P2, P3 These two nerves are branches of the right pedal nerve (P1), and innervate the genital organs from the ventral side.
- V1 Visceral nerve; branching off from the visceral loop.

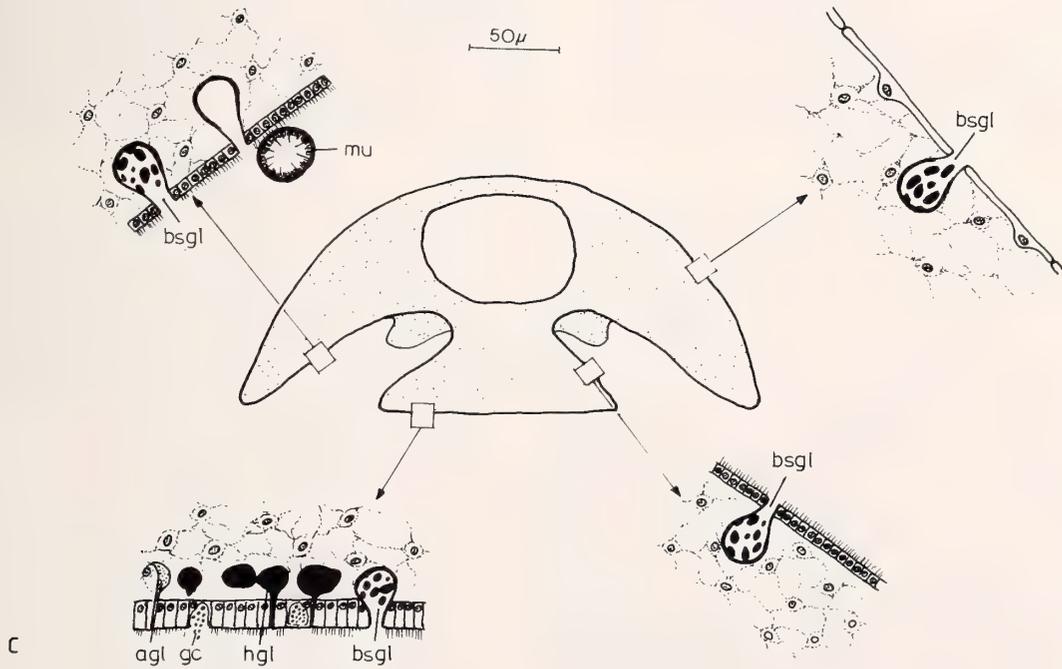
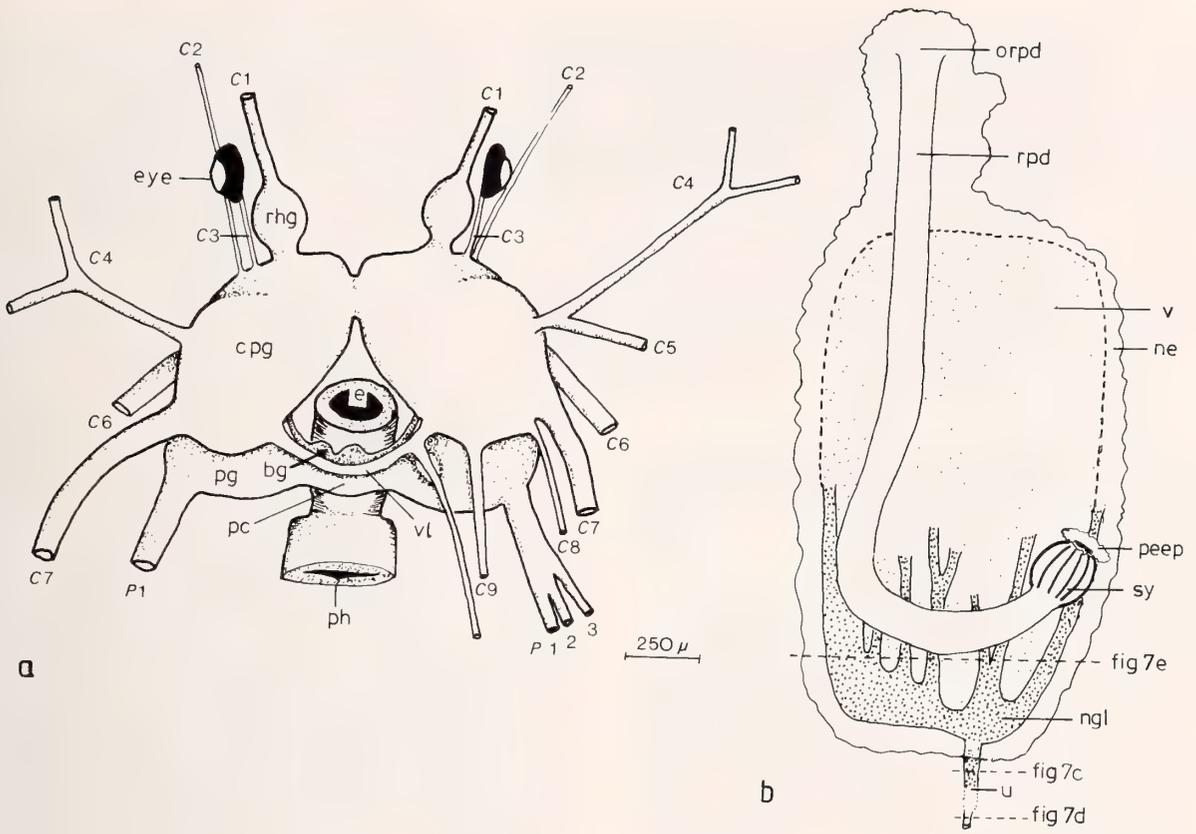
Figure 5

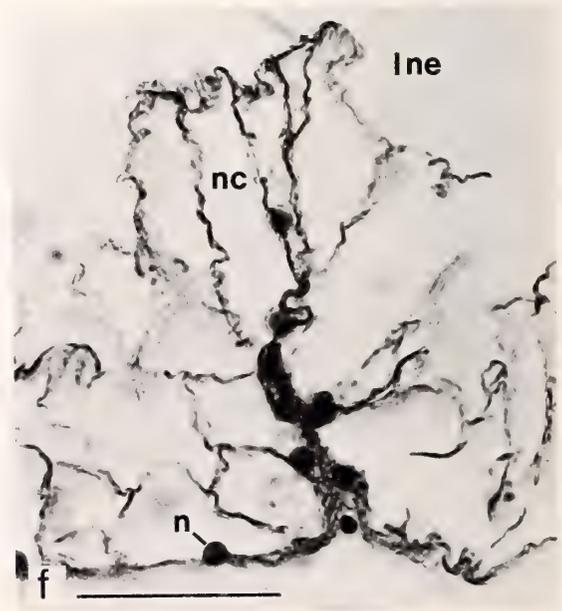
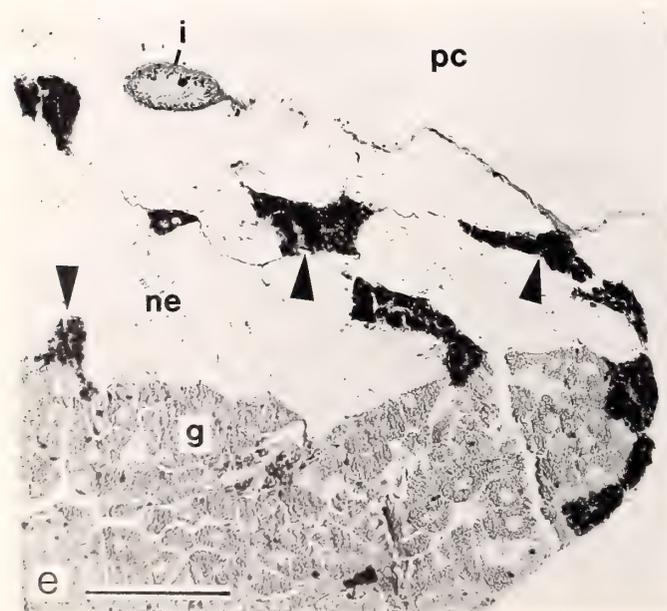
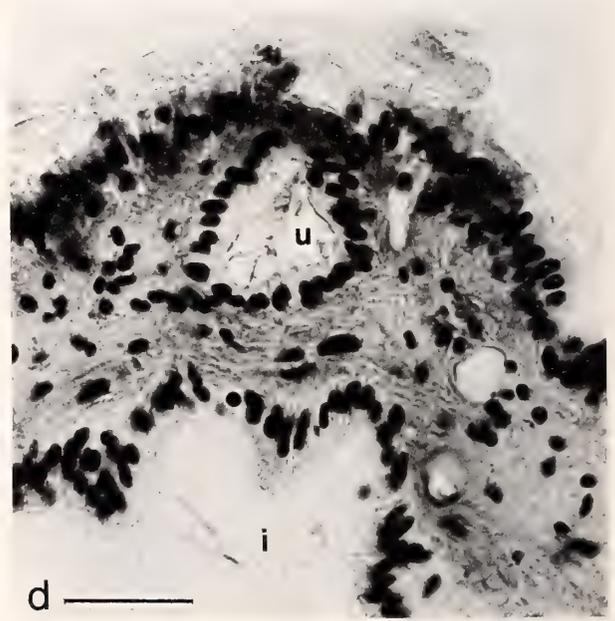
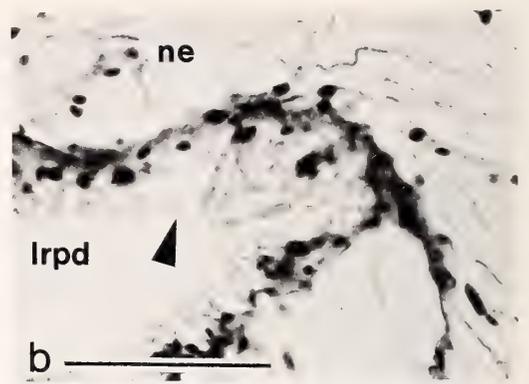
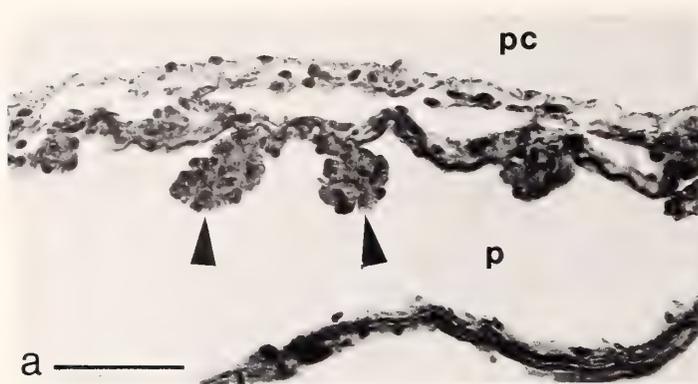
Histology of the genital apparatus. a. "Old" mucous cells of the mucous gland; May-Grünwald/Giemsa; scale 50 μm . b. Cross section of proximal oviduct: for position of the section see Figure 4b; arrows, sperm—note that their heads are turned toward the wall; May-Grünwald/Giemsa; scale 5 μm . c. Apocrine secretory epithelium of bursa copulatrix of small specimen L1; azan; scale 5 μm . d. Section of ampulla, with cuboidal epithelium; May-Grünwald/Giemsa; scale 10 μm . e. Specimen C1, section of the epithelium of the receptaculum seminis; the heads of the sperm are oriented toward the wall; May-Grünwald/Giemsa; scale 5 μm . f. Oocyte-like cell (oo) in the lumen of the bursa; arrow, epithelium of bursa; May-Grünwald/Giemsa; scale 5 μm . g. An aggregation of sperm and prostatic secretion granula; arrows, epithelium of bursa; May-Grünwald/Giemsa; scale 5 μm . Key: b, bursa copulatrix; dgl, digestive gland; lb, lumen of bursa; mgl, membrane gland; mugl, mucous gland; ogl, oral gland; oo, oocyte-like cells; r, receptaculum seminis; vad, vaginal duct.

Figure 6

a. Central nerve ring; dorsal side; at the transition of pharynx (ph), coming from ventrad, into esophagus (e); the esophagus is cut before it passes the nerve ring from ventrad. Key: bg, buccal ganglion; cpg, cerebropleural ganglion; pc, pedal commissure; pg, pedal ganglion; rhg, rhinophoral ganglion; vl, visceral loop. b. General outline of the excretory system. Key: ne, nephridium; ngl, gland in the nephridium; orpd, opening of the renopericardial duct into the nephridium; peep, pericardial epithelium; rpd, renopericardial duct; sy, syrinx; u, ureter; v, digestive gland and gonad covered by the nephridium. c. Epithelia and their position. The four types of glands: agl, acidophilic subepithelial glands (4); bsgl, basophilic subepithelial glands which stain granularly (3); gc, goblet cells (1); hgl, basophilic subepithelial glands which stain homogeneously (2); mu, "crystallized" mucus.







Histology: As mentioned above, two nerves run along the esophagus in the layer of the longitudinal muscle fibers (Figure 3d: nv). These nerves originate in the buccal ganglia and end before the esophagus passes into the stomach. Shortly after their origin in the buccal ganglia, a branch of these nerves runs in the opposite direction to the pharynx, where it shows on each side a ganglionic enlargement in the layer of the longitudinal muscles, exactly at the transition of the esophagus into the pharynx.

The epithelium of the rhinophores is composed of high columnar ciliated cells with basally lying nuclei. Gland cells were not detected. The interior part of the rhinophore contains hyaline tissue (HOFFMANN, 1939), spiculae, and small groups of longitudinal muscle fibers. Spiculae were also observed in the lamellae.

The oral tentacles have an epithelium similar to the ventral side of the notum. In the lateral grooves of the tentacles, larger aggregations of perikarya with well stained nuclei, but with little cytoplasm, were found. These aggregations always lie in hollow spaces of the hyaline tissue. They are probably nuclei of sensory cells, although they could not be recognized as such in this preparation (see HOFFMANN, 1939).

The statocyst of C1 has a diameter of approximately 90 μm . It is placed between the pedal and cerebropleural ganglia (Figure 1c). The inner side is lined by a pavement epithelium. Above this epithelium, toward the cerebropleural ganglion, lies the thin neurilemma (Figure 1c: arrows). The statocyst is filled with 15–20 statoliths of oval to globular form. The average size of the statoliths was 6–8 μm . Cilia were not detected by light microscopy.

Excretory System

Anatomy: The excretory system (Figure 6b) communicates with the pericardium by the so-called syrinx (sy), which lies ventral to the pericardium at the right side. From there, the renopericardial duct (rpd) leads forward under the pericardium to the region of the blood gland, where it enters the nephridium (ne) from the dorsal side.

The nephridium covers the gonad laterally and dorsally and also reaches anteriorly between the viscera. The ramified appearance of the nephridium is caused by the branched vessels in the wall, starting with the aorta posterior.

The ureter originates from the caudal end of the nephridium and opens to the outside on the right side at the base of the anal papilla.

Histology: The wall of the syrinx, a thick layer of longitudinally plicated tissue, is covered at the inner side with a cuboidal epithelium with long cilia. At the transition from syrinx to the renopericardial duct, the cuboidal cells are replaced by apocrine secreting cells (Figure 7b: arrows). In the posterior part of the body, the renopericardial duct is submerged into the nephridium, but in the anterior part it lies dorsal of the nephridium.

The lamellae and folds of the nephridial tissue are mainly formed by the ventral wall of the nephridium. In the posterior part they divide the nephridium into chamberlike areas (Figure 7e). In the folds a thin layer of tissue, with blood vessels in between, separates the cells from each side.

The nephrocytes are large cells with large, nonstaining spaces (Figure 7f).

At the posterior part of the specimen a glandular complex that lies mainly dorsally and laterally on the visceral mass was observed (Figure 6b: ngl). From there, tubuli with a unistriate glandular epithelium and lying in the nephridial tissue reach anteriorly. In specimen L1 these ducts were missing.

The gland is connected with the proximal ureter, where the same large secreting cells of the glandular mass are present between small epithelial cells (Figure 7c: u). The submerged, secreting cells have basal nuclei, whereas the nuclei of the epithelial cells lie apically. Near the end of the ureter the secreting cells are replaced by small ciliated, cuboidal cells (Figure 7d).

Pericardial glands (Figure 7a) which project into the lumen of the pericardium are attached to the anterior dorsal part of the pericardial wall.

Histology of the Epidermis

Figure 6c shows a general outline of the epidermis.

Dorsal notum epithelium: The epithelium is formed by large but flat cells (pavement epithelium) with submerged nuclei. Cilia were not observed. Some basophilic, submerged secretory cells (bsgl) are scattered all over the dorsal side. The contents of these secreting cells have a

Figure 7

Anatomy and histology of excretory system. a. Section of the dorsal pericardial epithelium with pericardial glands (arrows); hemalaun/lightgreen; scale 5 μm . b. Cross section of renopericardial duct; note the apocrine secretory cells (arrow); hemalaun/lightgreen; scale 10 μm . c. Proximal ureter with secretory cells; for position of section see Figure 6b; May-Grünwald/Giemsa; scale 10 μm . d. Distal ureter; May-Grünwald/Giemsa; scale 5 μm . e. Glandular ducts lying in the nephridial tissue (arrows); for position of the section see Figure 6b; May-Grünwald/Giemsa; scale 25 μm . f. Nephrocytes (nc) of a septum; hemalaun/lightgreen; scale 5 μm . Key: g, gonad; i, intestine; lne, lumen of the nephridium; lrpd, lumen of the renopericardial duct (rpd); n, nucleus; nc, nephrocytes; ne, nephridial tissue; pc, perivisceral cavity; pe, pericardium; u, ureter.

granular appearance. Sometimes the contents evidently had been secreted (mu), and only the lining of the epithelium was stained (dark violet: May-Grünwald/Giemsa). Submerged acidophilic glands (agl) were occasionally found.

Ventral notum epithelium: This epithelium consists of cuboidal ciliated cells. The submerged basophilic glands, mentioned above, are abundant here. Acidophilic glands are not present.

Dorsal foot epithelium: This appears to be the same as the ventral notum epithelium; only basophilic glands are represented.

Ventral foot epithelium: Columnar ciliated cells with basal nuclei dominate.

Four different types of glands are to be found in the ventral foot, and, of these, Types 1 and 2 are glands confined to the foot epithelium.

Type 1: goblet cells (gc) with basophilic granular contents interspersed in the epithelium (see also digestive tract: oral tube and oral gland);

Type 2: subepithelial basophilic glands, with contents stained homogeneously (hgl);

Type 3: subepithelial, granularly stained, basophilic glands;

Type 4: subepithelial acidophilic glands, especially at the margin of the foot.

DISCUSSION

External Morphology

The external appearance of the specimens found in Khalkidhiki and Malta agrees with that of the animals photographed (1974a; animals from Portofino) and described by BARLETTA (1974a, b) and by SCHMEKEL & PORTMANN (1982, animals from Capo Miseno and Ponza).

Digestive System

In accordance with HOFFMANN (1939) I regard the glandular complex at the opening of the mouth as the foot gland and not as the labial gland, because it lies mainly ventrally and laterally of the vestibulum, not dorsally.

BERGH (1868–69) shows drawings of cross sections through the distal oral tube of *Phyllidia pustulosa* Cuvier, 1804, and *P. varicosa* Lamarck, 1801. These clearly show that the oral tube has inner folds in addition to the lobed or papillate glands at the outside of the posterior oral tube. These outer glands are missing in *P. pulitzeri*. Bergh observed these inner folds in other species too, but did not describe them in detail. BERGH (1889) also mentioned in the first description of *Phyllidiopsis striata* foldlike features in the enlarged part of the oral tube. Because of the lack of anatomical examinations of the outer and inner oral glands and the total absence of histological examinations, possible homologies among different genera of the family Phyllidiidae cannot be discussed.

An “intrabulbous” part of the pharynx, such as observed by BERGH (1868–69) in several species (*Phyllidia varicosa*, *P. nobilis* Bergh, 1868–69), is not present. The pharynx shows some peculiarities in lacking features typical for other groups of the Opisthobranchia: no labial disc or other armament is present at the transition from the oral tube to the pharynx, and radula, mandible, and salivary glands are absent.

A stomach completely separate from the digestive gland, as possessed by other Doridacea, does not exist within the Phyllidiidae. The dorsal part of the central lumen of the digestive tract, where the openings of esophagus and intestine are located, is part of the stomach, whereas the ventral part, with the openings into the digestive gland, seems to represent the central collecting cavity of the digestive gland (see HOFFMANN, 1939). The digestive gland corresponds to the holohepatic type. A caecum is absent. No cuticular structures could be found in the entire digestive system.

Genital Apparatus

The anatomy of the genital apparatus of the specimens examined in this study agrees with the description given by SCHMEKEL & PORTMANN (1982). All examined specimens were sexually mature. The largest of the three histologically examined specimens (C1) seemed to be on the verge of oviposition. This is indicated by the ripe eggs of the gonad, the spermiogenesis restricted to the glandular margin, and the stout membrane gland. No eggs were found in the ampulla or in the distal parts of the genital ducts. This was to be expected, because eggs are transported through the gonoduct and oviduct only during oviposition (SCHMEKEL, 1971).

The smallest of the specimens examined histologically (L1) was in the protandrous phase. Eggs were not yet developed.

Whether the sperm in the proximal oviduct of the larger specimen were autospERM or not, could not be determined.

The structure and position of the membrane gland and the mucous gland are as in other Doridacea (see SCHMEKEL, 1970, 1971). The large mucous gland envelops the tightly coiled membrane gland.

The size of the receptaculum seminis in relation to the size of the bursa probably depends on the quantity of sperm present in the receptaculum. In accordance with this, the empty receptaculum of L1 is small in relation to the bursa, whereas the receptaculum of C1, which was filled with sperm, was larger than the bursa. In the bursa, a dissolution of sperm and of the prostate secretion takes place (SCHMEKEL, 1971).

Nervous System

The enumeration of the nerves and the records of the innervations of organs are still incomplete. To gain a more

accurate conception of innervation more material is necessary.

In some phyllidiids the connectives of the buccal ganglia are very long (see IHERING [1877] for *Phyllidia varicosa*; RISBEC [1956] for *P. honloni* Risbec, 1956; BOUCHET [1977] for *Phyllidiopsis gynenopla* Bouchet, 1977) and the buccal ganglia lie near the stomach. In others they are short (see RISBEC [1956] for *Phyllidia sereni* Risbec, 1956; MARCUS & MARCUS [1970b] for *Phyllidia tula* Marcus & Marcus, 1970) as in *Phyllidia pulitzeri*.

Several authors describe gastro-esophageal ganglia lying near the buccal ganglia (IHERING, 1877; RISBEC, 1928, 1956; MARCUS & MARCUS, 1970a; EDMUNDS, 1972). It may be possible that the ganglionic enlargements of the nerves in the pharyngeal layer of the longitudinal muscle fibers represent the gastro-esophageal ganglia in *Phyllidia pulitzeri*. This would mean that in this species these ganglia are only detectable by histological examinations.

Excretory System

A sphincter muscle around the opening of the syrxinx in the pericardium, as described by HANCOCK (1864) for some dorids, is absent in *Phyllidia pulitzeri*.

The renopericardial duct in other dorids is described as lying ventral to the nephridium (see SCHMEKEL & PORTMANN, 1982). In *Phyllidia pulitzeri* it is submerged into the nephridium and is very long as compared with the renopericardial ducts of other Doridacea.

The function of the great glandular complex in the posterior part of the visceral mass is not clear. Whether this gland also exists in other dorids has yet to be examined. BABA (1937) describes in *Okadaia* an accessory renal gland that is separated from the nephridium. This accessory gland opens with a duct into the middle of the ureter. Further investigations must be made before possible homologies can be discussed.

Epidermis

Whether the glands are single glandular cells or multicellular glands could not be determined in the present study.

The basophilic granular type of gland (type 3) seems to be responsible for the secretion of the mucus that "crystallizes" to small globules during fixation with formaldehyde. Sometimes these globular structures could be found even within the glands. Strangely enough, this phenomenon is only mentioned once in the literature (ELIOT, 1910, for *Phyllidiopsis carinata* Eliot, 1910), although Schmekel's specimen from Ponza and also that described by PRUVOT-FOL (1962) have this "crystallized" mucus. The existence of the crystallized mucus apparently depends on the use of certain fixatives. In the presence of acetic acid, which is part of Bouin's fluid and nearly all staining fluids, the globules dissolve. Whether this mucus is identical with the mucus in *Phyllidia varicosa*, described by JOHANNES (1963), is not clear. According to him this mucus, having

a pH of approximately 7, can be secreted in great quantities within a few seconds, and has a poisonous effect on many invertebrates and vertebrates.

Comparing the histological features of the oral gland and the ventral foot epithelium it is remarkable that, except for the basophilic granular type which is absent in the oral gland, both epithelia have the same gland types.

Taxonomic Remarks on the Mediterranean Species of *Phyllidia*

Three species of the genus *Phyllidia* are known from the Mediterranean at present: *P. rolandiae* Pruvot-Fol, 1951; *P. aurata* Pruvot-Fol, 1952; and *P. (Phyllidiopsis) pulitzeri* Pruvot-Fol, 1962.

PRUVOT-FOL (1952) was in doubt as to whether *Phyllidia rolandiae* and *P. aurata* should be placed within the genus *Phyllidia*. Although they differed in some features (e.g., they lack the black color so typical for almost all species of the family Phyllidiidae), she did not want to erect a new genus based on only two specimens. As she did not dissect *P. pulitzeri*, she was uncertain as to which genus it belonged. The present study settles this problem: similar to the descriptions of the type species of *Phyllidia* (*P. varicosa* Lamarck, 1801, described by BERGH, 1868-69), *P. pulitzeri* has a posterior club-shaped oral tube. Furthermore, there is no oral gland lying free ventral to the oral tube; therefore, it cannot belong to the genus *Phyllidiopsis*.

When the descriptions of *Phyllidia rolandiae* and *P. pulitzeri* are compared, no differences of taxonomic value can be detected. Unfortunately, information given on the same specimens differs in subsequent publications, and the first descriptions of these species were inadequate. Many features of *P. rolandiae* can only be inferred from PRUVOT-FOL's (1952) description of *P. aurata*. The gills of *P. aurata* are said to be "moins saillantes"; hence, those of *P. rolandiae* have to be bigger, similar to those of *P. pulitzeri*. Information on features such as size is not sufficiently reliable, especially in organs where different kinds of fixation may cause variability. The same applies to the form and size of the tubercles as demonstrated for *P. pulitzeri* in the present study.

The only differences between *Phyllidia rolandiae* and *P. pulitzeri* seem to be the shape of the surface of the tubercles ("bosselés" in *P. rolandiae* [PRUVOT-FOL, 1951: 37], smooth in *P. pulitzeri*) and the isolated gland near the posterior part of the oral tube in *P. rolandiae*, which is lacking in *P. pulitzeri*. In the first description of *P. pulitzeri*, PRUVOT-FOL (1962:568-569) differentiates between large tubercles, composed of five or six translucent "spherules" and smaller tubercles, composed of one, two, or three "spherules." She further states "Elles tiennent solidement au tégument; et ceci, en plus de la disposition plus ou moins régulière sur le manteau, exclut l'idée d'un artefact, qu'il fallut tout d'abord écarter, à cause de leur forme sphérique insolite." What she describes here very

likely is the mucus that, indeed, can hardly be removed from the surface, being partly crystallized in the epithelium. This assumption is supported by the fact that, in Pruvot-Fol's figure of *P. pulitzeri*, some globules are drawn on the ventral side of the notum.

Unfortunately a re-examination of the holotypes of the three Mediterranean species is not possible, as the holotypes of *Phyllidia rolandiae* and *P. pulitzeri* are considered to be lost (personal communication from Dr. P. Bouchet, Paris) and the holotype of *P. aurata*, located at the Muséum National d'Histoire Naturelle in Paris, is totally dissected, so that no organs are left except the notum.

The examination of this notum revealed that *Phyllidia aurata* is clearly distinguishable by the granular appearance of its tubercles. This granular surface is caused by the spiculae with their outwardly pointing ends. The tubercles of *P. aurata* are arranged in lines (not mentioned by PRUVOT-FOL, 1952), as can be seen in the fixed holotype, although this is difficult to make out, as it is in the fixed specimens of *P. pulitzeri*.

The possibility cannot be excluded that *Phyllidia rolandiae* is identical to one of the other two Mediterranean species of the genus. Most of the few features known (color not known, tubercles "bosselés," gills larger than in *P. aurata*) cannot be used to characterize a species. As to the only feature of importance, the "couche glandulaire," the possibility of confusion with the blood gland must be considered. *Phyllidia rolandiae* also has a small anal tubercle, which is thought to be absent in *P. aurata* but is present in *P. pulitzeri*. In my specimens of *P. pulitzeri*, however, this feature shows great variability. Therefore, at present *P. rolandiae* cannot be distinguished from the other species. Certainly, the "*P. rolandiae*" mentioned by BARASH & DANIN (1982) is a *P. pulitzeri*. Thus, all evidence seems to indicate that *P. rolandiae* has to be regarded as a *nomen dubium*.

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LITERATURE CITED

- BABA, K. 1937. 8. Contribution to the knowledge of a nudibranch *Okadaia elegans* Baba. Japanese Journal Zoology 7: 147-190.
- BARASH, A. & Z. DANIN. 1982. Mediterranean Mollusca of Israel and Sinai: composition and distribution. Israel Journal of Zoology 31(3-4):86-118.
- BARLETTA, G. 1974a. Genus: *Phyllidia* Cuvier, 1798. *Phyllidia pulitzeri* Pruvot-Fol, 1962. Schede Malacol. Mediterr. No. 43:1-4.
- BARLETTA, G. 1974b. Secondo reperto di *Phyllidia pulitzeri* Pruvot-Fol, 1962. Natura - Soc. Ital. Sci. Nat., Museo Civ. Ster. Nat. e Acquario Civ., Milano 65(1-2):25-32.
- BERGH, R. 1868-69. Bidrag til kundskab om Phyllidierne, en anatomisk Undersøgelse. Naturhist. Tidsskr. 5:357-542.
- BERGH, R. 1873. Neue Nacktschnecken der Südsee, malacologische Untersuchungen. J. Mus. Godeffroy (1):65-96.
- BERGH, R. 1875. Neue Nacktschnecken der Südsee, malacologische Untersuchungen. J. Mus. Godeffroy 8:91-116.
- BERGH, R. 1876. Neue Beiträge zur Kenntnis der Phyllidien. Verh. Zool.-Bot. Ges. 25:659-674.
- BERGH, R. 1889. Malacologische Untersuchungen, 16. Nudibranchien vom Meere der Insel Mauritius. In: C. Semper, Reisen im Archipel der Philippinen, 2. Teil, 2. Bd.:815-872.
- BOUCHET, P. 1977. Opisthobranches de profondeur de l'océan Atlantique: 2—Notaspidea et Nudibranchiata. J. Molluscan Stud. 43(1):28-66.
- EALLES, N. B. 1938. A systematic and anatomical account of the Opisthobranchia. John Murray Exped. (Brit. Mus. Natur. Hist.) Sci. Rep. 5, no. 4, London: 77-122.
- EDMUNDS, M. 1972. Opisthobranchiate Mollusca from the Seychelles, Tanzania, and the Congo, now in the Tervuren Museum. Revue Zool. Bot. Afr. 85(1-2):67-92.
- ELIOT, C. N. E. 1903. Nudibranchiata, with some remarks on the families and genera and description of a new genus, *Doridomorpha*. Pp. 540-573. In: J. S. Gardiner (ed.), The fauna and geography of the Maladive and Laccadive Archipelagoes 2. Cambridge.
- ELIOT, C. N. E. 1904. On some nudibranchs from East Africa and Zanzibar. 6. Proc. Zool. Soc. Lond. for 1904:268-298.
- ELIOT, C. N. E. 1910. Nudibranchs collected by Mr. Stanley Gardiner from the Indian Ocean in H. M. S. Sealark. Trans. Linn. Soc. Lond. 13:411-438.
- HANCOCK, A. 1864. On the structure and homologies of the renal organ in the nudibranchiate Mollusca. Trans. Linn. Soc. Lond. 24:511-530.
- HECHT, E. 1895. Contributions à l'étude des nudibranches. Mém. Soc. Zool. France 8:539-711.
- HOFFMANN, H. 1939. I. Opisthobranchia. In: H. G. Bronn (ed.), Klassen und Ordnungen des Tierreiches. Bd. 3, Abt. 2, Buch 3. 1247 pp.
- IHERING, H. VON. 1877. Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken. Verlag Wilhelm Engelmann: Leipzig. 290 pp.
- JOHANNES, R. E. 1963. A poison-secreting nudibranch (Mollusca: Opisthobranchia). Veliger 5:104-105.
- MARCUS, E. 1962. Opisthobranchs from Florida and the Virgin Islands. Bull. Mar. Sci. 12(3):450-488.
- MARCUS, E. & E. MARCUS. 1970a. Some gastropods from Madagascar and west Mexico. Malacologia 10(1):181-223.
- MARCUS, E. & E. MARCUS. 1970b. Opisthobranch mollusks from the southern tropical Pacific. Pacific Sci. 24:155-179.
- PRUVOT-FOL, A. 1951. Étude des nudibranches de la Méditerranée. Arch. Zool. Exp. Gén. 88(1):1-80.
- PRUVOT-FOL, A. 1952. Un nouveau nudibranch de la Méditerranée: *Phyllidia aurata* n. sp. Bull. Soc. Zool. Fr. 77(5-6):408-411.
- PRUVOT-FOL, A. 1962. Deux très rares nudibranches de la Méditerranée. Bull. Soc. Zool. Fr. 87(5-6):566-569.

- RISBEC, J. 1928. Contribution à l'étude des Nudibranches Néocalédoniens. Faune Colon. Fr. 2. 328 pp.
- RISBEC, J. 1956. Nudibranches du Viet-Nam. Archs. Mus. Natur. Hist. Natl. Paris (6)4:5-78.
- ROMEIS, B. 1968. Mikroskopische Technik. R. Oldenbourg Verlag: München, Wien, 16. Auflage. 757 pp.
- SCHMEKEL, L. 1970. Anatomie der Genitalorgane von Nudibranchiern (Gastropoda, Euthyneura). Pubbl. Staz. Zool. Nap. 38:120-217.
- SCHMEKEL, L. 1971. Histologie und Feinstruktur der Genitalorgane von Nudibranchiern (Gastropoda, Euthyneura). Z. Morph. Tiere 69:115-183.
- SCHMEKEL, L. & A. PORTMANN. 1982. Opisthobranchia des Mittelmeeres. Nudibranchia und Saccoglossa. Springer Verlag: Berlin, Heidelberg, New York. 410 pp.
- WÄGELE, H. 1984. Kiemen und Hämolympfkreislauf von *Phyllidia pulitzeri* (Gastropoda, Opisthobranchia, Doridacea). Zoomorphology 104:246-251.

The Nudibranch Genera *Onchidoris* and *Diaphorodoris* (Mollusca, Opisthobranchia) in the Northeastern Pacific

by

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Abstract. An anatomical review was conducted on the genus *Onchidoris* in the northeastern Pacific. Comparisons were based on the published literature and specimens obtained from both the North Atlantic and North Pacific oceans. *Onchidoris muricata* (Müller, 1776) occurs in both the Atlantic and Pacific oceans, and *O. varians* (Bergh, 1878) and *O. hystricina* (Bergh, 1878) are junior synonyms of this species. The nudibranch commonly considered in California to be *O. hystricina* was an unnamed species belonging to the genus *Diaphorodoris*. This new species, *D. lirulatocauda*, is described and compared with other species in the genus, including *Diaphorodoris mitsuii* (Baba, 1938) comb. nov. The relationships of the genus *Diaphorodoris* with other genera in the family Onchidorididae are discussed.

INTRODUCTION

FOUR SPECIES OF *Onchidoris* have been reported from the northeastern Pacific. The species *Onchidoris bilamellata* Linnaeus, 1767, and *O. muricata* Müller, 1776, have also been recorded from both sides of the Atlantic (THOMPSON & BROWN, 1976). *Onchidoris hystricina* (Bergh, 1878) and *O. varians* (Bergh, 1878) were described from the northeastern Pacific as cognate species of *O. muricata*. ABBOTT (1974) suggested that both these species are synonyms of *O. muricata*. Unfortunately, the type material is lost (Zoologisk Museum, Copenhagen, personal communication), and comparisons must therefore be made on the basis of the literature.

Three species of *Onchidoris* are found in British Columbian waters. *Onchidoris bilamellata* is easily recognized due to its mottled brown (rarely white) coloration and its unique habit of preying on barnacles. Another species is identical to the Californian species commonly referred to as *O. hystricina*. The third species is of the type referred to as *O. muricata* by BEHRENS (1980:67). An anatomical investigation of the latter two species was undertaken and comparisons made with *O. muricata* of the Atlantic and the literature.

Onchidoris muricata (Müller, 1776)

Doris aspera Alder & Hancock, 1842.

Doris diaphana Alder & Hancock, 1845.

Doris pallida Agassiz, 1850.

Doris ulidiana Thompson, 1845.

Lamellidoris varians BERGH, 1878:613-614; BERGH, 1879:365; BERGH, 1880a:216-219, pl. 11 (figs. 13, 14); BERGH, 1880b:67-70, pl. 11 (figs. 13, 14), pl. 13 (fig. 1); BERGH, 1890:985; BERGH, 1892:1153 (161); *syn. nov.*

Lamellidoris hystricina BERGH, 1878:605, 614, pl. 68 (figs. 17-23); BERGH, 1879:365; BERGH, 1880a:219-221; BERGH, 1880b:70-72; BERGH, 1890:985; BERGH, 1892:1153 (161); *syn. nov.*

Onchidoris hystricina (Bergh, 1878): MARCUS, 1961:28, 57, pl. 5 (figs. 89-91).

External morphology: I examined preserved specimens from Norway which ranged in length from 4 to 11 mm, from the Atlantic coast of the United States with lengths of 4 to 10 mm, and from British Columbia, Canada, from 1 to 10 mm in length. Most animals were 5-7 mm long. The body shape is oval, slightly wider and more truncate in front, with a low arch (Figure 1A). A small mantle margin overhangs the sides and foot. The mantle becomes disproportionately larger as the animal's size increases. The notum is covered with rounded tubercles, flattened and uneven on top, constricted at their bases, giving them a mushroom shape.

The tubercles are large, with a few, scattered, small tubercles. Towards the mantle edge all of the tubercles are small. The tubercles of specimens from the Canadian Pacific, Atlantic, and Norwegian Sea had the same average tubercle size. The larger tubercles of specimens from

these three areas were 0.51–0.56 mm high and 0.59–0.65 mm wide at the top.

Spicules run lengthwise in the tubercles (Figures 1B, 2A, B) and are capable of being protruded through openings in grooves along the flattened top (KRESS, 1981, figs. 5E, F). In a relaxed state the spicules do not protrude and the tubercle is an inflated mushroom shape. When contracted, the tubercles appear cylindrical with flattened spiculose tops. Short spicules radiate in a star-like pattern in the notum at the tubercle bases. In the notum there is a dense spicule arrangement that shines through the integument in a cross, transverse, circular, radiating pattern as diagrammed by ALDER & HANCOCK (1855, pl. 48 [fig. 2]). The margins of the rhinophores bear 2 (sometimes 3) tubercles, and there are 3 to 8 tubercles inside the branchial circlet, which is located on the posterior midline.

The simply pinnate, contractile gills are separate, arranged in a nearly complete, transverse oval, broken mid-posteriorly by the post-anal tubercle. Gill number varies between 6 and 18 in Pacific specimens, 8 to 14 in Atlantic specimens. The anterior-most gills are the largest, decreasing gradually in size toward the posterior.

The rhinophores are long and slender with a rectangular, flat-topped tip. The stalk is short, and most of the clavus has long sloping lamellae. The lamellae, except for the most distal one, are attached along the anterior line. Posteriorly only the first 3 or 4 are complete, with an ever-widening bare space proximally. Atlantic specimens had 9 to 20 lamellae, Pacific specimens had 6 to 10. The rhinophore margin is not raised and is smooth except for 2 (sometimes 3) tubercles which are positioned on either side of the anterior border.

The head has a semicircular velum, usually with folds to mark the triangular tentacles that are attached posteriorly.

The large foot is truncate anteriorly, thickened but not bilabiate. The foot is wider in front than behind and ends in a bluntly rounded tail which is covered by the mantle margin.

Living Pacific specimens were usually white, occasionally creamy-white, light yellow, or light orange. The notum is semitranslucent. Through it can be seen the bright red digestive gland, which in mature specimens becomes obscured by creamy gonads. In mature animals, a dark brown spot, the sperm-filled bursa copulatrix, can be seen through the anterior right side of the dorsum. Ventrally, the red digestive gland shows clearly for $\frac{2}{3}$ of the body length. It extends farther forward on the left side. The leaves of the rhinophores are dusky yellow or orange. The branchiae are lighter than the body, white or dusky yellow with an opaque white base. A color photograph appears in BEHRENS (1980:fig. 72). Atlantic specimens are either white or pale yellow, the latter color being more common at the northern end of its range (THOMPSON & BROWN, 1976).

Digestive tract and radula: The internally folded buccal tube is short, broad, and flaccid. The buccal bulb has a

dorsal rounded sucking crop with a broad median muscular band and a short stalk. The radular sac projects posteriorly. It is long, cylindrical, and usually bent to one side. The lip disk has been described as having a thick yellowish cuticle (BERGH, 1880).¹ With the aid of the scanning electron microscope, I found the lip disks of Atlantic and Pacific specimens to be finely papillate toward the central area. The opening is guarded by two ventral flaps (Figure 1C). The lip papillae were illustrated by BERGH (1878, pl. 68 [fig. 17]) for *Onchidoris hystricina*, and reported by BERGH (1880) in *O. varians*.

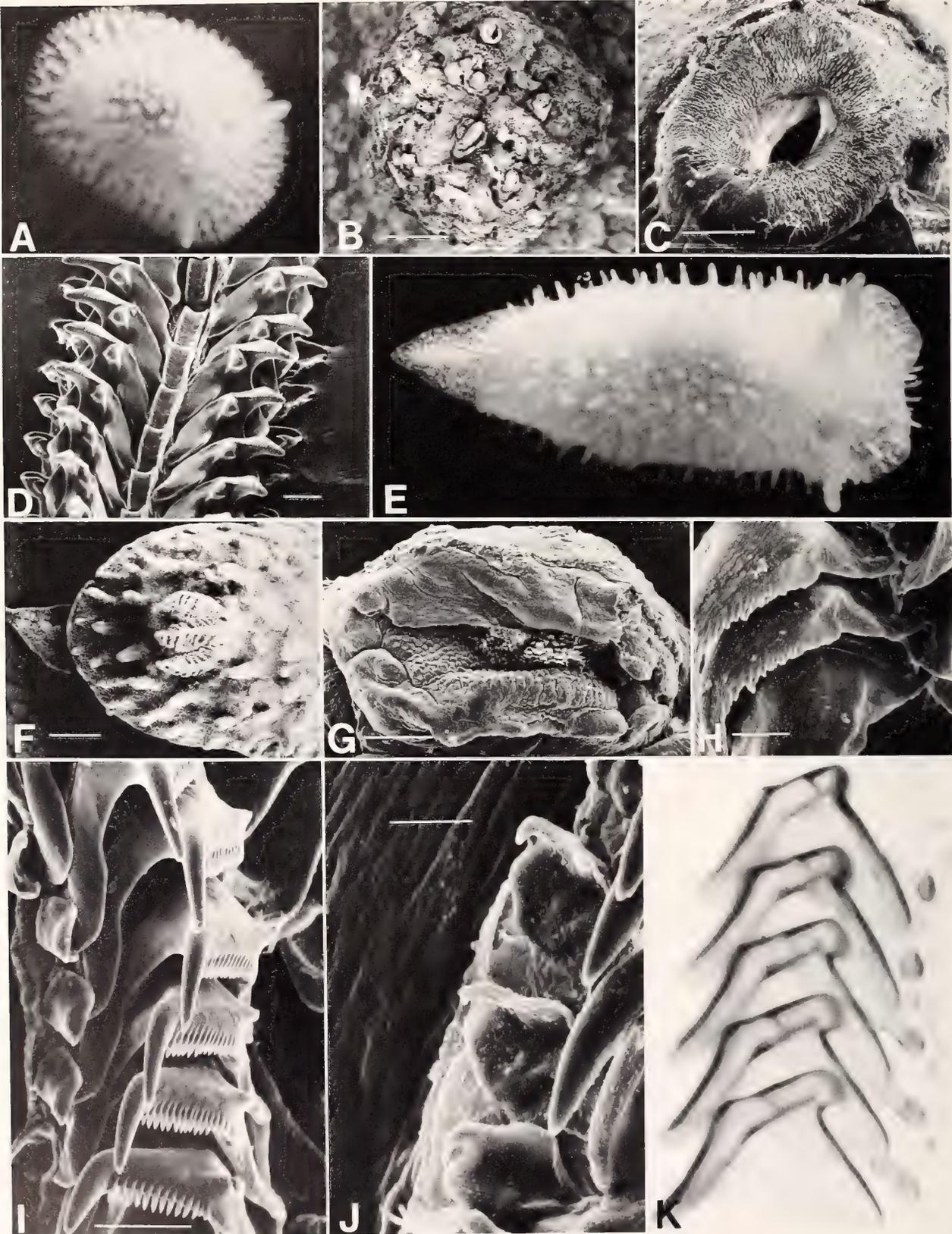
Atlantic specimens of *Onchidoris muricata* have been reported to have radulae ranging in length from 29 to 44 rows. I found that specimens from the Atlantic have from 27 to 34 rows and specimens from the Pacific have 20 to 33 rows.

The radula is narrow, with the formula 1.1.1.1.1 (Figure 1D). The central (rachidian) tooth is an elongate rectangular shape with thickened sides. In Atlantic specimens of *Onchidoris muricata* its length was 0.05 mm (BERGH, 1880). Specimens that I examined from the Atlantic had central-tooth lengths of 0.03–0.04 mm (\bar{X} = 0.04 mm; n = 9) and from the Pacific 0.02–0.06 mm (\bar{X} = 0.04 mm; n = 25).

Each large lateral tooth (Figure 1D) has a triangular-shaped base with a denticulate hook. At the base of the denticulations is a knoblike projection from which a small wing extends down the inner side of the tooth. Reported tooth height for *Onchidoris muricata* is 0.075–0.12 mm (BERGH, 1880; MEYER, 1971). My specimens from the Atlantic had a tooth height of 0.07–0.10 mm (\bar{X} = 0.08 mm; n = 8) and from the Pacific 0.04–0.10 mm (\bar{X} = 0.08 mm; n = 16). Bergh did not measure the lateral tooth height of *O. hystricina* but reported them to be smaller than the 0.12–0.17 mm he found in *O. varians*, although of the same shape (see Figures 9C, D). The number of denticles varied in Atlantic *O. muricata* from 9 to 16 and in Pacific specimens from 8 to 18. There was substantial variation in the strength of denticulation and the numbers of denticles. Older, worn teeth had the tips of the hooks ground away and the denticles extended almost to the tip as in *O. varians*. Younger teeth had a longer, straighter, smooth cusp with denticles only near the base as in *O. hystricina*.

The marginal teeth have a triangular base with a single strong recurved hook facing posteriorly (Figure 1D). *Onchidoris muricata* from the Atlantic had a marginal tooth height of 0.04 mm (BERGH, 1880). Atlantic specimens that I examined had a height of 0.03–0.04 mm (\bar{X} = 0.03 mm; n = 9), while those from the Pacific had a tooth height of 0.02–0.05 mm (\bar{X} = 0.03 mm; n = 19).

¹ Text references to BERGH (1880) refer both to BERGH (1880a) and (1880b) listed separately in the Literature Cited. They are the same paper published in two different journals.



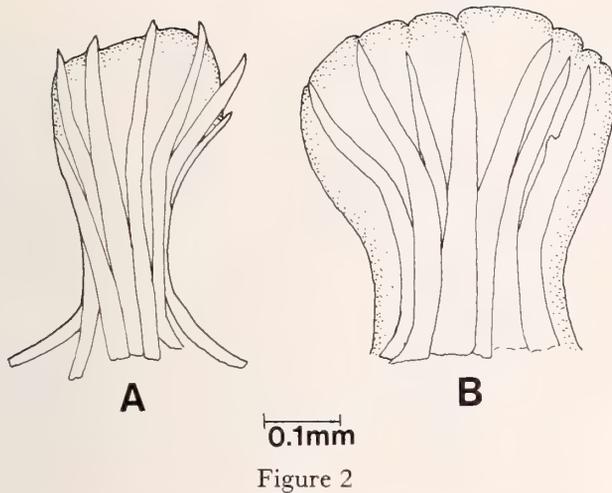


Figure 2

Tubercles of *Onchidoris muricata* showing the arrangement of the spicules. A. Contracted state. B. Relaxed state.

At the posterior end of the buccal bulb is a narrow tubular esophagus. The salivary glands are attached on either side of the base of the esophagus. BERGH (1880) described them as 2 or 3 thick, white coils in *Onchidoris muricata*, and as a large, whitish mass in *O. varians*. I found them to be small and U-shaped in both Pacific and Atlantic specimens. The stomach is buried in the digestive glands except at the junction of the intestine, where a small, round, stalked caecum is given off. The digestive glands appear as one oval reddish mass hollowed on the anterior right due to the reproductive organs. The narrow tubular intestine loops to the right around or over the caecum and runs straight to the anus, located at the posterior of the branchial cirrlet at the base of a large tubercle. The anal opening is simple and not raised. The inconspicuous renal pore is located within the cirrlet to the right of center, surrounded by tubercles.

Circulatory system: The pericardial sac contains a posterior, thin-walled, triangular auricle and a ventricle. The aorta ends in a large, granular, white, blood gland situated above the central nervous system.

Central nervous system: The central nervous system has been well described for *Onchidoris muricata* by BERGH (1880). He also described and illustrated this system for *O. varians* (pl. 13 [fig. 1]) and described it for *O. hystericina*. In all three species the cerebral and pleural ganglia are fused, ovate or rounded, and connected by a short commissure. The almost separate pedal ganglia are rounded and only slightly smaller than the cerebro-pleurals. The eyes are on moderately long, fine stalks. There were no discernible differences in this system in specimens from the Atlantic or the Pacific.

Reproductive system (Figure 3): The ovotestis consists of creamy-yellow lobules on the dorsal surface, sides, and part of the ventral surface of the digestive glands. Its histology and maturation have been studied by BEHRENTZ (1931) and TODD (1978a). The branched gonoducts of the ovotestis merge forming a thin pre-ampullary duct. This duct widens into a U-shaped ampulla, which is attached to the inner, lower curvature of the albumen gland. It narrows to form a thin post-ampullary duct, which ends at a triple junction. One branch becomes the vas deferens, another leads to the buried receptaculum seminis (fertilization chamber), and a third, the short oviduct, enters the female gland mass. The vas deferens is narrow and prostatic for a short distance. It becomes non-prostatic, looping dorsally, then enlarging into a muscular penial sac. Inside, the vas deferens coils and then straightens, ending in an unarmed, simple, bifurcate or trifurcate penis.

The vagina, which is short and muscular, has a separate opening posterior to the penial sac. The vagina leads to a bluntly rounded, blind sac, where on one side the moderately long duct to the large round bursa copulatrix is given off. The fertilization duct is long, muscular and convoluted, terminating in a buried, oval receptaculum seminis. The arrangement of the ducts is semiseriate.

The female gland mass has a separate nidamental duct ventral to the vagina. This mass has an anterior, yellowish, albumen gland and a posterior, inner, mucous gland. The receptaculum seminis is buried in the albumen gland.

The reproductive openings are located on the right side a short distance posterior to the anterior margin of the foot.

Figure 1

A. *Onchidoris muricata*, 7 mm. Photograph of a live Pacific specimen. B. Tubercle of *O. muricata*, SEM micrograph of a Pacific specimen. Scale = 100 μ m. C. Lip disk of *O. muricata*, SEM micrograph of an Atlantic specimen. Scale = 100 μ m. D. Radula of *O. muricata*, SEM micrograph of a Pacific specimen. Scale = 40 μ m. E. *Diaphorodoris lirulatocauda*, 12 mm. Photograph of a live specimen. F. Posterior half of *D. lirulatocauda* showing tubercles and gills. SEM micrograph. Scale = 1 mm. G. Lip disk of *D. lirulatocauda*, SEM micrograph. Scale = 50 μ m. H. Radula of *D. lirulatocauda*, SEM micrograph of medial area showing connecting membranous wing of laterals. Scale = 10 μ m. I. Radula of *D. lirulatocauda*, SEM micrograph of lateral and first marginal teeth. Scale = 20 μ m. J. Radula of *D. lirulatocauda*, SEM micrograph of inner marginal teeth. Scale = 10 μ m. K. Radula of *D. lirulatocauda*, light microscope photograph of one half row including reduced outer platelet.

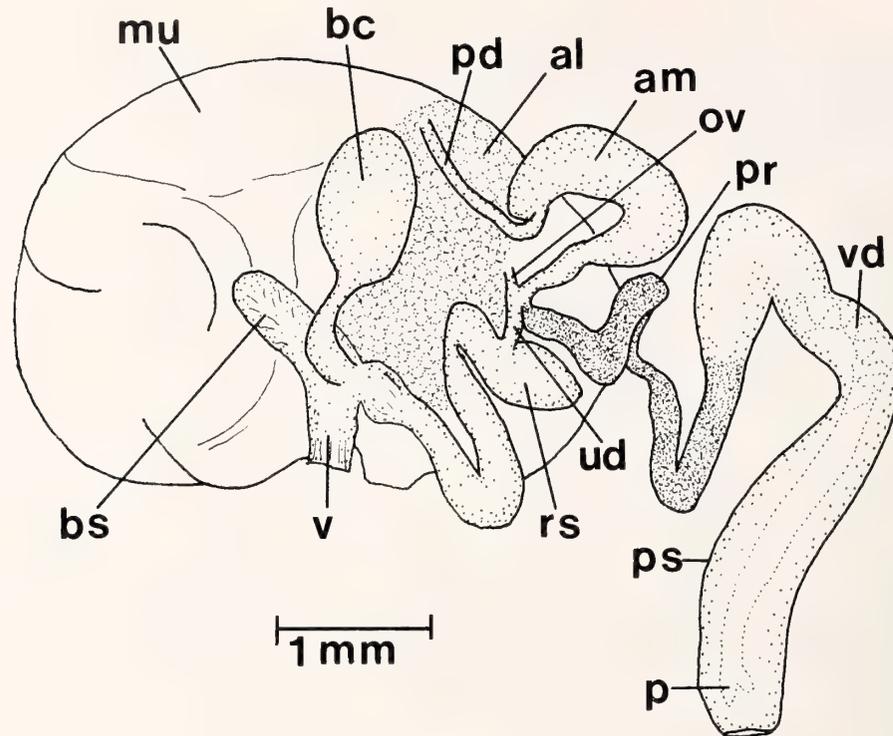


Figure 3

Onchidoris muricata reproductive system, drawn using a camera lucida. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; bs, blind sac; mu, mucous gland; ov, oviduct; p, penis; pd, preampullary duct; pr, prostate; ps, penial sac; rs, receptaculum seminis; ud, uterine duct; v, vagina; vd, vas deferens.

This system was found to be essentially the same for Atlantic and Pacific specimens. It agrees with the description given for *Onchidoris muricata* by BERGH (1880) and with his partial descriptions for *O. varians* and *O. hystricina*. It should be noted that Bergh did not consider the vas deferens (spermatoduct) of *O. hystricina* to be very long. The reproductive system was reconstructed by BEHRENTZ (1931, figs. 6–9) using serial sectioning. Behrentz noted that the penis has three “horns.” On specimens of *O. muricata* that I examined, the penis was often a simple cylinder or showed two lobes.

Ecology: *Onchidoris muricata* occurs in the low intertidal zone and shallow subtidal to 20 m (THOMPSON & BROWN, 1976). It ranges from the White Sea to Cape Finisterre, Greenland, from Nova Scotia to Rhode Island in the Atlantic, and from Kyska, Alaska, to California in the Pacific. The southern range limit is uncertain due to confusion with the next species and an undescribed *Adalaria* species. I examined specimens from as far south as Abalone Beach, Humboldt County, California and MARCUS's (1961) specimen came from Dillon Beach, California.

In Britain this species eats a variety of encrusting bryozoans, especially *Electra pilosa*, *Membranipora membranacea*, and *Alcyonidium polyoum* (THOMPSON & BROWN,

1976; TODD, 1978b, 1979a, 1981). In the Pacific it also eats a variety of encrusting bryozoans, most of which are cheilostomate. Specimens have been reported feeding on *Reginella mucronata*, *Eurystomella bilabiata*, and *Micro-porella cribosa* (MCDONALD & NYBAKKEN, 1978; GODDARD, 1984). In British Columbia the species feeds most often on *Schizoporella unicornis* but has also been found on *Hippodiplosia insculpta*, *Cheliopora praelonga*, *Lagenipora* sp., *Microporina borealis*, and *Membranipora serrilamella* (personal observations). It feeds by sucking the bryozoan polypides out of their skeletons, approximately 19–32 polypides being eaten per adult per day (TODD, 1979a, 1981) at a rate of 0.4–5.2 polypides per hour (TODD, 1979b, 1981). The nudibranchs are normally found on rocks and under boulders. TODD (1978b) found that their distribution on the undersurface of boulders showed aggregation, which was particularly pronounced during breeding season.

The life cycle has been studied in Sweden (BEHRENTZ, 1931) and in Britain (THOMPSON, 1961b; MILLER, 1962; TODD, 1979a, b, 1981). In both places this species was an annual, settling in the summer, growing until the early spring, when animals over 3 mm spawn. Spawning animals die in June, leaving a brief interval between gener-

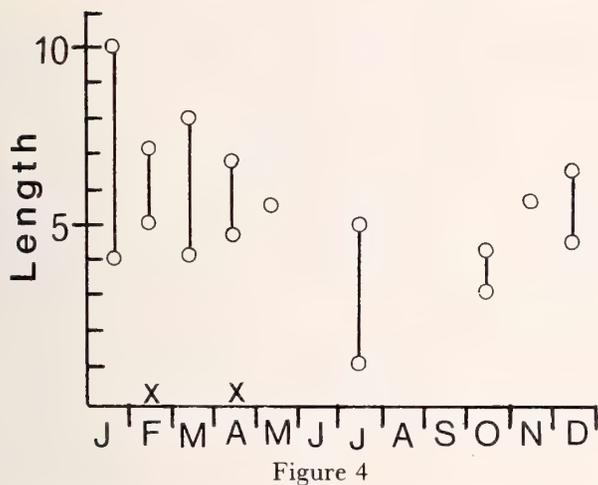


Figure 4

Onchidoris muricata. Annual cycle of Pacific animals. Preserved length in mm versus month collected. Spawn present in months marked "x." n = 91.

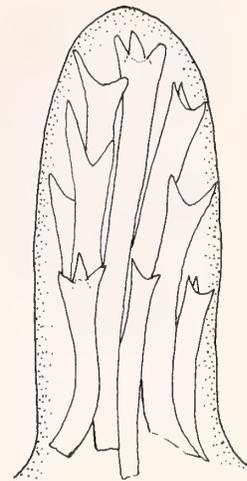
ations. Specimens collected from British Columbia (Figure 4) had a similar annual cycle.

The spawn mass is white or pale orange in 1½–2 whorls. The eggs are in a string folded up and down in the whorl, although this pattern is not obvious. The egg mass is quite thick and leans inward. The eggs are usually found one to a double-walled capsule. The eggs are 75.0–77.3 µm (GODDARD, 1984), 73–100 µm (THOMPSON, 1967), or 80–100 µm (TODD, 1979b) in diameter, with a capsule size of 99–117 µm (personal observation). There are approximately 2500 eggs/ribbon (THOMPSON, 1967; TODD, 1978a). Each animal lays approximately 15,000–34,000 eggs in its lifetime (TODD, 1979b). Egg masses are produced in a regular 4–5 day cycle, with mating necessary prior to each spawning (TODD, 1978b).

The eggs hatch in 7–20 days (MILLER, 1958; THOMPSON, 1967; HURST, 1967; GODDARD, 1984; personal observations) into Type-1 veligers of THOMPSON (1967), with shell Type 1 (THOMPSON, 1961a) and having a length of 117–136 µm (GODDARD, 1984; personal observations). The larvae are long-term planktotrophs with a larval life estimated at 12 wk (BEHRENTZ, 1931) or 7–8 wk (TODD, 1979a, b). I maintained larvae, fed on phytoplankton, in the laboratory at 8°C for 7 weeks, when they suddenly died without metamorphosing. This corroborates Todd's estimate. Animals in Britain preferentially settle on the bryozoan *Callopora aurita* even though as adults they prefer *Electra pilosa* (TODD, 1979a, b, 1981). Adult animals are quite active compared to other dorid nudibranchs and have the disconcerting habit of crawling out of their dish and drying up on the sides when kept in the laboratory.

Diaphorodoris lirulatocauda Millen, spec. nov.

Onchidoris hystericina (Bergh, 1878): BEEMAN & WILLIAMS, 1980:328 (section 14.42), pl. 105 (fig. 14.42) (*non*



0.1mm

Figure 5

Diaphorodoris lirulatocauda tubercle showing the arrangement of the spicules.

Bergh); BEHRENS, 1980:66–67 (fig. 71) (*non* Bergh); McDONALD & NYBAKKEN, 1981:16, 31, 44–45 (fig. 18) (*non* Bergh); NYBAKKEN & McDONALD, 1981:440, 442 (fig. 1H) (*non* Bergh); McDONALD, 1983:198–199 (fig. 36) (*non* Bergh); JAECKLE, 1984:209 (*non* Bergh).

Onchidoris sp. (cf. *Onchidoris hystericina*): GODDARD, 1984: 143–163.

Material: Holotype: British Columbia Provincial Museum, BCPM-984-347-1, 5 June 1979, Earls Cove, British Columbia, Canada (49°45'N, 124°01'W), 20 m depth, rocky substrate on bryozoans growing on *Rhabdocalypptus dawsonii*, spawning, coll. S. Millen.

Paratypes: In the British Columbia Provincial Museum three lots: BCPM-976-1037-6, 27 Mar. 1976, Juan Perez Sound, Queen Charlotte Islands, British Columbia, Canada (52°35.8'N, 131°25.2'W), 10–20 m, rock with coralline algae, 3 specimens, coll. P. Lambert; BCPM-976-1057-5, 18 June 1976, Arbutus Island, British Columbia, Canada (48°42.4'N, 123°26.1'W), <13 m, rocky substrate, 4 specimens, coll. P. Lambert; BCPM-976-1073-10, 2 Aug. 1976, Discovery Passage, British Columbia, Canada (50°19.7'N, 125°26.4'W), <25 m, rock with hydroids, 6 specimens, coll. P. Lambert. In the California Academy of Sciences two lots: CASIZ 031680, 8 Aug. 1968, Hazard Canyon, San Luis Obispo Co., California, 1 specimen, coll. D. Roller; CASIZ 031682, 8 Aug. 1964, Moss Beach, California, 1 specimen, coll. L. Andrews.

Etymology: The name *lirulatocauda* is derived from the Latin *lirulatus*, meaning "ridged," and *cauda*, meaning "tail," and refers to the mid-dorsal ridge on the tail. This feature distinguishes this species from similar small white dorids in the family Onchidorididae.

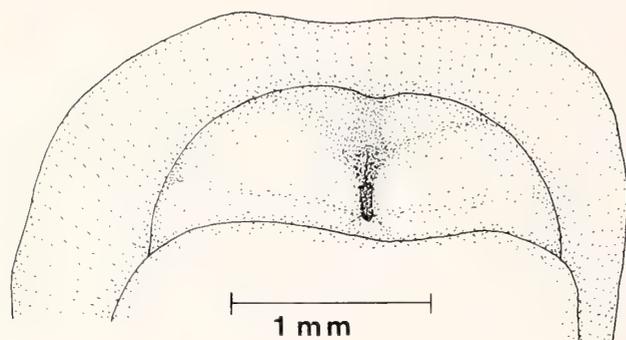


Figure 6

Head of *Diaphorodoris lirulatocauda*.

External morphology: I examined 44 specimens from British Columbia and California ranging in length from 3 to 12 mm. The body shape is elongate-oval (Figure 1E), wider in front than behind, with a trailing, keeled tail. The mantle margin is not wide, but covers the high sides and is slightly longer in front, covering the head. The notum bears elongate, slender, cylindrical tubercles with blunt but not inflated ends. The tubercles taper slightly from their bases. They are soft and capable of slight contraction. The tubercles show little variance in size, although smaller tubercles predominate toward the mantle edges. They are spaced fairly far apart, not crowded. In some specimens, the tubercles appear to form longitudinal rows. Larger tubercles are from 0.34 to 0.64 mm high and 0.13 to 0.28 mm wide.

Spicules are found in the tubercles, but they do not protrude, even when the tubercle contracts (Figure 1F). The spicules are densely packed in the central core of the tubercles and have trifurcate ends (Figure 5). At the bases of the tubercles the spicules extend in a radial, star-like pattern through the notum. In the notum there are large, curved spicules with side prongs and slightly smaller S-shaped spicules scattered in the connective tissue. These spicules do not form a definite pattern, nor are they visible in living animals. In the foot, the spicules form a crisscross pattern. The margins of the rhinophores bear three tubercles, two anterior and one posterior. There are no tubercles within the branchial cirlet. The branchial margin is smooth except for one large posterior tubercle, but several slightly smaller tubercles are sometimes present (Figure 1F).

The simply pinnate, contractile, branchiae are non-retractable, enclosed in a common sheath, and joined at their bases. There are 4–9 gills, the most anterior being the longest and the most posterior two being very small.

The rhinophores are long and slender, with a long, blunt tip. The stalk is long and most of the clavus bears sloping lamellae. The 6–10 lamellae are attached along a vertical, anterior line, except for the most distal one or

two. The lamellae slope ventrally and meet posteriorly forming a chevron, except for the most proximal two or three which are incomplete.

The head (Figure 6) is rounded, not extended into a large veil, but appearing as a double, rounded mound, separated by the vertical mouth opening. There are small, longitudinal, lateral tentacle grooves.

The foot is narrow and elongate, wider and truncate anteriorly. The anterior foot edge is not bilabiate. Dorsally the protruding tail, which ends in a sharp point, has a medial ridge.

Living specimens are white or creamy-white, with opaque white, granular flecks in the notum, the top of the foot, and head, but not on the tubercles. In mature animals, the mid-dorsal region appears darker yellow due to the creamy gonads underneath. Sometimes there is a brown spot on the anterior right, indicating the location of the sperm-filled bursa copulatrix. Ventrally the dark-brown digestive gland is visible through the foot, although it is often obscured by the creamy-yellow gonads. The rhinophores are creamy-yellow, as are the gills. The gills may have white granulations near their bases and an opaque white line up the central shaft. Color photographs appear in BEEMAN & WILLIAMS (1980: pl. 105 [fig. 14.42]), BEHRENS (1980:fig. 71), and McDONALD & NYBAKKEN (1981: fig. 18).

Digestive tract and radula: The soft buccal tube is surrounded by glands made up of large granules. The buccal bulb has a dorsal, rounded sucking crop which is sessile. The crop has a broad muscular band dorsally, but only a thin muscular strip posteriorly. On the ventral surface a small radular sac projects posteriorly. The lip disk is smooth, except in the central passageway, where it has small, oval papillae that are 7–8 μm in diameter (Figure 1G).

The radula has 29–33 rows. The radular formula is 2.1.0.1.2, with no central (rachidian) tooth. A membranous wing runs from the inner posterior corner of each lateral tooth to join just inside the inner base of the following tooth (Figure 1H). The large lateral teeth (Figure 1I) have a wide triangular base with a small, needlelike recurved hook. At the inner base of the hook extends a comblike row of 11–13 denticles. Above and inside the row of denticles is a prominent knob. The lateral teeth range in height from 0.05 to 0.06 mm. The innermost marginal tooth has an oval base with a posterior-facing middle hook (Figure 1J). The height is 0.02 mm. On the outside of this is a small, insubstantial, oval plate (5–10 μm long), representing a rudimentary second lateral tooth (Figure 1K).

At the posterior end of the buccal bulb is the long, thin esophagus. The salivary glands insert at its base. These are long, thin straps running down the sides of the digestive gland for half its length before bending ventrally. The small stomach is buried in the digestive gland, but a round, short, stalked caecum extends from it to the surface. In

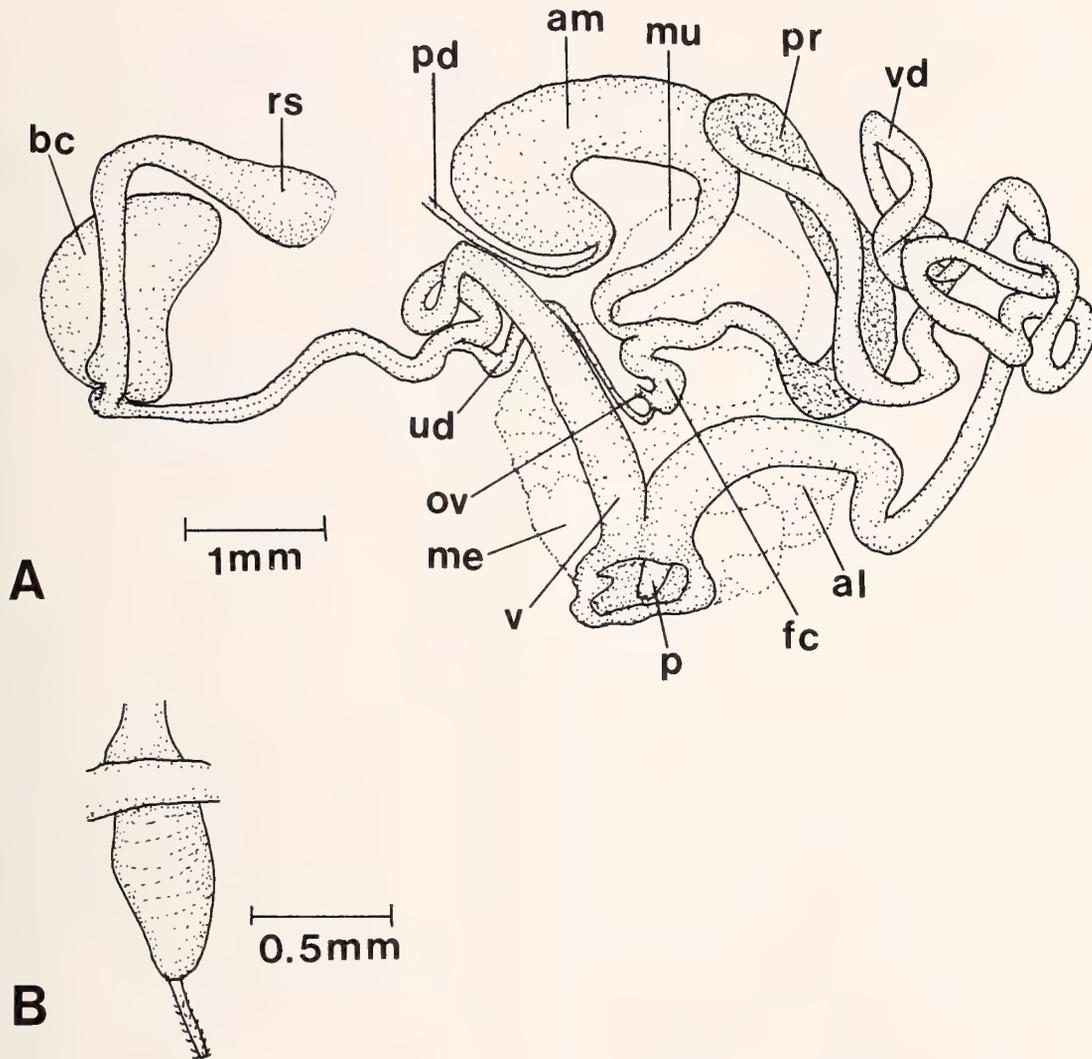


Figure 7

A. *Diaphorodoris lirulatocauda* reproductive system, drawn using a camera lucida. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; fc, fertilization chamber; me, membrane gland; mu, mucous gland; ov, oviduct; p, penis; pd, preampullary duct; pr, prostate; rs, receptaculum seminis; ud, uterine duct; v, vagina; vd, vas deferens. B. Conical penis with everted, armed, central core.

mature animals the digestive gland is covered by the gonads. The oval, brown digestive gland appears as one mass. The intestine emerges beside the caecum, curves to the right, and runs as a long, thin tube to the anus, located in the center of the branchial cirlet. The renal pore is to the right and slightly anterior to the anal opening.

Circulatory system: The auricle is large, triangular, and thin. The ventricle is small, muscular, and rounded. The muscular aorta ends in fluffy, white, blood glands located just posterior to and slightly over the central nervous system.

Central nervous system: The cerebro-pleural ganglia are fused, large, and elongate oval in shape. The smaller,

rounded pedal ganglia are ventrally located and are connected by a short circumesophageal commissure. The olfactory bulbs have a short stalk. The eyes are connected to the cerebro-pleural ganglia by long optic nerves with small bulbs at their bases. The paired buccal ganglia are separated by a short commissure and each has a gastroesophageal ganglion attached by a short stalk.

Reproductive system (Figure 7): The ovotestes are creamy-yellow lobules entirely covering the digestive gland, including the ventral side. The gonoducts are broad, shiny white and conspicuous, uniting to form a central preampullary duct, which widens into the U-shaped ampulla. This ampulla is attached to the inner side of the female

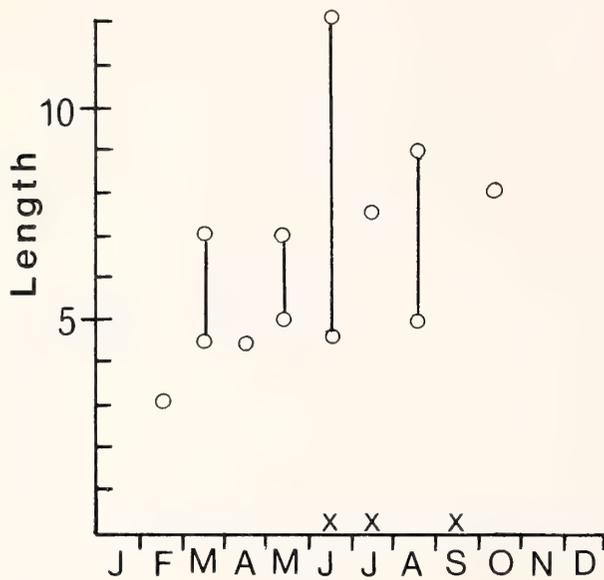


Figure 8

Diaphorodoris livulatocauda. Annual cycle. Preserved length in mm versus month collected. Spawn present in months marked "x." n = 40.

gland mass. The post-ampullar duct bifurcates into a short, wide fertilization duct and an extremely long, coiled vas deferens. The inner portion of the vas deferens widens into a soft granular prostatic section, then narrows to a coiling, muscular portion. Near the outer body wall the vas deferens widens slightly to join a common atrium with the vagina. This atrium has a plicate edge. The conical penis is located at the anterior of the atrium, and has a central protrusible core bearing spines. The core, which can extend 300–400 μm , bears approximately 8 irregular rows of 15–25 spines. The spines are simple rods with pointed, downward-tipped ends. They vary in length from 8 to 23 μm , the shortest being most proximal.

The vagina is long and cylindrical, wider near its posterior opening in the atrium and gradually narrowing into a long duct leading to the sessile bursa copulatrix. Just after it narrows, the uterine duct branches off. The vaginal duct beyond this point has a double-partitioned interior. The bursa copulatrix is a large, round thin-walled sac, dark-brown when filled with sperm. At its junction with the vagina, the moderately long duct of the club-shaped receptaculum seminis bends anteriorly. The arrangement of the ducts is vaginal. The uterine duct is combined with the vagina for one-half of its length. It then separates from the vaginal duct and crosses the posterior portion of the female gland mass. It terminates in a slightly swollen fertilization chamber next to the short oviduct, which in turn enters the female gland mass.

The female gland mass consists of a membrane gland, mucous gland, and albumen gland. Its exit is located just

ventral to the vaginal opening. A short duct widens into an interior, white membrane gland and then widens further into a more dorsal, yellow, highly convoluted albumen gland. On top of the albumen gland is the soft, granular, white coil of the mucous gland. The oviduct enters the mucous gland at its junction with the albumen gland.

The genital openings are located on the right side, a short distance behind the anterior margin of the foot.

Ecology: The habitat and life cycle of this species has been frequently confused with those of *Onchidoris muricata*. I will therefore restrict my observations to specimens that I have examined. This species occurs in the low intertidal down to 126 m subtidally. It ranges from Juan Perez Sound, Queen Charlotte Islands, British Columbia, to Point Loma, California.

This species has been observed eating the ctenostome bryozoan *Nolella stipitata*. The nudibranchs are usually found under rocks intertidally or crawling on rocky surfaces and sponges subtidally. They have been found from February to October, reaching their largest size in the summer (Figure 8). Spawning has been observed in June, July, and September (GODDARD, 1984; personal observations). The spawn mass and development time have been described by GODDARD (1984). He found the spawn mass to be white, in a sausage-shaped cord laid in a disorderly spiral of 1–4 turns. The single egg per capsule had a diameter of 62.6–64.0 μm and hatched in 9–11 days (at 12–16°C) into Type-1, eyeless veligers of THOMPSON (1967). The veligers have shell Type 1 of THOMPSON (1961a) and a length of 113.3–116.6 μm . The duration of the larval stage is unknown.

DISCUSSION

Synonyms of *Onchidoris muricata*

Onchidoris muricata from the Atlantic has the same internal and external morphology as the animals from the Pacific that are described as *O. varians*. I therefore consider them synonymous. BERGH (1880) distinguished *O. varians* on the basis of its bluish color as opposed to the light yellowish, white, or yellowish-white colors of *O. muricata*. Nevertheless, he conceded that a variety of *O. varians* is yellowish-white or yellowish. The radula formula for *O. varians* is 30–41 \times 1.1.1.1.1, with 15–20 denticles reaching to the end of the hook (Figure 9C). This is within the range for *O. muricata* from Norway (Table 1, Figure 9A). Live specimens from the eastern Atlantic are reported to reach a length of 17 mm (BEHRENTZ, 1931), whereas the largest live specimen found on the Pacific coast was 12 mm. When Pacific animals from Vancouver Island were compared with Norwegian animals (Table 1, Figure 9B), the following differences were found. Identically sized specimens were alike, but some larger animals had been collected in Norway. These latter specimens bore disproportionately large tubercles and a similarly oversized mantle margin. They had been labeled *Adalaria loveni*

Table 1

Morphological features of the species of *Onchidoris* and *Diaphorodoris* examined.

	<i>O. muricata</i>	<i>O. muricata</i>	<i>O. hystricina</i>	<i>O. varians</i>	<i>D. lirulatocauda</i>
Location	Atlantic	Pacific	Pacific	Pacific	Pacific
Color	white, yellowish	white, yellowish	bluish, yellowish	bluish	yellowish
Body	oval	oval	oval	oval	elongate
Head	veliform	veliform	veliform	veliform	knobbed
Foot	short	short	short	short	elongate
Branchiae	disk large separate pits	disk large separate pits	disk large separate pits	disk large separate pits	disk small common pit
	8-14	6-18	12	12-20	4-9
Tubercles	knobbed club spicules project	knobbed club spicules project	clubbed spicules project	clubbed ?	cylindrical not projecting
Skin	spicules show	spicules show	spicules show	no spicules	spicules buried
Radula	27-44 (1.1.1.1.1)	20-33 (1.1.1.1.1)	40 (1.1.1.1.1)	30-41 (1.1.1.1.1)	29-33 (2.1.0.1.2)
Denticles	9-16 fine	8-18 fine	6-8 fine	15-20 stronger	11-13 very strong
Vas deferens	short	short	short	short	long
Penis	large	large	large	large	small
Receptaculum	buried	buried	?	?	free

(Alder & Hancock, 1862) on the basis of their external anatomy. However, when compared with equal-sized bona fide *A. loveni*, it could be seen that the tubercles of the large Norwegian specimens of *O. muricata* were not as large and were more constricted at their bases. Internally, the single marginal tooth per half row, as opposed to the 8-12 found in *A. loveni*, provided positive identification of these mislabeled animals. The only unexplained difference noted by Bergh for *O. varians* is the lack of spiculation. This was probably an artifact of preservation.

The species *Onchidoris hystricina* has been the object of confusion on the Pacific coast. BERGH (1878, 1880) obtained one specimen that Dall found in Alaska. He separated it from *O. muricata* by its color (bluish rather than yellowish-white). He separated it from *O. varians* apparently because of slight differences in the nervous system, a thinner belt of denticles on the lip cuticle, and smaller lateral plates (0.075 versus 0.12 mm in height). The denticulation on the lateral teeth was weaker, there were fewer denticles (8 versus 20), and the denticles did not extend as far out toward the tip. Bergh did not consider these differences to be great, and he concluded that "... the possibility cannot be denied that further investigations may show both the Pacific 'species' to be merely varieties of the old *Lamellidoris muricata* of the Atlantic." *Onchidoris hystricina* is compared with the other two species (Table 1, Figure 9D). The differences noted by Bergh fall within the range of variability of *O. muricata*. *Onchidoris muricata* can be an almost translucent bluish color, opaque white, or pale yellow. MEYER (1971) reported teeth with a height of 0.075 mm in *O. muricata*, the same height that Bergh found in *O. hystricina*. I found *O. muricata* from Norway with 9-16 denticulations, usually ending before the tip, but at times continuing to the end. Tooth heights varied from 0.057 to 0.090 mm. Younger teeth had longer,

straighter hooks; older, worn teeth had shorter, blunter, more curved hooks, much as shown by THOMPSON (1958: 51, fig. 2) for *Adalaria proxima* (Alder & Hancock, 1854). BERGH's (1879:pl. 68 [figs. 18-23]) drawings of the teeth of *O. hystricina* are consistent with newer, unworn teeth (Figure 9D). I therefore consider *O. hystricina* to be a junior synonym of *O. muricata*.

Misidentification of *Diaphorodoris lirulatocauda* and *Onchidoris muricata*

Confusion has arisen in the literature due to the mistaken association of the distinctive new species *Diaphorodoris lirulatocauda* with the name *Onchidoris hystricina*. Three factors probably led to this error. Firstly, *O. muricata* had its known range extended to California by MARCUS (1961) under the misnomer of *O. hystricina*. Because later researchers realized two species occurred in California, one was correctly identified as *O. muricata*; the other (*D. lirulatocauda*) was given the name *O. hystricina*, as this was the only other name reported from California for a similar appearing animal. Secondly, both *O. hystricina* and *D. lirulatocauda* have tooth denticles that do not extend to the end of their strongly hooked laterals. This reinforced the misidentification even though the lateral teeth differ in shape (Figures 9D, E). Thirdly, the tubercles of *O. hystricina* are mistakenly reported by BERGH (1880) as being 1.2 mm high, which is much higher than the 0.51-0.56 mm actually found in *O. muricata*. *Diaphorodoris lirulatocauda* has slightly longer tubercles than *O. muricata*, and this reinforced its identification with the name *O. hystricina*. However, the longest tubercles of *D. lirulatocauda* are only 0.64 mm long, which is not nearly as long as in Bergh's report. When the features of *D. lirulatocauda* are compared closely with *O. hystricina* as described by Bergh, many important differences emerge

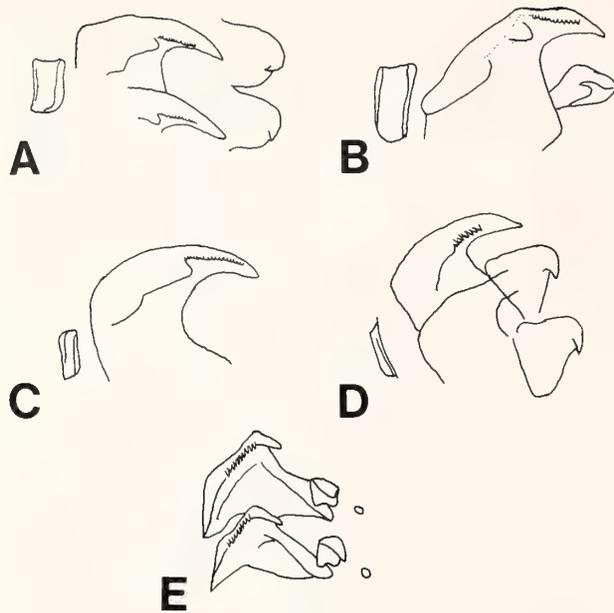


Figure 9

Radular teeth. A. *Onchidoris muricata* (Atlantic) from BERGH, 1880:pl. 11 (fig. 10). B. *Onchidoris muricata* (Pacific). C. *Onchidoris varians* from BERGH, 1880:pl. 11 (figs. 13, 14). D. *Onchidoris hystericina* from BERGH, 1878:pl. 68 (figs. 18, 21). E. *Diaphorodoris lirulatocauda*. Not drawn to scale.

(Table 1). These differences, particularly those of the head shape, gill arrangement, radula, and length of vas deferens, show that Bergh's *O. hystericina* belongs with the species *O. muricata* rather than the animal we have been commonly calling *O. hystericina*. This latter animal is in fact a new species, which I have described in this paper.

Discussion of *Diaphorodoris*

This new species, *Diaphorodoris lirulatocauda*, has been placed in the genus *Diaphorodoris* Ireland & O'Donoghue, 1923, because it has broadly based, triangular, denticulate teeth with no central tooth, an elongate body with a trailing keeled tail, a double-knobbed head, and a reproductive system similar to that of the type species *D. luteocincta* (M. Sars, 1870). Another important feature distinctive to this species is branchiae that are enclosed in a common sheath much as in the cryptobranch dorids, although in *Diaphorodoris* the branchiae are nonretractable as the sheath does not close over the branchiae. The genus *Diaphorodoris* was first created by IREDALE & O'DONOGHUE (1923) as a genus of Onchidorididae for the species *D. luteocincta*, although no distinctive characters were given. PORTMANN & SANDMEIER (1960) provide a history of the genus, redescription of the type species, and describe a new species, *D. papillata*, which varies only in color and tubercle shape from the type. Since then, no new species have been added and the generic status of *Diaphorodoris*

Table 2
Anatomical characters separating *Onchidoris* and *Diaphorodoris*.

	<i>Onchidoris</i>	<i>Diaphorodoris</i>
Shape	oval	elongate
Head	veliform	lobiform
Tail	not extending	trailing
Branchiae	separate pits enclosing tubercles	common sheath no tubercles enclosed
Radula	central present or absent	no central
Reproductive	vagina short bursa stalked receptaculum buried	vagina elongate bursa sessile receptaculum free
	semiserial	vaginal

is usually ignored. FRANC (1968) considers *Diaphorodoris* to be a subgenus, although he does not state of which genus. He places it in the family Lamellidoridae A. Pruvot-Fol, 1954, although the name Onchidorididae Alder & Hancock, 1845, has priority. THOMPSON & BROWN (1976) and THOMPSON (1976) place the species *luteocincta* in the genus *Onchidoris*. It is clear that in spite of the early arguments of PRUVOT-FOL (1932), the completeness of PORTMANN & SANDMEIER's (1960) description, and its recent use by SCHMEKEL & PORTMANN (1982), the establishment of *Diaphorodoris* as a distinct genus has not been universally accepted. I believe *Diaphorodoris* should retain its generic status. In support of this, I have summarized the important differences between the two genera in Table 2.

Comparison of Species in the Genus *Diaphorodoris*

Diaphorodoris lirulatocauda conforms closely to the morphology of *D. luteocincta*. It differs externally in having slimmer rhinophores, longer dorsal tubercles (0.6 versus 0.2 mm) and more branchial gills (7-9 versus 5-7). *Diaphorodoris luteocincta* normally has a yellow marginal ring and dorsal crimson blotching, but the red color is missing in the variety *alba* although the yellow ring is present. *Diaphorodoris papillata* can be distinguished from *D. lirulatocauda* by its red-colored, soft, inflated tubercles, which reach up to 0.8 mm in length. Internally *D. lirulatocauda* differs from the others by having an extra, reduced, outer external plate giving it the formula 2.1.0.1.2. In addition, the vas deferens of *Diaphorodoris lirulatocauda* is longer, with more coils, and the penis is armed with spines.

Diaphorodoris mitsuui (Baba, 1938) comb. nov.

The species *Lamellidoris mitsuui* (for which BABA, 1938, created a new subgenus *Lamellidorella* because it has an

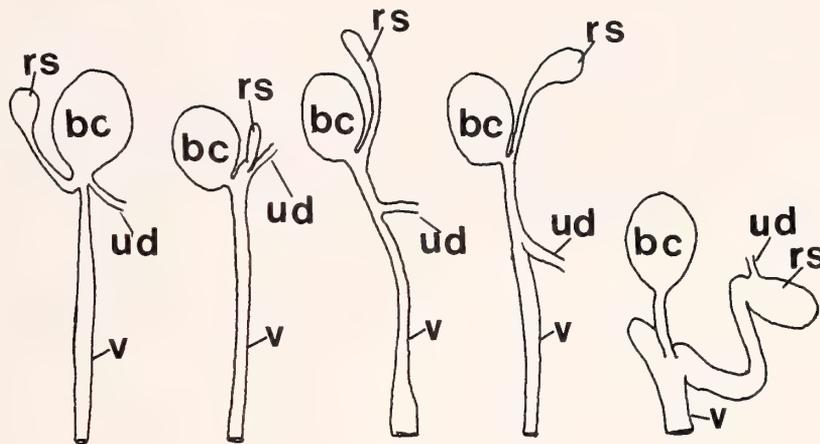


Figure 10

Reproductive systems—female portion. A. *Acanthodoris* from BERGH, 1880:pl. 13 (fig. 5). B. *Aciodoris* from BERGH, 1880:pl. 6 (figs. 18, 19). C. *Calycidoris* from ROGINSKAYA, 1972:pl. 1 (fig. 16). D. *Diaphorodoris*. E. *Onchidoris*. Not drawn to scale.

armed lip cuticle) must also be compared with the genus *Diaphorodoris*. The teeth have the same triangular, denticulate shape and lack a central plate. The body is also elongate with cylindrical tubercles and a trailing tail. Most importantly the branchiae are enclosed by a common cavity into which, according to BABA (1938, 1949), they can retract. This species has a rounded, double-lobed head like other *Diaphorodoris* species. The orange-yellow marginal ring is reminiscent of *D. luteocincta* var. *alba*. The small scales on the lip disk, which BABA regarded as distinctive (1938:131 [fig. 1B]), are similar to the small papillae on the lip cuticle of *D. lirulatocauda*. Unfortunately, the reproductive system of this species is not known, but externally, and according to its radular morphology, it appears to be conspecific with *Diaphorodoris*. I therefore designate it *Diaphorodoris mitsuui* (Baba, 1938) comb. nov.

Discussion of Generic Relationships in the Family Onchidorididae

One of the major characteristics separating *Diaphorodoris* and *Onchidoris* is that the branchiae do not possess separate pits, but emerge from a common cavity. This is similar to the branchial arrangement of cryptobranch dorids, although the gill pocket does not close over to protect the gills and thus the gill system can still be classified as nonretractile. Of the genera in the family Onchidorididae, *Aciodoris*, *Adalaria*, *Arctadalaria*, *Doridunculus*, *Onchidoris*, and *Prodoridunculus* have nonretractile branchiae that contract and are arranged in separate cavities. The genus *Acanthodoris* has gills that connect at their bases. However, the branchial margin of the acanthodorids indents between each gill and the gills usually enclose a tuberculated portion of the notum. *Calycidoris* and *Diaphorodoris* both have a single cavity containing gills that join at their bases. ROGINSKAYA (1972) proposed a new family,

Calycidorididae, for the monotypic genus *Calycidoris* because its gills retract into a common sheath. However, in specimens that I examined it appears that the gill margin does not close over the gills and, thus, even when the gills are maximally contracted the system can still be considered nonretractile. The gills of *Diaphorodoris mitsuui* are probably similarly contracted, rather than retracted as claimed by BABA (1938, 1949). This branchial arrangement is very close to that of true cryptobranchs (which is termed retractile) differing only in that the gill margin does not close itself over the gills.

Diaphorodoris can be distinguished from *Calycidoris* by its broad, triangular-based, denticulate lateral teeth and its elongate body shape with a trailing, keeled tail. It is separated from other genera in the family Onchidorididae because its branchial gills are arranged in a common sheath. *Diaphorodoris* is more closely allied to the genera *Calycidoris*, *Acanthodoris*, and *Aciodoris* on the basis of the vaginal arrangement of the uterine duct than to *Onchidoris*, which has a semiserial arrangement (Figure 10). As in *Aciodoris*, the penis can be armed with spines. The radular teeth are most similar to some of the species in the genus *Onchidoris*. The elongate body shape, knobbed head, trailing keeled tail, common branchial pit, and vaginal arrangement of the copulatory bursa are all characteristics that validate the generic separation of *Onchidoris* and *Diaphorodoris*.

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LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells, the marine Mollusca of the Atlantic and Pacific coasts of North America. 2nd ed. Van Nostrand Reinhold: New York. 633 pp.
- ALDER, J. & A. HANCOCK. 1855. Monograph of the British Nudibranchiate Mollusca 7. Ray Society: London. 54 pp.
- BABA, K. 1938. Three new nudibranchs from Izu, Middle Japan. *Annot. Zool. Japon.* 17(2):130-133.
- BABA, K. 1949. Opisthobranchia of Sagami Bay. Iwanami Shoten: Tokyo. 194 pp.
- BEEMAN, R. D. & G. C. WILLIAMS. 1980. Opisthobranchia and Pulmonata. Pp. 308-354. In: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal invertebrates of California*. Stanford Univ. Press: Stanford, Calif.
- BEHRENS, D. W. 1980. Pacific coast nudibranchs: a guide to the opisthobranchs of the northeastern Pacific. Sea Challengers Inc.: Los Osos, California. 112 pp.
- BEHRENTZ, A. 1931. Trekk av *Lamellidoris muricata's* biologi og av dens generasjonsorganer bygning. *Nyt mag. Naturv. Oslo* 70:1-26.
- BERGH, L. S. R. 1878. Malacologische Untersuchungen. Pp. 603-645, pl. 66-68. In: C. G. Semper, *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper*. Zweiter Theil. Wissenschaftliche Resultate. 2,2(14).
- BERGH, L. S. R. 1879. Gattungen Nordischer Doriden. *Archiv. für Natur.* 45(1):340-369, pl. 19.
- BERGH, L. S. R. 1880a. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. *Sci. Results Explor. Alaska* 1(6) 2:189-276, pl. 1-16.
- BERGH, L. S. R. 1880b. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. 2. *Proc. Acad. Natur. Sci. Philadelphia.* 32: 40-127, pl. 9-16.
- BERGH, L. R. S. 1890. Malacologische Untersuchungen. Die nudibranchien des "Sunda-Meer." Pp. 873-991, pl. 85-89. In: C. G. Semper, *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper*. Zweiter Theil. Wissenschaftliche Resultate. 2,3(17).
- BERGH, L. R. S. 1892. Malacologische Untersuchungen. System der nudibranchiaten Gastropoden. Pp. 995-1165 (3-173). In: C. G. Semper, *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper*. Zweiter Theil. Wissenschaftliche Resultate. 2,3(18).
- FRANC, A. 1968. Sous-Classe des Opisthobranches. Pp. 608-893. In: P. Grassé (ed.), *Traité de Zoologie* 5:3. Mollusques Gasteropodes et Scaphopodes. Masson et Cie: Paris.
- GODDARD, J. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. *Veliger* 27(2):143-163.
- HURST, A. 1967. The egg masses and veligers of thirty north-east Pacific opisthobranchs. *Veliger* 9(3):255-288.
- IREDALE, T. & C. H. O'DONOGHUE. 1923. List of British nudibranchiate Mollusca. *Proc. Malacol. Soc. Lond.* 15(4-5):195-233.
- JAECKLE, W. B. 1984. Opisthobranch mollusks of Humboldt County, California. *Veliger* 26(3):207-213.
- KRESS, A. 1981. A scanning electron microscope study of notum structures in some dorid nudibranchs (Gastropoda: Opisthobranchia). *J. Mar. Biol. Assoc. U.K.* 61:177-191.
- MARCUS, E. 1961. Opisthobranch mollusks from California. *Veliger* 3(Suppl.):1-85.
- MCDONALD, G. R. 1983. A review of the nudibranchs of the California coast. *Malacologia* 24(1-2):114-276.
- MCDONALD, G. R. & J. W. NYBAKKEN. 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. *Veliger* 21(1):110-119.
- MCDONALD, G. R. & J. W. NYBAKKEN. 1981. Guide to the nudibranchs of California. American Malacologists Inc.: Melbourne, Florida. 72 pp.
- MEYER, K. B. 1971. Distribution and zoogeography of fourteen species of nudibranchs of northern New England and Nova Scotia. *Veliger* 14(2):137-152.
- MILLER, M. C. 1958. Studies on the nudibranchiate Mollusca of the Isle of Man. Doctoral Thesis, University of Liverpool [not seen].
- MILLER, M. C. 1962. Annual cycles of some Manx nudibranchs, with a discussion of the problem of migration. *J. Anim. Ecol.* 31(3):545-569.
- NYBAKKEN, J. W. & G. R. MCDONALD. 1981. Feeding mechanisms of west American nudibranchs feeding on Bryozoa, Cnidaria and Ascidiacea, with special respect to the radula. *Malacologia* 20(2):439-449.
- PORTMANN, A. & E. SANDMEIER. 1960. Zur kenntnis von *Dia-phorodoris* (Gastr., Nudibranchia) und ihrer mediterranen formen. *Verh. Nat. Gesel.* 71:174-183.
- PRUVOT-FOL, A. 1932. Notes de systématique sur les Opisthobranches. *Bull. Mus. Nation. Hist. Nat.* 2(4):322-331.
- ROGINSKAYA, I. S. 1972. *Calycidoris guentheri* (Gastropoda, Nudibranchia). Taxonomy and distribution. *Akad. Nauk S.S.S.R. Zool. Zh.* 51(6):913-918.
- SCHMEKEL, L. & A. PORTMANN. 1982. Opisthobranchia des Mittelmeeres: Nudibranchia und Saccoglossa. Springer-Verlag: New York. 410 pp.
- THOMPSON, T. E. 1958. Observations on the radula of *Adalaria proxima* (A. & H.) (Gastropoda Opisthobranchia). *Proc. Malacol. Soc. Lond.* 33:49-56.
- THOMPSON, T. E. 1961a. The importance of the larval shell in the classification of the Saccoglossa and the Acoela (Gastropoda Opisthobranchia). *Proc. Malacol. Soc. Lond.* 34(5): 233-238.
- THOMPSON, T. E. 1961b. Observations on the life history of the nudibranch *Onchidoris muricata* (Muller). *Proc. Malacol. Soc. Lond.* 34(5):239-242.
- THOMPSON, T. E. 1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *J. Mar. Biol. Assoc. U.K.* 47(1):1-22.
- THOMPSON, T. E. 1976. Nudibranchs. T. F. H. Publications Inc.: Neptune, New Jersey. 96 pp.
- THOMPSON, T. E. & G. H. BROWN. 1976. British opisthobranch molluscs. Mollusca: Gastropoda. Synopsis of the British fauna (new series) 8. Linnean Soc. London. Academic Press: New York. 203 pp.
- TODD, C. D. 1978a. Gonad development of *Onchidoris muricata* (Müller) in relation to size, age and spawning (Gastropoda: Opisthobranchia). *J. Moll. Stud.* 44(2):190-199.
- TODD, C. D. 1978b. Changes in spatial pattern of an intertidal

- population of the nudibranch mollusc *Onchidoris muricata* in relation to life-cycle, mortality and environmental heterogeneity. *J. Anim. Ecol.* 47:189-203.
- TODD, C. D. 1979a. The annual cycles of two species of *Onchidoris* (Opisthobranchia: Nudibranchia). Pp. 65-72. In: E. Naylor & R. G. Hartnoll (eds.), *Cyclic phenomena in marine plants & animals*. Proc. 13th Eur. Mar. Biol. Symp. Pergamon Press: Toronto.
- TODD, C. D. 1979b. Reproductive energetics of two species of dorid nudibranchs with planktotrophic and lecithotrophic larval strategies. *Mar. Biol.* 53:57-68.
- TODD, C. D. 1981. The ecology of nudibranch molluscs. *Oceanogr. Mar. Biol. Ann. Rev.* 19:141-234.

A New Subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae)

by

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Abstract. A new subgenus *Rothelix* is described for the land snail genus *Helminthoglypta* in southern California. It is distinguished from the nominate subgenus by its long, sausage-shaped, lower sac of the penis and by its atrial sac in which the vagina enters just below the dart sac instead of near the genital pore.

INTRODUCTION

THE SPECIOSE GENUS *Helminthoglypta* comprises over 100 species and subspecies of western North American land snails. Classification within the genus has consisted mainly of allocating species into series whose characteristics are primarily based on shell sculpture, size, shape, and color.

Subgeneric classification has been limited to the designation of two subgenera, namely the nominate subgenus, whose type species is *Helminthoglypta tudiculata* (Binney, 1843), and *Charodotes* Pilsbry, 1939, whose type species is *H. traskii* (Newcomb, 1861). *Helminthoglypta* s.s. is characterized by a double-walled penis with an outer tube (i.e., an eversible inner tube with an outer tube) and *Charodotes*, as reported by PILSBRY, 1939, by a single, thick, muscular tube. PILSBRY (1939:68) also prepared a key in which *Charodotes* was listed as having a large dart sac with a short common duct of the mucus glands, while *Helminthoglypta* s.s. was divided into two main groups of species, one group having the dart sac and common duct as in *Charodotes* and the other having the dart sac small and much shorter than the common duct.

Between 1956 and 1964, the late Wendell O. Gregg and I undertook to conduct a careful examination of the anatomy of nearly every known (and many yet undescribed) species and subspecies of *Helminthoglypta* in order to find characteristics that could be used to establish additional subgeneric categories. Publication of our findings was delayed by Gregg's declining health and eventual death. Foremost among our determinations was the fact that all species examined, including *H. traskii*, had a double-tubed penis, of varying length, thereby synonymizing

Charodotes with *Helminthoglypta* s.s.; this information has been reported by MILLER (1981), and the name *Charodotes*, while available, is invalid because it is a junior synonym. Furthermore, we found that the comparative measurements of dart sac and common duct of the mucus glands were generally useless diagnostically, because we could find specimens with a large sac and short duct in the same populations with specimens with a small sac and long duct. On the other hand, the studies revealed that the lower sac of the penis, which PILSBRY (1939:69) refers to as "a short neck with a simple wall," differed considerably and consistently in one group of species which includes *H. lowei* (Bartsch, 1918), *H. cuyamacensis cuyamacensis* (Bartsch, 1916), and several additional species yet to be described. The reproductive anatomy of this group of species differs so markedly from that of all other species of the genus, including the type species, *H. tudiculata*, that it warrants classification in a separate, new subgenus, described below. It is imperative, in comparing reproductive system anatomies, that the terms used in describing the accessory organs be unequivocally defined. BERRY (1953) described and compared the reproductive systems of *H. lowei* and *H. thermimontis* Berry, 1953, in minute detail. In *H. lowei*, however, he considered the epiphallus to include the double-tubed, eversible portion, and he then identified the lower sac of the penis, which is long and saccular in this species, as the entire penis. In this report, in order to be consistent with Pilsbry's earlier definitions, the epiphallus (Figure 1, ep) is considered to be the muscular, single-tubed duct which begins at the junction of the vas deferens and the epiphallic caecum, and ends at the beginning of the double-tubed, eversible duct. The penis, then, consists of an upper part (Figure 3, upe)

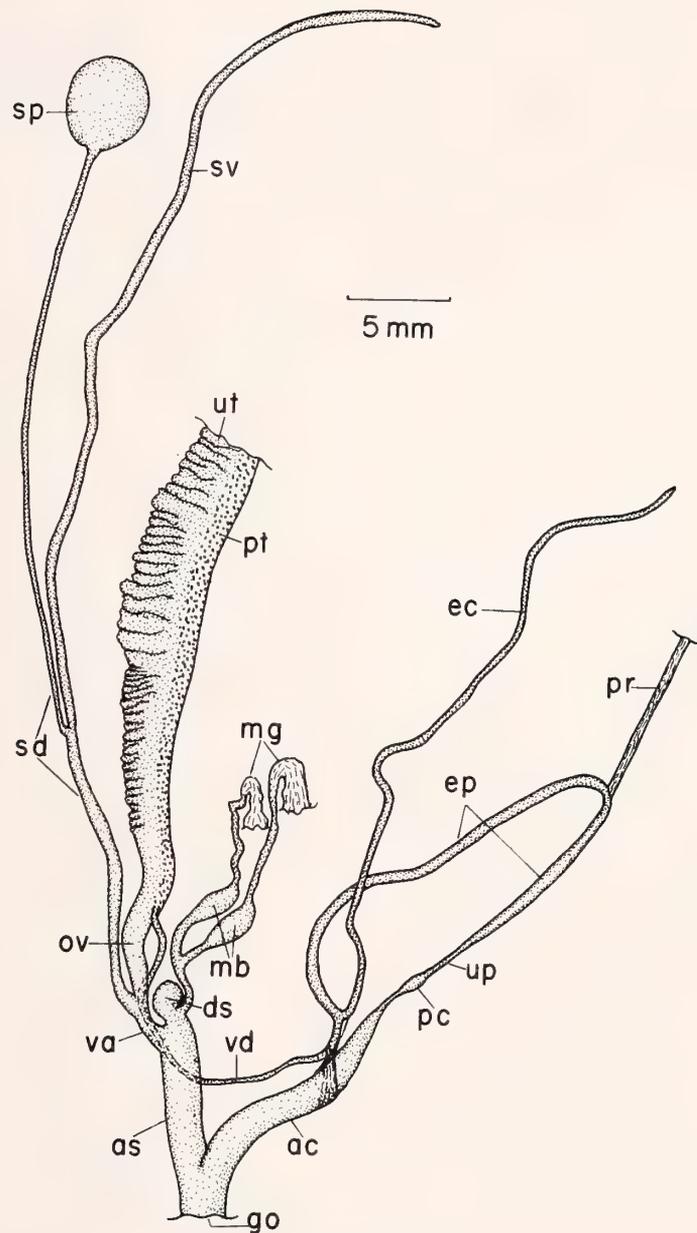


Figure 1

Reproductive system of *Helminthoglypta (Rothelix) lowei* (Bartsch); ovotestis and albumen gland region omitted. Drawing made from projection of stained whole mount, WBM 7366, collected on Palomar Mountain, San Diego County, California, along bank of Fry Creek at about 1500 m (4800 ft) elevation, 5 January 1984. ac, anterior chamber of lower part of penis; as, atrial sac; ds, dart sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; mb, mucus gland bulbs; mg, mucus gland membranes; ov, oviduct; pc, posterior chamber of lower part of penis; 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.

which is the double-tubed, eversible duct, and a lower part (Figure 3, lpe) which is a single-walled, saccular duct that connects with the atrium. The penial retractor muscle is always attached to the epiphallus. This is in accord with

the description of the epiphallus and the penis of the typical subgenus *Helminthoglypta* in PILSBRY (1939:67). The term "atrial sac" also is in accord with Pilsbry's definition of that term (PILSBRY, 1939:63 and fig. 31).

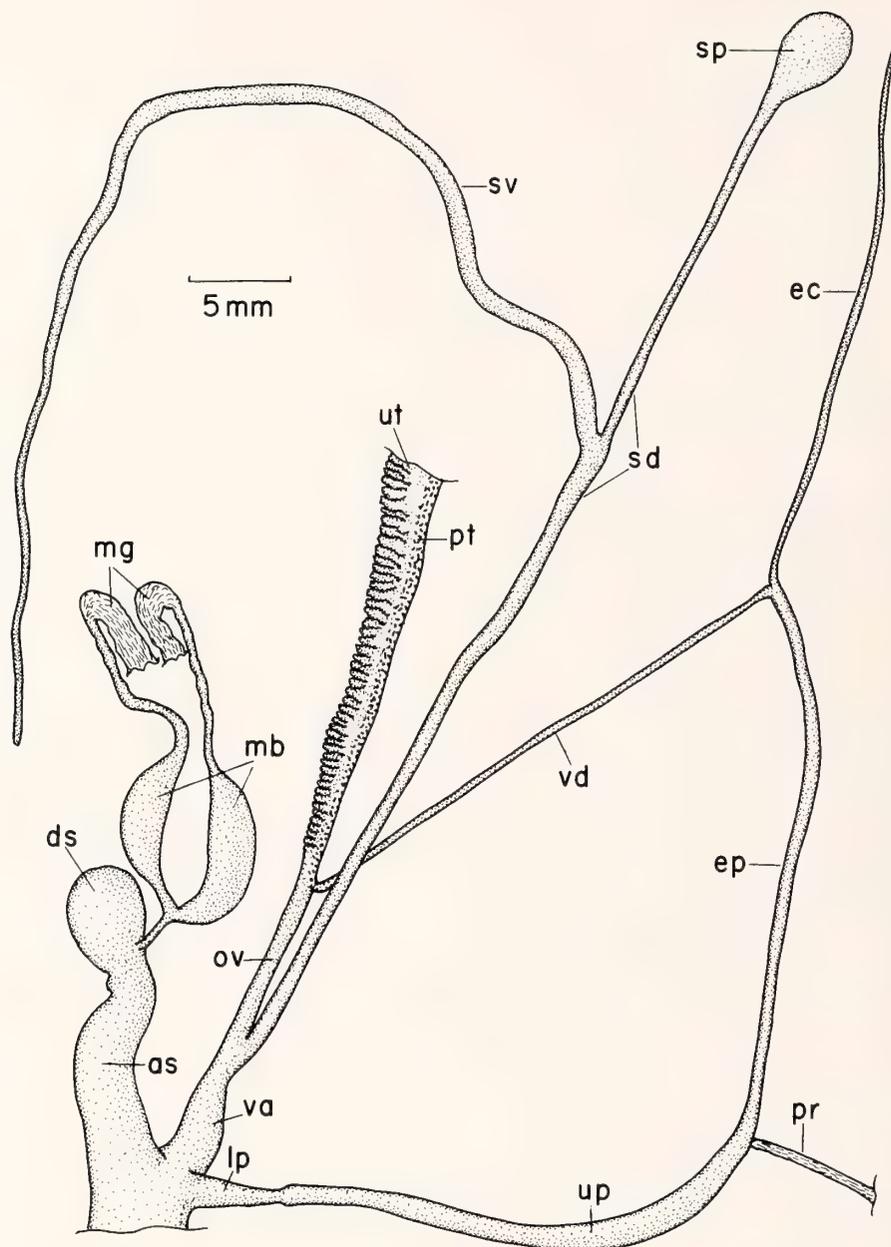


Figure 2

Reproductive system of *Helminthoglypta tudiculata* (Binney); ovotestis and albumen gland region omitted. Drawing made from projection of stained whole mount, WBM 4426-A, collected along Sweetwater River, 2.6 km (1.6 mi) upstream from confluence of Harbison Creek, San Diego County, California, 9 February 1963. as, atrial sac; ds, dart sac; ec, epiphallal caecum; ep, epiphallus; go, genital orifice; lp, lower part of penis; mb, mucus gland bulbs; mg, mucus 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.

DESCRIPTION

Rothelix W. B. Miller, subgen. nov.

Diagnosis: Shell varying from medium to small for the genus, finely papillose above and below. Reproductive

anatomy distinguished by the long, sausage-shaped, lower sac of the penis and by the vagina which enters the atrial sac at its apex, next to the dart sac.

Type species: *Helminthoglypta (Rothelix) lowei* (Bartsch, 1918).

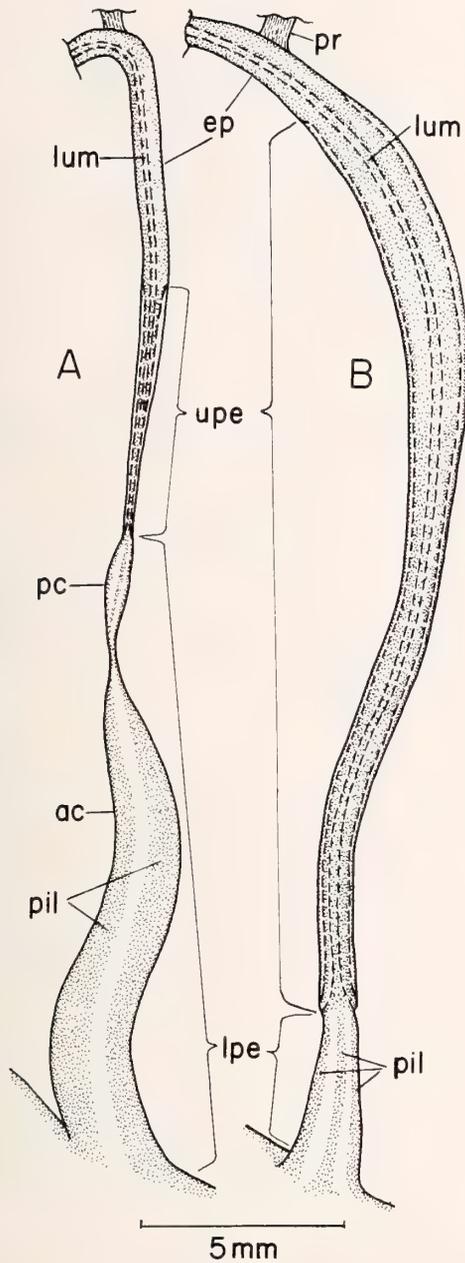


Figure 3

Enlargement of penes shown in Figures 1 and 2, showing inner structures in dotted lines. A, penis of *Helminthoglypta* (*Rothelix*) *lowei*; B, penis of *H. (H.) tudiculata*. ac, anterior chamber of lower part of penis; ep, epiphallus; lpe, lower, saccular part of penis; lum, lumen of epiphallus and penis; pc, posterior chamber of lower part of penis; pil, pilasters; pr, penial retractor muscle; upe, upper, double-tubed part of penis.

Description of penis and dart apparatus of type species (Figure 1): The penis consists of a double-tubed, upper part, which is relatively short and narrow, and a single-tubed, saccular, lower part which is long, sausage-shaped,

and consists of a small, short, thin, bulging, posterior chamber and a long, thick, wide, anterior chamber lined with spongy, glandular, anastomosing pilasters; the two chambers connect via a very narrow venturi-shaped constriction. The dart sac and mucus glands are typical for the genus, but the atrial sac, below the dart sac, connects with the vagina at its posterior end, immediately below the dart sac. The mucus gland membranes completely envelop the mucus bulbs, dart sac, and atrial sac, as well as the base of the anterior chamber of the lower part of the penis where they anastomose with additional connective tissues to form a penial sheath that attaches by several strong strands to the vas deferens, the epiphallus, and the epiphallal caecum, where the three ducts join together.

DISCUSSION

The reproductive system (Figure 2) of the type species of the nominate subgenus, *Helminthoglypta tudiculata*, is characterized by a long, cylindrical, double-tubed, upper part of the penis, and a very short, thin, saccular, lower part of the penis. The dart apparatus consists of a large dart sac, mucus glands, and a capacious atrial sac, in which the vagina and the penis enter at its anterior end, next to the genital orifice. The mucus membranes completely envelop the dart apparatus, including the lower part of the penis where they form a thin penial sheath that attaches to the vas deferens where it connects with the epiphallus (not shown in Figure 2, in order to show individual structures fully stretched).

In *Rothelix*, the upper part of the penis is relatively short and thin, compared to that of *Helminthoglypta* s.s. (Figures 3A, B), while the lower part of the penis is long and large. Furthermore, the penial sheath in *Rothelix* is long and tough, whereas it is short and fragile in *Helminthoglypta* s.s.

Included in this subgenus are *Helminthoglypta cuyamacensis* (Bartsch, 1916) and several additional species, yet to be described, from the vicinity of the Cuyamaca Mountains. Not included are *H. cuyamacensis piutensis* Willett, 1938, and *H. c. avus* (Bartsch, 1916), whose anatomy is typical of *Helminthoglypta* s.s., thereby requiring that they be elevated to specific rank, namely *H. (H.) piutensis* and *H. (H.) avus* respectively. *Helminthoglypta lowei* was originally described by Bartsch as *Epiphragmophora cuyamacensis lowei* and was subsequently raised to specific status by BERRY (1953). It is selected as the type species of the subgenus because its type locality, Palomar Mountain, is precisely known, and it has been collected and dissected by several workers, including Berry, Gregg, and the author. The type locality of *H. cuyamacensis cuyamacensis* on the other hand, "Cuyamaca Mountains, San Diego Co.," covers a large area that is home to many species of *Helminthoglypta*, several of which are undescribed and, therefore, topotypes could not be obtained for dissection. Gregg and I have obtained anatomies from snails whose shell measurements and characters correspond closely with those of the holotype and may pos-

sibly be topotypes; these anatomies reveal them to belong in the subgenus *Rothelix*. PILSBRY (1939:146, fig. 73) illustrates the "genitalia of a *Helminthoglypta* of uncertain status"; it is obviously a member of the subgenus *Rothelix*, and probably came from the same lot whose shells were described by Bartsch as *Epiphragmophora cuyamacensis cuyamacensis*.

Zoogeography: At present, the subgenus *Rothelix* is known only from San Diego County where it inhabits the inland montane region from Palomar Mountain in the north to the Cuyamaca Mountains in the south, including several intervening localities. It is primarily a log snail, living in rotting logs of oaks, firs, and incense cedars, but it can be found also in large rat nests. It is sympatric with species of the *Helminthoglypta traskii* group, which is widespread in southern California and northern Baja California. Accordingly, it probably evolved from an *H. traskii*-like ancestor and spread, during pluvial times, throughout the area that it now occupies.

Etymology: This subgenus is named after Barry Roth, a friend and colleague, who has taken up systematic re-

search of western North American terrestrial mollusks from his tutor, the late and beloved Allyn G. Smith.

ACKNOWLEDGMENTS

I am indebted to the late Wendell O. Gregg for pointing out the salient features of the anatomies of *Helminthoglypta lowei* and *H. cuyamacensis* and for companionship on many field trips to collect specimens of these species as well as other species yet to be described. I wish to thank Carl C. Christensen and Barry Roth for their critical reviews of this manuscript.

LITERATURE CITED

- BERRY, S. S. 1953. Two Californian mountain snails of the genus *Helminthoglypta*—a problem in the relationship of species. *Transactions San Diego Soc. Natur. Hist.* XI(12): 329–344 (17 April 1953).
- MILLER, W. B. 1981. *Helminthoglypta reederi* spec. nov. (Gastropoda: Pulmonata: Helminthoglyptidae) from Baja California, Mexico. *Veliger* 24(1):46–48 (1 July 1981).
- PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). *Acad. Natur. Sci. Phila., Monogr.* (3)I(1):i–xviii + 1–573 + i–ix; figs. A, B, 1–377 (6 December 1939).

The Archaeogastropod Family Addisoniidae Dall, 1882: Life Habit and Review of Species

by

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Abstract. The family Addisoniidae is reported for the first time in the eastern Pacific with the description of *Addisonia brophyi* spec. nov., which lives within spent egg cases of two species of cat sharks (family Scyliorhinidae). The thin shell and the characteristic radular morphology are adaptations to this habitat. Illustrations of the gill structure, hermaphroditic gonad, and the open seminal groove are given. The other two species in the family are reviewed: *A. lateralis* (Requien, 1848), from the Mediterranean and eastern Atlantic, and *A. paradoxa* Dall, 1882, type species of the genus, from the western Atlantic.

INTRODUCTION

Addisonia in the eastern Pacific was first collected off southern California by Pat Brophy, of Pacific Bio-Marine Laboratories, who obtained it on four separate occasions during the summer months of 1968 and 1972 while salvaging biological specimens as a guest on trawling vessels. Based on this material, HICKMAN (1983) included a radular illustration of the new species in her discussion of radular morphology in deep-sea limpets. The new species *A. brophyi* is validated here.

Prior to the discovery of the new species, *Addisonia* had been considered to include only the western Atlantic type species, *A. paradoxa*, and the European species, *A. lateralis*. These two taxa have been variously recognized, synonymized, or related as "varieties" by different authors. Here they are redefined and recognized as distinct.

Notes on external anatomy in *Addisonia paradoxa* were given by DALL (1882a, 1889a), VERRILL (1884), and THIELE (1908), the latter under the name *A. lateralis*. I include here notes on anatomy in the new species and discuss the significance of the association of the genus with spent egg cases of sharks.

MATERIALS

I have been able to locate shells of the east Atlantic *Addisonia lateralis* in the collections of the Paris Museum and the Brussels Museum. Shells with dried animals of the western Atlantic *A. paradoxa* were located in the U.S. National Museum of Natural History. Preserved specimens of *A. brophyi* have been used for radular prepara-

tions and histologic sectioning. Light microscope preparations of radulae of *A. brophyi* and *A. paradoxa* were made; preparations of the same two species were examined by C. S. Hickman, using scanning electron microscopy (SEM). Transverse and sagittal sections of *A. brophyi* were made, but the initial fixation in alcohol was not adequate for histological work and the sections of the internal organs were shattered. However, the sections suffice to demonstrate the condition of the gill and the hermaphroditic gonad. The shark egg cases were identified by comparison with illustrations of COX (1963).

Abbreviations for museum collections cited here are: CAS, California Academy of Sciences, San Francisco; IRSNB, Institut Royal des Sciences Naturelles de Belgique; LACM, Los Angeles County Museum of Natural History, Los Angeles; MNHNP, Museum of National d'Histoire Naturelle, Paris; USNM, United States National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Order ARCHAEOGASTROPODA

Suborder LEPTELLINA

Superfamily LEPETELLACEA

Families: Addisoniidae Dall, 1882; Bathypeltidae Moskalev, 1971; Bathyphytophilidae Moskalev, 1978; Bathysciadiidae Dautzenberg & Fischer, 1900; Cocculinellidae Moskalev, 1971; Cocculinidae Dall, 1882; Lepetellidae Dall, 1882; Pseudococculinidae Hickman, 1983. Each family has a characteristic radula.

The Lepetellacea (sole superfamily here recognized in the suborder Lepetellina) occupy a position intermediate between that of archaeogastropods and mesogastropods. Gill characters suggest neither archaeogastropods nor mesogastropods, as the gill (if present) is secondary. As in archaeogastropods, the radula is rhipidoglossate (or degeneratively rhipidoglossate). As in lower mesogastropods, the heart is monotocardian and the right kidney is lacking. However, a true pallial gonoduct, which replaces the right kidney of archaeogastropods in the lower mesogastropods, has not developed. All members are simultaneously hermaphroditic and have a seminal receptacle; in some, the right tentacle bears a sperm groove and functions in copulation.

Anatomy in these families has been treated only by THIELE (1903, 1908), who illustrated serial sections of three genera, reporting first on *Cocculina* (1903) and subsequently on *Lepetella* and *Bathysciadium* (1908). External features of *Addisonia* were compared in the second paper. He concluded (THIELE, 1908) that these four genera are closely related anatomically, despite major differences in radular configuration.

Two families, the Cocculinidae and Pseudococculinidae, have rhipidoglossate radulae in which lateral teeth are generally like those of adjacent laterals in size and shape. The remaining families have lateral teeth that are not similar to adjacent laterals and, except for the Bathyphytophilidae, lack marginals. THIELE (1929) interpreted these radulae to be degeneratively rhipidoglossate. Support for this interpretation is provided by the recently named Bathyphytophilidae, a transitional group in which there are 6–20 pairs of marginal teeth and non-repeating “lateral” elements that most closely resemble those of the Lepetellidae.

Systematic papers treating these families are those of THIELE (1909), MOSKALEV (1971, 1973, 1976, 1978), WARÉN (1972), and MARSHALL (1983). HICKMAN (1983) gave SEM radular illustrations for many of these groups; only the radula of the Bathyphytophilidae remains to be illustrated with SEM.

MOSKALEV (1971, 1973, 1976, 1978), in papers published in Russian (translations available, see Acknowledgments), has proposed three of these families. His family definitions are accepted because each family has radular characters that are different enough to warrant recognition. However, he inflated the classification to contain four superfamilies. I do not follow Moskalev in this action because he did not offer sufficient justifications and he made no original contributions of his own to an understanding of anatomy. Moreover, his classification (see translation of 1978, summary section) did not properly take Thiele’s work into account. He did not cite THIELE’s (1903) paper on the Cocculinidae, claiming that anatomy in that family had not been investigated; and, although he cited THIELE (1908), he followed PELSENEER (1900) in relating the Bathysciadiidae to the docoglossate patellaceans, despite the fact that THIELE (1908) amply dem-

onstrated that Pelseener’s conclusions were wrong. Thus, MOSKALEV (1978) erroneously placed the families Bathysciadiidae and Bathypeltidae in the order Docoglossa.

Until major anatomical differences among the families under discussion can be demonstrated, I accept THIELE’s (1908) conclusion that all members are closely related anatomically, and following MARSHALL (1983), recognize only the superfamily Lepetellacea (which has priority over Cocculinacea). I do not relate the suborder Lepetellina to other archaeogastropods or to lower mesogastropods, but arbitrarily retain the suborder in the order Archaeogastropoda on the strength of the rhipidoglossate radula.

Family ADDISONIIDAE Dall, 1882

Addisonia Dall, 1882

Addisonia DALL, 1882a:404. Type species (original designation): *A. paradoxa* Dall, 1882. Recent, northwestern Atlantic.

The single genus *Addisonia*, with three species, comprises the family Addisoniidae. Radular characters are unique. Although BOSS (1982), following THIELE (1908), placed *Addisonia* in the Lepetellidae, genera in that family differ in having a symmetrical shell and an entirely different radula.

Dall’s generic name honored his contemporary, Addison E. Verrill.

Shell (Figures 1–6): Cap-shaped, thin, non-nacreous; periostracum thin, smooth. Margin sharp and fragile, ends slightly raised relative to sides. Outline asymmetrical, anterior either broader or narrower than posterior. Apex of young shells (to 6 mm in length) near mid-dorsal line, ¼ shell length from posterior margin; apex in larger shells offset toward left, curved backward and downward. Protoconch deciduous, apical tip sealed over. Radial sculpture of fine striae; concentric sculpture of microscopic growth lines. Muscle scar horseshoe-shaped, narrow throughout, not broken into discrete bundles, anterior terminations curved inward and directed posteriorly; termination of right side with broader inward curve than that of left. A narrow pallial line extends in broad arch from anterior limitation of muscle scar.

The shell edge is so thin that all specimens tend to have broken and chipped margins.

Radula (based on *Addisonia brophyi* and *A. paradoxa*, Figures 15, 16): The following description is based upon the SEM illustration of HICKMAN (1983), one of which is reproduced here (Figure 15), and partially paraphrases her description: Rachidian subcylindrical, uncusped, fitting with rachidian elements anterior and posterior to it to form continuous, jointed cylindrical column along central longitudinal axis; rachidian flanked by two pairs of uncusped, solid rhomboidal plates in a V-shaped alignment; these plates flanked by two pairs of narrow sigmoid elements; outermost 3 plates complexly interlocked; first

of these triangular and bicuspid; second large and bicuspid, overlapping the first; third a narrow element separating the large bicuspid plate from the corresponding plate anterior and posterior to it.

Hickman's description of this radula was the first clear understanding of it, as earlier interpretations of light microscope preparations (see Figure 16) were incorrect.

As Hickman noted, this radula is neither rhipidoglossate nor docoglossate, nor has it any features to suggest relationships with other families in the superfamily with which it shares anatomical characters. The other families in the superfamily also have odd and essentially unique radulae.

Addisonia brophyi and *A. paradoxa* differ in the morphology of the rachidian element as discussed in the species accounts; no intact specimens of *A. lateralis* were available.

Anatomy (based on Thiele's description of *Addisonia paradoxa* and my examination of *A. brophyi*, Figures 7–10, 12): Foot oval, thin at center, where it reveals darker digestive gland tissue within; edge of foot thin, projecting; epipodial processes lacking. Mantle edge simple, thickened. Secondary gill in right mantle groove, extending on right side adjacent to right cephalic tentacle to adjacent to foot tip; leaflets produced by folding of mantle skirt, each leaflet with a thin extension at tip (Figure 10). Eyes lacking, snout expanded at tip, mouth opening triangular, lacking oral lappets. Cephalic tentacles bent ventralward, nearly equal in size; right tentacle with sperm groove on lateral side; sperm groove leading to right tentacle clearly visible on neck and outer body wall (Figures 9, 17).

According to THIELE's description of *Addisonia paradoxa* (1908): "The dorsal side contains the gonad in the center, the duct of which runs anteriorly and on the right. Next to it lies the hindgut, while more to the left the heart is visible." These organs are readily apparent on the intact specimen illustrated here (Figure 8), in which the developing eggs are visible in the central gonad. The gonad is simultaneously hermaphroditic; male and female cells are closely associated, as can be seen in sections (Figure 12).

THIELE (1908) observed a swelling at the base of the right tentacle, which reminded him of the sperm groove of the copulatory organ of *Bathysciadium*. Here I confirm that there is a sperm groove in *Addisonia*, visible in illustrations of two species—on the preserved specimen *A. brophyi* (Figure 9), and a dried specimen of *A. paradoxa* (Figure 17). This had been missed by DALL (1882a, 1889a) and VERRILL (1884). VERRILL's statement (1884) that males and females differ in appearance is incorrect, as the species is hermaphroditic.

DALL's drawing of the animal of *Addisonia paradoxa* (1889a, b), which has been the principal cited figure—copied by PILSBRY (1890) and ABBOTT (1974)—is incorrect in showing a ventral axis connecting the gill filaments. The first figure of the species, that of VERRILL (1884), correctly showed the gill, but this figure has been ignored by most subsequent authors.

The pronounced asymmetry of the mature shell is a result of asymmetry in the animal: the enormous secondary gill on the right side requires extra space, forcing this side of the shell to become inflated and the shell apex to be diverted to the left.

Three broadly allopatric species are known in the genus *Addisonia*. Specific characters include relative size and differences in proportions of the rachidian element in two of the three species. However, the radula of one species is not available. These differences are admittedly few. Unfortunately, sufficient specimens are not available to allow rigorous study. It may well be that the differences among the three are purely quantitative, but in the absence of sympatry the question is moot. A pragmatic approach is taken here in accepting three species, although it is recognized that equal justification could be offered for the recognition of three subspecies of a single, widely distributed species.

Addisonia paradoxa Dall, 1882

(Figures 1, 2, 16, 17)

Addisonia paradoxa DALL, 1882a:405; 1882b:737; VERRILL, 1882:533; VERRILL, 1884:256, pl. 29, figs. 10, 11, 11a, 11b; DALL, 1889b:158, pl. 25, figs. 1a–e, pl. 44, figs. 10, 11–11b, pl. 63, fig. 100; THIELE, 1909:25, pl. 4, figs. 20–23; ABBOTT, 1974:35, fig. 206 [copy Dall figs.]; HICKMAN, 1983:81, fig. 10 [radula].

Addisonia lateralis var. *paradoxa*: DALL, 1889a:344, pl. 25, figs. 1a–e; PILSBRY, 1890:139, pl. 25, figs. 1–3 [copy Dall figs.].

Addisonia lateralis paradoxa: JOHNSON, 1934:66.

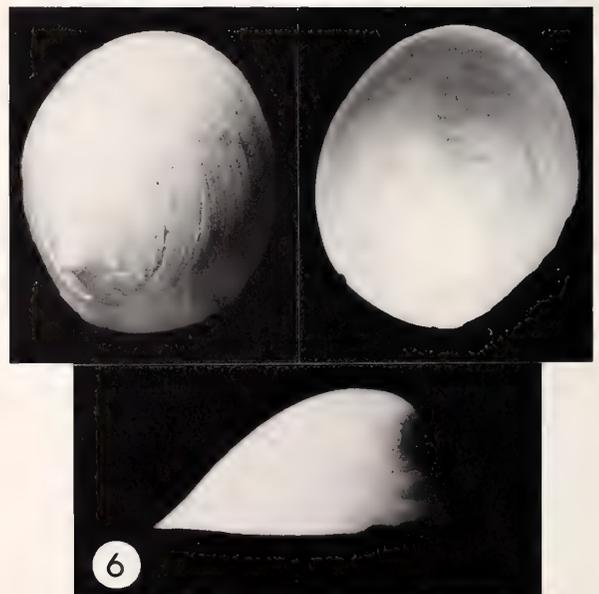
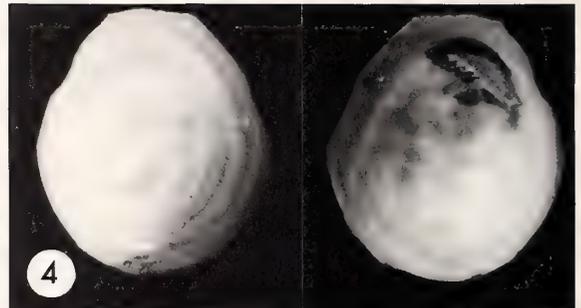
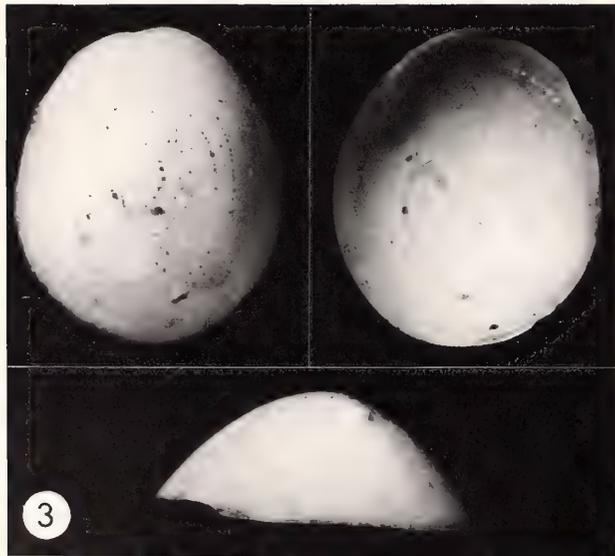
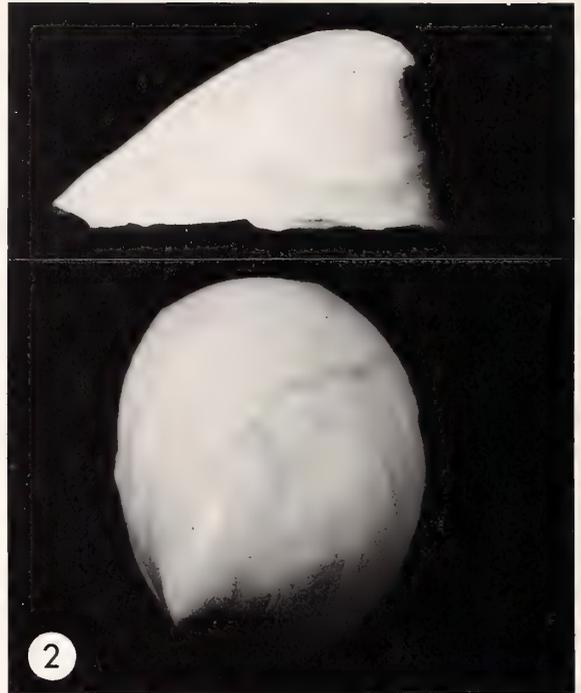
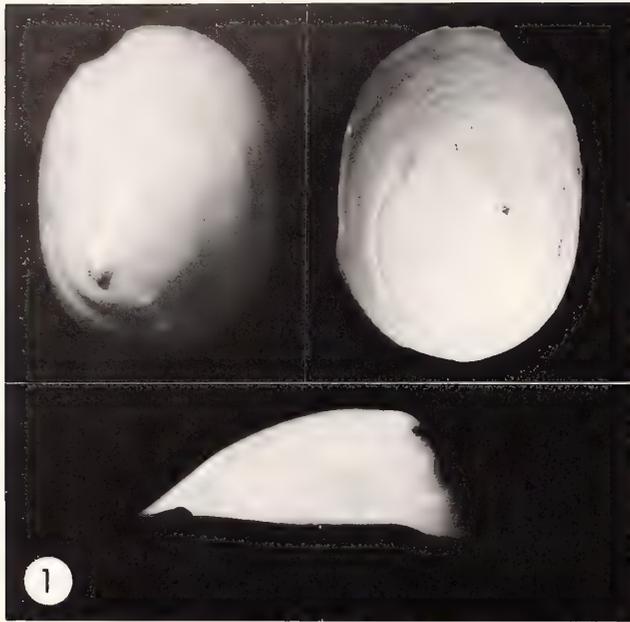
Diagnosis: Differing from both *Addisonia lateralis* and *A. brophyi* in its much larger size and having only a trace of the interior radial sculpture that is so pronounced in *A. lateralis*. The subcylindrical rachidian element differs from that of *A. brophyi* in having convex rather than parallel sides (compare Figures 15 and 16).

Dimensions: Lectotype: length 10.8, width 8.0, height 4.0 (Figure 1). Largest specimen: length 20.3, width 16.0, height 10.5 mm (Figure 2, USNM 50404, off North Carolina).

Type material: Original specimens of *Addisonia paradoxa* were collected in 1881 from three U.S. Fish Commission stations (923, 940, 950) off Martha's Vineyard Island, Massachusetts, 126–238 m. A lectotype, USNM 43741 (Figure 1), from station 950 is here designated; two paralectotypes USNM 333747, same station; 3 paralectotypes USNM 33748, sta. 923. The material from sta. 940 has not been located.

Distribution: Grand Banks, Nova Scotia, to Kingston, Jamaica, in depths of 119–1170 m.

Material examined: All USNM: USNM 226271, "Grand Banks, USFC"; 7 lots off Martha's Vineyard; 1 lot off St. Augustine, Florida; 3 lots off Virginia and North Caro-



lina; 3 lots off Florida Keys; 1 lot (USNM 811797) off Kingston, Jamaica (R/V *Oregon* sta. 3560). Depth range 115–878 m.

USNM 43743 (Martha's Vineyard) contained two dried animals, one of which is illustrated (Figure 17), the other was prepared for the radular mount (Figure 16). USNM 47345 (Martha's Vineyard) has an original label that reads "from skate egg." This was overlooked in all the published accounts, but confirms the association of this species with elasmobranch egg cases.

Remarks: When first proposed, DALL believed *Addisonia* to be monotypic; however, he shortly thereafter (1882b: 737) allocated *Gadinia excentrica* Tiberi, 1857, to the genus. A year later JEFFREYS (1883) placed Dall's species in the synonymy of *A. excentrica* (Tiberi). DALL subsequently wavered; in (1889b) he recognized his own species but in (1889a) he considered it a "variety" of the European species. DALL (1889a) noted that the "figures, descriptions, and specimens I have seen of European origin all indicated the shell as very much smaller than our American specimens . . ." Recent authors (ABBOTT, 1974; HICKMAN, 1983) have used the name *A. paradoxa*, without mentioning the unresolved taxonomic question. I consider the size difference to be sufficiently important to warrant the recognition of separate species.

Addisonia lateralis (Requien, 1848)

(Figures 3, 4)

- Gadinia lateralis* REQUIEN, 1848:39; PETIT, 1869:92, 264.
Addisonia lateralis: DAUTZENBERG, 1886:1; PILSBRY, 1890: 139, pl. 25, figs. 26, 27 [copy Tiberi figs.]; THIELE, 1909:25, pl. 4, figs. 18, 19 [copy Tiberi figs.]; HUBENDICK, 1946:77; NORDSIECK, 1968:35, fig. 21.10.
Gadinia excentrica TIBERI, 1857:27, pl. 2, fig. 6; PETIT, 1869: 92, 264; WEINKAUFF, 1870:90; LOCARD, 1898:93.
Addisonia excentrica: DALL, 1882b:737; WATSON, 1886:32.
Addisonia excentros: JEFFREYS, 1883:673 [emendation of *excentrica* Tiberi].

Diagnosis: Differing from both *Addisonia paradoxa* and *A. brophyi* in having a less deflected apex; smaller than *A. paradoxa*.

Dimensions: Length 10.5, width 8.9, height 4.2 mm (Figure 3, holotype *Addisonia excentrica*).

Type material: *Gadinia lateralis* Requien, 1848, was never figured, and, according to DANCE (1966:299), the Requien Collection was neglected and abandoned. Philippe Bouchet of the Paris Museum reports (personal communication) that he had searched unsuccessfully for Requien's type material in Avignon and Toulouse. The description was included in Requien's catalogue of mollusks of the French Mediterranean island Corsica. Although short, the description is adequate and subsequent authors have accepted the synonymy.

A specimen marked "type" of the junior synonym *Gadinia excentrica* Tiberi, 1857, has been examined (Figure 3). The published locality is the Italian Mediterranean island Sardinia, from the "coral fishery." PILSBRY (1890) copied the illustrations and translated the Latin description to English. The above cited measurements are less than the published dimensions of 17 × 14 × 11 mm.

Distribution: Mediterranean Sea: Sicily to Corsica; Eastern Atlantic: Bay of Biscay to Morocco.

Material examined: MNHNP: Single specimens of LOCARD (1898:93): sta. 26 off Portugal; sta. 35, off Atlantic Morocco (Figure 4); 5 specimens from Atlantic Morocco (33°59'N, 07°50'W), *N. O. Vanneau* sta. 37, 1923–1929. IRSNB: 4 lots: Sciacca, Sicily; South of Sicily (*Princesse Alice*); Ile Yeu, Bay of Biscay (cited by Dautzenberg, 1886); *N. O. Vanneau* sta. 46, Atlantic Morocco.

Remarks: DAUTZENBERG (1886) accepted JEFFREYS' (1883) conclusion that Dall's genus *Addisonia* was represented in the eastern Atlantic, but used the oldest name, *Gadinia lateralis* Requien, 1848, for the Atlantic species.

None of the published accounts has mentioned an association with elasmobranch egg cases. According to P. Bouchet, there are no recent collecting records of *Addisonia lateralis* in European waters and no accounts in recent literature. The synonymy given by DAUTZENBERG (1886) includes several references not mentioned here.

The radula of this species has not been illustrated.

Explanation of Figures 1 to 6

Exterior, interior (anterior at top), and lateral (left side) views of shells of *Addisonia* species. Shell edges of all specimens are chipped; shell apex is posterior and deflected to left in mature specimens (Figures 1 to 3, 6), posterior and near mid-dorsal line in immature specimens (Figures 4, 5). Interior views show the narrow muscle scar and anterior pallial line. Dimensions are given as length, width, and height.

Figure 1. *A. paradoxa* Dall, lectotype, USNM 43741. USFC sta. 950, 130 m off Martha's Vineyard Island, Massachusetts. 10.8 × 8.0 × 4.0 mm.

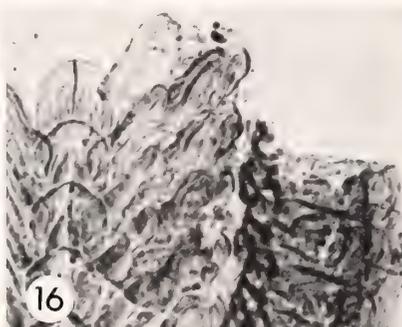
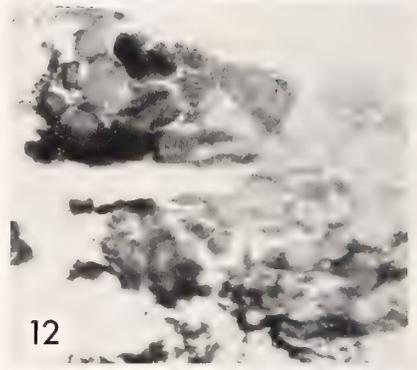
Figure 2. *A. paradoxa* Dall, USNM 50404. USFC sta. 2425, 218 m off North Carolina. 23.3 × 16.0 × 10.5 mm.

Figure 3. *A. lateralis* (Requien), MNHNP, uncatalogued. Holotype of *Gadinia excentrica* Tiberi. Off Sardinia, Mediterranean Sea. 10.5 × 8.9 × 4.2 mm.

Figure 4. *A. lateralis* (Requien), MNHNP uncatalogued. LOCARD (1898) sta. 35, off Atlantic Morocco. 7.3 × 6.4 × 2.8 mm.

Figure 5. *A. brophyi*, spec. nov., LACM 111551. 91 m off Catalina Isthmus, California. 6.0 × 5.3 × 1.9 mm.

Figure 6. *A. brophyi* spec. nov., holotype, LACM 2082, 155–174 m off Gaviota, California. 10.1 × 8.5 × 4.8 mm.



MOSKALEV (1978) erred in stating that HUBENDICK (1946) "convincingly showed that *G. excentrica* Tiberi is an independent species" [of *Gadinia*]. In actuality, HUBENDICK (1946:77) merely listed it in a catalog of names and referred it to *Addisonia lateralis*.

Addisonia brophyi McLean, spec. nov.

(Figures 5–12, 15)

Addisonia n. sp., HICKMAN, 1983:81, figs. 38a, 38b (radula).

Diagnosis: Smaller than *Addisonia paradoxa* and with apex more displaced than that of *A. lateralis*.

Although half the size of large specimens of *Addisonia paradoxa*, the apex is fully displaced to the left; on specimens of *A. paradoxa* of comparable size (for example, the lectotype, Figure 1), the apex is only partially offset to the left. The subcylindrical rachidian differs (Figure 15) from that of *A. paradoxa* (Figure 16; HICKMAN, 1983, fig. 10) in having parallel rather than convex sides.

Description: Cap-shaped, thin, non-nacreous; periostracum thin, smooth. Margin sharp and fragile, ends slightly raised relative to sides. Outline asymmetrical, anterior either broader or narrower than posterior. Apex near midline, $\frac{1}{4}$ shell length from posterior margin in young shells (to 6 mm in length); apex in larger shells offset toward left, curved backward and downward. Protoconch lost, apical tip sealed over. Radial sculpture of fine striae; concentric sculpture of microscopic growth lines. Muscle scar horseshoe-shaped, narrow throughout, not broken into discrete bundles, anterior terminations curved inward and

directed posteriorly; termination of right side with broader inward curve than that of left side. A narrow pallial line extends in broad arc from anterior limitation of muscle scar.

Dimensions: Holotype: Length 10.1, width 8.5, height 4.8 mm. Largest specimen: length 10.2, width 9.5, height 4.4 mm (CAS 056077).

Type locality: 85–95 fm (155–174 m) off Gaviota, Santa Barbara County, California (approx. 34°12'N, 120°12'W).

Type material (all collected by Pat Brophy on trawling vessels working at or near the type locality): 10 specimens extracted from 7 egg cases (Figure 11) identified by McLean as brown cat shark *Apristurus brunneus* (Gilbert), 28 August 1968, distributed as follows: Holotype LACM 2082, 7 paratypes (with egg cases) LACM 2083, 2 paratypes USNM 784754. Additional paratypes: LACM 2084, 3 specimens, 17 July 1968, "in shark egg cases." CAS 056076, 1 specimen with egg case (Figure 13) identified by McLean as swell shark *Cephaloscyllium uter* (Jordan & Gilbert), 17 July 1968. CAS 056077, 5 specimens, 25 July 1968, "in shark egg case."

Referred material: LACM 111551 (Figure 5), 3 immature specimens, not with egg case, but with original label reading "in swell shark egg case," 91 m (50 fm) off Catalina Isthmus, Catalina Island, California, June 1972. As in other juveniles, the apex in these specimens is near the mid-dorsal line.

Distribution: Gaviota, Santa Barbara County, to Cata-

Explanation of Figures 7 to 17

Figure 7. *Addisonia brophyi* spec. nov., paratype. Ventral view of preserved animal, showing mantle cavity gill on right side, foot with digestive gland (dark patch) showing through, head with large oral disc and cephalic tentacles bent down. Length of preserved specimen 6.5 mm.

Figure 8. Same specimen as Figure 7. Dorsal view, showing gill extending to right, large light colored heart near anterior termination of gill; gonad with light colored eggs, dark digestive gland bordered by narrow shell muscle.

Figure 9. Same specimen as Figure 7. Right lateral view showing structures noted above and the sperm groove (light colored with dark channel) leading from base of right tentacle toward 7:00 o'clock position.

Figure 10. *Addisonia brophyi*, histologic section through 5 filaments of gill on right side, showing that each filament is an outpocket of epithelium. Smooth mantle edge at left edge of frame, mantle cavity space at right. Horizontal dimension of field 1.5 mm.

Figure 11. Egg capsules of brown cat shark *Apristurus brunneus* shown with paratypes of *Addisonia brophyi* in vial, LACM 2083. Actual size, horizontal dimension of field 54 mm.

Figure 12. *Addisonia brophyi*, histologic section through her-

maphroditic gonad, showing large eggs and dark staining testes cells interspersed. Horizontal dimension of field 1.5 mm.

Figure 13. Egg case of swell shark *Cephaloscyllium uter* from which a paratype specimen of *Addisonia brophyi* was collected, CAS 056076. Actual size, horizontal width of field 53 mm.

Figure 14. SEM view of inside wall of egg case illustrated in Figure 13. Undamaged interior of egg case in upper right, grooves identified as radular scraping marks made by *Addisonia brophyi* present at lower left. 100 \times .

Figure 15. SEM view of radular ribbon of paratype of *Addisonia brophyi*, showing columnar rachidian elements running diagonally, two rhomboidal plates in V-shaped alignment, and the outer bicuspid plates (see text for more detailed description). Horizontal dimension of field 200 μ m.

Figure 16. *Addisonia paradoxa*, light microscope preparation of radula, to show the rachidian elements with convex sides and to illustrate the difficulty of interpretation of such radular preparations. Horizontal dimension of field 200 μ m.

Figure 17. *Addisonia paradoxa*, specimen with dried animal, sperm groove clearly visible on body wall (the dark groove in lighter area extending from base of right tentacle), USNM 43743. Shell length 11.0 mm.

lina Island, Los Angeles County, California (records above).

Remarks: All collecting records of *Addisonia brophyi* have been associated with the spent egg cases of the cat shark family Scyliorhinidae, as discussed below.

DISCUSSION

Other deep-sea limpet families in the suborder Lepetelina are associated with, and feed upon, various kinds of organic debris that have a frequent but scattered occurrence in the deep sea (HICKMAN, 1983). Cocculinids and pseudococculinids are usually associated with wood, although some have adapted to cephalopod beaks (MOSKALEV, 1976); bathysciadiids and bathypeltids are associated with cephalopod beaks (MOSKALEV, 1973); bathyphytophilids are associated with turtle grass debris (MOSKALEV, 1978); lepetellids reside within polychaete tubes (MOSKALEV, 1978); cocculinellids derive their nutrition from fish bone (MARSHALL, 1983). Therefore, it comes as no surprise to learn that *Addisonia* has an obligate association with shark egg cases.

Egg cases are produced by three shark families: the cat sharks (family Scyliorhinidae), of which there are more than 85 species in the world (ESCHMEYER *et al.*, 1983), the bullhead or horn sharks (family Heterodontidae), and the skates (family Rajidae). COX (1963) and ESCHMEYER *et al.* (1983) illustrated the egg cases of the Californian species in these families. *Addisonia* is now known to live within old egg cases of two species of cat sharks; it should also be expected to inhabit the spent egg cases of skates and horn sharks, although the single Californian species in the latter group occurs in shallower water than known for *Addisonia*.

WOURMS (1977) reviewed the literature on shark egg case structure and formation. Egg cases are composed primarily of layers of the structural protein collagen, that of the egg cases having unique chemical and physical properties. The egg cases protect the shark embryos for up to nine months, after which there is little evidence of deterioration. Data are not available, but the spent egg cases probably endure for a number of years in the marine environment. This is, therefore, a persistent and reliable food source, but one that must require enzymes capable of digesting collagen. One other prosobranch gastropod, the North Atlantic *Choristella tenera* (Verrill, 1882), is known to be associated with elasmobranch egg cases (VERRILL, 1882; HICKMAN, 1983:86), upon which it presumably feeds (for current taxonomy of *Choristella*, see BOUCHET & WARÉN, 1979:225).

The wall thickness in preserved egg cases of the brown cat shark (LACM 2083) is 0.1 to 0.2 mm. Specimens preserved in alcohol and viewed with transmitted light show thinner areas on the inner surface and some holes. Grooves presumed to be tooth scraping marks made by *Addisonia* on the inner surface of a dried specimen of swell shark egg case (CAS 056076) are illustrated here in an

SEM micrograph (Figure 14). It is apparent that *Addisonia* feeds upon inner layers of the egg case. The low relief of the functional teeth (the bicuspidate outer elements) can penetrate the complex layering of the inner lining of the egg case without rupturing the egg case and thereby exposing the limpet to predators.

Bone-feeding *Cocculinella* have not the same constraint, as the bone itself provides no containment. Thus the teeth of *Cocculinella*, illustrated by MARSHALL (1983), have comparatively high relief for feeding upon bone softened by bacterial activity.

Partially digested collagen within the hindgut of the preserved specimens of *Addisonia brophyi* may account for the dark-brown coloration of the digestive gland, which matches that of the egg cases. The hardness of the collagen particles may also have been a contributing factor in the shattering of the digestive organs in the serial sections of the present material.

Although early development is unknown, the veliger stage must be brief, owing to the small protoconch. Demersal veligers probably enter the spent cases and grow to maturity within. The egg cases provide shelter and protection from predators for the thin-shelled limpets. The shell margin with raised ends enables the limpet to have a good fit on the concave surface within the confines of the egg cases.

The largest specimen of *Addisonia brophyi* reported here is 10.2 mm in length, much smaller than the largest specimen of *A. paradoxa* (20.3 mm in length). The egg cases supporting *A. brophyi* were too small to support larger limpets. Therefore, the egg cases that support *A. paradoxa* must be larger.

It is surprising that only one of the records of *Addisonia paradoxa* noted the association of the limpets with shark egg cases. Collection by trawling usually produces immense masses of bottom debris; large limpets could have been clinging to partially disintegrated remains of the cases, so that the association could easily have been missed. Shark egg cases are sufficiently common in the accumulations of debris brought up by trawlers to suggest that more records of *Addisonia* will come to light when an effort is made to examine old egg cases, particularly in the summer months, the time at which the specimens of *A. brophyi* were collected.

ACKNOWLEDGMENTS

The addition of *Addisonia* to the eastern Pacific fauna is entirely due to the careful observation and collection of all the material by Pat Brophy, of Venice, California, to whom I am greatly indebted. The late Allyn G. Smith of the California Academy of Sciences initially loaned me those specimens on deposit at that institution. Macrophotography of an immersed preserved specimen is the work of Bertram C. Draper. Serial sectioning was done by JoCarol Ramsaran of the LACM Malacology Section. Carole S. Hickman of the University of California, Berkeley,

provided the SEM radular illustration. Copies of Moskalev's papers, translated by George Shkurkin, were provided by Hickman. THIELE (1903) was translated by David R. Lindberg and THIELE (1908) by Silvard Kool. Specimens of *A. lateralis* were loaned by Philippe Bouchet of the Paris Museum and J. van Gothem of the Brussels Museum; those of *A. paradoxa* were loaned by R. Houbriek and J. Rosewater of the U.S. National Museum. J. P. Wourms sent additional information about shark egg cases. I am grateful to Eugene Coan, David R. Lindberg, and Bruce A. Marshall for reading the manuscript and offering helpful suggestions.

LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold: New York. 663 pp.
- BOUCHET, P. & A. WARÉN. 1979. The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. *Sarsia* 64:211-243.
- BOSS, K. J. 1982. Mollusca. Pp. 945-1166. In: S. P. Parker (ed.), *Synopsis and classification of living organisms*, vol. 1, McGraw-Hill: New York.
- COX, K. W. 1963. Egg-cases of some elasmobranchs and a cyclostome from Californian waters. *Calif. Fish & Game* 49(4):271-289.
- DALL, W. H. 1882a. On certain limpets and chitons from the deep waters off the eastern coast of the United States. *Proc. U.S. Natl. Mus.* 81(26):401-414.
- DALL, W. H. 1882b. Note on *Gadinia excentrica* Tiberi. *Amer. Natur.* 16:737.
- DALL, W. H. 1889a. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico . . . by the U.S. Coast Survey Steamer "Blake" . . . XXIX. Report on the Mollusca. II. Gastropoda and Scaphopoda. *Bull. Mus. Comp. Zool. (Harvard Univ.)* 18:1-492, pls. 10-40.
- DALL, W. H. 1889b. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. *U.S. Natl. Mus. Bull.* 37, 221 pp., 74 pls.
- DANCE, S. P. 1966. *Shell collecting: an illustrated history*. Univ. Calif. Press: Berkeley. 344 pp.
- DAUTZENBERG, P. 1886. Note sur l'*Addisonia lateralis*. *J. Conchyl.* 1886:1-6.
- DAUTZENBERG, P. & H. FISCHER. 1900. Description d'un mollusque nouveau. *Bull. Soc. Zool. France* 24:207-209.
- ESCHMEYER, W. N., E. S. HERALD & H. HAMMANN. 1983. A field guide to Pacific Coast fishes of North America. Peterson Field Guide Series, Houghton Mifflin Company: Boston. 336 pp.
- HICKMAN, C. S. 1983. Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *Veliger* 26(2):73-92.
- HUBENDICK, B. 1946. Systematic monograph of the Patelliformia. *Kungl. Svenska Vetenskapsakademiens Handlingar* 23(5):1-93, pls. 1-6.
- JEFFREYS, J. G. 1883. On the Mollusca procured by the *Lightning* and *Porcupine* expeditions. V. *Proc. Zool. Soc. Lond.* (1882):656-687.
- JOHNSON, C. W. 1934. List of marine Mollusca of the Atlantic coast from Labrador to Texas. *Proc. Boston Soc. Natur. Hist.* 40(1):1-204.
- LOCARD, A. 1898. Expéditions scientifiques du *Travailleur* et du *Talisman* pendant les années 1880, 1881, 1882, 1883. Mollusques testacés, tome 2, Paris, 515 pp., 18 pls.
- MARSHALL, B. A. 1983. The family Cocculinellidae (Mollusca: Gastropoda) in New Zealand. *Natl. Mus. New Zealand Records* 2(12):139-143.
- MOSKALEV, L. I. 1971. New data on the systematic position of the gastropod mollusks of the Order Cocculinida Thiele, 1908. *Abstr. of Repts., Fourth Conference on the Investigation of Mollusks, Acad. Sci. U.S.S.R. Nauka, Leningrad*, pp. 59-60 [in Russian].
- MOSKALEV, L. I. 1973. Pacific Ocean Bathysciadiidae (Gastropoda) and forms similar to them. *Zool. Jour.* 52(9):1297-1303 [in Russian].
- MOSKALEV, L. I. 1976. Concerning the generic diagnostics of the Cocculinidae (Gastropoda, Prosobranchia). *Works of the P. P. Shirshov Institute of Oceanology, Acad. Sci. USSR* 99:57-70 [in Russian].
- MOSKALEV, L. I. 1978. The Lepetellidae (Gastropoda, Prosobranchia) and forms similar to them. *Works of the P. P. Shirshov Institute of Oceanology, Acad. Sci. USSR* 113:132-146 [in Russian].
- NORDSIECK, F. 1968. Die europäischen Meeres-Gehäuseschnecken (Prosobranchia) vom Eismeer bis Kapverden und Mittelmeer. Gustav Fischer: Stuttgart. 273 pp.
- PELSENEER, P. 1900. Note sur l'organisation du genre *Bathysciadium*. *Bull. Soc. Zool. France* 24:209-211.
- PETIT DE LA SAUSSAYE, S. 1869. *Catalogue des mollusques testacés des mers d'Europe*. Savy: Paris. 312 pp.
- PILSBRY, H. A. 1890. Stomatellidae, Scissurellidae, Pleurotomariidae, Haliotidae, Scutellinidae, Addisoniidae, Cocculinidae, Fissurellidae. *Manual of Conchology*, v. 12, 321 pp., 65 pls.
- REQUIEN, E. 1848. *Catalogue des coquilles de l'île de Corse*. Avignon. 110 pp.
- THIELE, J. 1903. Die beschalten Gastropoden der deutschen Tiefsee-Expedition 1898-1899. A. Die Anatomie und systematische Stellung der Gattung *Cocculina* Dall. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*, 7:149-156, pls. 6, 7.
- THIELE, J. 1908. Ueber die Anatomie und systematische Stellung von *Bathysciadium*, *Lepetella*, und *Addisonia*. *Bull. Mus. Comp. Zool. (Harvard Univ.)* 52(5):79-89.
- THIELE, J. 1909. Cocculinoidea und die Gattungen *Phenacolepas* und *Titiscania*. In: *Kuester, Systematisches Conch. Cabinet von Martini und Chemnitz*. Bd 2, Abt. 11a. Nurnberg, 1-48.
- THIELE, J. 1929. *Handbuch der systematischen Weichtierkunde. I. Prosobranchia (Vorderkiemer)*. Gustav Fischer: Jena. 376 pp.
- TIBERI, N. 1857. Testacea Mediterranei novissima. *J. Conchyl.* 6:37-39, pl. 2.
- VERRILL, A. E. 1882. Catalogue of marine Mollusca added to the fauna of New England during the past ten years. *Trans. Conn. Acad. Sci.* 5:447-587.
- VERRILL, A. E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England Coast and adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Trans. Conn. Acad. Sci.* 6:139-294.
- WARÉN, A. 1972. On the systematic position of *Fissurisepta granulosa* Jeffreys, 1882, and *Patella laterocompressa* de Rayneval & Ponzi, 1854 (Gastropoda Prosobranchia). *Sarsia* 51:17-24.
- WATSON, R. B. 1886. Report on the Scaphopoda and Gastropoda collected by H.M.S. *Challenger* during the years in

- 1873-1876. Report on the Scientific Results of the Voyage of H.M.S. *Challenger*, 1873-1876. Zoology 15, part 42: 1-680, pls. 1-50.
- WEINKAUFF, H. C. 1870. Supplemento alle conchiglie del Mediterraneo, la loro distribuzione geografica e geologica. Bull. Malac. Ital. 3:14-24, 33-37, 74-100, 128-129.
- WOURMS, J. P. 1977. Reproduction and development in chondrichthyan fishes. Amer. Zool. 17:379-410.

NOTE ADDED IN PROOF:

Too late for inclusion in the text, P. Bouchet has sent me a copy of a paper published in an Italian journal in which the same habitat for *Addisonia* is described:

Villa, R. 1985. Note su habitat ed ecologia di *Addisonia lateralis* (Réquien, 1848). Notiz. CISMA, "1983," 5(1-2):9-12.

Villa reported the collection of *A. lateralis* within the egg cases of the elasmobranchs *Scyliorhinus canicula* and *Raja* sp. from Fiumicino on the Mediterranean coast near Rome. "The specimens of *Addisonia* were found inside the egg case and there is no opening that would permit the mollusk to enter. I suppose the mollusk penetrates the egg case at an early stage." [translation]

Redescription and Systematic Position of *Pleurobranchaea obesa* (Verrill, 1882) (Opisthobranchia: Pleurobranchaeidae)

by

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Abstract. Rediscovery of specimens of *Koonsia obesa* Verrill, 1882, has permitted the amplification of the original description and provided information that permits the reassessment of its generic status. *Koonsia* Verrill, 1882, is regarded as a junior subjective synonym of *Pleurobranchaea* Meckel in Leue, 1813. *Pleurobranchaea confusa* Marcus & Gosliner, 1984, is regarded as a junior subjective synonym of *Pleurobranchaea obesa* (Verrill, 1882).

INTRODUCTION

THE STATUS OF *Koonsia obesa* Verrill, 1882, has been the subject of controversy and confusion, largely owing to the incomplete original description of the species. Compounding the problem are the facts that specimens from Verrill's type series have been considered as a distinct species, *Pleurobranchaea confusa* Marcus & Gosliner, 1984, and that the reproductive organs of the holotype have been removed and apparently lost.

Koonsia obesa Verrill, 1882, is the type species of *Koonsia* Verrill, 1882, by monotypy. The genus has been considered as distinct (VERRILL, 1882; PILSBRY, 1896; ABBOTT, 1974; MARCUS, 1977; MARCUS & GOSLINER, 1984) or as a junior synonym of *Pleurobranchaea* Meckel in Leue, 1813 (BERGH, 1896; WILLAN, 1983). MARCUS & GOSLINER (1984) suggested that it was likely that specimens matching the description of *Koonsia obesa* would be rediscovered and that a definitive judgement about the status of the genus must await re-examination of the type species.

During the course of examining material in the collections of the Division of Mollusks, National Museum of Natural History, specimens that are identifiable with *Koonsia obesa* were found. This paper more fully describes the morphology of the species and discusses its generic placement and affinities with other members of the family.

DESCRIPTION

Pleurobranchaea obesa (Verrill, 1882)

Koonsia obesa VERRILL, 1882:545; 1884:pl. 28 (fig. 7); 1885:571, fig. 107. ABBOTT, 1974:349, fig. 2046. MARCUS & GOSLINER, 1984:46, fig. 25C.

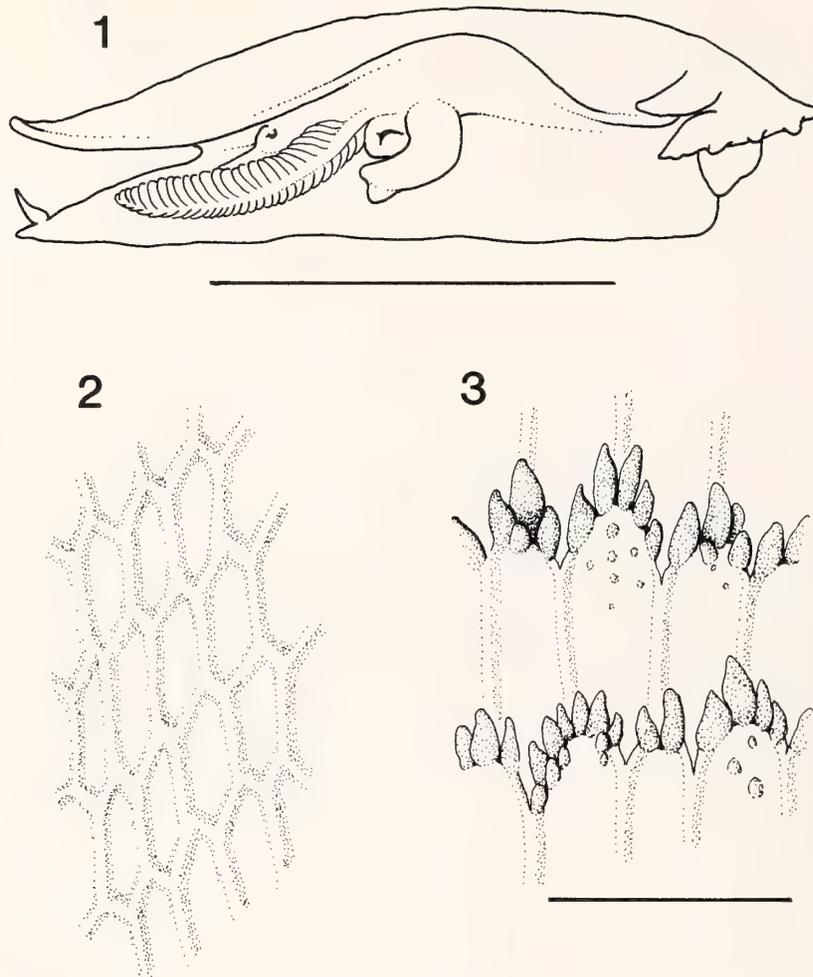
Pleurobranchaea obesa (Verrill, 1882). BERGH, 1897:30, pl. 7 (figs. 19-21).

Pleurobranchaea confusa MARCUS & GOSLINER, 1984:12, fig. 3, *syn. nov.*

Material examined: (1) **Holotype:** National Museum of Natural History, Washington, D.C., USNM 784655, 1 specimen, "off Martha's Vineyard" (off Delaware) (39°53'N, 69°50'30"W), 258 fm (472 m), *Fish Hawk*, USFC station 939, 4 August 1881. (2) **Paratype** (holotype of *Pleurobranchaea confusa* Marcus & Gosliner, 1984): USNM 784657, 1 specimen, "off Delaware Bay" (38°35'N, 73°13'W), 400 m, 10 October 1881. (3) USNM 784658, 1 specimen, "off Martha's Vineyard" (39°55'31"N, 70°39'W), 193 fm (353 m), *Fish Hawk*, USFC station 1154, 4 October 1882. (4) USNM 40132, 1 specimen, "off Nantucket Shoals," RV *Albatross*, station 2262, September 1884. (5) USNM 812662, 1 specimen, 161 km (100 mi) S of Mobile, Alabama (29°10'N, 88°09'W), 260 fm (476 m), RV *Oregon*, 5 March 1955. (6) USNM 578212, 3 specimens, off Bahama Islands (29°59'N, 80°08'W), 210-220 fm (384-403 m), RV *Oregon*, 9 February 1965.

The anatomy of all the material was examined and the following re-description is based on a composite of the material. The radula of the holotype was broken into several pieces and its formula could not be determined. The reproductive organs of the holotype had been removed and are no longer present.

External morphology: The preserved specimens (Figure 1) range from 50 to 100 mm in length. The holotype is the largest specimen examined (although VERRILL [1882] mentioned that the holotype was 128 mm in length, it is



Explanation of Figures 1 to 3

Figure 1. *Pleurobranchaea obesa* (Verrill, 1882). Lateral view of preserved animal (U.S.N.M. 578212). Scale = 25 mm.

Figures 2 and 3. *Pleurobranchaea obesa* (Verrill, 1882). Jaw

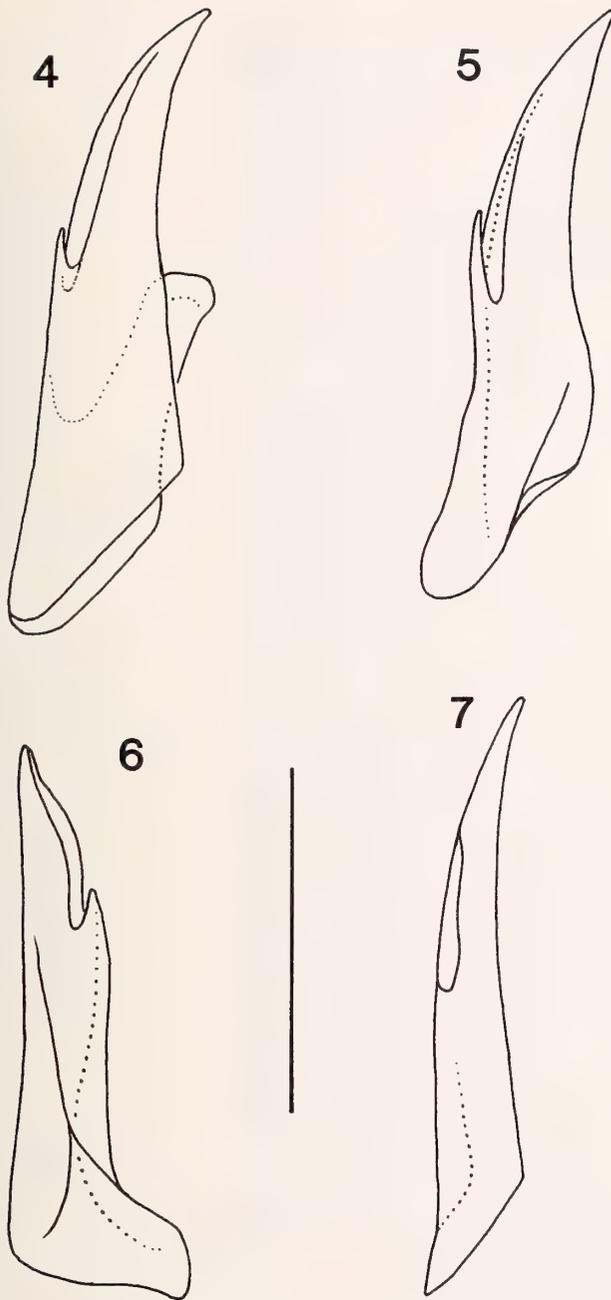
platelets from different portions of jaw (U.S.N.M. 578212). Scale = 50 μ m.

presently more contracted). The smooth notum covers most of the animal and overhangs the foot. The oral veil is broad with scattered tubercles along its margin. The oral tentacles and the well-separated rhinophores are involute. A spur is present on the posterodorsal portion of the foot in all specimens examined. A pedal gland is situated on the posteroventral portion of the foot. The genital apertures are located anterior to the base of the gill. The tri-pinnate gill consists of 31–35 primary leaflets on either side of the central rachis. Immediately behind the posterior base of the gill is the anus.

Internal morphology. The buccal mass is large, comprising one-third to one-half of the body length. The jaws are thin and fragile and are composed of numerous polygonal platelets. The shape of the platelets varies as does the number of irregular denticles on their outer surface

(Figures 2, 3). The radula is broad and golden brown in color. The radular formula in one specimen (U.S.N.M. 578212) examined is $31 \times 75.0.75$. The teeth in the holotype (Figures 4–8) and a second specimen (U.S.N.M. 578212) are elongate and sharply acute with a single denticle present on the inner side of most teeth. The outer 5 or 6 teeth lack a denticle.

The reproductive system (Figure 11) is androdiaulic. The narrow preampullary duct expands into an elongate, convoluted ampulla. The ampulla bifurcates into the oviduct and vas deferens. The oviduct expands into a lobate, glandular receptaculum seminis and again narrows. The ectal (distal) portion of the oviduct is elongate and convoluted. The oviduct joins the bulbous vagina near the base of the large saccate bursa copulatrix. The vagina is joined with the female gland mass near the female gon-



Explanation of Figures 4 to 7

Figures 4 to 6. *Pleurobranchaea obesa* (Verrill, 1882). Inner lateral teeth of holotype. Scale = 500 μ m.

Figure 7. *Pleurobranchaea obesa* (Verrill, 1882). Outer lateral tooth of holotype. Scale = 500 μ m.

pore. The mucous gland forms the largest portion of the female gland mass and a smaller albumen gland is present near the junction of the gland mass with the vagina. A distinct membrane gland was not discernible. A short dis-

tance beyond the bifurcation of the ampulla, the vas deferens expands into a globular prostate which is composed of numerous anastomosing tubules. The vas deferens again emerges from the ectal (distal) portion of the prostate where it is elongate and convoluted. It enters the penial sheath at the ental (proximal) end. The penis sheath is contained within the membranous penial sac, which has a retractor muscle at its ental (proximal) end. The penial sheath has a ridged, bifurcate apex. The penis proper (Figure 9) is thick and muscular basally and gradually narrows and becomes laterally compressed. The penis has an external cuticle over much of its length. The tip of the penis bears five to nine tubercles (Figure 10).

DISCUSSION

The status of *Koonsia* Verrill, 1882, has remained in question since its original description. Several workers have regarded *Koonsia* as a junior subjective synonym of *Pleurobranchaea* Meckel in Leue, 1813 (BERGH, 1897; VAYSSIÈRE, 1901; WILLAN, 1977, 1983), while others (PLSBRY, 1896; ABBOTT, 1974; MARCUS, 1977) have considered it as a distinct genus.

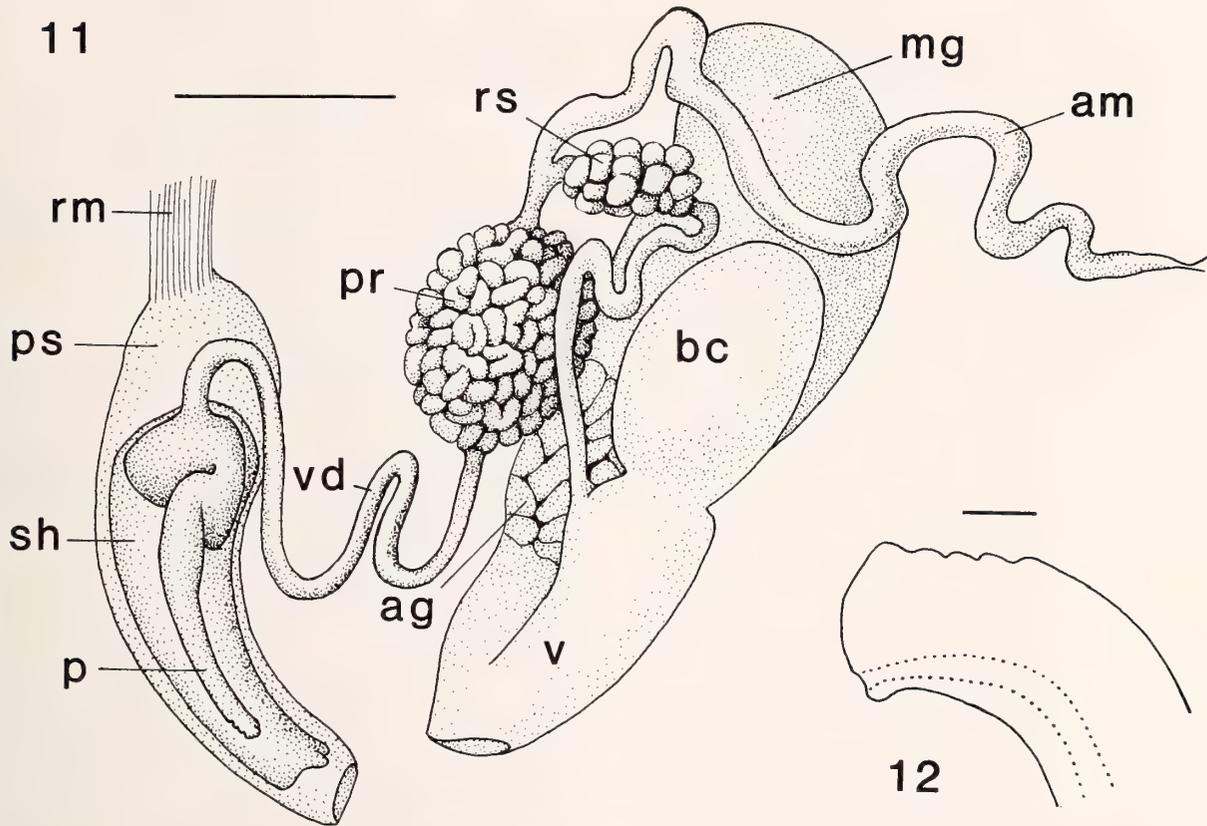
The original description of *Koonsia obesa* Verrill, 1882, emphasized two differences between *Koonsia* and *Pleurobranchaea*. In *Koonsia* the mantle has a distinct edge which overhangs the body laterally and posteriorly, and the penis is armed with small hooks.

Part of the confusion regarding *Koonsia obesa* stems from the fact that VERRILL described the genus as being characterized by having an overhanging mantle edge, but later (1884, pl. 28, fig. 7) depicted a specimen in which the mantle edge does not overhang the foot. There is some question as to whether the animal depicted in the figure is conspecific with *Koonsia obesa* or whether its shape is simply an artifact of preservation. In the figure legend, Verrill noted that in the specimen that he figured "the dorsal part of the body is much contracted." This suggests that its appearance is due to contraction during preservation. It should be emphasized that the systematic status of the specimen that Verrill depicted has no bearing on the taxonomy of *Koonsia obesa*. In the holotype, which I re-examined, the mantle is overhanging with a distinct edge, as Verrill originally described. If the specimen he figured is distinct, then it must receive a new name. The examination of material in this study yielded no specimens with a contracted mantle.

BERGH (1897) examined a paratype of *Koonsia obesa* and stated that the penis was unarmed. I also found that a second paratype had an unarmed penis (MARCUS & GOSLINER, 1984), but suggested that these specimens represent a distinct species and described them as *Pleurobranchaea confusa*. The holotype of *Koonsia obesa* was also examined by Bergh. As the reproductive organs have been removed from the specimen, the question of penial armature of *K. obesa* remains unanswered.

The present material possesses an overhanging mantle





Explanation of Figures 11 and 12

Figure 11. *Pleurobranchaea obesa* (Verrill, 1882). Reproductive system (U.S.N.M. 578212): ag, albumen gland; am, ampulla; bc, bursa copulatrix; mg, mucous gland; p, penial papilla; pr, prostate; ps, penial sac; rm, retractor muscle; rs, receptaculum seminis; sh, penial sheath; v, vagina; vd, vas deferens. Scale = 10 mm.

Figure 12. *Pleurobranchaea obesa* (Verrill, 1882). Penis of paratype specimen (holotype of *Pleurobranchaea confusa* Marcus & Gosliner, 1984). Scale = 250 μ m.

and a row of cuticular papillae on the tip of the penis. The geographical proximity of the localities from which the present material was collected to the type locality, and the morphological similarity of it to Verrill's material, strongly suggest that all the present material is conspecific with *Koonsia obesa*.

With an increase in the knowledge of the morphology of *Koonsia obesa* it is appropriate to reassess the status of the genus within the Pleurobranchaeidae. *Euselenops* Pilsbry, 1896, *Pleurobranchella* Thiele, 1925, and *Giganto-*

notum Lin Guangyu & Tchang Si, 1965, possess unicuspid teeth, while in *Pleurobranchaea* Meckel in Leue, 1813, and *Koonsia* Verrill, 1882, the majority of the teeth is bicuspid. A variable number of outer teeth may be unicuspid in *Pleurobranchaea* species, and the bicuspid cusps of *P. californica* are rudimentary. *Euselenops* has soft conical papillae covering the penis and in *Pleurobranchella* there are chitinous hooks. The reproductive morphology of *Gigantonotum* remains unknown. *Euselenops* is unique among the Pleurobranchaeidae in that the prostatic cells

Explanation of Figures 8 to 10

Figure 8. *Pleurobranchaea obesa* (Verrill, 1882). Scanning electron micrograph of radular teeth of holotype. Scale = 200 μ m.

Figure 9. *Pleurobranchaea obesa* (Verrill, 1882). Scanning electron micrograph of penis (U.S.N.M. 578212). Scale = 5.0 mm.

Figure 10. *Pleurobranchaea obesa* (Verrill, 1882). Scanning electron micrograph of penial papilla (U.S.N.M. 578212). Scale = 500 μ m.

are contained within the vas deferens rather than forming a distinct prostate gland. The penial morphology of *Pleurobranchaea* is variable (MARCUS & GOSLINER, 1984), although there appears to be little intraspecific variability (present study). Some species possess an entirely unarmed penis, while in others there may be either an internal stylet or an external cuticle.

The overhanging mantle, described by VERRILL (1884) as a distinctive feature of *Koonsia* and observed in all of the present material, is not unique to *K. obesa*. It is also found in *Pleurobranchella nicobarica* Thiele, 1925, *Pleurobranchaea confusa*, *P. brockii* Bergh, 1897, and *Gigantotum album* Lin Guangyu & Tchang Si, 1965 (MARCUS & GOSLINER, 1984) and cannot be utilized for generic separation. *Koonsia obesa* closely resembles members of the genus *Pleurobranchaea* in all aspects of its external and internal anatomy. There is no basis for maintaining the separation of genera. I, therefore, agree with BERGH (1897), VAYSSIÈRE (1901) and WILLAN (1977, 1983) that *Koonsia* should be regarded as a junior subjective synonym of *Pleurobranchaea*.

Pleurobranchaea obesa is similar in its external appearance to *P. confusa* Marcus & Gosliner, 1984. Owing to the fact that the holotype of *P. confusa* is also a paratype of *P. obesa*, it is imperative to compare these taxa. Both species have an overhanging mantle and are similar in most aspects of their external and internal morphology. MARCUS & GOSLINER (1984, fig. 3D) reported that the tip of the penis of *P. confusa* possesses two cuticular bulbs. The cuticular tubercles described for *P. obesa* were not observed. However, upon re-examination of the penis of the holotype of *P. confusa* (present study) it was determined that the penis has an external cuticle and that five low-lying tubercles are present (Figure 12). It was also noted that the dorsalmost of the cuticular bulbs was actually an air bubble trapped in the mounting medium. Therefore, there is no significant morphological difference between the two taxa, and *P. confusa* Marcus & Gosliner, 1984, is regarded as a junior synonym of *P. obesa* (Verrill, 1882).

The penial morphology of the seven specimens of *Pleurobranchaea obesa* examined in this study varied only in the number of tubercles on the papilla. The shape of the penis and the elaboration of the cuticle were consistent in all material. The only other member of *Pleurobranchaea* that has an external penial cuticle is *P. notmec* Marcus &

Gosliner, 1984. In this species the penis has about six loops within the penial sac, in contrast to the simple penis of *P. obesa*.

Consistent and fundamental differences in penial morphology, cuticularization, and elaboration clearly distinguish five species of *Pleurobranchaea* in the western Atlantic (MARCUS & GOSLINER, 1984). These characteristics do not vary significantly with size or age of the animals and provide the basis for the separation of species.

ACKNOWLEDGMENTS

I thank Dr. Eveline Marcus for her suggestions and advice about the systematic problems discussed in this paper. The late Joseph Rosewater of the National Museum of Natural History kindly provided help in locating specimens and for making them available to me. Barbara Weitbrecht of the California Academy of Sciences prepared the final figures and her assistance is greatly appreciated.

LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells. 2nd ed. van Nostrand Reinhold: New York. 663 pp.
- BERGH, R. L. S. 1897. Malacologische Untersuchungen 5. In: Semper, C. (ed.), Reisen im Archipel der Philippinen 7, 4 Abt., 1 Abschn., Die Pleurobranchiden 1-2. Kreidel's Verlag: Wiesbaden. Pp. 1-115.
- MARCUS, E. 1977. An annotated checklist of the Atlantic warm water opisthobranchs. J. Moll. Stud., suppl. 4:1-22.
- MARCUS, E. & T. M. GOSLINER. 1984. Review of the family Pleurobranchaeidae (Mollusca, Opisthobranchia). Ann. S. Afr. Mus. 93(1):1-52.
- PILSBRY, H. A. 1896. Manual Conch. 16:I-VII, 1-262.
- VAYSSIÈRE, A. 1901. Monographie de la famille des Pleurobranchides, II. Anns. Sci. Natur. Zool. (8)12:1-85.
- VERRILL, A. E. 1882. Catalogue of marine Mollusca added to the fauna of the New England Region. Trans. Conn. Acad. Arts Sci. 5:447-587.
- VERRILL, A. E. 1884. Second catalogue of Mollusca added to the fauna of the New England region. Trans. Conn. Acad. Arts Sci. 6:139-294.
- VERRILL, A. E. 1885. Third catalogue of Mollusca added to the fauna of the New England Region. Trans. Conn. Acad. Arts Sci. 6:395-452.
- WILLAN, R. C. 1977. A review of *Pleurobranchella* Thiele, 1925 (Opisthobranchia: Pleurobranchaeinae). J. Conchol. (Lond.) 29:151-155.
- WILLAN, R. C. 1983. New Zealand side-gilled sea slugs (Opisthobranchia: Notaspidea: Pleurobranchidae). Malacologia 23:221-270.

NOTES, INFORMATION & NEWS

Some Preliminary Observations on the
Homing of the West Indian Chiton
Acanthopleura granulata
byDavid Mook
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RR 1, Box 196,
Fort Pierce, Florida 33450

The West Indian chiton *Acanthopleura granulata* (Gmelin, 1791) exhibits a marked homing behavior, especially on lower energy shorelines. Individuals generally remain stationary at their homes during the daylight hours and forage for their surficial and endolithic algal food during the night, returning to their homes by morning (Mook, 1983). The purpose of this preliminary study is to investigate some of the possible mechanisms that may be involved in the homing behavior of *A. granulata*.

Chitons and their homes along a low energy, limestone shoreline on northern San Salvador Island, Bahamas, were marked with fingernail polish. All marking of chitons and their homes was done during the day at low tide. Stations were located approximately 10 m apart to minimize the chances of marked chitons exchanging homes with adjacent marked chitons. Three experimental manipulations (scrubbing treatment, chopping treatment, and magnetic treatment) were done. Controls consisted of observing whether marked, unmanipulated chitons returned to their homes. In all cases, experimental manipulations were done at low tide during the night after marking, and the effects of the manipulation (whether the chitons homed or not) were observed at low tide the following day. Because all of the chitons did not leave their homes every night to forage, only chitons that were away from their homes at the time of nighttime observations were manipulated or used as controls. Each manipulation (treatment) was repeated (replicated) several times on different nights (2-4 nights). Results of each manipulation were compared to the controls (no manipulation) using a chi-square test.

To determine whether the chitons used their outward bound trail, old trails from previous excursions, or distant chemoreception to relocate their homes, the limestone substrate in and around the home (30 cm radius) was rinsed with 0.5 N HCl and scrubbed with a wire brush to remove and/or hydrolyze any traces of trails and/or pheromones (scrubbing treatment). After scrubbing with the acid, the scrubbed region was rinsed thoroughly with seawater to remove any traces of the acid.

To test whether terrain memorization was a factor in relocation of homes, all rock was removed to a depth of several centimeters below the original rock surface in a

Table 1

Number and percent of treated chitons homing, and chi-square values after various treatments.

Treatment	Total treated	Total homing	% homing	Chi-square	Replicates
Scrubbed	23	16	70	0.22	3
Chopped	16	13	81	0.65	2
Magnetic	31	24	77	0.21	4
Control	60	42	70	—	4

band approximately 15 cm in width around the home (chopping treatment). Care was taken to assure that no original rock surface remained and that the original relief of the rock surrounding the hole was totally changed.

Because magnetic fields may be used by some organisms for navigation (MARLER & HAMILTON, 1966), magnetic tape was epoxied onto the plates of chitons to disrupt the earth's magnetic field around the chiton (magnetic treatment). A simple test with a compass showed that the earth's magnetic field was disrupted in a radius of 2-3 cm around the chiton.

Chi-square values all indicate an alpha value of greater than 0.5, suggesting that neither trail removal (scrubbing treatment), terrain alteration (chopping treatment), nor disruption of the earth's magnetic field around the chiton (magnetic treatment) had any significant effect on the homing frequency of manipulated chitons (Table 1).

These observations suggest that the homing in chitons either (1) may not be a one mechanism system, such as trail following or terrain memorization alone, or (2) that the animals possess a more complex homing system, such as kinesthetic memory. Future, more rigorous experiments are necessary to determine the exact mechanism or mechanisms that *A. granulata* uses to home.

Acknowledgments

I would like to thank Donald and Kathy Gerace at the College Center of the Finger Lakes on San Salvador for their hospitality during this study. This is Harbor Branch Contribution Number 450 and College Center of the Finger Lakes Contribution Number 33-B109.

Literature Cited

- MARLER, P. & W. J. HAMILTON. 1966. Mechanisms of animal behavior. John Wiley & Sons, Inc.: New York. 771 pp.
MOOK, D. H. 1983. Homing in the West Indian chiton *Acanthopleura granulata* Gmelin, 1791. *Veliger* 26:101-105.

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For more information, contact:
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Box 2739 California Lutheran College
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Faye B. Howard, 1907–1984

The Santa Barbara Museum of Natural History recently lost one of the driving forces behind the development of malacology in the Department of Invertebrate Zoology. Della Faye Ballou was born at home in Crumpler, North Carolina, on February 15, 1907. At the age of ten her family moved to California. She attended Fullerton City College and the University of California, Berkeley, where she was introduced to shells by her neighbor, John Jones. Beginning in 1932 until shortly before her death, Faye engaged in private research in conchology. In 1961 she was appointed as a Research Associate in Conchology at the Museum. From 1961 to 1968 she personally funded the position of Assistant in Conchology at the Museum. During the same period Faye organized, financed, and led six major expeditions to West Mexico to study and collect mollusks. With the impetus of Faye's enthusiasm and support, the Santa Barbara Malacological Society was founded in 1962. She served on the Editorial Board of the Society's publication, the *Tabulata*, from 1967 to 1974. Faye was a member of the Conchological Club of Southern California for 54 years and was also a member of the Hawaiian Malacological Society. She authored a total of 22 publications on mollusks and famous malacologists. She described two new species of marine gastropods, and had four new species and one new subspecies named in her honor. Faye's dream of establishing a major center for the study of mollusks in Santa Barbara will become a reality, supported by her large collection and a bequest that she leaves to the Museum. This legacy will forever preserve her memory but will never fill the void she leaves behind.

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We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709. Foreign correspondents should enclose one international postal reply coupon.

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 42, part 1, on 2 April 1985:

Opinion No. 1292 (p. 27). *Voluta papilio* Link, 1807 (Gastropoda): conserved.

Opinion No. 1296 (p. 37). Request for the use of the plenary powers to conserve *Nettastomella* Carpenter, 1865 (Bivalvia) refused.

Direction 117 (p. 43). Correction of Entry No. 462 in the Official List of Generic Names in Zoology concerning *Sphaerium* Scopoli, 1777 (Mollusca, Bivalvia) (Correction to Opinion 94).

Also, the Commission has given six months notice of the possible use of its plenary powers in the following cases, published in the *Bulletin of Zoological Nomenclature*, volume 42, part 1, as of 2 April 1985, and would value comments and advice on them from interested zoologists. Correspondence should be addressed to Dr. R. V. Melville, Secretary, ICZN, % British Museum (Natural History), Cromwell Road, London, SW7 5BD.

Case No. 2340. *Spiroglyphus* Daudin, 1800 and *Stoa* De Serres, 1855 (Mollusca, Gastropoda, Vermetidae): proposed suppression of two equivocal generic names.

Case No. 2331. Homonymy in the families HARPIDAE Hawle & Corda, 1847 (Trilobita) and HARPIDAE Bronn, 1849 (Mollusca, Gastropoda).

BOOKS, PERIODICALS & PAMPHLETS

The Freshwater Snails of Connecticut

by EILEEN H. JOKINEN. Connecticut State Geological and Natural History Survey, Bulletin 109. 1983. 83 pp.; 35 text figures, 1 table. Paperback \$4.00.

At last there is available a guide to a large and important component of the freshwater invertebrate fauna of New England. Jokinen's book on freshwater snails of Connecticut provides an in depth and comprehensive study of a heretofore neglected group of animals. Although it may seem to many that the freshwater mollusk fauna of New England was "studied out" by the early twentieth century, Jokinen's contribution clearly establishes how little was actually known about these animals in the region.

The book is generally arranged in three parts. The first part consists of several sections, including an introduction to the natural history of Connecticut gastropods. A historical review of the knowledge of gastropods in Connecticut is followed by a section on classification, which incorporates recent studies, a section on biological, ecological, and physical parameters controlling snail distribution and abundance in Connecticut, and a section on "Rare and Missing Species." The historical review is complete. The discussion on biological, ecological, and physical factors is impressive and is probably the most useful section in this part of the book. However, students of freshwater gastropods, particularly students of the Pleuroceridae, may not agree with Jokinen's statement that gastropods are not "good indicators of stream drainage history" (page 2). The section on "Rare and Missing Species" is largely repeated from JOKINEN & PONDICK (1981). A useful glossary of gastropod shell morphology is provided. A description and map of the physiographic and drainage characteristics of Connecticut is presented along with a "Methods and Materials" section. Readers might have difficulty distinguishing site numbers on the locality map (fig. 5). A detailed account describing methodologies used in collecting and preserving gastropods rounds out the first part.

The second part of the book commences with an illustrated key which incorporates shell features and anatomical characters (requiring some dissection to observe). The key is followed by individual species accounts, including data on taxonomy, distribution, and ecology. Distributions are presumably based on Jokinen's own collections. Records documenting the occurrence of *Aplexa elongata* (Physidae) or those demonstrating a wider distribution of *Valvata tricarinata* (Valvatidae) in Connecticut are present in the Museum of Comparative Zoology at Harvard University. Extensive information is presented on the Viviparidae, a family poorly known in New England; however, it should have been noted that *Viviparus georgianus*

is possibly an introduced species in the region (see CLENCH, 1929).

The last part of the book contains a list of references, all but a few cited in the text, and three extremely useful appendices which supply particulars of the water chemistry of Connecticut sites where gastropods were collected, specific localities of collection, and species diversity at each site.

The book is well written (I found only six typographical errors), clear, and inexpensive. The large amount of information presented should make it useful not only to students of New England mollusks but to environmental consultants, wildlife managers, and educators as well. It should also be noted that the book appears in time to announce the decline of certain species at the edge of their range in Connecticut.

Literature Cited

- CLENCH, W. J. 1929. Freshwater shells of New England. Bulletin Boston Society of Natural History 52:3-8.
 JOKINEN, E. H. & J. PONDICK. 1981. Rare and endangered species: freshwater gastropods of southern New England. Bulletin American Malacological Union 1981:52-53.

Douglas G. Smith

TWO-HUNDRED TEREBRIDS IN COLOR

Terebridae (Mollusca: Gastropoda)

by UMBERTO AUBRY. 1984. Via Degli Aranci 80, 80067 Sorrento (NA), Italia. 48 pp.; 15 color plates. (privately published by the author)

Although the author of this illustrated catalog is a collector who insists that his contribution is without scientific pretense, he has provided a remarkable work of considerable scientific interest and merit. There are, admittedly, a number of things that this volume is not: it is not an evaluation of the systematics of terebrids and makes no attempt to group related species either by generic assignment or morphological similarity; it does not contain keys or references to morphological characters useful in identification; and the quality of the photographic documentation is not always sufficiently detailed to provide a reliable visual identification guide.

What this handsome volume does contain may be of much greater value to the professional than to the amateur collector. It provides an excellent visual summary of variation in shell form and sculpture in the family, and the 200 species that are illustrated may provide a relatively accurate assessment of the species diversity in a family in

which more than 400 names have been proposed. For each specimen figured, Aubry provides a measurement, geographic locality, and depth. Perhaps the most useful feature, however, is the quality of the nomenclatural documentation, which includes not only authors and dates for each species but a bibliography of more than 100 references, providing a summary of and rapid entry into the literature dealing with the family.

C. S. Hickman

MARINE ARCHAEOGASTROPODS OF NORTHWESTERN SPAIN

Fauna Marina de Asturias. No. 1. Moluscos.

1. Archaeogastropods (Prosobranchia)

by EVA MARIA LLERA GONZALEZ, JESÚS ANGEL ORTEA RATO & ALBERTO VIZCAINO FERNANDEZ. 1983. Centro de Investigaciones acuáticas de Asturias (CRINAS). Priced at 1.000 ptas. 12 \$. 75 pp. Available from CRINAS, Consejería de Agricultura y Pesca, Apdo. 4067, Gijón (12), Asturias, España.

This volume is the first in a series dedicated to documentation of the marine fauna of Asturias, a stretch of the northern Iberian Peninsular coastline with a rich molluscan fauna exceeding 700 species. The series is to be based in part on recent re-collections of 600 species. The first volume treats ten archaeogastropod families, including 30 species. It is the high quality of the illustrations and the detail of documentation that make this volume worthy of note. Not only are the drawings of the shells particularly fine, but there are illustrations of the living animals, radular dentition, and operculae. Distribution maps for Asturias provide indications of relative abundance, and maps are also provided showing the entire geographic ranges of species in Europe and north Africa. When complete, this series should constitute an invaluable reference.

C. S. Hickman

THREE MONOGRAPHIC TREATMENTS OF CENOZOIC MOLLUSK FAUNAS

Molluscan Paleontology, Paleoecology, and North Pacific Correlations of the Miocene Tachilni Formation, Alaska Peninsula, Alaska

by LOUIE MARINCOVICH, JR. 1983. *Bulletins of American Paleontology*, Vol. 84, No. 317. 155 pp.; 12 pls. \$17.50.

Molluscan Paleontology and Biostratigraphy of the Lower Miocene Upper Part of the Lincoln Creek Formation in Southwestern Washington

by ELLEN J. MOORE. 1984. Contributions in Science No. 351, Natural History Museum of Los Angeles County. 42 pp.; 180 figs. \$5.00.

Megapaleontology of the Eocene Lajas Formation, Simi Valley, California

by RICHARD L. SQUIRES. 1984. Contributions in Science No. 350, Natural History Museum of Los Angeles County. 76 pp.; 19 figs. \$7.50.

Three recent molluscan faunal monographs are noteworthy as examples of a resurgence of documentation of the history of the northeastern Pacific mollusk fauna. All three appear in large format (8½ × 11 inches) and share exceptionally high quality illustrations. Paleontologists have always maintained higher standards for photographic documentation of mollusks than have their neontological counterparts, and this becomes even more apparent in the printing of these volumes by Allen Press, using fine halftone screens and high quality ink and paper. The new format and high quality of the plates in *Bulletins of American Paleontology* is particularly impressive.

The early Miocene fauna described by Ellen Moore is part of a series of unusually well-preserved faunal zones that have been meticulously collected by a pair of amateurs, James L. and Gail H. Goedert. This monograph describes a number of interesting new deep-water mollusk species and is noteworthy particularly for the detailed review and illustration of the eastern Pacific species of the spectacular large volute *Musashia* and treatment and illustration of the exceptional collection of 180 specimens of nautiloid cephalopods of the genus *Aturia*.

Louie Marincovich's monograph of 53 molluscan taxa from the western end of the Alaska Peninsula records a cold-water fauna, also of Miocene age, that is not only unusually well preserved but one that is critical as a link between north American and Asian Miocene mollusk faunas. The quality of scholarly detail in this monograph surpasses that of the other two as a reflection of the high, uncompromising standards set by the Paleontological Research Institution. For example, the index is detailed and useful (not a "token index"); authors and dates of publication are provided for all taxa mentioned; and, more importantly, full citations for authors of taxa are included in the "References Cited."

Richard Squires' monograph treats 96 Eocene mollusk species and stands as a major contribution to our understanding of the more widespread, warm-water, Early Tertiary mollusk faunas of our eastern Pacific coast with their curious mixture of cosmopolitan, Tethyan, Caribbean, and North American elements.

C. S. Hickman

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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.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

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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.

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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 tables.

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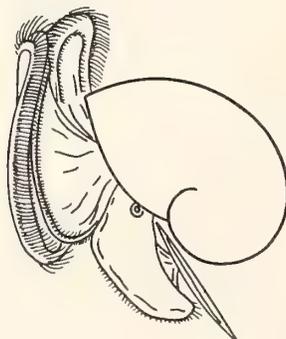
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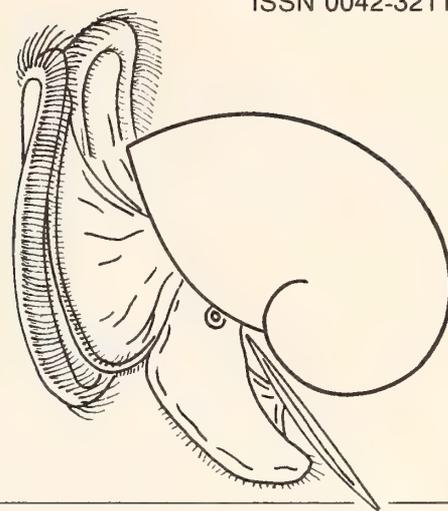
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THE VELIGER

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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Synopsis of the Supraspecific Classification of Living Oysters (Bivalvia: Gryphaeidae and Ostreidae)

by

HAROLD W. HARRY

4612 Evergreen St., Bellaire, Texas 77401

Abstract. Recent members of the superfamily Ostreacea are subdivided into two families, four subfamilies, ten tribes (all new) and 24 genera and subgenera (12 new). Based on the examination of the gross anatomy of the flesh of all but four of the 36 known species of living oysters, and the shells of each, the supraspecific units are defined sufficiently to differentiate coordinate taxa. Illustrations are provided of the shells of type species of the new genera and subgenera, as well as of significant anatomical features. Two junior homonyms are renamed at the species level.

IN STUDYING the large collection of oysters of the U.S. National Museum of Natural History on several visits during the last few years, and other material collected by myself or provided by many friends, I have found it necessary to extend the classification of the living species beyond that proposed by STENZEL (1971), in order to indicate their diversity and relationships more precisely. The purpose of the present synoptic account is to remedy the deficiency by introducing several new taxa at the level of subgenus, genus, and tribe. The type species at the generic level are described and illustrated in sufficient detail to differentiate them from coordinate taxa and to give them nomenclatorial validity. Other species within genera having multiple species, although listed, are not treated in such detail. Complete bibliographic references to previously established genera and their types, as well as illustrations of the latter, are to be found in STENZEL (1971); references to the proposed nominal species of living oysters are provided by LAMY (1929-1930) and HARRY (1981). Because the limits of morphological variation, habitat, and zoogeography of most species are poorly known, a more extensive account, discussing those factors and the complicated synonymies, must await further study.

The shells of all species, and the flesh of most, have been available for study. Several new characters have thereby been discovered, some of which were briefly noted in two short abstracts (HARRY, 1981a, 1983). TORIGOE (1981) independently found some of these new characters. Considering not only the structure of the flesh and shell but also the environments, geographic range on a world-wide basis, and behavior (habits) of oysters produced more character series (see HARRY, 1968, 1971) than are usually

used in systematic works on bivalves. Although no new species are proposed, apart from renaming two junior homonyms, it is necessary to introduce new taxa at several levels in order to express the degrees of relationship, or classification, adequately. Such a procedure is inevitable, as pointed out by SCHENK & McMASTERS (1948:3) and CROWSON (1970).

STENZEL's (1971) classification has been reviewed and somewhat modified by HARRY (1981), TORIGOE (1981), and HARRY & DOCKERY (1983). Torigoe elevated one subfamily of the three that Stenzel recognized in the Gryphaeidae to family rank, Pycnodonteidae. This seems of little use, and merely confuses the issue of relating the two extinct subfamilies, Gryphaeinae and Exogyrinae, to the Pycnodonteinae. On the other hand, Torigoe recognized the need of separating *Crassostrea* and related genera from the Ostreinae as the subfamily Crassostreinae, a step foreshadowed by Stenzel in his arrangement of genera, but not definitely taken by him. Torigoe followed Stenzel in placing the Lophinae after the Ostreinae (and Crassostreinae); but the Lophinae share with the Pycnodonteinae several characters which are absent or much modified in the Ostreinae. Conversely, new characters appear in the Lophinae which are shared with the Ostreinae and Crassostreinae, but are absent in the Pycnodonteinae, and additional characters appear in the Ostreinae which are shared only with the Crassostreinae. Details supporting this arrangement are summarized after the definitions of the appropriate subfamilies.

In some of the earlier literature on the anatomy of oysters there was much confusion about their proper orientation (see below, "promyal passage"). In this paper the

hinge is considered to be dorsal, and when one has the outer surface of the right, or unattached, valve facing them, with the hinge uppermost, the anterior margin is to the right, the posterior one on the left, and the ventral margin is opposite the hinge. This orientation was used by GALTSOFF (1964) and STENZEL (1971), in whose works general anatomical accounts of oysters are presented. The height of a specimen is measured along a line perpendicular to the axis of the ligament, and length along a line perpendicular to the height and parallel to the ligamental axis. Small oysters are those whose maximum dimension (usually height) is about 30 mm or less; medium sized ones extend to about 50–70 mm; and larger ones are greater than that size. Normal oceanic salinity is 35 parts per thousand (ppt), varying about 2 ppt; in warm climates some restricted bodies of water may have salinities that are several ppt higher than normal (Red Sea, Persian Gulf, etc.). In brackish water the salinity is usually much lower, and more variable, than where normal salinity prevails. USNM refers to the collection of Recent mollusks of the United States National Museum of Natural History.

The intraspecific variation of oyster shells, which is probably greater than in any other group of living bivalves, precludes the preparation of a simple and satisfactory taxonomic key. The systematic format presented below should allow the identification of any living species to the generic level, or lead to the conclusion that it belongs to an undescribed genus. However, this requires that one know considerably more about the species to be identified than the limited characters inherent in a single dry shell, such as that which is usually thrust on some presumed authority for an immediate identification, or subjected to a taxonomic key. Moreover, the format here presented goes beyond the taxonomic key, because the first entry (superfamily definition) allows the exclusion of several oyster mimics, such as species of *Anomia*, *Plicatula*, *Spondylus*, *Hinnites*, *Chama* and related genera, as well as other monomyarian bivalves such as the sponge oysters (Vulsellidae), pearl oysters (Pteriidae), hammer oysters (Malleidae), and indeed of all other bivalves of the order Pterioida. Three tables are appended to summarize the more prominent variable characters of the true, or common, oysters of the two families Gryphaeidae and Ostreidae.

I am much obliged to the personnel of the U.S. National Museum of Natural History, particularly Joseph Rosewater, Harald Rehder, Richard Houbriek, Thomas Walker, Frederick Bayer, and Druid Wilson, for their generous hospitality while I studied there. To B. J. Gallaway and Marion Fischel of the LGL Ecological Research Associates, Bryan, Texas, I am indebted for numerous specimens from offshore oil drilling platforms in Louisiana, which initiated my present study of the systematics of oysters. For her assistance in studying the oyster collection of the British Museum of Natural History I thank Solene Morris, and also Thomas E. Pulley and Constance E.

Boone for their help in studying the growing mollusk collection and library of the Houston Museum of Natural Sciences.

Constance E. Boone also generously loaned oysters, which she personally collected, with most material preserved with flesh, from West Africa, Mauritius, Australia, the Philippine Islands, Fiji, Tahiti, the Tuamotu Islands, Gulf of Mexico, and western Mexico, as well as other lots of shells which she had obtained by exchange.

To John W. Tunnell, Jr., I am very obliged for making available a collection of 34 lots of oyster shells, of 14 species, which had evidently been assembled about 1950 by personnel of the Texas Game and Fish Commission at the Rockport Laboratory, where they had since been stored. This collection is now in the custody of the Biology Department of Corpus Christi State University. He also loaned much oyster material in alcohol, which he had collected in western Florida, and in the Persian Gulf.

Others who have provided significant material and information are: C. A. Beddinger, Tom and Beatrice Burch, Thomas Calnan, Hays Cumins, David T. Dockery III, Valerie Ernst, Mario Lasta, Paul and Paula Mikkelsen, Bryan Morton, Ellen J. Moore, Takeshi Ogawa, Juan Parodiz, Hugh Porter, Eric Powell, Dale Steinke, Jose Stuardo, and Margaret Teskey; to all of them I express my heartfelt thanks. *Reviewers of the ms?*

Superfamily OSTREACEA Rafinesque, 1815

Bivalve mollusks (Order Pterioida, Suborder Ostreina) that are epifaunal, and in which the shell is usually attached by cementation of its left valve to a firm substrate, during at least early post-larval life (exception: *Cryptostrea*). The shell shape is varied and irregular, conforming to the situation. The umbos may be small and inconspicuous, in which case they are nearly equal in size, but the left one varies from only slightly to many times larger than the right in some species. The shells are usually nearly equilateral, but inequivalve, and the left valve is generally more inflated. The umbos are usually opisthogyrous but they are often orthogyrous or prosogyrous, even within a species, among shells of adjacent specimens.

The periostracum is thin, smooth, nearly colorless, and quickly deciduous beyond the shell margin (possibly excepting *Cryptostrea*). The prismatic shell layer is always present, either forming a continuous sheet or thin, projecting lamellae (sometimes thickened by the foliar layer). The lamellae may be closely spaced and imbricate, or reflexed to varying extent, and in some instances they form subcylindrical, tubular spines of varying length, called hyote spines. The inner, or foliar shell layer, is vitreous and translucent when thin and homogeneous (subnacreous in *Striostrea* and *Pustulostrea*), becoming white and opaque when thicker. Besides the myostracal shell, underlying the adductor muscle attachment and progressively enclosed in the foliar layer as the shell grows, several

other interruptions of the foliar layer may occur, depending on the species: in a process of chambering, the surface of a mantle lobe is pulled away from the foliar layer, then secretes a new layer, leaving a hollow space between the two; non-cellular, organic patches (conchiolin) of varied size, shape and thickness may be secreted, especially in more erodable shells (e.g., *Striostreini*) and as an initial covering to shell injury; this layer is light green when thinnest, becoming light to dark brown when thicker. Pure white or colored, irregular, chalky deposits of varied size and thickness may also form.

The basic color of the shells is white or grayish, and shells of small species and the spat of larger ones may be golden brown from the organic material of the prismatic layer. The shells may be variously washed or radially striped with red or blue pigment, or a purplish combination thereof. Green or brown washes internally seem to result from covering the organic patches noted above. The color is highly variable within most species.

The functioning part of the ligament is an elongate, thin, semicylindrical mass extending before and behind the umbos (thus, it is amphidetic), along the hinge of the shell, with the convex surface facing the interior. Its internal surface is continuously increased along its length and at both ends. Above the inner surface the functional ligament is gradually superseded, losing its elasticity and becoming brittle; this part is external, and attached to a variable extent to a triangular ligamental scar on the medial face of each valve, below the umbos. From much of this scar the ligament is usually worn away. The ligamental scars are divided vertically into three equal triangular parts, the central resifier and anterior and posterior bourrelets (except in the extinct subfamily *Exogyrinae*: see HARRY & DOCKERY, 1983).

There are no hinge teeth comparable to those of most other bivalves, but most species of oysters have some form of ridges or pustules along the margin of the shell. These are usually near the ligament when present, sometimes limited to a short strip there, but often extending downward on anterior and posterior shell margins for a variable distance, and even across the ventral margin. These marginal denticles, collectively called chomata by STENZEL (1971), are of systematic importance. They are all apparently derived from faint structural bands which are narrow, parallel to each other, and normal to the shell margin; these can be seen on the surface of the foliar shell layer in an occasional specimen of many species. They are here termed *protochomatal* bands. In *Alectryonella* they are generally present and much exaggerated.

Post-larval oysters are monomyarian, retaining only the morphologically posterior shell adductor muscle, which is placed posteroventrally; it is divided into "quick" (translucent, dorsal) and "catch" (opaque, ventral) parts. The shape of this muscle is indicated in the scar it leaves on the inner surface of the shell, and the shape varies significantly at the level of families and some lower taxa; but

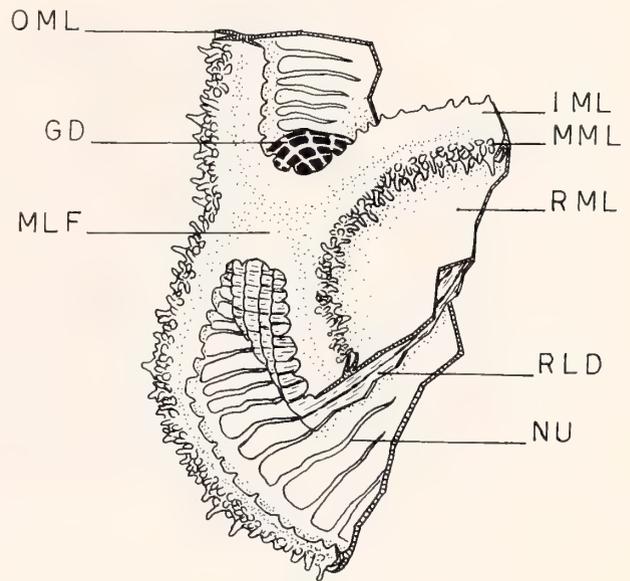


Figure 1

Fusion of mantle lobes at posteroventral curve of shell. From a specimen of *Crassostrea virginica* from Galveston, Texas; accessory heart not shown (hidden by diaphragm). GD, gill diaphragm; IML, inner mantle margin lamella; MLF, mantle lobe fusion; MML, middle mantle margin lamella; NU, neobranch unit; OML, outer mantle margin lamella; RLD, right lateral demibranch of gill; RML, right mantle lobe.

the two parts of the muscle seem never to be shown in the scars.

The foot is entirely lost early in post-larval life, when the larva settles and attaches. This condition of early foot loss is here termed *paedapody*, to emphasize its near uniqueness in this group (possibly also occurring in *Dimyidae*?) and the several distinctive morphological features resulting from it. Nearly all other bivalves that experience foot loss or atrophy (an occasional species in several distantly related families) do so late in post-larval life, a condition here termed *gerontapody*. The usual superficial musculature of the visceral mass, both the sphincter component which functions to extend the foot, and the rectilinear pedal retractors, is absent throughout post-larval life of oysters. Small, short gill protractor muscles are generally prominent in oysters, attaching to the shell below the umbos, where they may leave a scar; these were named Quenstedt's muscles by STENZEL (1971:N965), who mistakenly considered them to be remnants of pedal retractor muscles.

Besides the usual confluence of the mantle lobes below the hinge (the isthmian mantle, which secretes the ligament), they are only fused to each other elsewhere by short extensions of the inner mantle margin lamellae at the posteroventral curve of the shell margin (Figure 1); the potential excurrent opening thus occupies the whole of the

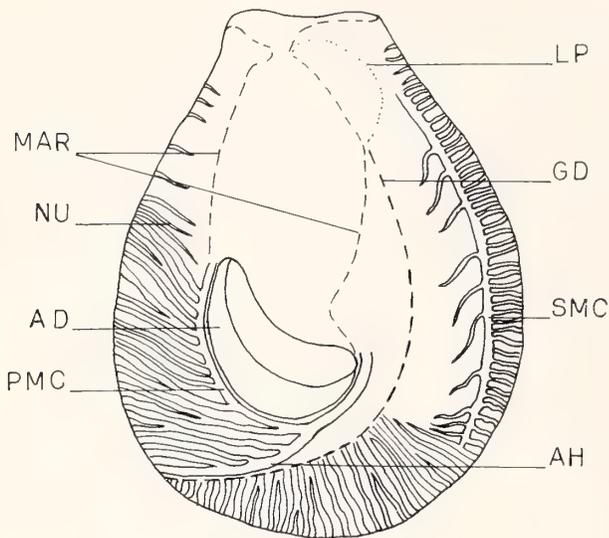


Figure 2

Diagram of the neobranch of left mantle lobe of *Ostrea puelchana* from Port Phillip Bay, Victoria, Australia (USNM 767650). AD, adductor muscle; AH, accessory heart; GD, gill diaphragm; LP, labial palp; MAR, limit of attachment of right mantle lobe to visceral mass; NU, neobranch unit; PMC, perimyal collecting vessel; SMC, submarginal collecting vessel.

posterior shell margin, the incurrent opening both the ventral and anterior parts of the margin.

The margin of each mantle lobe is divided into three lamellae. The inner mantle margin lamella is only moderately high, and in life it stands at right angles to the mantle lobe; along its free margin there are small, tapering papillae, usually separated by a space several times as long as their diameters; the middle lamella is held parallel to the mantle lobe's surface, forming between it and the outer lamella a narrow, shallow periostracal groove. The outer mantle margin lamella, as in all bivalves, is without papillae. There are no papillae along the free margin of the middle lamella, but its medial (exposed) surface is densely set with long and short, tapering papillae, irregularly arranged. Contrary to TORIGOE (1981) and previous workers, I have not found the size and arrangement of these papillae to be of systematic value.

In both incurrent and excurrent mantle chambers, submarginally along the medial surface of both mantle lobes, there are tubular ridges, normal to the mantle margin. These begin shortly below the isthmian mantle junction, increasing in size and becoming more closely spaced toward the ventral margin. They taper inward, occasionally branching at one or both ends. They are protrusions of vascular recessions (or "blood vessels," although undefined by special cells lining their interiors) of the parenchymatous tissue between the two epithelial layers bounding the surface of the mantle lobes. These tubes are here

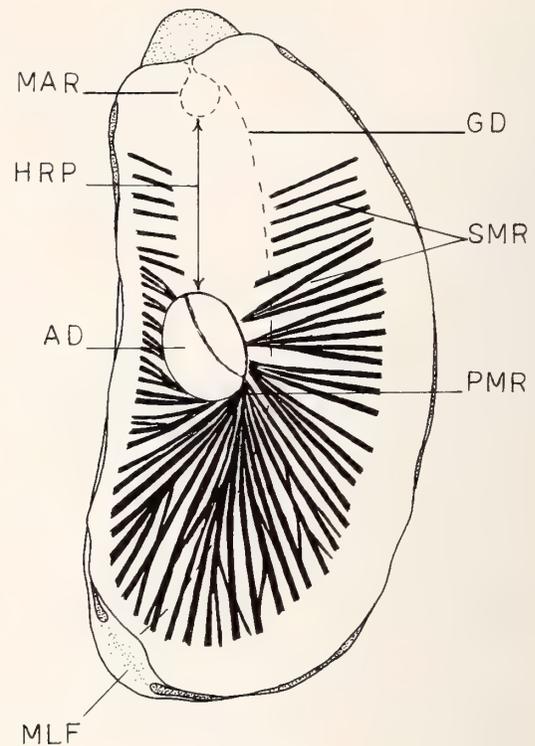


Figure 3

Distribution of pteriomorph mantle margin retractor muscles, diagrammed from a specimen of *Neopycnodonte cochlear* from Algiers, Algeria, loaned by H. B. Stenzel. Marginal papillae not shown. AD, adductor muscle; GD, gill diaphragm; HRP, height of right promyal passage; MAR, limit of attachment of right mantle lobe to visceral mass; MLF, mantle lobe fusion; PMR, primary mantle margin retractor muscle; SMR, secondary mantle margin retractor muscles.

termed *neobranch units*, and collectively termed the *neobranch*, structures universally present but hitherto unnoticed in oysters (Figure 2). In the incurrent mantle chamber there is usually a longitudinal protruding vessel in each mantle lobe, parallel to the mantle margin. These begin near the isthmian mantle, some distance inward from the margin, which they parallel to a rather abrupt termination at the anteroventral curvature of the shell margin. There, these *submarginal collecting vessels* disappear in the musculature of the mantle margin.

No such submarginal collecting vessels are present in the excurrent mantle chamber, but the neobranch units immediately behind and above the gill diaphragm, in each mantle lobe, are often enlarged. Such enlarged neobranch units extend inward along the anterior margin of the adductor muscle, where they fuse with other vessels (venous) from the ventral ends of the axial suspensory septa of the gills (explained below), and occasionally with a circummyal vessel along each margin of attachment of the adductor muscle (Figure 2), immediately before entering the

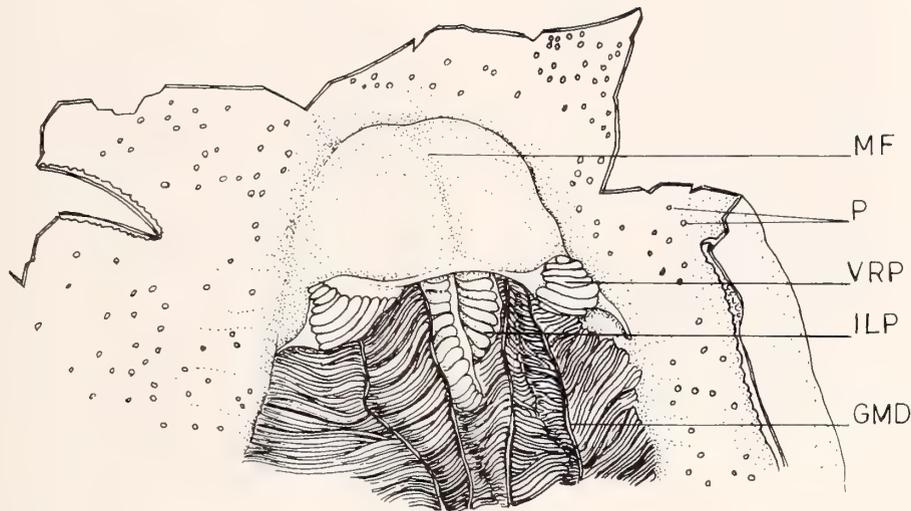


Figure 4

Labial palps of *Neopycnodonte cochlear*. Specimen from Algiers, Algeria, loaned by H. B. Stenzel. GMD, groove on free margin of demibranch; ILP, inner labial palp; MF, median fusion of outer labial palp; P, papillae on inner surface of mantle; VRP, reflected tip of outer labial palp.

auricles of the heart. When enlarged and passing forward to enter the heart, the two post-diaphragmal units of the neobranch are known as accessory hearts. They pulsate, carrying blood to the heart auricles. Whether the accessory hearts receive as tributaries the several adjacent neobranch units varies at the generic level (Figures 2, 5). The most recent extensive account of the accessory hearts, by GALTISOFF (1964, *q.v.* for references to earlier works) is incorrect in many details.

Besides muscle fibers in the mantle lobes adjacent and parallel to the mantle margin, which subtend the three mantle margin lamellae and constitute circular musculature, there are also mantle margin retractor muscles inserting in this area, and normal to the margin. The major and sometimes the only mantle margin retractor muscle in oysters originates as one source on the anterior curvature of the adductor muscle margin, at a slight indentation between the quick and catch parts of the latter, but it never leaves a scar on the shell's surface. A few similar but smaller ones may originate along the ventral and posterior margin of the adductor muscle in some species. From these origins large muscle bundles radiate and branch repeatedly before inserting on the mantle margin. These distinctive muscles have previously been undescribed and lacked a name; they are here termed the *pteriomorphic mantle margin retractor muscles*, because they also occur in some other monomyarian bivalves (Figure 3).

Secondary mantle margin retractor muscles (Figure 3) may originate at isolated spots in a line about at the level of the gill diaphragm, each extending as a single bundle or branching several times before inserting along the mantle margin. These occasionally leave an irregular, inter-

rupted line of scars in the position of a pallial line on the shell (often prominent in *Saccostrea*).

The broad fusion of the mantle lobes to the left and right sides of the visceral mass is a factor of systematic importance. A lobe not so attached leaves a promyal passage between the anterior and posterior parts of the excurrent mantle chamber; this passage is morphologically supramyal, but the term "promyal passage" will be retained for it because of long established usage. A promyal passage may be present on left and right sides (*Hyotissa*), on the right side only (Crassostreinae, Pycnodonteinae except *Hyotissa*), or closed on both sides (Lophinae and Ostreinae).

The mantle lobes may be thin and transparent, in which case they are generally extensively papillate on their inner surfaces; in other species, the lobes are thick and opaque, used for food storage (glycogen), and papillation is local and rarely present. These extremes have intermediates (reduction of papillation and slight thickening of the lobes), and precise characterization for most species must await the study of more specimens than have been presently available.

In many oysters there is medial fusion of the two moieties, right and left, of the outer labial palp, forming a hood over the two branches of the inner palp, which never has such fusion (Figure 4). The amount of fusion varies among different species and is described under subordinate taxa.

In all oysters there are two gills, right and left, each with two demibranchs, medial and lateral; each demibranch consists of a descending and ascending lamella. The demibranchs are eulamellibranch (*i.e.*, with adjacent filaments of one lamella fused by tissue connections, leav-

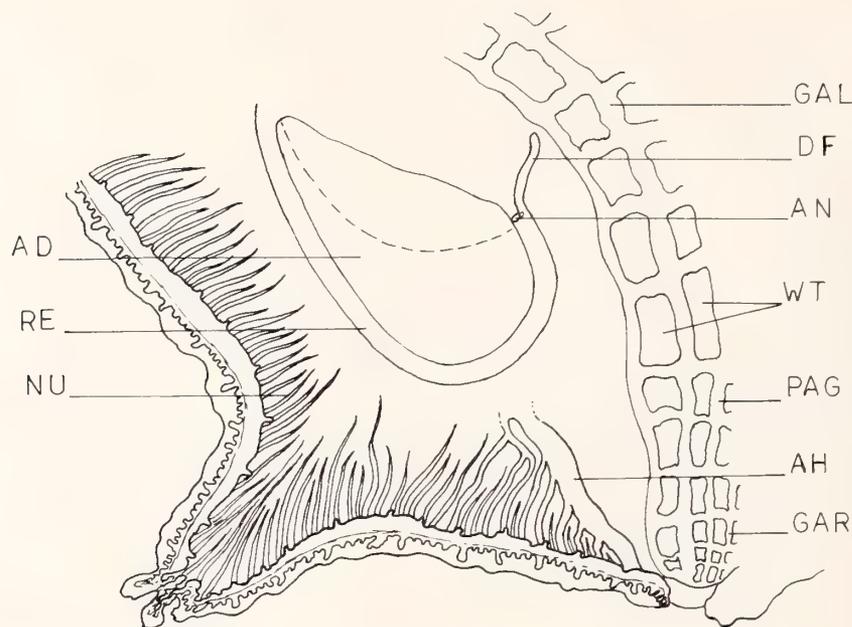


Figure 5

Internal view of posteroventral part of left mantle lobe of *Lopha cristagalli* from the New Hebrides Ids. (USNM 793723) to show anal appendage. Note extent of rectum around adductor muscle and tributaries to accessory heart. AD, adductor muscle; AN, anus; AH, accessory heart; DF, anal appendage; GAL, left gill axis; GAR, right gill axis; NU, neobranch unit; PAG, pseudoaxis of gill (fused junction of ascending lamellae of medial demibranchs); RE, rectum; WT, opening of water tubes of gill on surface of diaphragm.

ing small holes, or ostia, between them) and plicate (several small filaments of uniform size bulging outward to form a ridge between larger filaments in the grooves between the plicae), and all demibranchs are grooved along their free margin (Figure 4). There are regularly spaced, primary interlamellar septa extending from the free margin of each demibranch to the diaphragm; these septa define the water tubes, which are in oysters evenly coordinate in transverse rows in all four demibranchs. Thus they form a pattern of quadrate openings of the water tubes on the posterior (or excurrent) surface of the gill diaphragm (Figure 5). The gill diaphragm is completely attached by tissue continuity to the mantle lobes along the distal margins of the ascending lamellae of the lateral demibranchs. The diaphragm extends from the lower end of the labial palps to the inner surface of the post-ventral fusion of the mantle lobes, and thus the profile of the gills is J-shaped.

Along its dorsal half, the posterior surface of the diaphragm is attached to the anterior surface of the visceral mass by three narrow, non-muscular suspensory septa which are parallel to each other. The two lateral septa are attached along the gill axes, and they do not extend as far ventrad as the medial one, which is here termed the *pseudoaxial suspensory septum* (Figure 6). The latter resembles in all respects the axial septa, except in its extent and in attaching to the margins of the ascending lamellae

of the inner demibranchs, which are here and lower down, beyond the septum, fused to each other by permanent tissue continuity. The pseudoaxial septum is a consequence of paedapody, and it is limited to the Ostreacea among living bivalves. It seems not to have been previously named or described.

In lateral view the three suspensory septa of the gills are elongate triangles, tapering to a point at the ventral ends of the labial palps (which surround the dorsal ends of the four demibranchs), and gradually widening to their terminations near the base (for the axial septa) or ventral end (for the pseudoaxial septum) of the metasoma (defined below). The ventral or free margins of all three septa are arched, being concave ventrally, and along this margin in the two gill axial septa, but not that of the pseudoaxial, there courses a prominent branchial nerve, originating from the visceral ganglia (see below). In most oysters the three septa are continuous sheets from the dorsal apices to the ventral free margins, but in at least two species—*Parahyotissa (Pliohyotissa) quercinus* and *Striostrea prismatica*—the septa are discontinuous, being broken up into several segments (probably variable within a species) with large holes between, or the septa are entirely absent except for a short strip at their ventral ends, thus allowing passage of water between the three dorsal extensions of the anterior part of the excurrent mantle chamber which these three septa bound. The condition of discontinuous sus-

pensory septa was only discovered late in my examination of oyster anatomies, and its presence in other species may have been overlooked.

The visceral mass extends as a short, tapering sac along the anterior curvature of the adductor muscle, to which it is attached; this projection is here termed the metasoma (Figure 6). It contains the distal end of the crystalline style sac (which opens throughout its length to the initial part of the intestine), allowing the long style to be straight, so that it can rotate on its axis.

The metasoma also contains an extension of the gonad, surrounding the style sac and intestine, and on its anterior surface open a pair of renopores and gonopores, medial to the cerebro-visceral connectives of the central nervous system. The position of the renopores relative to the tip of the metasoma differs at the family level.

After leaving the posteroventral part of the visceral mass the intestine, now termed the rectum, passes through the pericardium and along the posterior curve of the adductor muscle. Its extent across the ventral curve of this muscle before terminating at the anus varies at different taxonomic levels. Moreover, in most oysters there is an anal appendage attached to the anus (Figures 5, 8). The form of this appendage varies at different taxonomic levels.

There are no pedal ganglia or statocysts in post-larval oysters (a further consequence of paedapody). The visceral ganglia are flattened masses, fused to each other medially, located under the mantle epithelium on the anterior curvature of the adductor muscle, immediately ventrad of the distal end of the metasoma. From these ganglia radiate several pairs of nerves, the most prominent of which are the pair of branchial nerves cited above, the cerebro-visceral connectives, lateral to them, and the osphradial nerves, described below. A pair of small cerebral ganglia are by the mouth, attached to each other dorsally by a short commissure and each to a cerebro-visceral connective, but little attention was given to these ganglia in the present study.

A pair of sense organs, termed osphradia (possibly not homologous to the osphradia of other mollusks), is present on the ventral surface of the adductor muscle (Figure 6). Each is a low, transverse, semilunar lamella, projecting into the mantle cavity, extending medially from the margins of attachment of the muscle, and each osphradium is connected to the visceral ganglion on its side by a prominent osphradial nerve. The osphradia are usually white, even when the adjacent mantle is darkly colored; the right osphradium is always larger than the left, and situated closer to the anus than the left one, regardless of the extent of the rectum around the ventral curvature of the adductor muscle.

THIELE (1889) first described these "abdominal sense organs," noting their presence in species of *Arca*, *Glycymeris*, *Pteria*, *Pinctada*, *Pinna*, *Pecten*, *Lima*, and *Spondylus* (some of his generic names are here modernized), as well as in *Ostrea edulis*. He could not find the organs in the Mytilidae, the protobranchs of the genera *Nucula* and *Nuculana*, nor any siphonate bivalves. He did not find the

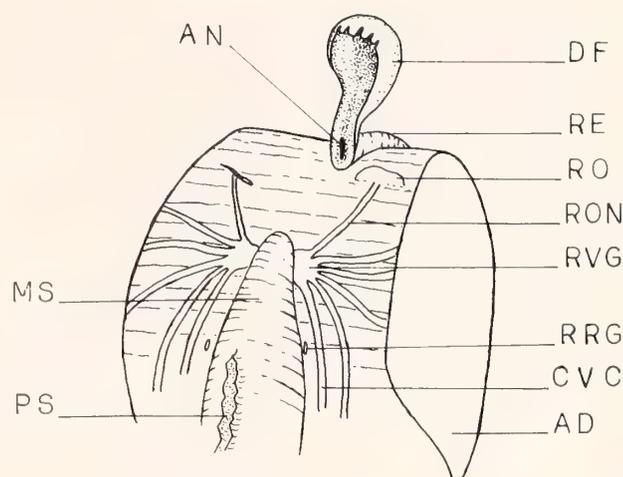


Figure 6

Oblique view of anteroventral curve of the free surface of the adductor muscle of a specimen of *Dendostrea folium*, 22 mm high, from Port Victoria, Seychelles Ids. (USNM 778093). AD, adductor muscle; AN, anus; CVC, cerebro-visceral connective; DF, anal appendage; MS, metasoma; PS, pseudoaxial suspensory septum of gills (cut); RE, rectum; RO, right osphradium; RON, right osphradial nerve; RRG, right reno-gonopore; RVG, right visceral ganglion.

minute left organ in *O. edulis*, but his figure (*loc. cit.*, fig. 9) shows very well the cardiform shape of the anal appendage of this species, although he did not mention it in the text.

The right and left parts of the heart are brought together in front of the rectum, and the auricles are always fused to each other, so that their cavities communicate, but they separate before entering independently into the single, bilobed ventricle (Figure 9). Variation within the heart, and its relation to the rectum and kidney are explained below, at the family level.

Based on studies of a few species of the Ostreidae, oysters have long been known to be hermaphroditic. But members of that family are sequential hermaphrodites, *i.e.*, they produce both sperm and ova in the same follicles of a single pair of gonads, but at different seasons. At least some of the Gryphaeidae are concurrent hermaphrodites, having a pair of testes and a pair of ovaries present together in the same individual.

Nothing is known of the reproductive habits of the living Gryphaeidae; of the Ostreidae, the Crassostreinae that have been studied are oviparous, shedding the gametes into the sea, where fertilization and development occur. The Lophinae and Ostreinae both seem to be larviparous, retaining the fertilized ova in the mantle cavity until the larvae have shells and can swim. Those two subfamilies are unique among incubating bivalves, in that the larvae occur only in the incurrent mantle cavity, nearly filling it and the area around the labial palps (at least in preserved specimens). Little emphasis has been given to this unusual

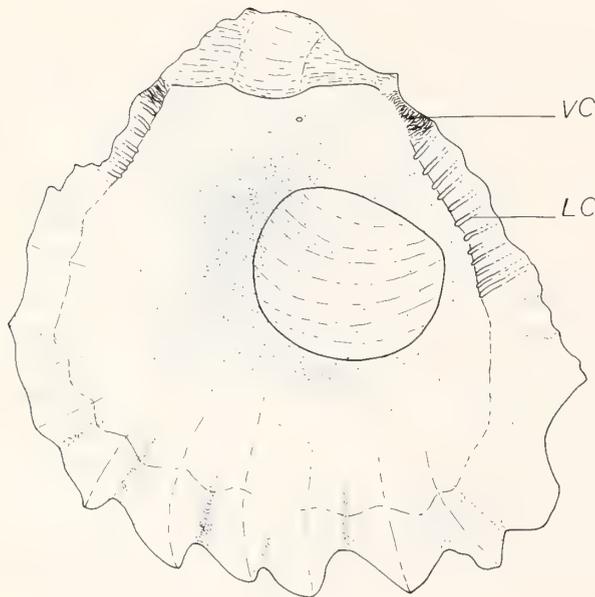


Figure 7

Hyotissa hyotis. Interior of a right valve, 180 mm high, showing lath chomata (LC) below vermiculate chomata (VC). From Okinawa, Ryukyu Ids. (USNM 670956).

condition, and the hypothetical explanations of how the gametes (or zygotes?) attain the incurrent chamber when they are released in the excurrent one are not convincing (see GALTISOFF, 1964).

All Ostreacea are marine, occurring from tropical to cool temperate seas, but they are most diversified in warmer areas. None occurs in the Arctic or Antarctic zones. There is considerable variation in the preferred range of salinity, temperature, water turbulence, substrate type, and depth for different species.

Family GRYPHAEDAE Vyalov, 1936

Ostreacea in which the adductor muscle scars are circular or only slightly flattened dorsally.

Two of the three subfamilies, the Gryphaeinae and Exogyrinae, are extinct; they were reviewed by STENZEL (1971) and briefly redefined by HARRY & DOCKERY (1983). All living gryphaeid oysters belong to a single subfamily, as follows.

Subfamily PYCNODONTEINAE Stenzel, 1959

Gryphaeidae in which the chalky deposits interspersed in the foliar matter of the inner shell layer have vesicles (hollow, subspherical or polyhedral cavities) easily seen with magnification of 10× or more. This is termed vesicular shell structure; it is well illustrated in RANSON (1967), STENZEL (1971), and TORIGOE (1981). The inner edge of the commissural shelf, along the shell margin, is usually well defined by a prominent angle of the shell surface.

Chomata are always present. These are of three types in this subfamily: (1) *Vermiculate chomata* (Figure 7) are small, rounded ridges, closely spaced, normal to the margin; they are slightly twisted, tapering out so that they are of varied lengths, or dividing and fusing. They are always present near the ligament on the front and hind margins of both valves, but those of opposite valves do not interdigitate. Usually the surface on which they occur is flat, but it may be creased to various degrees in the left valve, parallel to the margin, with a corresponding ridge in the right valve, fitting into the crease. When well manifest, these will be referred to as the chomatal troughs and ridges. (2) The *neopycnodontine chomata* are modifications of the vermiculate type, having very pronounced ridges and troughs, with the vermiculate chomata greatly enlarged as they cross the crests of the ridges on the right valve (Figure 16, but the ridges and troughs are not well shown); there are pits to receive the individual enlargements in the chomatal troughs of the left valve. This type is also limited to the shell margin near the ligament. It is intermediate between the vermiculate and ostreine types (see below, under Ostreidae) of chomata. (3) *Lath chomata* (Figure 7) are elongate, straight, well defined ridges, spaced about as far apart as their widths, and normal to the margin. They occur ventral to the vermiculate chomata, on both right and left valves, but they seem to coincide rather than interlock, or alternate, with those of the opposite valve. These are present only in some specimens of *Hyotissa hyotis*, among living oysters.

The mantle lobes are thin, transparent in smaller specimens, and probably not used to store glycogen; their inner surface is usually extensively papillate, becoming more densely so in older individuals. The first neobranch unit behind the diaphragm is not expanded nor extended inward to form an accessory heart. The outer labial palp is fused medially for most of its length. The anus is surrounded by a fleshy, collarlike flange, often rolled outward to appear as a bulbous mass in preserved specimens (Figure 8). The right promyal passage is broadly open, reaching from the adductory muscle nearly to the isthmian mantle.

The bilobed ventricle of the heart is distinctly penetrated by the rectum. The auricles of the heart are fused to each other, and also extensively adnate to the ventral wall of the pericardium, over the adductor muscle; they are irregularly outpocketed, appearing lobate (Figure 9); internally they are packed with granulocytes containing a dark brown, granular pigment, but a central, tubular lumen persists in each auricle for passage of blood to the ventricle. The renopericardial passage, if present, has not been located.

The granulocytes in the auricles of bivalves were extensively treated by GROBBEN (1888), who thought they are excretory cells. These cells are less abundant in those species of Ostreidae in which they occur (e.g., *Ostrea edulis*), but insufficient observations were made on the his-

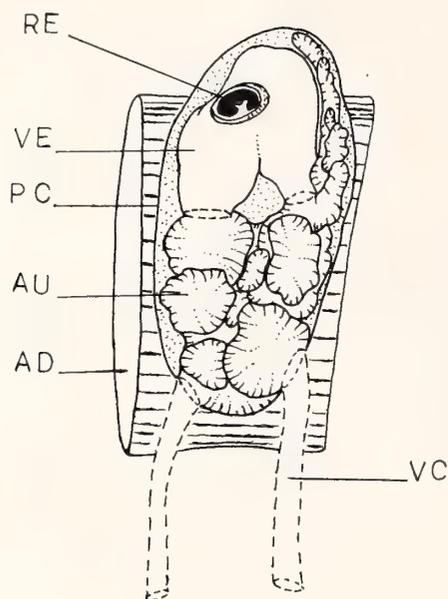


Figure 9

Dorsal view of heart of *Hyotissa hyotis* from Galapagos Ids. (USNM 796193). Note the many lobes of the auricles; the thin walled kidney, between the pericardium and adductor muscle, is not shown. AD, adductor muscle; AU, auricle of heart; PC, pericardium; RE, rectum; VC, left vena cava; VE, ventricle of heart.

very wide, so that the gills appear to be more voluminous than those of the Ostreidae.

When alive, the species that grow to large size, at least, have brilliant orange pigment in the gonad (ovary) and adductor muscle. The pigment may be seasonal and it is alcohol soluble, so that it is not apparent in the flesh of most preserved specimens. Specimens preserved in alcohol usually have a dark brown pigment in the parenchyma, which is more abundant in older (larger) oysters.

Tribe *Hyotissini* Harry, new tribe

Pycnodontinae in which the shells are thin to thick, small to very large, with vermiculate chomata always present near the hinge. The interior of the valves have a moiré luster; the right valve is often inflated to a variable extent. The prismatic layer of the right valve is thin, frequently lost through erosion. Tuck grooves (see next tribe) on the right valve are rare. These generally live in shallower depths than the Neopycnodontini. The condition of the promyal passages varies at the generic level.

Genus *Hyotissa* Stenzel, 1971

Type, by original designation: *Mytilus hyotis* Linné, 1758, Syst. Nat., Ed. 10, p. 704, No. 270. See Figures 7, 10 and 11; also STENZEL (1971) fig. J85, p. N1111.

Hyotissini with medium to very large shells (to 250 mm height or more), occasionally subcircular but usually

oval, dorsoventrally elongate; both of the valves are thick, and both usually have rounded plications, from which semicylindrical lamellae may project as hyote spines. The marginal commissure is usually zigzag, with vesicular chalky deposits developing internally in the troughs between the plicae. The ventral margin of the adductor muscle scar is usually elevated, at least in larger shells. Lath chomata (Figure 7) occasionally develop. The valves are variously colored, washed with red, blue, or purple. Some specimens are light brown externally, and occasionally specimens will have dark purple, almost black margins internally, or the whole inner surface may be so colored.

The left promyal passage is open, but limited to the area of the pericardium and lower part of the visceral mass (Figure 8); it is thus not as extensive as the right passage, which extends from the adductor muscle nearly to the hinge. In larger specimens the papillate inner surface of the mantle is rough to the touch.

As here restricted, the genus is monotypic, but *Hyotissa hyotis* extends from Madagascar to the Tuamotu Islands in the Indo-West Pacific tropics, and it also occurs in the tropical part of the eastern Pacific faunal realm. It lives in shallow subtidal depths, often on coral reefs. Junior synonyms of the population of the eastern Pacific include *Ostrea fischeri* Dall, 1914. There are numerous junior synonyms of the Indo-West Pacific population.

Genus *Parahyotissa* Harry, gen. nov.

Type: *Ostrea thomasi* McLean, 1941, Notulae Naturae (Acad. Nat. Sci. Philadelphia), No. 67, p. 7, pl. 3, figs. 1, 2; pl. 4, figs. 1, 2. Not *Ostrea sellaeformis* var. *thomasi* "Conrad" Glenn, 1904, Maryland Geol. Surv., Miocene, p. 380, pl. C, figs. 5a, 5b. McLean's species is here renamed *Parahyotissa mcgintyi* to preserve his original intention to honor Thomas L. McGinty, noted student of malacology of Florida. See Figures 12 and 13; also STENZEL (1971) fig. J27, p. N987.

Hyotissini in which the shell is smaller than *Hyotissa*, without lath chomata, but with vermiculate chomata always present and restricted to the subligamental margin. The ventral margin of the muscle scar is not elevated. Plications, occasionally with short hyote spines, are potentially present on both valves. The valves are often washed with red or light purple, tending to be white inside. In contrast to *Hyotissa*, the left promyal passage is always closed.

Parahyotissa (Parahyotissa) mcgintyi occurs subtidally and to 98 m depth or slightly more in the tropical eastern and western Atlantic Ocean, extending slightly into subtropical areas in the latter realm (to North Carolina and Texas). Another species of the typical subgenus, *P. (Parahyotissa) imbricata* (Lamarck, 1819), occurs in the central part of the Indo-West Pacific tropics (Australia to the Ryukyu Islands of Japan); its shells may be difficult to distinguish from juveniles of *H. hyotis*, but the left promyal passage is closed.

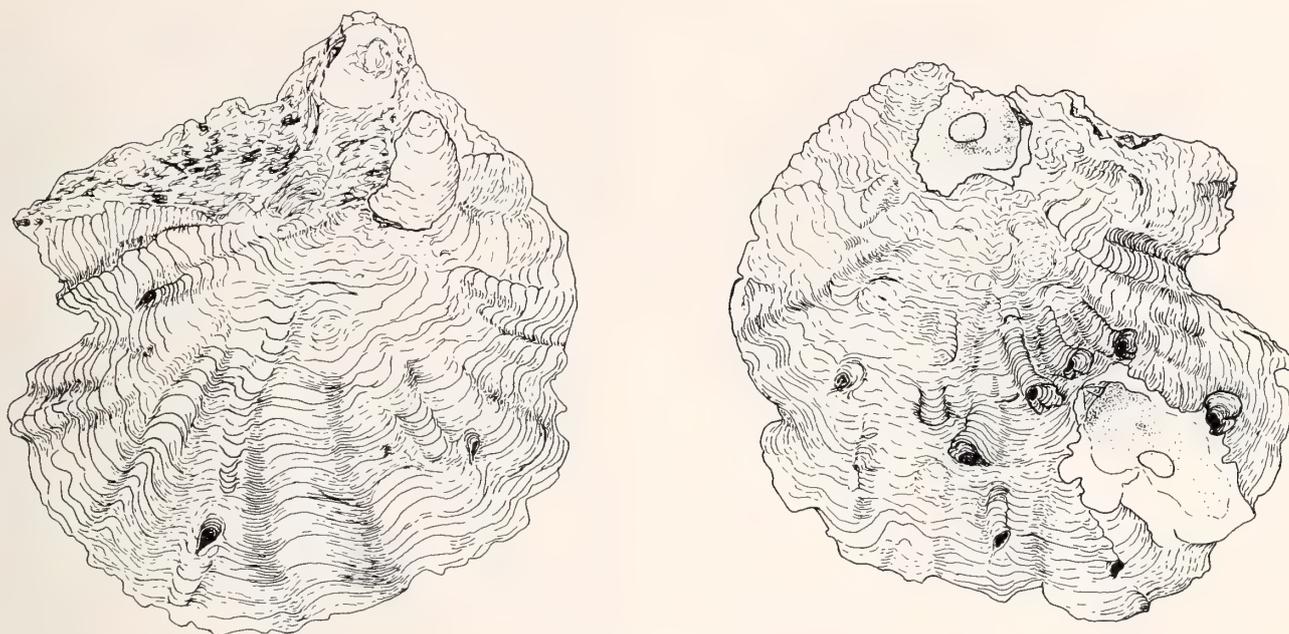


Figure 10

Hyotissa hyotis. Exterior of valves (left one on left), 130 mm high. Galapagos Ids. (USNM 796193).

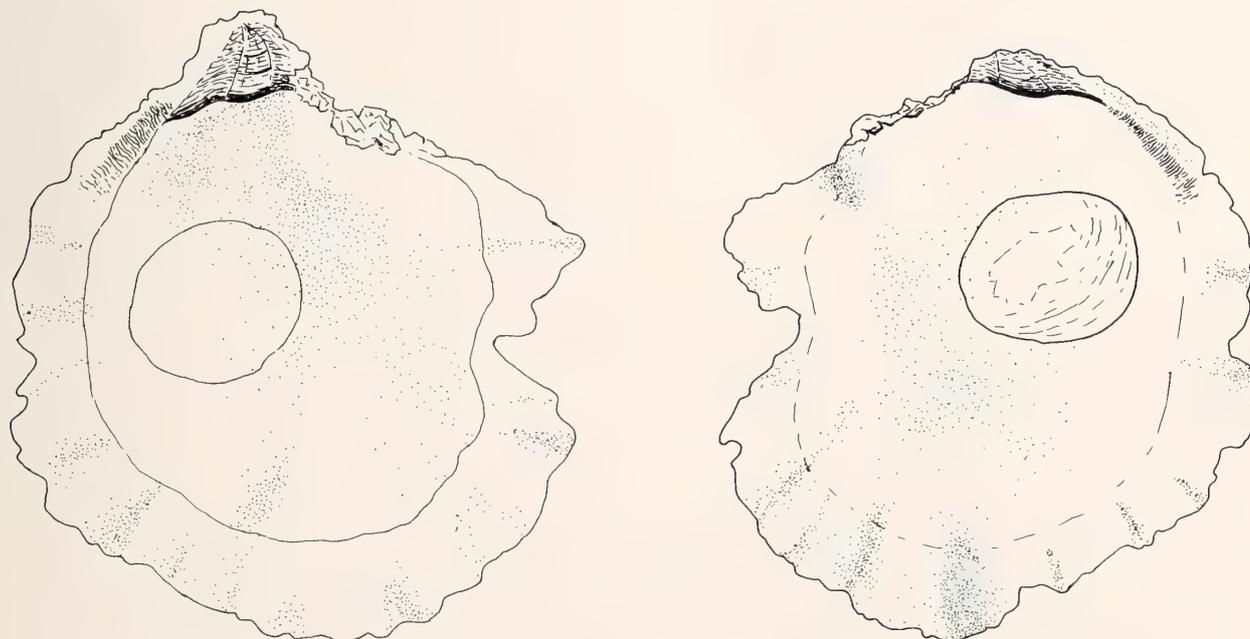


Figure 11

Hyotissa hyotis. Interior of valves of shell of Figure 10.

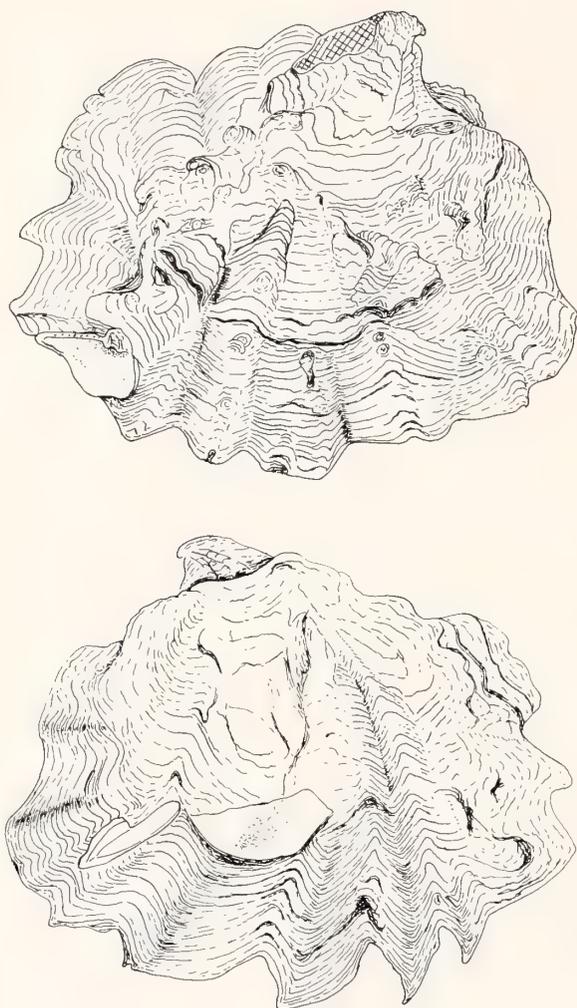


Figure 12

Parahyotissa mcgintyi. Exterior of left (above) and right valves of a specimen 65 mm long, from several meters depth on a support of an oil drilling platform, several kilometers south of Timbalier Island, Louisiana. Shell loaned by C. A. Beddinger. Small attachment area of left valve, cross hatched, only partly visible.

Subgenus *Parahyotissa* (*Pliohyotissa*)
Harry, subgen. nov.

Type: *Ostraea quercinus* Sowerby, 1871, in *Ostraea* of Reeve's Conch. Icon., 18, pl. 19, figs. 43a, 43b. See Figure 14.

Pliohyotissa differs from the typical subgenus in the nearly complete absence of plications and spines on the valves, which otherwise grow to a size comparable to that of *Parahyotissa* s.s., by the oaken color (irregular light brown wash) of the shell's interior (which may occur in the typical subgenus also), and by the frequent presence of narrow, marginal rays of purple. *Parahyotissa* (*Pliohyotissa*) *quercinus* (Sowerby, 1871) was originally de-

scribed from unknown locality. It lives in the eastern Pacific, particularly along the east coast of Baja California, where it was rediscovered by Constance E. Boone. The holotype of Sowerby's species in the British Museum of Natural History has a few small plicae on the slightly upturned margin of the left valve, but the marginal commissure is not zigzag. As presently known, this subgenus is monotypic.

Subgenus *Parahyotissa* (*Numismoida*)
Harry, subgen. nov.

Type: *Ostrea numisma* Lamarck, 1918, Hist. Nat. Anim. sans Vert., Vol. 6, pt. 1, p. 205, No. 8. Not figured. See Figure 15.

Parahyotissa in which the shell is small (40 mm high or usually less), extensively cemented by the left valve; the right valve is slightly convex, without plicae or spines; it is usually white, occasionally with a few small purple spots near the umbo. The only known species, *P. (Numismoida) numisma* (Lamarck, 1819) is widely distributed in the Indo-West Pacific tropics from East Africa to Hawaii and the Tuamotu Islands. Junior synonyms include *Ostrea thaanumi* Dall, Bartsch & Rehder, 1938, of Hawaii.

Tribe *Neopycnodontini* Harry, new tribe

Pycnodontinae in which the shells are thin and of small to moderate size, with the left valve very inflated and right valve flat. The chomata are of the neopycnodontine type. The right valve has a few peculiar linear, radiating grooves, each margined by a small ridge near the shell margin of larger specimens, resembling tucks in a piece of cloth. The left valve rarely shows a few plications (large, vague, discontinuous) but none are present on the right valve. The shells are generally light gray, occasionally washed with light pink or lavender. The interior surface of the shell does not have moiré luster. The left promyal passage is always closed; the right one is broadly open.

Genus *Neopycnodonte* Stenzel, 1971

Type, by original designation: *Ostrea cochlear* Poli, 1795. Testacea utriusque Siliciae, Vol. 2, p. 179. See Figure 16.

The single species of this genus, *Neopycnodonte cochlear* (Poli, 1795), is nearly circumglobal in lower latitudes. Although some specimens of *Parahyotissa* may extend to the shallower limit of depth of *N. cochlear*, this species extends to greater depths than any other Recent oyster: 27 to 2100 m; but the populations seem to be very localized throughout its range. It has been abundantly recorded in the eastern Atlantic from the Mediterranean and Atlantic coasts of France; the U.S. National Museum of Natural History has much material from the western Atlantic, from Bermuda, North Carolina, and the east coast

of Florida, and I have a specimen found off south Texas (27°18'N, 96°23'W, 131 m depth). In the Indo-West Pacific realm it is represented in the USNM by specimens from the Red Sea to Madagascar, the Philippines, China Sea, Japan and Hawaii. The species is unknown from the eastern Pacific faunal realm. There are numerous junior synonyms.

Family OSTREIDAE Rafinesque, 1815

Ostreacea in which the dorsal margin of the adductor muscle scar is concave or flat, so that the shape of the scar is gibbous, or more frequently reniform or lacrimoid. The valves generally lack moiré luster internally. Chalky deposits of the foliar layer, when present, do not show vesicles at lower magnification, although at high magnification these deposits may be seen to be minutely vesicular (CARRIKER *et al.*, 1980). A marginal commissural shelf is generally not defined (exception: *Planostrea*).

Chomata may be absent throughout life (*Booneostrea*, *Crassostrea*) or occasionally lost in larger (older) shells of some species (*Ostrea*, *Striostrea*, *Pustulostrea*), or absent in some ecomorphs of a species in which they are generally present (*Saccostrea*); but chomata are present in most species, and of two distinct types: (1) *Lophine chomata*, limited to the Tribe **Lophini**, consist of minute pustules in adjacent lines which are normal to the shell margin, with one to several pustules per line. The lines of pustules are on the protochomatal bands usually manifest in the underlying shell structure. Lophine chomata may form a broad, continuous band completely around the shell margin, or occur only at a few places along it; the pattern may change drastically within the life of an individual. They may be present on both valves, or limited to the right valve only, but in either case there are no pits to receive them in the opposite valve. Occasionally lophine and ostreine chomata may occur in the same specimen (*Dendostrea*, *Alectryonella*), in which case the ostreine chomata are limited to the margin close to the hinge. (2) *Ostreine chomata* consist of pustules, sometimes elongate normal to the shell margin, in a single line parallel to the shell margin; they occur only on the right valve, and there are pits to receive them in the left one. Ostreine chomata may be only a few, in which case they are usually near the ligament, or they may extend ventrally for variable distances, sometimes to or even across the ventral margin. Only this type of chomata is present in the tribe **Myrakeenini** of the Lophinae, and in the Ostreinae and Crassostreinae (with exceptions noted above).

The left promyal passage is always closed; the right one is closed in Lophinae and Ostreinae, but partially open in the Crassostreinae. The first neobranch unit behind the diaphragm usually is enlarged and extends inward (upward) to form an accessory heart. The rectum passes completely behind the ventricle of the heart rather than through it. The heart auricles are not outpocketed, nor are they adnate to the ventral wall of the pericardium. Generally

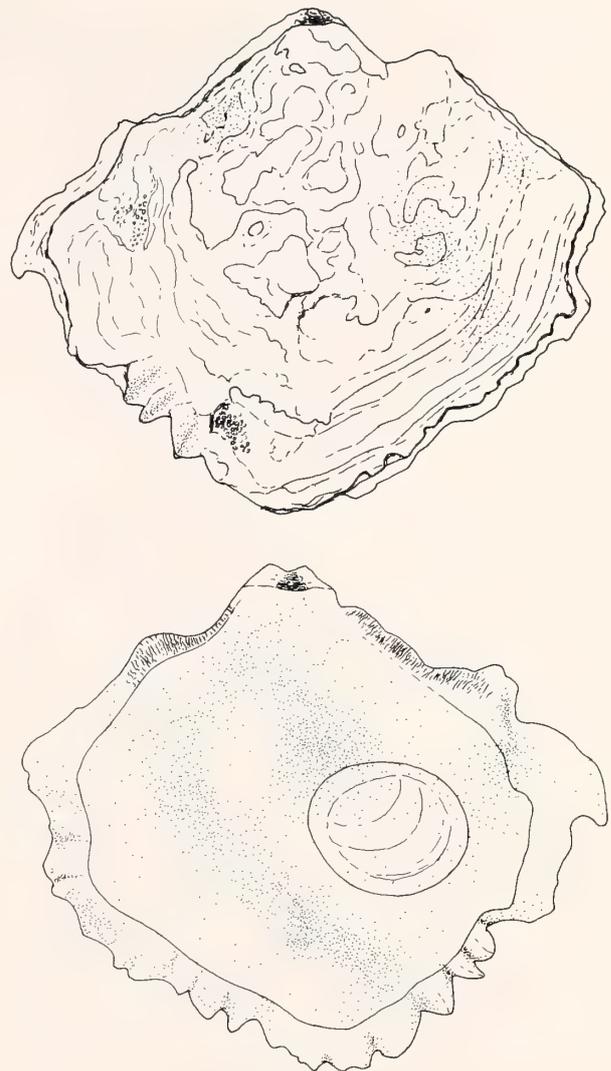


Figure 13

Parahyotissa mcgintyi. Shell 89 mm long. Exterior of right valve (above) with margin of left showing, and interior of same below. Note extreme erosion and poorly developed plicae; left valve was almost entirely cemented to bedrock. Shell is from Stetson's Reef, near the edge of the continental shelf, off the northern Texas coast; collected and loaned by Thomas E. Pulley.

parenchyma and pigmented granulocytes are sparse in the heart auricles.

The main sac of the kidney of the Gryphaeidae is reduced to a small, transverse tube at the anterior curve of the adductor muscle, between it and the front end of the pericardium; there are no posterior kidney caecum or internal trabeculae; the anterior horns of the kidney are present, lateral to the metasoma, and these extend above and below the transverse tube. A large lateral tube is often present, extending backward from the anterior horns lateral to the dorsal part of the pericardium. All these tubes

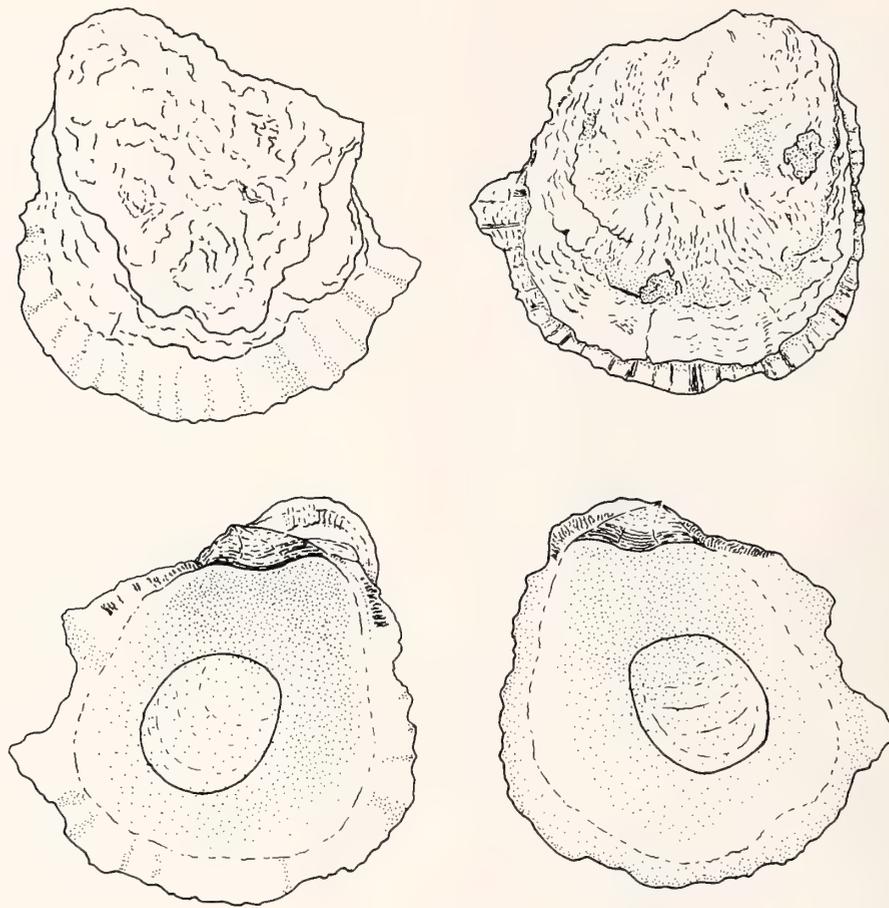


Figure 14

Parahyotissa (Pliohyotissa) quercinus. Height, 65 mm. Concepción, Baja California Sur, Mexico, low intertidal zone. Shell collected and loaned by Constance E. Boone.

are obscured because they have arising from them short, closely spaced, dendritically branched foliols, and the whole kidney mass is often nearly colorless, or sometimes pure white.

The reno-pericardial passage consists of two large openings between the pericardium and the transverse kidney tube. These openings are just above the lateral ends of the auricles. The renopores are at the lower ends of the anterior kidney horns, and they open with the gonopores in small pits, lateral to the free end of the metasoma (Figure 6).

Subfamily LOPHINAE Vyalov, 1936

Ostreidae of small to large size, usually with plicate surfaces on both valves and generally having a zigzag marginal commissure. The area of cementation of the left valve may be large, but it is usually small and often accompanied by thin, recurved hyote spines which may be of considerable length or mere rudiments, often free

throughout their length and only attached to a solid object terminally; these clasper, or lophine, spines arise at the crests of plications of the left valve only, and at or close to the outer margin of the area of cementation. The outer (prismatic) layer of the shell is usually continuous, not projecting as lamellae at growth rests.

The interior of the shell often has a metallic luster, and frequently it is of some color other than white (brown, greenish, or reddish). The adductor muscle scars are generally not colored differently from the rest of the shell's interior. Chalk deposits are absent (as noted also by TORIGOE, 1981), but shell chambering is frequent. Chomata are always present, either lophine or ostreine or both.

The mantle lobes are usually thin (exception: *Myra-keena*) and occasionally their inner surfaces are papillate. Both promyal passages are closed. The outer labial palp is fused medially, usually for the greater part of its length. The rectum extends well under the adductor muscle, sometimes curving upward around the anterior part of the

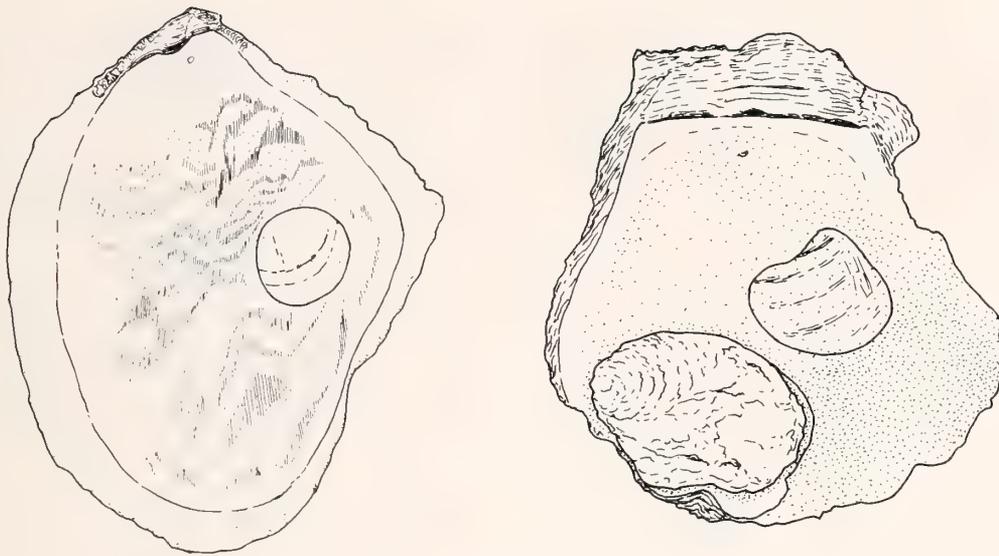


Figure 15

Parahyotissa (Numismoida) numisma. Right: exterior of right valve, attached to left valve, the latter cemented completely by its outer surface to the inner surface (near ventral margin) of a slightly worn right valve of *Pustulostrea tuberculata*. Left: interior of same right valve, showing moiré luster. The *P. (N.) numisma* shell is 28 mm high. From Efate Island, New Hebrides Ids. (USNM 787771).

muscle for a short distance. The anus has a large, digitiform process extending from the outer part of its rim (Figure 5).

The gonad may be brightly colored (yellow) seasonally by a pigment that quickly leaches out in alcohol. The species are larviparous (where reproductive habits are known).

Lophine oysters live in tropical or warm temperate marine waters from shallow subtidal levels to a few meters depth, generally in situations where they are not subject to turbulence and where the water is of constant temperature and normal oceanic salinity. Several species are typically coral reef associates.

The Lophinae show their close relationship to the Pycnodonteinae in several characters that are lost or much modified in the rest of the Ostreidae; thus, both valves are usually strongly plicate (lost in some species of both subfamilies); the outer labial palp is more extensively fused medially than in the rest of the Ostreidae; mantle lobes are usually thin and papillate on the inner surface. They are more strictly limited to the tropics than the other living oysters, and are primarily coral reef associates. Conversely, new characters appear in the Lophinae which are also present in the Ostreinae but not in the Pycnodonteinae: ostreine chomata; a digitiform anal appendage; a closed right promyal passage and habit of brooding the larvae; modification of the first neobranch unit behind the gill diaphragm to become an accessory heart; and a tendency in some (*Myrakeena*) to lose the papillation of the inner surface of the mantle lobes and to thicken them for storing

glycogen. TORIGOE (1981:pls. 1-5) illustrated and described a pattern of the intestine within the visceral mass in which the intestine does not loop around the stomach in the Pycnodonteinae and Lophinae, but does do so in the Ostreinae and Crassostreinae; but I have made no observations on this point.

Tribe **Lophini** Vyalov, 1936, new tribe

Nom. trans. Harry, herein, *ex* Lophinae Vyalov, 1936.

Lophinae in which only lophine chomata occur (*Lopha*), or both lophine and ostreine types may occur, together or separately (*Alectryonella*, *Dendostrea*). Clasper spines may arise from the left valve, but these are often reduced or absent. Although the species may have completely white shells, the shells are usually deeply colored, red, brown, blue, or purple (or combinations thereof), either by washes or by prominent radial stripes or both. There is no circular flange around the anus, which has a prominent digitiform appendage on its outer margin.

Genus *Lopha* Röding, 1798

Type, by subsequent designation of Dall (1898): *Mytilus cristagalli* Linné, 1758, Syst. Nat., Ed. 10, p. 704. STENZEL (1971) figured this species, fig. J129, p. N1156, under the name "*Lopha folium ecomorph cristagalli*."

Lophini in which the shell becomes large (to 100 mm high) and is subcircular to oval-reniform in profile, with about five very large, interlocking, radial plicae on both

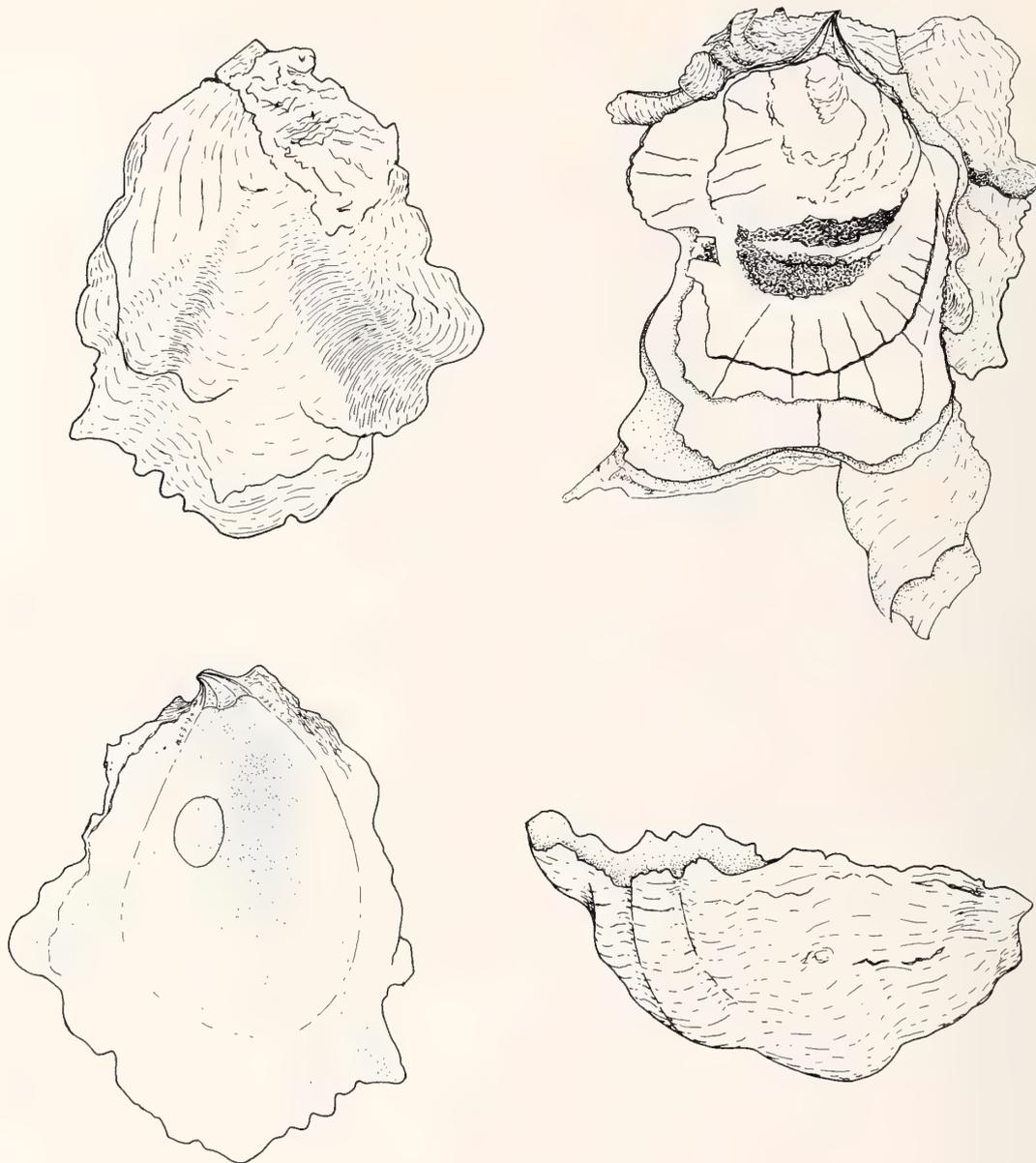


Figure 16

Neopycnodonte cochlear. Upper right: exterior of right valve, still attached to left valve (54 mm high), which is cemented to a cluster of other specimens. Note crescent-shaped abraded areas in middle of valve, revealing vesicular chalk deposits, and radial "tuck marks" peripherally. Specimen is one of lot USNM 196421, from Sicily, part of the Jeffreys Collection. The other three figures are of a left valve, 63 mm high, one of lot USNM 249152, from 270 m depth in the China Sea, off Pratas Island (116°40'E, 20°40'N).

valves; the ridges and troughs of these plications are acutely angled, and the sides flattened. There are nearly always some low, rounded or quadrate pustules, very small, arranged in radial rows, covering the surface of both valves or present only in limited areas. These are smaller than the pustules of *Alectryonella* and *Pustulostrea*. The area of cementation is generally small; clasper spines are usu-

ally present, and they are often long (to several cm) and irregularly recurved. The right valve usually has externally a distinct indentation over each spine of the left valve.

The shells are thin, with the inner surface usually metallic, bronzed or rarely white. No chalk deposits seem to form, but chambering is used to smooth the interior and

eliminate the plications inward from the narrow marginal zone. Chomata are lophine only; they are prominent, often extending to and around the ventral margin; they are present in both valves or the right valve only.

Mantle lobes of the two alcoholic specimens examined (from the New Hebrides Ids., USNM 793723) are thin, transparent, and papillate on their inner surfaces. The first neobranch unit behind the diaphragm is enlarged and receives as tributaries the next two or three units above it (Figure 5). The outer labial palp is fused in the midline almost to its tip. The rectum passes ventrally under the adductor muscle and ends on the anterior curvature; the anus has a very large, flattened, fingerlike appendage, narrow and tapering to an acute tip, arising from the outer curve of the lip (Figure 5). Both promyal passages are closed.

STENZEL (1971:N1005) cites WADA (1953, a paper not available to me) as saying this species and the next (*Alectryonella plicatula*) incubate their larvae.

The genus is here considered to be monotypic, and the two other species that STENZEL (1971) included as synonyms are placed in *Dendostrea*. TORIGOE (1981) reached the same conclusion. As thus restricted, *Lopha cristagalli* is limited to the tropics of the Indo-West Pacific faunal realm, associated with coral reefs at a few meters depth; it extends from the east coast of Africa and the Red Sea to the Ryukyu Islands of Japan, and to 165°E longitude. While it is not uncommon in the Philippines and Indonesia, it seems to be rare in the waters of northern Australia. Junior synonyms include *Ostrea townsendi* Melville, 1898, and the two specimens on which this name was based were examined in the British Museum; both are white, inside and out, but one is faintly washed with pale pink and the other with pale lavender on the exterior near the umbos.

Genus *Alectryonella* Sacco, 1897

Type, by original designation: *Ostrea plicatula* Gmelin, 1791, Syst. Nat., Ed. 13, p. 3336, No. 111. See STENZEL (1971) concerning the interpretation of Gmelin's species, and for excellent photographs of it: fig. J29, p. N990; J134, p. N161; J135, p. N1162.

Lophini with shells of moderate size (but to 110 mm long), subcircular, slightly inflated, usually cemented by about half of the left valve. Clasper spines are rarely formed, and usually they are short and adnate throughout their length. Numerous (up to 20) regular, rounded radial ribs are present on both valves. These plications are roughened by closely spaced growth rests, but no lamellae seem to be formed along them. Low, rounded pustules, closely spaced and irregularly arranged, may occur on adumbonal parts of the shell before the plications are formed; these are larger than those of *Lopha*, and they resemble those of *Pustulostrea* (see below). The beaks are moderately large, and the ligament is short to long.

The exterior is usually dark bluish purple or brown, uniformly colored.

The interior is often dark brown, submetallic. No chalk deposits are formed, but chambering is common in the deeper parts of the left valve, at least. Chomata may be ostreine near the hinge, but typically lophine on the rest of the shell margin, where they are often prominent on both valves, or the right one only.

Protochomatal bands are manifest in small patches by narrow, thin strips of brown, organic material (conchiolin) deposited at any place on the shell interior (rare on the muscle scars); these bands are closely spaced, mostly parallel to each other and chiefly normal to the shell margin, especially near it, but inward they may become whorled and branched, forming a pattern similar to a human fingerprint. The organic strips (the ends of which curl away from the surface in dried shells) become gradually covered by the foliose shell layer, beginning first between the strips and around the margin of each patch, enhancing the fingerprint effect.

I have not seen the flesh of this species, but TORIGOE (1981) reports that the right promyal passage is closed, the outer labial palp is extensively fused medially, and the anal appendage is digitiform.

The single living species, *Alectryonella plicatula* (Gmelin, 1791), may be rare and local, probably living in shallow subtidal depths, judging from the few lots in collections. It is known from the Indo-West Pacific faunal realm, from Madagascar to the Philippines, Ryukyu Islands, and western Caroline Islands. The organic strips regularly deposited along the protochomatal bands are unique to this species, and their alignment with the chomata furnishes the most convincing evidence that the chomata are derived from these bands.

Examination of the type specimens in the British Museum of Natural History showed that *Ostrea dubia* Sowerby, 1871, is a juvenile specimen, and *O. solida* Sowerby, 1871 (erroneously cited from the Gulf of Panama by him), is a completely white shell, externally, of *Alectryonella plicatula*.

Genus *Dendostrea* Swainson, 1835

Type, by subsequent designation of Herrmannsen, 1847: *Ostrea folium* Linné, 1758, Syst. Nat., Ed. 10, p. 699, No. 178. See Figures 17 and 18.

Lophini mostly of small to medium size (but to 85 mm high), irregularly subcircular to elongate dorsoventrally, with thin shells cemented by a variable part of the left valve, often with clasper spines which are usually short and adnate throughout their length. Both valves may be convex, the left more so than the right, and generally plicate, although the right valve may have plications limited to a small region; the plications are small, rounded, closely spaced, with rounded grooves between. The shell margin is generally zigzag along some part, even when plications of the right valve are poorly developed. The

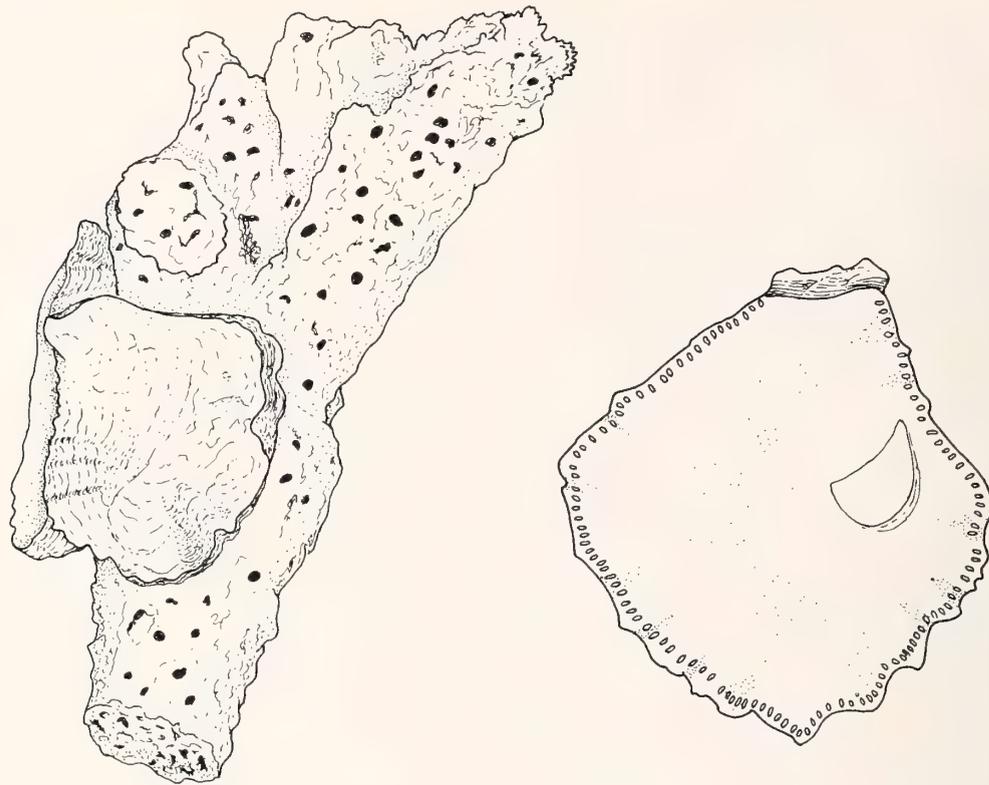


Figure 17

Dendostrea folium. Specimen on coral (*Acropora* sp.) at left, and the interior of the right valve, 23 mm high, of the front shell on the coral. From Abu Dhabi, Persian Gulf, 1 m deep, collected and loaned by John W. Tunnell, Jr.

external surfaces are without pustules, and usually smooth, often with a waxy texture, rarely with short lamellae at growth rests, which may form a few hyote spines on both valves. The exterior is often white, but usually blue or purple, sometimes rayed with darker stripes.

The shell interior is often white, varying to light or dark green; the chomata are usually only ostreine, limited to the margin near the hinge, but occasionally supplemented by lophine chomata in the right valve also, extending to the ventral margin.

The mantle lobes are thin, and often papillate internally; the outer labial palp is extensively fused in the midline, to three-fourths of its length. An accessory heart is developed behind the diaphragm, and it lacks tributaries. The anus has a large, fingerlike appendage (Figure 6), generally with sides inrolled and a cupped tip in the type species, *Dendostrea folium* (Linné, 1758), but it is flat and pointed in the other two known species.

Two of the three living species (there are no data for *D. mexicana*) are larviparous. *Dendostrea folium* is extensively distributed in the Indo-West Pacific faunal realm; *D. frons* (Linné, 1758) occurs in the western, and probably also in the eastern Atlantic realms. *Dendostrea mexicanum* (Sowerby, 1871) occurs in the eastern Pacific (coast of Baja California), where specimens were rediscovered by

Thomas Pulley and Constance Boone. The species live at shallow subtidal depths in protected waters of normal salinity in tropical and warm temperate seas. They are often associated with gorgonians, usually forming a leaflike, clasping ecomorph thereon, and on stony coral.

Tribe **Myrakeenini** Harry, new tribe

Lophinae in which only ostreine chomata are present; clasper spines are unknown in the living species. The outer surfaces of the shells are almost or entirely white, never extensively colored as in **Lophini**. A circular flange around the anus, drawn out to a fingerlike appendage on the outer margin, is present in *Myrakeena angelica*, the only species of the tribe of which the flesh has been available for study.

Genus *Myrakeena* Harry, gen. nov.

Type: *Ostrea angelica* Rochebrune, 1895, Mus. d'Hist. Nat. Paris, Bull., 1:241-242. Not figured. Holotype figured by KEEN (1971:81, fig. 167 [lower of the two]); see also Figure 19.

Myrakeenini in which the shells are mostly of moderate size (but to 100 mm high), subcircular, attached by cementation for half or less of the left valve's area. Both

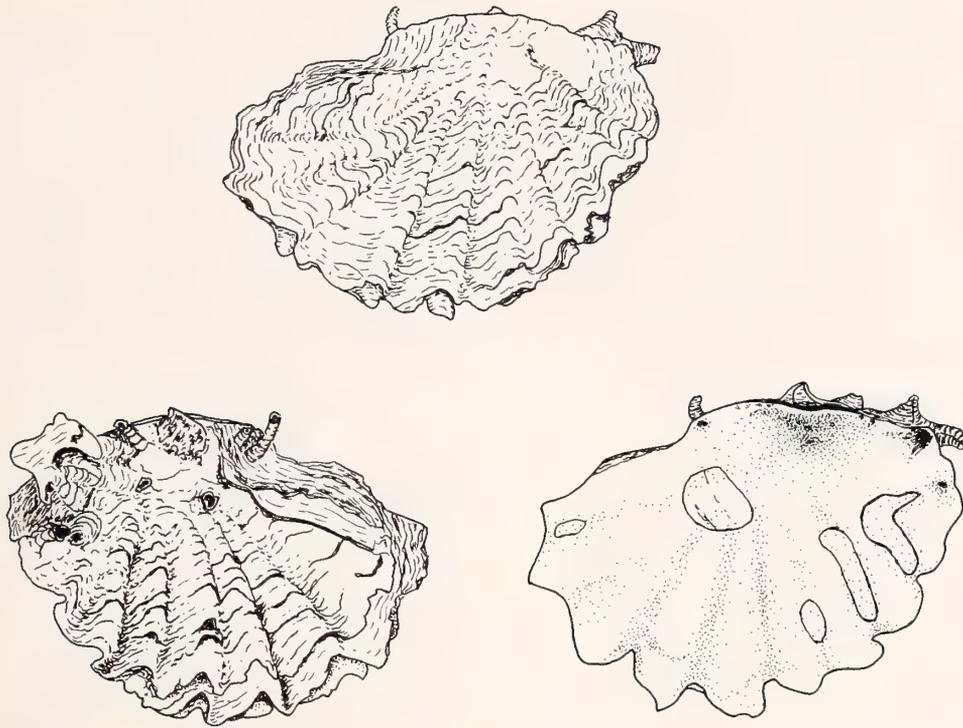


Figure 18

Dendostrea folium. Exterior of right valve above. Exterior of left valve at lower left, and interior of same at lower right. Shell is 43 mm high. Note patches of foliar layer of shell, forming chambers in the troughs near the periphery of the left valve interior. Only a few ostreine chomata are present, near the hinge. Three clasper spines of the left valve have holes opening to the interior, near the hinge. From Weld Island, Western Australia, shallow subtidal, collected and loaned by Constance E. Boone.

valves are slightly inflated, regularly plicate beyond attachment area by low, rounded ribs, ending in a zigzag marginal commissure. No hyote or clasper spines seem to form. The exterior is grayish white, occasionally with a linear stripe of dark purple in a few of the troughs between the ribs. The beaks are small, but the ligament is usually relatively long. The interior of the shell is white or light green. Lophine chomata are never formed, but ostreine ones always are, though small and occasionally only a few, near the ligament, or extending down the upper fourth of the valve margin.

The flesh is grayish, with thickened, opaque mantle lobes; the first neobranch unit behind the diaphragm is enlarged, and reaches to the heart; it does not receive tributaries. The outer labial palp is fused medially for about half of its length; the anus is surrounded by a circular flange which at the outer margin extends as a fingerlike appendage, tapering to an acute point, with sides curved so that it is semicylindrical. The reproductive habits are unknown.

The genus is named for A. Myra Keen, noted malacologist. *Myrakeena angelica* (Rochebrune, 1895), the only known species, seems to be limited to the Gulf of Califor-

nia, contrary to some statements in the literature. It lives in water of normal oceanic salinity, in protected situations at very low tide level and slightly deeper.

Genus *Anomiostrea* Habe & Kosuge, 1966

Type, by original designation: *Ostrea pyxidata* Adams & Reeve, 1850, Voy. Samarang, Moll., p. 72, pl. 21, fig. 19. Not *Ostrea pyxidata* Born, 1778, Index Mus. Caes. Vindobon., p. 93 (Pectinidae); renamed *Anomiostrea coralliophila* Habe, 1975.

Myrakeenini that are small, with the left valve hemispherical, the right one flat; the prismatic layer is light tan, but the interior of the shell is pure white. There are no clasper spines or chalk deposits. Numerous very small radial ribs, well defined, are on the peripheral part of the right and left valves. The ventral margin of the muscle scars is elevated. STENZEL (1971:N167) reproduced the original illustration of this species and that of SOWERBY (1871:pl. 9, figs. 16a, 16b) of the same specimen, but he thought it of uncertain affinity and possibly not an oyster. The following description of *Anomiostrea coralliophila* Habe, 1975, is based on this specimen, the holotype, which I studied at the British Museum of Natural History.

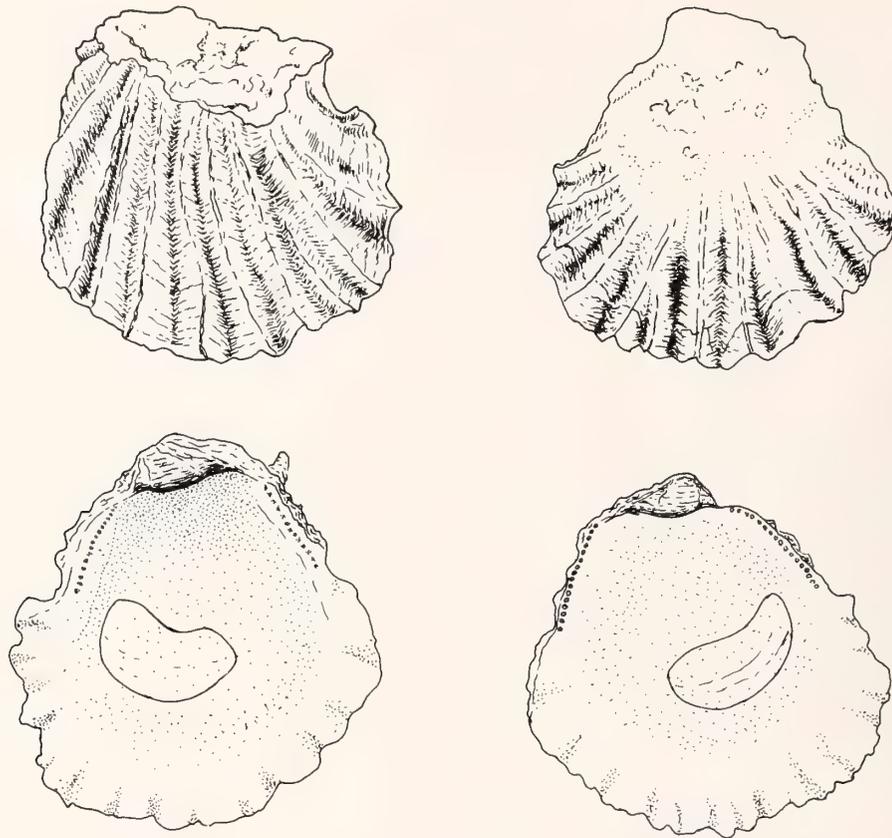


Figure 19

Myrakeena angelica. A shell 77 mm high, from Bahía de Los Angeles, Baja California Norte, Mexico. Collected and loaned by Constance E. Boone.

The shell is small, 25 mm high, 25 mm long, 12 mm wide, and both valves are thin; it is subcircular in profile; the left valve is evenly swollen, nearly hemispherical, and the right valve is flat. The specimen is very light tan outside, and pure white within. The left valve was cemented to a flat, roughened surface by the umbonal fourth of its area, the attachment area being nearly at a right angle to the median plane of the shell. Thirty-six small, well defined, subacute radial ribs begin at the attachment area, and are separated by spaces about as wide as their diameters; some branch once, and a few short, intercalated ribs occur, so that the diameters of the rib-ends, around the shell margin, are those of their origin. Numerous growth rests give the ribs a subnodular appearance.

The initial third of the right valve's exterior is roughened, subnodular, with a waxy texture, being the xenomorphic representation of the coral to which the shell was evidently attached. Beyond that area the valve has ribs of the same size as those of the left valve. The marginal commissure is straight, not zigzag (but see below). The hinge is long (10 mm), the beaks low, orthogyrus, the ligamental scar divided into three equal parts. About 10

small pustules are in a line on the hind margin of the right valve, near the hinge, extending downward as far as the muscle scar and representing ostreine chomata. None were found on the anterior margin, and no pits were found on the margins of the left valve (possibly worn off through much handling of this delicate specimen). There is a moderate subumbonal cavity in the left valve and a smaller one in the right.

The adductor muscle scars are white and large; they appear to be subcircular with a flattened dorsal margin, but the latter is indistinct. The ventral margin of the scars in both valves are prominently elevated above the level of the shell surface, and the space ventral to the scar is partially covered by chambering.

The holotype was collected in the Philippines, and the specimens described by HABE & KOSUGE (1966) were from Zamboanga, Mindoro, Philippines. They noted an "ovate" muscle scar which was "elevated," and a "crenulated" (zigzag) shell margin. The two lots at the U.S. National Museum of Natural History are from North Borneo (USNM 632887) and Jolo Id., Philippines (USNM 255013); they contain only five slightly worn left valves,

evidently collected on the beach. Some show a crenulated shell margin, and distinctly reniform muscle scar, with lower margin elevated. The inner surface of some are corrugated by the ribs, and in others the corrugations are partially smoothed by chambering. RANSON (1967:272-273) listed the type specimen of this species in the British Museum and, based on specimens which he considered to be conspecific in other museums, he cited the species from Borneo, Ceylon, the Moluccas, and Java; he apparently overlooked the specimens in the U.S. National Museum, although he studied that very large collection.

The anatomy of the flesh is unknown.

Subfamily OSTREINAE Rafinesque, 1815

Ostreidae of small to medium or rarely large size; usually subcircular or subtriangular, rarely elongate dorsoventrally or falcate. Shell plications, when present, are limited to the left valve and frequently variable in development (but see *Undulostrea*); the marginal commissure is rarely zigzag, and spines never develop on the shell exterior. The right valve tends to be flat; sculpture of the valves is varied, and distinctive for each genus. The beaks are small (exception: *Pustulostrea*) and valves are not excessively thickened. The interior of the valves is usually white (less frequently in *Ostreola* and *Pustulostrea*), often with chalky deposits or thin organic patches. The muscle scars are of the same color as the rest of the valve (exception: *Pustulostrea*) and level with the shell surface. Ostreine chomata are generally present, except in *Booneostrea*, and older specimens of *Ostrea* and *Pustulostrea*.

The flesh is grayish, occasionally with black melanin pigment, usually limited to the margins of the mantle lobes, but bright orange or yellow pigments are absent. The right promyal passage is closed; the free surface of the mantle is rarely papillate in limited areas; the mantle lobes are thickened for glycogen storage in some species. A prominent accessory heart is present behind the diaphragm (except possibly in some *Cryptostreini*); it is a simple tube in most species, but receives as tributaries the adjacent neobranch units in *Ostrea*. The outer labial palp is slightly to extensively fused medially. The anal appendage, when present, is variable in form at the species level. Those species of which the reproductive habits are known are larviparous.

The species live subtidally to several meters depth, rarely extending to the lower intertidal zone in waters of constant, near normal salinity; most are tropical, but a few extend into warm temperate waters, and the species of one genus, *Ostrea*, are limited to cool temperate seas.

The Ostreinae show a close relationship to the Lophinae in the completely closed right promyal passage and larviparous habit; these two phenomena are functionally associated in much of the literature, but without convincing justification. The bathymetric and salinity preference of the two subfamilies is about the same. The Ostreinae have regressed to various degrees in the amount of fusion

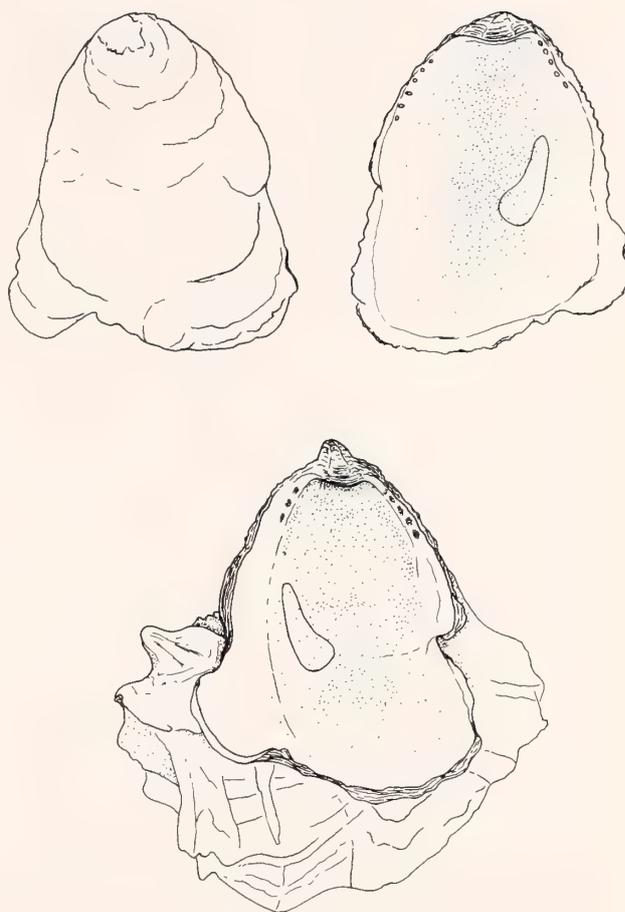


Figure 20

Ostreola stentina. Height, 35 mm. Left valve (below) is completely cemented to another shell. From Lake Tunis, Tunisia. Loaned by H. B. Stenzel.

of the outer labial palp medially, in the presence and shape of the anal appendage, and in the plication of the shell becoming much reduced; but they have retained the ability to produce chalk deposits, which the Lophinae have lost.

Three new characters have appeared in the Ostreinae which extend into the Crassostreinae: they have extended further into temperate areas than the Lophinae; the mantle has been thickened for storage of food (foreshadowed in *Myrakeena* in the Lophinae); and the right valve in several genera has developed peculiar imbricating lamellae along closely spaced growth lines (*Ostrea*, *Booneostrea*, *Teskeyostrea*, *Pustulostrea*).

Tribe *Ostreini* Rafinesque, 1815, new tribe

Nom. trans. Harry, herein, ex Ostreidae Rafinesque, 1815.

Ostreinae in which the shell is small to large, subcircular to subtriangular to slightly elongate dorsoventrally,

in which the right valve is nonplicate and flat or only slightly convex, the left valve more inflated and with plicate sculpture usually well defined. The right valve is sometimes washed or more often radially striped with blue, red, or purple.

Genus *Ostreola* Monterosato, 1884

Type, by original designation: *Ostrea stentina* Payraudeau, 1826, Cat. Moll. Corse, p. 81, pl. 3, fig. 3. See Figure 20; also fig. J112, p. N1140 in STENZEL (1971), who erroneously considered this genus to be a junior synonym of *Ostrea*.

Ostreini in which the shells are of small to medium size, and irregularly subcircular to somewhat elongate dorsoventrally. The prismatic layer of the right valve is light tan, non-lamellose, frequently with a wash or radial markings of various shades and tints of red, blue, and purple. The unattached part of the left valve is generally plicate. The interior of the shell is usually white, or green. Chomata are present throughout life, extending well down the anterior and posterior margins, and occasionally across the ventral part also.

The outer labial palp is fused medially for a fourth to a half of its length; the anus has a fingerlike appendage extending from the outer curve of its lip. The accessory heart does not receive adjacent neobranch units as tributaries.

Chiefly in shallow subtidal waters to a few meters depth, in tropical and temperate seas. Three species are known: *Ostreola stentina* (Payraudeau, 1826) in the eastern Atlantic, from the Mediterranean southward, possibly to South Africa; *Ostreola equestris* (Say, 1834) in the western Atlantic, from North Carolina to Argentina (*Ostrea spreta* Orbigny, 1841, is a junior synonym), and *Ostreola conchaphila* (Carpenter, 1857) in the eastern Pacific, from Alaska to Panama (*Ostrea lurida* Carpenter, 1864, is a junior synonym). The genus as restricted here is not known from the Indo-West Pacific faunal realm.

Genus *Ostrea* Linné, 1758

Type, by subsequent designation of Children, 1823: *Ostrea edulis* Linné, 1758, Syst. Nat., Ed. 10, p. 699. See fig. J190, p. N1137 in STENZEL (1971).

Ostreini with shells of moderate to large size, subcircular or subtriangular or rarely elongate dorsoventrally, the right valve nearly flat, with wide, overlapping, appressed, very thin and brittle lamellae, arising from rather closely spaced, evenly formed growth lines. The left valve is moderately inflated, with variable but usually distinct, small radial plicae, and a few growth rests which have only narrow, thick lamellae, or none at all. Chalk deposits in the inner shell layer are regularly present, in a distinctive pattern in older shells: a broad area behind and below the adductor muscle scar, with narrower extensions dorsad along both margins. The interior is usually white,

occasionally washed with lavender or purple; similar color on the exterior of the shell is chiefly limited to young stages of growth. The chomata are very small, inconspicuous, ostreine, limited to the margin near the hinge, and sometimes disappearing in older specimens. No commissural shelf is defined in the shell.

The outer labial palp is fused medially for only a fourth of its length; the anus has a distinct circumferential flange, typically tapering to an obtuse point along the outer margin, so that it is heart shaped. The mantle lobes are thick. The accessory heart receives several adjacent neobranch units as tributaries.

The species live in cool temperate, euryhaline waters, usually at several meters depth, but an occasional specimen may be found at low tide level. Two subgenera are recognized.

Subgenus *Ostrea* s.s.

Shells generally grow to a larger size than those of the subgenus *Eostrea*; at the time of release the veligers have inflated umbos, extending well above the hinge line. The larval swimming period is about one to two weeks. Species of this subgenus are restricted to the northern hemisphere.

Two species are recognized: *Ostrea (Ostrea) edulis* Linné, 1758, in the eastern Atlantic, from Norway to Morocco and in the Mediterranean (with many junior synonyms); and *Ostrea (Ostrea) denselamellosa* Lischke, 1869, along the main islands of Japan and the adjacent shore of Asia.

Subgenus *Eostrea* Ihering, 1907

Type, by subsequent designation of Iredale, 1939: *Ostrea puelchana* Orbigny, 1841. Junior synonyms include *Anodontostrea* Sutter, 1917 (type: *Ostrea angasi* Sowerby, 1871, by subsequent designation of Finlay, 1928) and *Tiostrea* Chanley & Dinamani, 1980 (type, by original designation: *Ostrea lutaria* Hutton, 1873). See fig. J113, 1 and 2, p. N1141 in STENZEL (1971), which represents this species.

The umbos of the veligers are very flattened, not extending above the hinge line at time of release from the adult (see RANSON, 1967; CHANLEY & DINAMANI, 1980); the larval swimming period is about four days. A single species is recognized, *Ostrea (Eostrea) puelchana* Orbigny, 1841, which is circumglobal between 35° and 50°S latitude, including both coasts of South America, also southern New Zealand, southern Australia, and South Africa. Among the many junior synonyms are *Ostrea chilensis* Philippi, 1845, *Ostrea angasi* Sowerby, 1871, *Ostrea algoensis* Sowerby, 1871, and *Ostrea lutaria* Hutton, 1873.

Genus *Nanostrea* Harry, gen. nov.

Type: *Ostrea deformis* Lamarck, 1819, Anim. s. Vert., Vol. 6, pt. 1, p. 209. Not figured. Not *Ostrea deformis* Lamarck, 1806, Ann. Mus. Nat. d'Hist. Natur., Vol. 8, p. 164, Velin No. 57, fig. 4 (Palmer reprint, 1978)

which is fossil, near Paris. *Ostrea deformis* Lamarck, 1819, is here renamed *Nanostrea exigua*. See Figure 21.

Ostreini in which the shells are very small (to 12–15 mm high). The outer surface of the right valve is not lamellose, and the original light tan surface is frequently eroded to reveal shells entirely white, inside and out, or rarely radially streaked externally with lavender; they are usually cemented by most of the left valve, which has the upturned part plicate. The chomata are prominent, persistent, extending often completely around the margin. The outer labial palp is fused medially for three-fourths of its length; no anal appendage was present in the single preserved specimen of which the flesh was examined (USNM 769911, from Lizard Island, Queensland, Australia, at 10–11 m depth), but a pre-anal constriction gave the anus a knobbed appearance. The accessory heart is a simple tube, without tributaries.

Nanostrea exigua generally attaches to empty shells of other mollusks, in shallow lagoonal waters of coral reefs or on mudflats, in the tropical Indo-West Pacific faunal realm from the Red Sea to Hawaii. The original description of *Ostrea deformis* Lamarck, 1819, said the species is 8–11 mm long; the type locality was cited as “seas of Europe, etc, on other abandoned shells, most often in the interior of pinnae.” RANSON (1967) examined the types in the Paris Museum and recognized this species as one from the Indo-West Pacific faunal realm.

Genus *Planostrea* Harry, gen. nov.

Type: *Ostrea pestigris* Hanley, 1846, Proc. Zool. Soc. London (for 1845), pp. 106–107. Not figured. See Figure 22.

Ostreini with shells of moderate size (to 75 mm high), very compressed, generally in one plane. The valves are not lamellose, the outer shell layer being continuous, with few growth rests, and little shell erosion. Small, semicylindrical plicae, widely spaced, are variously developed on the left valve only, and the surface is flat between these ribs. The chomata are exceptionally well developed, small, uniform, closely spaced near the hinge, along front and hind margins, which diverge in straight lines from the small umbos, forming an acute angle. In the left valve there is a wide marginal commissural shelf which is flat, well defined along its inner edge, and regularly thickened with chalk deposit. The outer surface of both valves is usually light to dark lavender, and often with numerous narrow, closely spaced, darker radial stripes of the same color.

A specimen with flesh from Hong Kong, dissected at the British Museum, had been dredged from 10 m depth. Additional specimens dissected were collected at low tide by Constance E. Boone, at Rowe's Bay, Townsville, Queensland, Australia. The mantle lobes are thin, transparent. Both left and right promyal passages are closed,

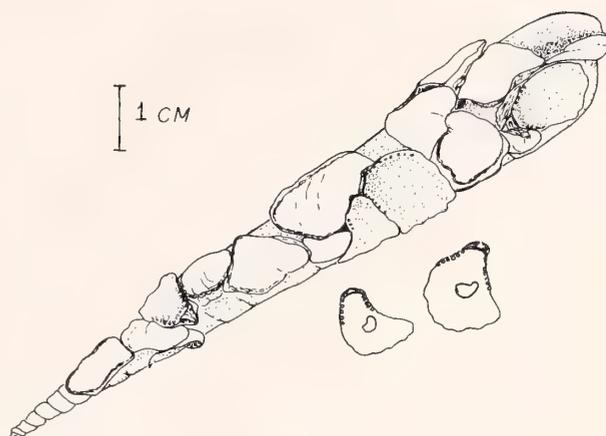


Figure 21

Nanostrea exigua. Several specimens on large, worn shell of *Terebra* sp. Tawi Tawi Ids., Philippine Ids. USNM 242291.

but there is an incipient pocket on each side, narrow and deep, lateral to the pericardium, opening posteriad; the outer labial palp is fused medially for a fourth of its length. The anus seems to be surrounded by a narrow, circular flange of uniform width. The accessory heart is a simple tube, which does not receive adjacent neobranch units as tributaries.

The single species, *Planostrea pestigris* (Hanley, 1846), is known only from a limited area in the Indo-West Pacific, being abundantly represented at the U.S. National Museum from the Philippines (type locality), but extending to Formosa, Thailand and North Borneo. An occasional specimen may occur at low tide, but most seem to have been dredged from a few to 100 m depth. Most are attached to shells of other mollusks, often to *Placuna placenta* (Linné, 1758).

Junior synonyms include *Ostrea rivularis* Gould, 1861, *Ostrea paulucciae* Crosse, 1869, and *Ostrea palmipes* Sow-erby, 1871.

Tribe **Cryptostreini** Harry, new tribe

Ostreinae of small size, with delicate shells lacking radial plications on both valves. The coloring is uniformly light tan, with no purple washes or stripes. The chomata are reduced ostreine, or absent (*Booneostrea*). Irregular chalk deposits are infrequently present. The species live secluded in protected situations, usually in reduced light, in tropical and subtropical waters of normal oceanic salinity, subtidally to a few meters depth. Although neobranch units are present in the excurrent mantle chamber, an accessory heart was detected, with some doubt, only in *Booneostrea*.

The species of the three monotypic genera each have distinctive form and sculpture, and they may not be a monophyletic group; the characters of the shell and flesh

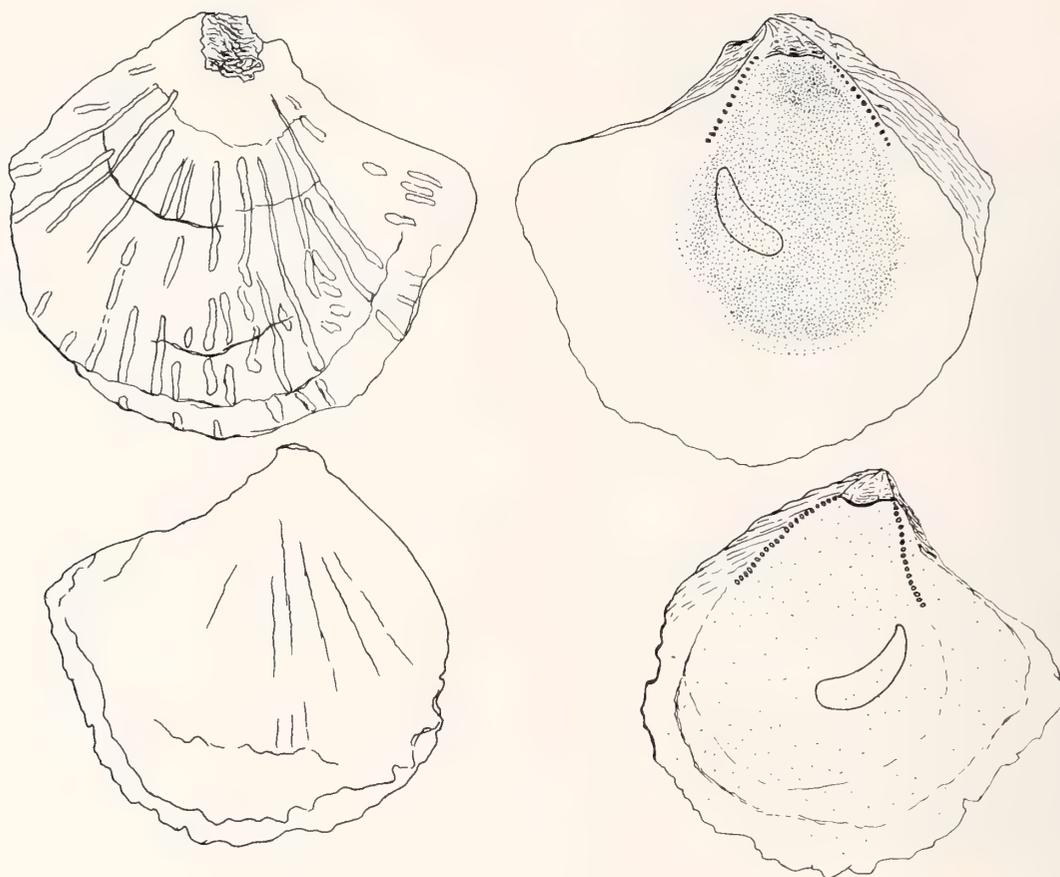


Figure 22

Planostrea pestigris. Height, 75 mm. Upper left: exterior of left valve, to show the small radial ridges. Lower left: exterior of right valve. Interiors of same valves are on right. Specimen collected by trawl, at 10 m depth, off Tambizan, North Borneo. USNM 666809.

suggest diminution or loss, which may result from their reclusive life habits. Larviparous specimens were found in all three species.

Genus *Cryptostrea* Harry, gen. nov.

Type: *Ostrea permollis* Sowerby, 1871, in Reeve's Conch. Icon., *Ostraea*, pl. 10, fig. 18a (18b is here excluded). See Figure 23.

Cryptostreini which are imbedded in sponge in post-larval life, rather than being cemented to firm substrate. The shells are small (30 mm high), very thin, only slightly inflated, inequivalve, but either valve may be the more inflated. The profile is subtriangular, subcircular or slightly elongate dorsoventrally; the beaks are of equal size, or the right one is smaller, and they are usually strongly twisted posteriad, rarely orthogyrous; the ligament tends to be drawn out along the dorsal third or more of the posterior margin; the anterior shell margin forms a large, acute angle with the axis of the ligament, and the posterior

margin forms a large obtuse angle, sometimes nearly a straight line.

The outer shell layer is continuous over the surface, not interrupted by growth rests, and neither lamellose nor plicate, but often irregularly roughened. The color is uniformly light tan to darker brown. Small ostreine chomata are present, extending farther down along the anterior than the posterior margin. The interior of the shell is white, often slightly thickened with chalk deposit; it is not nacreous.

The outer labial palp is fused medially for the basal fourth of its length; the anus is surrounded by a distinct circular flange, extending as a flattened, tapering finger on the outer part of the rim.

Cryptostrea permollis (Sowerby, 1871) lives imbedded in the "bread sponge," a species of *Stellata* identical with or similar to *S. grubii* (see FORBES, 1964:454); the bathymetric range is from the very low intertidal zone to 154 m depth, in water of near oceanic salinity. It occurs in the northeastern Gulf of Mexico and off the coast of North

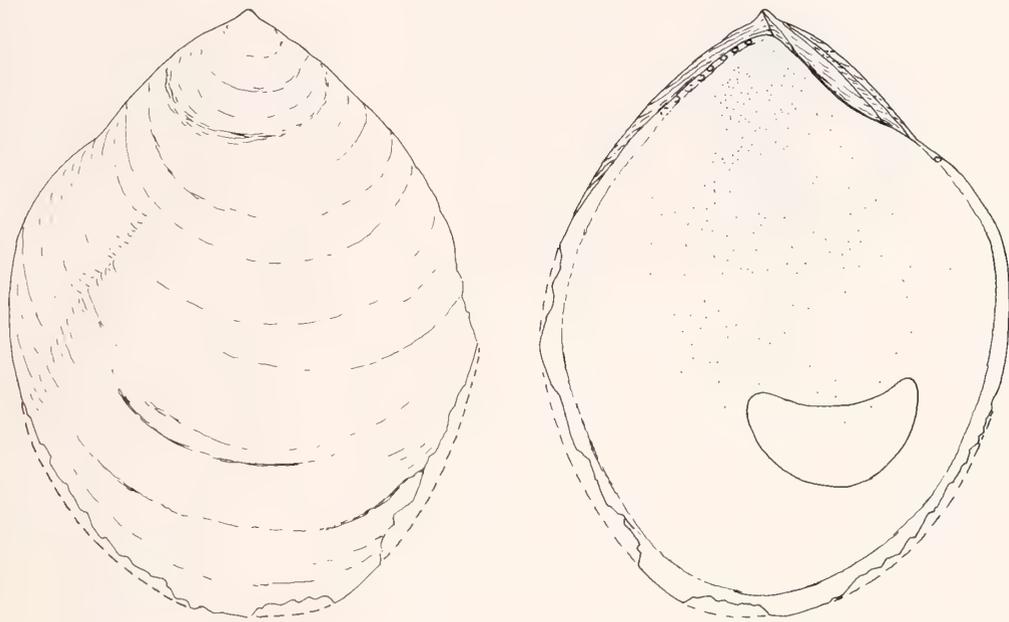


Figure 23

Cryptostrea permollis. Right valve exterior and interior, of a shell 30 mm high, collected by Milton L. Forbes near Alligator Harbor, Florida, and loaned by H. B. Stenzel.

Carolina; literature records from the West Indies need verification.

STENZEL (1971) was unwilling to accept this species as a member of the Ostreacea, because of its peculiar habitat (personal communication), although it has been the most thoroughly studied of the non-commercial oysters, thanks to the papers by FORBES (1964, 1966). I have studied the anatomy of the flesh and shell from specimens collected by Forbes and given to Stenzel, as well as much other material collected by John W. Tunnell, Jr., from Florida, and several other sources.

Cryptostrea permollis (Sowerby, 1871) was described from unknown locality; the specimens on which Sowerby's species was based were not found in the British Museum in October 1983, nor did RANSON (1967) seem to have found them.

Genus *Teskeyostrea* Harry, gen. nov.

Type: *Ostrea weberi* Olsson, 1951, *Nautilus* 65(1), pp. 6-7, pl. 1, figs. 1-4. See Figure 24.

Cryptostreini of small size (to 37 mm high), thin, sub-circular, of uniform dark golden brown color. The left valve is extensively cemented to a rock, usually on the under side. The right valve is slightly convex, with appressed, lamellose extensions of the prismatic layer at numerous growth rests; the lamellae are thin, brittle, scarcely overlapping, and in larger specimens they show minute, radial ridges, evenly rounded, closely spaced, low, with

linear grooves between; the interior is porcellaneous, often with one or two chalky pads. The chomata are ostreine, small, a few occurring on both anterior and posterior margins near the hinge.

The outer labial palp is fused for the basal fourth of its length; the anus is without any flange or appendage. The species is larviparous, and one specimen was gravid when collected in mid-December 1980.

The minute riblets of the lamellae of the right valve are similar to those of *Striostrea*, as noted by OLSSON (1951), who stated the type locality is Key West, Florida. The genus is named in honor of Margaret Teskey, for many years the Secretary of the American Malacological Union. She sent me live specimens with bits of the rock to which they were attached, from Big Pine Key, Florida, and empty valves collected at about 33 m depth off the Florida Keys by Pete Rosin. The U.S. National Museum has a single specimen (USNM 682581) taken by a diver in 2-4 m depth, off Cocoa Point, Barbuda, West Indies, and Constance E. Boone collected a specimen in the lagoon behind the island of Cancun, Yucatan, Mexico.

Genus *Booneostrea* Harry, gen. nov.

Type: *Ostrea cucullina* Deshayes, 1836, *Cat. Moll. de l'Île de la Reunion*, pp. 36-37, pl. 32, figs. 7-8. See Figure 25.

Cryptostreini having small shells (to 28 mm high), which are thin, fragile, variously shaped but usually elon-



Figure 24

Teskeyostrea weberi. Exterior and interior of a right valve, 25 mm high; shell was attached to the underside of limestone rock, at low tide level, Big Pine Key, Florida. Collected and donated by Margaret Teskey.

gate oval dorsoventrally; the beaks are not prominent; the right valve is flat to slightly convex, and the left valve is very inflated. The right valve exterior is covered by a thin, light tan or white prismatic layer, which produces numerous, prominent, very fragile, imbricated lamellae beyond the first few millimeters of growth. These lamellae become more elevated ventrally, as the shell grows, and tend to be crossed by a few minute radial ridges, the radial sculpture becoming linear clefts in the edge of the lamellae near the ventral margin, giving the lamellae a scalloped appearance.

The left valve exterior is light tan or whitish, attached by cementation for about a third of its area in larger shells; there are no plications on the left valve, but prominent, broad lamellae may develop at growth rests, which are rather widely spaced; the lamellae are fragile, but thicker than those of the right valve, and they tend to project more from the shell surface; there is a slight tendency to develop the minute radial striae.

The internal surface is porcellaneous, whitish, and flushed with light tan. Chomata are completely absent, but the anterior and posterior ends of the bourrelet part of the ligament are extended as thin, tapering, organic lamellae, very delicate, for a short distance down both front and hind margins of the shell, in both valves.

The outer labial palp is fused medially for about a fourth of its length. The anus lacks a flange or appendage. The accessory heart was detected only in one of the several specimens examined; it is a simple tube without tributaries. Anatomical studies were made on four specimens found under an intertidal rock at Weld Island, about 30 km off Onslow, Western Australia, and three more from under a rock at Coconut Wells, 25 km north of Broome, Western

Australia; one specimen of the latter lot, collected 10 September 1983, was larviparous. All of the above material was collected by Constance E. Boone, Secretary of the American Malacological Union, in whose honor the genus is named.

Booneostrea cucullina (Deshayes, 1836) is an oyster of the Indo-West Pacific faunal realm, known to extend from Reunion (type locality) to Australia and Japan. The U.S. National Museum has a few lots, from indefinite localities within this general area. It seems to live at low intertidal levels and to a few meters depth, in tropical waters of normal salinity. I found two left valves attached in a protected position to a mass of staghorn coral on the beach at Larentuka, Indonesia, evidently discarded by a fisherman. Junior synonyms include *Ostrea sedea* Iredale, 1939, from Australia, and *Ostrea sedea setoensis* Habe, 1957, from Japan. By the latter name the species was well illustrated by TORIGOE (1983).

Tribe *Undulostreini* Harry, new tribe

Ostreinae in which the shells are of moderate size (but to 90 mm high), thin, compressed, cemented by only a small area of the left valve, subcircular until about 20 mm high, then with disproportionate growth along the posteroventral margin of the shell, so that it becomes falcate, or L-shaped; several (two to four) large undulations develop along the anteroventral margin, with evenly rounded, broad troughs and crests, extending only a short way inward, and thus distinctly different from the usual plications of oysters. A single genus and species are recognized.

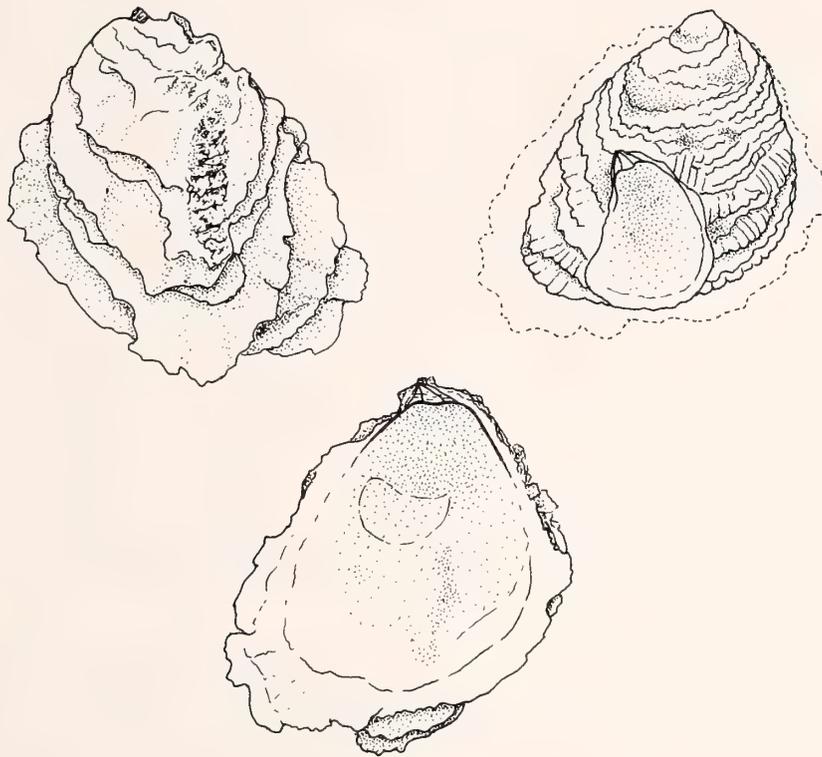


Figure 25

Booneostrea cucullina. Exterior of left and right valves, and (below) interior of left valve. Height, 25 mm. Low intertidal zone, Weld Island, Western Australia. Collected and loaned by Constance E. Boone.

Genus *Undulostrea* Harry, gen. nov.

Type: *Ostrea megodon* Hanley, 1846, Proc. Zool. Soc. London (for 1845), p. 106. Not figured. See Figure 26.

The more conspicuous features of the unique species have been noted above; the outer shell layer of both valves is continuous, not lamellose at growth rests. The right valve is uniformly colored, purplish to light reddish brown, the left valve similarly colored or grayish, usually lighter than the right. The interior of both valves is grayish white. The chomata are ostreine, prominent, in a single line extending well down front and hind margins, but not to the ventral part. The beaks are small.

The outer labial palp is fused medially for about half its length. The accessory heart does not receive tributaries. There is no flange or appendage along the anal rim. Reproductive habits are unknown.

Undulostrea megodon (Hanley, 1846) occurs infrequently from the Gulf of California and the lower west coast of Baja California to Peru (type locality), from low intertidal level to several meters depth, in water of normal salinity. It is generally attached to a shell fragment or even to the shell of a live mollusk, but possibly not to other oysters.

Tribe *Pustulostreini* Harry, new tribe

Ostreinae in which the beak of the left valve is enormously developed; both valves lack radial plicae, the left valve is not lamellose and usually it is extensively covered with pustules; the right valve exterior is densely covered with appressed lamellae. The single species closely resembles *Striostrea* in some shell characters, but it is distinctly ostreine in having a closed right promyal passage.

Genus *Pustulostrea* Harry, gen. nov.

Type: *Ostrea tuberculata* Lamarck, 1804, Ann. Mus. Nat. d'Hist. Natur. (Paris) 4:358, pl. 67, fig. 1. See Figures 27 and 28.

The shells are of medium to large size (to 90 mm high), compressed, elongate dorsoventrally, generally arched (concave to left) along the axis of height; the beak of the left valve is disproportionately large, often being half the height of the shell. The attachment area is small, and apparently absent on some shells. The left valve exterior is without plications, but usually has low, rounded pustules, closely but irregularly spaced, variably produced on the surface. The right valve is flat, subcircular, with its

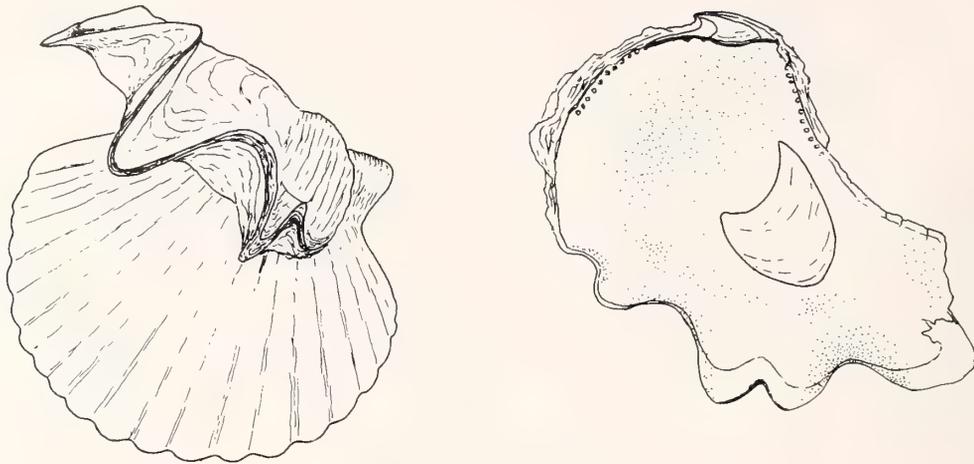


Figure 26

Undulostrea megodon. Specimen 35 mm high, attached to *Argopecten circularis* (Sowerby, 1835), from low intertidal zone in Laguna San Ignacio, Baja California, Mexico. Collected and loaned by Thomas E. Pulley.

beak only slightly produced, and its outer shell layer covered with closely spaced, smooth, fragile, appressed lamellae at the growth rests. The outer surface of the left valve is pale gray, that of the right valve light brown.

The hinge is exceptionally long, and the left umbral cavity is often deep; the muscle scar of the left valve is usually dark brown (the color not limited to the scar, but

extending beyond), that of the right valve is white. The interiors of both valves tend to be subnacreous and washed with brown or blue. The chomata are ostreine, large, elongate normal to the valve margin, widely spaced, extending downward two-thirds of the height on both margins, and occasionally absent in older shells.

The outer labial palp is extensively fused medially for

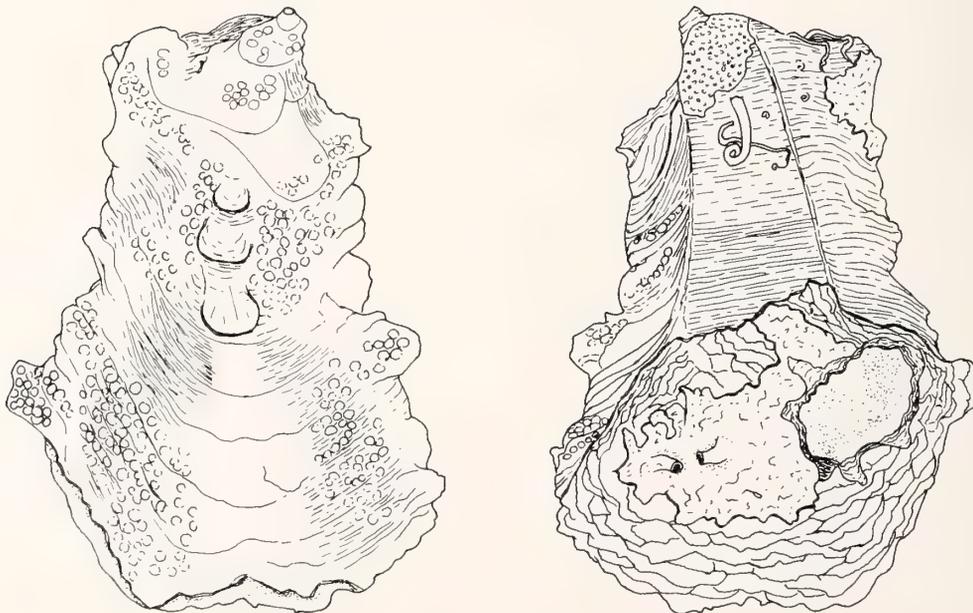


Figure 27

Pustulostrea tuberculata. Exterior of valves of a shell 70 mm high. New Hebrides Ids. USNM 787959. See Figure 28.

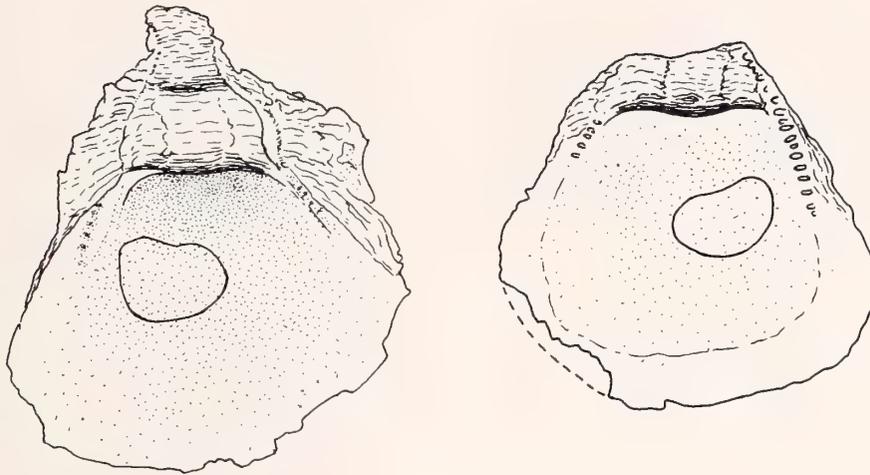


Figure 28

Pustulostrea tuberculata. Height, 90 mm. Interior of the valves of a second specimen from lot USNM 787959, from the New Hebrides Ids. See Figure 27.

two-thirds of its length. The anus is surrounded by a distinct flange, drawn out to a tapering, fingerlike appendage on the outer rim. The mantle lobes are thick. Flesh of several specimens of the U.S. National Museum were examined; these were collected by Thomas Waller in the New Hebrides Islands, after RANSON (1967) had completed his study of oysters at that museum.

This species is evidently rare and local; according to the records published by RANSON (1967), it occurs from the islands off the west coast of the Malay Peninsula to Singapore, throughout Indonesia and eastward to the New Hebrides, evidently in shallow water of high salinity, and probably usually associated with coral reefs. Reproductive habits are unknown. Junior synonyms include *Ostrea rufa* Lamarck, 1819, and *Ostrea australis* Lamarck, 1819.

Subfamily CRASSOSTREINAE Torigoe, 1981

Ostreidae with shells of medium to large size, usually elongate dorsoventrally, occasionally subcircular. The left valve is usually deeply concave, and the right one is usually nearly flat. Shell plications are usually limited to the left valve, often indifferently developed or absent. The early part of the right valve exterior has continuous growth of the outer shell layer, and later it often forms fragile, appressed, overlapping lamellae, but the outer surface is frequently eroded during life, obliterating the sculpture. The chomata are ostreine, or absent. The muscle scars tend to be more darkly colored than the surrounding shell, in one or both valves.

The mantle lobes are thickened and used for storage of glycogen. The right promyal passage is open over the pericardium and lower half of the visceral mass, and thus is about half as extensive as that of the Pycnodonteinae. The outer labial palp is only slightly fused medially, one-fourth

its length or less, and in some species it is unfused. The anus is usually without an appendage, but in some species it has a circular flange. The accessory heart is well developed, various in form, but it does not receive adjacent neobranch units as tributaries. The species that have been studied do not brood their larvae.

Species are chiefly tropical and subtropical, but some species of *Crassostrea* extend also into cool temperate water. These oysters tend to live intertidally or at shallow subtidal depths.

The Crassostreinae have retained the ability to secrete non-vesicular chalk deposits. They have continued the reduction of the fusion of the labial palp and formation of an anal appendage. Whether the partly open (or partly closed) right promyal passage is a regressive or progressive character is a moot question. The species of this subfamily have moved into shallower depths, thus experiencing greater fluctuation of environmental factors, than all other oysters. They tend to be large, with thick, food storing mantle lobes in all species, and they are generally abundant where they occur, being, by these characters, preeminent as the oysters of commerce.

Tribe *Striostreini* Harry, new tribe

Crassostreinae in which ostreine chomata are usually prominent (lost in some larger shells of *Striostrea*, and lacking in some ecomorphs of *Saccostrea*), often extending to the ventral margin. Thick, broad conchiolin deposits are frequent, chiefly in the right valve. The left valve has a propensity, variable within a species, to become enormously thickened by chambering, so the thickness may equal or exceed the height of the valve. Chalk deposits are infrequent. The hinge line is usually long in proportion

to other shell dimensions, and the left beak is often produced, with a large subumbonal cavity.

Limited to the tropics and subtropics, these oysters prefer normal salinity; although occasionally associated with red mangroves, most species live exposed to strong surf, attached to rock, but they avoid coral and limestone. The tribe is present in the eastern Atlantic, Indo-West Pacific and eastern Pacific faunal realms, but is apparently absent from the shores of the western Atlantic.

Genus *Saccostrea* Dolfuss & Dautzenberg, 1920

Type, by monotypy: *Ostrea saccellus* Dujardin, 1835, Mem. Geol. Soc. France 2(2):272 (Miocene fossil of France), which is a junior synonym (*vide* STENZEL, 1971) of *Ostrea cucullata* Born, 1778. See fig. J104, p. N1132 and fig. J105, p. N1133 in STENZEL (1971).

Striostreini in which the shell is of medium size, the attached part of the left valve of larger shells forming about half the total area of the valve or less, and the upturned part of the left valve with prominent, regular and continuous plications, often acutely crested, with broad, flat or concave troughs between. The right valve is flat, but projecting along the margin are short lobes, coordinate with the plications of the left valve; a few flattened plications, closely spaced, may develop on the right valve as the marginal lobes are extended.

Juvenile shells (to 30 mm high) may develop on the right or on both valves a few to many short, recurved, semicylindrical spines, usually colored dark purple; these may be abundant on one specimen and absent on an adjacent one of the same size; they are generally worn off in larger shells. In protected situations the right valve of larger shells may be densely covered with imbricated lamellae, brown or purple, which have no radial striations (contrast *Striostrea s.s.*), but most right valves, exposed to the action of the waves, are eroded in a characteristic fashion. The abrasion forms broad, irregularly rounded pits, showing sharp or beveled contours, with the bottom of the pits often floored by a sheet of dark brown, thick conchiolin (which becomes very brittle and fractures in dry shells).

The hinge line is long, the left beak is often very large, and the left subumbonal cavity may often be as large as the rest of the shell's interior; ostreine chomata are present, small but prominent, often widely spaced and extending to and across the ventral margin. Inside, the valves are essentially white, but a wide blue or purple margin may be present; the interior is porcellaneous; large brown patches of thick conchiolin are frequent, chiefly in the right valve. The attachments of the secondary mantle margin retractor muscles often leave a line of small, circular scars parallel to the front and hind margins of the shell. The valves are not brittle and flaky as in *Striostrea s.s.* One or both adductor muscle scars may be darker than the general shell interior.

The outer labial palp is fused medially about a fourth

of its length; there is no anal flange or appendage. In preserved specimens the accessory heart is an enormous, inflated, thin walled, flabby sac. The mantle margin is generally lightly washed with black pigment and there are a few granules of bright yellow pigment on the inner and middle mantle margin lamellae and their papillae; this yellow pigment is characteristic of the genus and often persists in specimens preserved in alcohol.

Limited to the tropics or slightly beyond, the species are sometimes attached to prop roots of red mangroves, but they live chiefly attached to non-calcareous rock in the intertidal zone, where they are subject to strong wave action. They probably do not live naturally subtidally.

Two species are known. *Saccostrea cucullata* (Born, 1778) occurs along the tropical coast of West Africa and offshore islands, around the Cape of Good Hope and into the Indo-West Pacific to southern Japan, southeast Australia, northern New Zealand, and possibly somewhat eastward, but it seems not to reach the extreme eastern part of the Indo-West Pacific faunal realm (Hawaii to Society Islands). The list of junior synonyms is long. A second species, *Saccostrea palmula* (Carpenter, 1857), occurs in the eastern Pacific, from San Ignacio Lagoon, west coast of Baja California, to Panama and the Galapagos Islands.

Genus *Striostrea* Vyalov, 1936

Type, by original designation: *Ostrea procellosa* "Valenciennes" Lamy, 1929, which is a junior synonym of *Ostrea margaritacea* Lamarck, 1819. See Figure 29. Also see fig. J107, p. N1135, and fig. J108, p. N1136, in STENZEL (1971).

Two subgenera are recognized.

Subgenus *Striostrea s.s.*

Striostreini in which the shell grows to large size (to 200 mm or more high), usually elongate dorsoventrally but sometimes subcircular, generally attached by nearly the entire area of the left valve, which, especially in elongate shells, may become enormously thickened, forming a broad pedicel, with no upturned (or idiomorphic) part, but merely a surface formed by earlier shell margins. Right valve not plicate, but covered with imbricated, brown, brittle lamellae, which usually have closely spaced, very small radial riblets or striae continuous across them. In larger shells, the lamellae are mostly worn off.

The hinge line is usually long, and the left beak enlarged; the valves are very brittle, breaking with a flaky, jagged margin and often separating smoothly between successive deposits of the foliar shell layer. The interior is distinctly subnacreous, iridescent, occasionally white but more often mottled and washed with dark brown, blue, or purple. The chomata are large, often elongate, widely spaced, usually extending far down both front and hind margins, but sometimes absent from larger shells. One or both muscle scars are often distinctively colored.

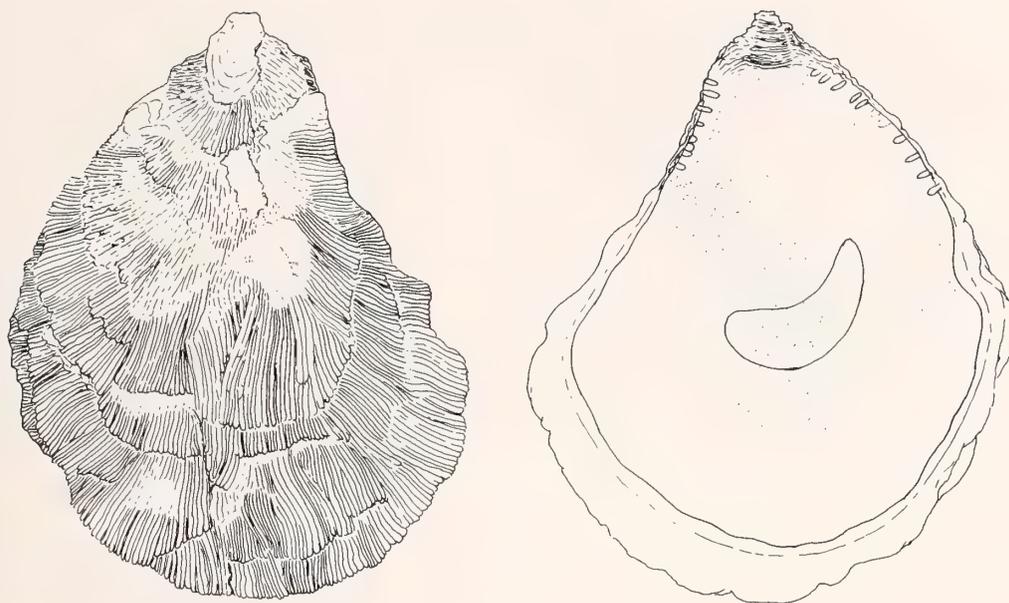


Figure 29

Striostrea prismatica. Exterior and interior of right valve, of a juvenile shell only 45 mm high. Collected at Puerto Vallarta, Jalisco, Mexico, by the author.

The outer labial palp is fused medially for a fourth of its length. The anus is simple, without flange or appendage. The accessory heart is large, but compact and cylindrical. There is no bright yellow pigment in the mantle margin; the mantle lobes are thick and muscular toward their margins. In the only species of which the flesh has been available for study, *Striostrea prismatica* from western Mexico, the gill suspensory septa are discontinuous.

Three species are known in the typical subgenus, each from a limited area: *Striostrea* (*Striostrea*) *margaritacea* (Lamarck, 1819) is found along the coast of tropical West Africa to South Africa (records of it from Madagascar may be based on the next subgenus?); *S.* (*Striostrea*) *circumpicta* (Pilsbry, 1904) occurs in southern Japan; and *S.* (*Striostrea*) *prismatica* (Gray, 1825) lives in the tropical eastern Pacific (Figure 29). The species live chiefly in the shallow subtidal zone, attached to non-calcareous rock in strong surf of normal salinity.

Subgenus *Striostrea* (*Parastriostrea*)

Harry, subgen. nov.

Type: *Ostrea mytiloides* Lamarck, 1819, Anim. s. Vert., Vol. 6, pt. 1, pp. 207-208. Not figured. See Figure 30.

Striostrea of large size (to 120 mm high), generally adhering to red mangrove roots, the left valve not excessively thickened, but attached by half the valve or less, the free part of the valve not plicate but occasionally vaguely undulate. Right valve covered with imbricated, dark purple lamellae which have no radial striations.

The hinge is long, but the left beak is rarely enlarged; the interior is porcellaneous. There are large ostreine chomata similar to those of *Striostrea s.s.*, which in larger shells usually extend completely around the ventral margin. The shell interior is white or washed or mottled with brown or various shades of purple, and the margin is usually dark purple.

The flesh is similar to that of the typical subgenus, but whether the suspensory septa of the gills are continuous has not been determined. This monotypic genus extends from Samoa to the Philippines, Indonesia (type locality), northwestern Australia, India, and Zanzibar. The species was figured by SOWERBY (1871:pl. 2, fig. 3).

Tribe *Crassostreini* Torigoe, new tribe

Nom. trans. Harry, herein, ex *Crassostreinae* Torigoe, 1981.

Crassostreinae in which the chomata are absent throughout life; the large shells tend to be elongate dorsoventrally, but are often subcircular. The adductor muscle scars of both valves tend to be colored dark purple, brown or blue, but in some populations, particularly in the tropics, one or both scars may be lightly colored or white. The interior of the valves is white, often washed with purple marginally, especially in tropical populations. Chalk deposits are frequent and extensive; conchiolin deposits occur, but chiefly as thin, small patches formed as preliminary reactions to shell invaders. Chambering is occasional, but the left valve never becomes as thick as it

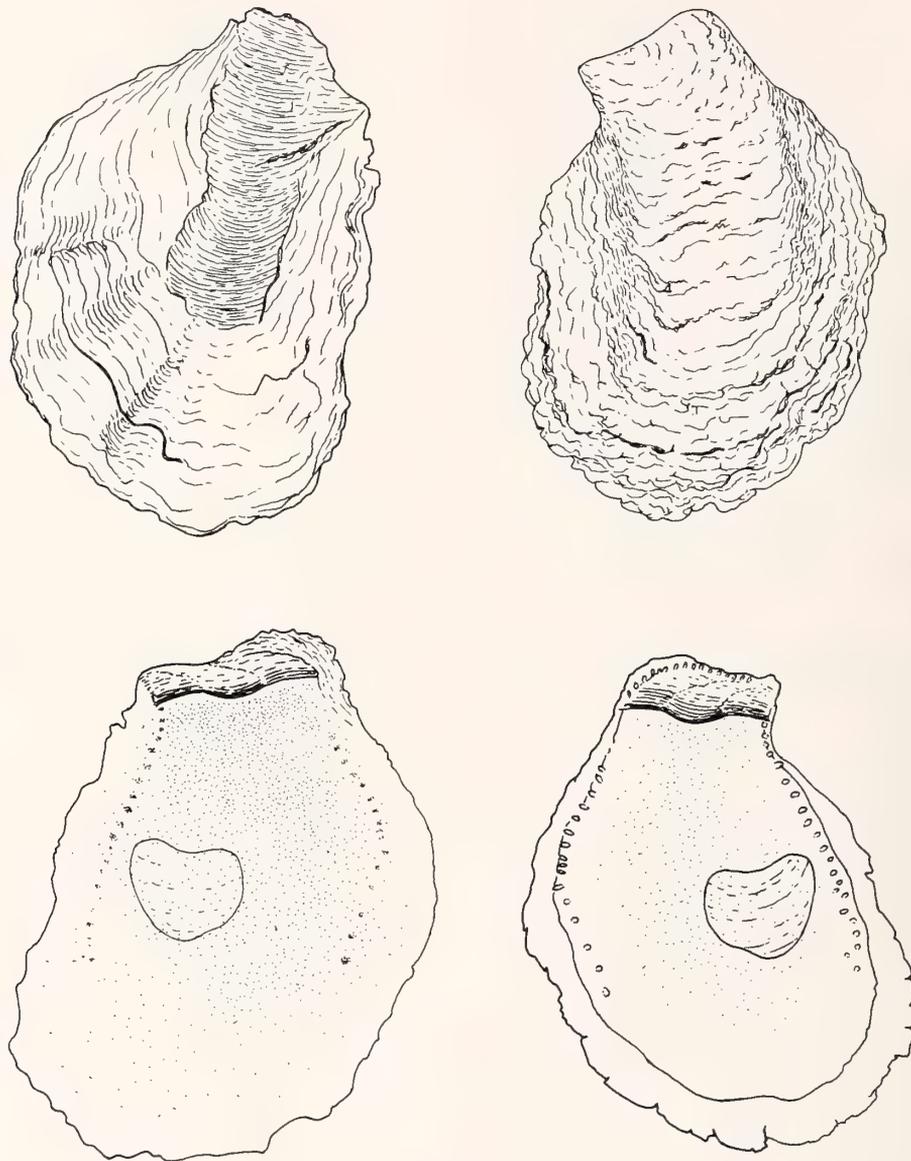


Figure 30

Striostrea (Parastriostrea) mytiloides. Height, 120 mm. Left valve (upper and lower left) cemented to prop root of a red mangrove. Right valve exterior (upper right) covered by closely appressed, deep bluish purple lamellae. From Efate Id., New Hebrides Ids., collected by Thomas Waller.

does in the *Striostreini*. The hinge line is usually short, and the left beak is rarely extended.

The species are chiefly limited to estuarine conditions, preferring brackish water of about 15–30 ppt salinity; in the tropics they are often associated with mangroves, sometimes where hypersaline conditions occur. Where they occur naturally, they seem limited to the shores of continents and larger islands nearby, and although present in all four major faunal realms, they seem nearly limited to the northern hemisphere; natural populations may extend only slightly below the equator (Brazil, possibly Indonesia also?).

Genus *Crassostrea* Sacco, 1897

Type, by original designation: *Ostrea virginica* Gmelin, 1791, *Syst. Nat.*, Ed. 13, p. 3336. See the extensive illustrations in GALTSOFF (1964) and fig. J101 (1a–h only), p. N1129, in STENZEL (1971).

The characters of the shell noted for the tribe are those of the single genus. The outer labial palp is not fused medially in *Crassostrea virginica*, but is slightly fused in *C. gigas*. The rectum ends at the posteroventral curve of the adductor muscle, being thus very short, and the anus is usually without any appendage (but a circular flange

Table 1

Comparison of the number of species, distribution and environment of the genera and subgenera of living oysters.

Family	Subfamily	Tribe	Genus and subgenus	No. of species	Geographic location ¹				Climatic zones ²			Depth ³		Special habitat ⁴		Salinity ⁵		
					East Atlantic	West Atlantic	East Pacific	Indo-West Pacific	Tropical	Warm temperate	Cool temperate	Most below 50 m	Subtidal to a few m	Low intertidal	Mid intertidal	Mangrove associate	Coral reef associate	Exposed to strong surf
Gryphaeidae	Pycnodontinae	Hytissini	<i>Hytissa</i>	1		X	X		X			X		X	?	X		
			<i>Parahytissa</i> s.s.	2	X	X			X	X		X			?	X		
<i>P. (Pliohytissa)</i>	1				X			X	?		?	X		X				
<i>P. (Numismoida)</i>	1					X		X			X		X		X			
		Neopycnodontini	<i>Neopycnodonte</i>	1	X	X	X		X	X	?	X				X		
Ostreidae	Lophinae	Lophini	<i>Lopha</i>	1			X		X			X		X		X		
			<i>Alectryonella</i>	1			X		X			X		X		X		
			<i>Dendostrea</i>	3	X	X	X	X		X	X		X		X		X	
		Myrakeenini	<i>Myrakeena</i>	1			X			X			X	X			X	
			<i>Anomiostrea</i>	1				X		X		X		X		X		
	Ostreinae	Ostreini	<i>Ostreola</i>	3	X	X	X		X	X	X		X	X			X	
			<i>Ostrea</i> s.s.	2	X			X			X		X				X	
			<i>O. (Eostrea)</i>	1	X	X	X	X			X		X				X	
			<i>Nanostrea</i>	1				X		X			X		X		X	
			<i>Planostrea</i>	1				X		X			X		?		X	
		Cryptostreini	<i>Cryptostrea</i>	1		X			X				X				X	
			<i>Teskeyostrea</i>	1		X			X			X	?			X		
		<i>Booneostrea</i>	1				X		X		X	X			X			
		Undulostreini	<i>Undulostrea</i>	1			X		X	X		X	?			X		
		Pustulostreini	<i>Pustulostrea</i>	1				X		X		X	?	X		X		
Crassostreinae	Striostreini	<i>Saccostrea</i>	2	X	X	X		X	X			X		X	X	X	?	
		<i>Striostrea</i> s.s.	3	X	X	X		X	?		X	X		?	X	X	?	
		<i>S. (Parastriostrea)</i>	1				X		X	?		X		X	?	X	?	
		Crassostreini	<i>Crassostrea</i>	4	X	X	X	X	X	X		X	X	?	X		X	

¹ Geographic location: includes all species of each genus and subgenus. Some species occur in two areas (*Hytissa hyotis*, *P. (Parahytissa) mcgintyi*, *Neopycnodonte cochlear*, *Dendostrea frons*, *Saccostrea cucullata*), but other species are limited to one of the four areas.

² Climatic zones: includes all species of a genus or subgenus.

³ Depth, very generalized; the depth indicated is considered the "optimum," or where the species is most abundant, based on data presently available.

⁴ Special habitat: the special habitat attributed to the taxa shown does not mean that the species are limited to that situation; no special habitat is known for species of some taxa.

⁵ Salinity: very generalized.

is present in *C. gigas*); the accessory heart is a thick, muscular, cylindrical tube without tributaries.

Four species are recognized, each with a long list of junior synonyms. *Crassostrea angulata* (Lamarck, 1819) occurs in the eastern Atlantic, from the equator northward

to the Mediterranean and Atlantic coast of the Iberian Peninsula; it has been introduced into southwestern France. *Crassostrea virginica* (Gmelin, 1791) is found in the western Atlantic, from Brazil northward through the Caribbean and Gulf of Mexico, including the Antilles, to the

Table 3

Comparison of characters of the flesh and reproductive habits of genera and subgenera of living oysters.

Family	Subfamily	Tribe	Genus and subgenus	Mantle lobes thin ¹	Mantle lobes thick ¹	L promyal passage open ²	R promyal passage wide ²	R promyal passage narrow ²	promyal passages closed ²	Ht.-kid.-rec. complex gryphaeid ³	Ht.-kid.-rec. complex ostreid ³	Labial palp fusion long ⁴	Labial palp fusion short ⁴	No fusion of palp ⁴	Anal appen. a bulbous collar ⁵	Anal appen. a thin circular collar ⁵	Anal appen. digitiform ⁵	Anal appen. cardiform ⁵	No anal appendage ⁵	No accessory heart ⁶	Accessory heart has tributaries ⁶	Accessory heart lacks tributaries ⁶	Broods larvae ⁷		
				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gryphaeidae	Pycnodontinae	Hyotissini	<i>Hyotissa</i> <i>Parahyotissa</i> s.s. <i>P. (Pliohyotissa)</i> <i>P. (Numismoida)</i>	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	X X X X	?		
		Neopycnodontini	<i>Neopycnodonte</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	?	
Ostreidae	Lophinae	Lophini	<i>Lopha</i> <i>Alectryonella</i> ⁸ <i>Dendostrea</i>	X ? X	X ?	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	yes yes yes		
		Myrakeenini	<i>Myrakeena</i> <i>Anomiostrea</i> ⁹	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	?	
	Ostreinae	Ostreini	<i>Ostreola</i> <i>Ostrea</i> s.s. <i>O. (Eostrea)</i> <i>Nanostrea</i> <i>Planostrea</i>	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	X X X X X	yes yes yes ? ?	
		Cryptostreini	<i>Cryptostrea</i> <i>Teskeyostrea</i> <i>Booneostrea</i>	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	yes yes yes	
		Undulostreini	<i>Undulostrea</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	?	
		Pustulostreini	<i>Pustulostrea</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	?	
		Crassostreinae	Striostreini	<i>Saccostrea</i> <i>Striostrea</i> s.s. <i>S. (Parastriostrea)</i>	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	X X X	no ? ?
			Crassostreini	<i>Crassostrea</i> ¹⁰	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	no

¹ Mantle: thickness may be determined in part by age and nutritional state.² Promyal passage: the left one is closed in all species but *Hyotissa hyotis*.³ Heart-kidney-rectum complex: in the gryphaeid condition the heart auricles are outpocketed, fused to the pericardium wall by their ventral surfaces, with very abundant brown granulocytes internally; the rectum distinctly penetrates the heart ventricle; the kidney is large, covering the dorsal curvature of the adductor muscle (which is circular in profile), with posterior caecum, and little outpocketing; renopores are at the dorsal ends of the anterior horns. In the ostreid condition, the auricles are not outpocketed, nor fused ventrally to the pericardium, and the amount of brown granulocytes is variable, but usually small; the rectum passes immediately behind the ventricle, the kidney is much reduced, with no large sac over the dorsal surface of the adductor muscle (which is reniform in profile), not posterior caecum, and the whole is much outpocketed as short, dendritic alveoli, with the renopores at the ventral ends of the anterior horns.⁴ Outer labial palp: the extent of fusion in the Ostreidae presents almost a continuous variable, but is here reduced to three alternatives.⁵ Anal appendage: this was difficult to determine in the limited amount of material available for some species (see text).⁶ Accessory heart: this was often difficult to determine precisely in the limited amount of preserved material available for some species.⁷ Reproductive habits: data are partly from the literature.⁸ Data on the flesh of *Alectryonella* are entirely from TORIGOE (1981).⁹ The flesh of *Anomiostrea* has not been available for study.¹⁰ *Crassostrea*: the labial palp is unfused, and there is no anal appendage in *C. virginica*, the genotype; but there is slight fusion of the palp, and a distinct circular flange on the anus in *C. pivas*.

St. Lawrence River estuary in eastern Canada (*O. rhizophorae* Guilding, 1827, is a junior synonym); in the eastern Pacific, *C. columbiensis* (Hanley, 1846) occurs from Ecuador northward to the Gulf of California (*O. corteziensis* Hertlein, 1951, is a junior synonym). *Crassostrea gigas* (Thunberg, 1793) occurs in the Indo-West Pacific from Pakistan to Japan and Korea, and in the Philippine Islands, Borneo, and Sumatra, but possibly not in the rest of Indonesia, or southward.

SUMMARY TABLES

Some of the more important characters which vary among Recent oysters are summarized in the preceding three comparative tables (pp. 153-155). The data refer to all known species of each genus and subgenus, not merely to the type species of the taxa cited, and they include variation found within the species. Therefore some characters which would seem to be mutually exclusive, as type of chomata in *Neopycnodonte*, *Alectryonella* and *Dendostrea*, and shape of the anal appendage and fusion of the labial palps in *Crassostrea*, appear in more than one column. For more precise information one must refer to the text.

LITERATURE CITED

- ADAMS, A. & L. REEVE. 1850. Zoology of the voyage of *H.M.S. Samarang*. Reeve and Benham: London. Mollusca. (1848-1850)
- BORN, I. VON. 1778. Index rerum naturalium musei Caesarei Vindobonensis, Pars I, Testacea. Verzeichniss der natürlichen Setenheiten des K.K. naturalien Kabinet zu Wien, Erster Theil, Schalthiere. Officina Krausiana: Vienna. 458 plus several unnumbered pages.
- CARPENTER, P. P. 1857. Catalogue of the collection of Matatlan shells in the British Museum collected by Frederick Reigen. London: British Museum. Pp. i-iv + 552. Reprinted, Paleontological Research Institute, 1957.
- CARPENTER, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the West Coast of North America. Rept. British Assoc. Adv. Sci. for 1863:517-686.
- CARRIKER, M. R., R. E. PALMER & R. S. PREZANT. 1980. Functional ultramorphology of the dissoconch valves of the oyster *Crassostrea virginica*. National Shellfisheries Association, Proc. 70(2):139-183.
- CHANLEY, P. & P. DINAMANI. 1980. Comparative descriptions of some oyster larvae from New Zealand and Chile, and a description of a new genus of oysters, *Tiostrea*. New Zealand J. Mar. Freshw. Res. 14(2):103-120.
- CHILDREN, J. G. 1822-1824. Lamarck's genera of shells, translated from the French, with plates from original drawings by Miss Anna Children. Quarterly J. Sci., Lit. Arts, 14:64-86 (Oct. 1822); 14:298-322 (Jan. 1823); 15:23-52, 2 pls. (Apr. 1823); 15:216-258, 2 pls. (July 1823); 16:49-79, 2 pls. (Oct. 1823); 16:241-264 (Jan. 1824). Designation of the type of *Ostrea* Linné is 1823, 15:44, pl. 2, fig. 94.
- CROSSE, H. 1869. Diagnoses molluscorum novorum. J. de Conchyl, Ser. 3, 9:183-188 (and pl. 2 of vol. 10, 1870).
- CROWSON, R. A. 1970. Classification and biology. Heinemann Educational Books, Ltd.: London. 350 pp.
- DALL, W. H. 1898. Contributions to the Tertiary fauna of Florida with especial reference to the Silex Beds of Tampa and the Pliocene Beds of the Caloosahatchie River including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Wagner Free Inst. Sci., Philadelphia, Trans., 3(4):viii + 571-947, pls. 23-35.
- DALL, W. H. 1914. Notes on West American oysters. Nautilus 28:1-3.
- DALL, W. H., P. BARTSCH & H. A. REHDER. 1938. A manual of Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. Bernice P. Bishop Mus. Bull. 153:233 pp., 57 pls.
- DESHAYES, G. P. 1863. Catalogue des mollusques de l'île de la Réunion (Bourbon). Pp. 1-144, pls. 28-41. In: L. Mailhard, Notes sur l'île de la Réunion.
- DUJARDIN, F. 1835. Mémoire sur les couches du sol en Touraine et descriptions des coquilles de la craie et des faluns. Soc. Geol. France, Mém. 2(2):211-311, pls. 15-20.
- FINLAY, H. J. 1928. The Recent mollusca of the Chatham Islands. New Zealand Inst., Trans. and Proc. 59(2):232-286, pls. 38-43.
- FORBES, M. L. 1964. Distribution of the commensal oyster, *Ostrea permollis*, and its host sponge. Bull. Mar. Sci. Gulf Caribb. (Univ. Miami) 14(3):453-464.
- FORBES, M. L. 1966. Life cycle of *Ostrea permollis* and its relationship to the host sponge, *Stellata grubii*. Bull. Mar. Sci. Gulf Caribb. (Univ. Miami) 16(2):273-301.
- GALTISOFF, P. S. 1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Bureau of Commercial Fisheries, Fish. Bull. 64:1-480, 400 figs.
- GLENN, L. C. 1904. Pelecypoda. Vol. 1:274-401. In: Maryland Geological Survey, Miocene. Text, pp. i-xix, 1-543; atlas of pls., 10-135.
- GMELIN, J. F. 1791. Caroli a Linné Systema naturae per regna tria naturae. Ed. 13, vol. 1, pt. 6, pp. 3021-3910. G. E. Beer: Leipzig.
- GOULD, A. A. 1861. Descriptions of shells collected in the North Pacific Exploring Expedition under Captains Ringgold and Rodgers. Boston Soc. Natur. Hist., Proc. 8:33-40.
- GRAY, J. E. 1825. A list and description of some species of shells not taken notice of by Lamarck. Ann. Philos. 25:134-140, 407-415 (sometimes cited as Ser. 2, vol. 9).
- GROBEN, C. 1888. Die Pericardialdrüse der Lamelibranchiaten. Ein Beitrag zur Kenntniss der Anatomie dieser Molluskenklasse. Arbeit des Zoolog. Institutes zu Wien 7(3): 355-444, 6 pls.
- GUILDING, L. 1828. Observations on the zoology of the Caribbean Islands. Zool. Journal Vol. 3, no. 12, art. 61, pp. 527-544.
- HABE, T. 1957. Descriptions of four new bivalves from Japan. Venus (Fukuyama) 19(3/4):177-183.
- HABE, T. & S. KOSUGE. 1966. New genera and species of the tropical and subtropical Pacific molluscs. Venus 24(2):312-341, pl. 29.
- HANLEY, S. C. T. 1846. A description of new species of *Ostreae*, in the collection of H. Cuming, Esq. Zool. Soc. London, Proc., for 1845:105-107.
- HARRY, H. W. 1968. An alternate view on the phylogeny of the Mollusca. Proceedings of the Symposium on Mollusca, Pt. 1. Marine Biol. Assoc. of India, Ramanathapuram District, Madras, India. Pp. 170-187.
- HARRY, H. W. 1971. Reconciling biological nomenclature and the phylogeny of organisms. The Echo (Abstracts and Proceedings of the Third Annual Meeting of the Western Society of Malacologists) 3:41-53.

- HARRY, H. W. 1981. Nominal species of living oysters proposed during the last fifty years. *Veliger* 24(1):39-45.
- HARRY, H. W. 1981a. Newly discovered anatomical characters useful in classifying oysters (Ostreacea, Gryphaeidae and Ostreidae). *Amer. Malacol. Bull.* for 1981:34.
- HARRY, H. W. 1983. Homology of the five types of marginal denticles (chomata) of living oysters (Gryphaeidae and Ostreidae). *Amer. Malacol. Bull.* 1:90.
- HARRY, H. W. & D. T. DOCKERY. 1983. Notes on the Lower Oligocene oysters of Mississippi. *Mississippi Geology* 4(2): 7-14.
- HERRMANNSEN, A. N. 1846-1852. *Incicis generum malacozoorum primordia*. 2 vols. Theodor Fischer: Cassel.
- HERTLEIN, L. G. 1951. Descriptions of two new species of marine pelecypods from West Mexico. *So. Calif. Acad. Sci., Bull.* 50(2):68-75, pls. 24-26.
- HUTTON, F. W. 1873. *Catalogue of the Tertiary Mollusca and Echinodermata of New Zealand*, in the collection of the Colonial Museum. *New Zealand Colonial Mus. and Geol. Surv. Dept.*, xvi + 48 pp. (Wellington).
- IHERING, H. VON. 1907. *Les mollusques fossiles du Tertiaire et du Crétacé supérieur de l'Argentine*. *Museo. Nac. Buenos Aires, Ann.*, ser. 3, 7:xiii + 611 pp., 16 figs., 8 pls.
- IREDALE, T. 1939. *Mollusca*, Pt. I. *Brit. Mus. Nat. Hist., Rec.* 19:267-340, pls. 20-24.
- KEEN, A. M. 1971. *Sea shells of tropical West America*. 2nd ed. Stanford Univ. Press: Stanford, Calif. 1064 pp.
- LAMARCK, J. B. P. DE M. 1802-1809. *Sur les fossiles des environs de Paris, comprenant la détermination des espèces qui appartiennent aux animaux marins sans vertèbres, et dont la plupart sont figures dans la collection des velins du Museum*. *Annales du Museum National d'Histoire Naturelle* (Paris). Various places in Vols. 1-14; reprinted, 1978, by the Paleontological Research Institution, Ithaca, New York.
- LAMARCK, J. B. P. DE M. 1804. Une nouvelle espèce de Trigonie, et sur une nouvelle espèce d'huitre, découvertes dans le voyage du capitaine Baudin. *Annales du Museum National d'Histoire Naturelle* (Paris) 4:351-359, pl. 67.
- LAMARCK, J. B. P. DE M. 1815-1822. *Histoire naturelle des animaux sans vertèbres*. Paris. 7 vols. (Vol. 6, 232 pp., appeared 1819; oysters are in part 1 of it, pp. 195-220.)
- LAMY, E. 1929-1930. *Revision des Ostrea vivants du Museum National d'Histoire Naturelle de Paris*. *J. de Conchyl.* 73 (ser. 4, vol. 27), No. 1 (30 April 1929):1-46, 3 figs.; No. 2 (20 July 1929):71-108; No. 3 (30 October 1929):133-168; No. 4 (28 February 1930):233-257, pl. 1.
- LINNÉ, C. 1758. *Systema naturae per tria regna naturae*. Ed. 10, vol. 1. Stockholm. 823 pp.
- LISCHKE, C. E. 1869-1874. *Japanische Meeres-Conchylien, mit besonderer Rücksicht auf die geographische Verbreitung derselben*. *Novitates Conchologicae*. W. Dunker (ed.), Suppl. 4, 3 pts. in 1.
- MCLEAN, R. A. 1941. *The oysters of the western Atlantic*. *Notulae Naturae*, (Acad. Natur. Sci. Philadelphia) No. 67: 1-14, 4 pls.
- MELVILL, J. C. 1898. *Further investigations into the molluscan fauna of the Arabian Sea, Persian Gulf and Gulf of Oman, with descriptions of forty species*. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 42(2):1-40 (reprint), 2 pls.
- MONTEROSATO, T. A., MARCHESE DI. 1884. *Nomenclatura generica e specifica di algune conchiglie mediterranee*. Virzi: Palermo. 152 pp.
- OLSSON, A. A. 1951. *New Floridian species of Ostrea and Vermicularia*. *Nautilus* 65(1):6-8, pl. 1.
- ORBIGNY, A. D'. 1835-1847. *Voyage dans l'Amérique Méridionale . . . exécuté pendant les années 1826-1833*. 7 vols. of text, 2 vols. of atlas. Paris (Mollusques, 1847, in vol. 5, pt. 3, 83 pls.).
- PAYRAUDEAU, B. C. 1826. *Catalogue descriptif et methodique des annelides et de mollusques de l'Isle de Corse*. Paris. 218 pp., 8 pls.
- PHILIPPI, R. A. 1845-1847. *Abbildungen und Beschreibung neuer oder wenig bekannter Conchylien*. Vol. 2 (in parts issued at intervals, pages and plates not consecutively numbered). Theodor Fischer: Cassel. (The part on *Ostrea*, pp. 81-82, is dated Feb. 1846.)
- PILSBRY, H. A. 1904. *New Japanese marine Mollusca: Pelecypoda*. *Proc. Acad. Natur. Sci. Philadelphia* 56:550-560, pl. 40.
- POLI, J. X. 1791-1827. *Testacea utriusque Siciliae eorumque historia et anatomie tabulis aeneis illustrata*. 3 vols. Parma, Italy.
- RAFINESQUE, C. S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palermo. 224 pp.
- RANSON, G. 1967. *Les espèces d'huitres vivant actuellement dans le monde définies par leurs coquilles larvaires ou prodissoconques*. *Revue des Travaux de l'Institut des Pêches Maritimes*, Paris 31 (part 2, June):127-192, 25 figs.; (part 3, September):205-247, figs. 26-55.
- ROCHEBRUNE, A.-T. DE. 1895. *Diagnoses des mollusques nouveaux, provenant du voyage de M. Diguët en Basse-Californie*. *Bull. Mus. d'Hist. Nat. (Paris)* 1:239-243.
- RÖDING, P. F. 1798. *Museum Boltenianum sive catalogus cimeliorum. Pars secunda continens conchyliam*. C. J. Trapitz: Hamburg. viii + 199 pp.
- SACCO, F. 1897. *Pelecypoda (Ostreidae, Anomiidae e Dimyidae) of L. Bellardi & Federico Sacco, 1872-1904*, I molluschi dei terreni Terziarri di Piemonte e della Liguria (30 pts. separately paged, pt. 23, 66 pp., 11 pls.). Carlo Clausen: Torino.
- SAY, T. 1834. *American conchology, or descriptions of the shells of North America illustrated by coloured figures from original drawings executed from nature*. Vol. 1, No. 6. School Press: New Harmony, Indiana. 42 pages (unnumbered), pls. 51-60.
- SCHENCK, E. T. & J. H. McMASTERS. 1948. *Procedure in taxonomy* (revised ed.). Stanford Univ. Press: Stanford, Calif. 93 pp.
- SOWERBY, G., JR. 1870-1871. *Monograph of the genus Ostrea*. In: L. Reeve, 1843-1878, *Conchologia Iconica; or illustrations of the shells of molluscos animals* (20 vols.) vol. 18, 33 pls. and index (2 pp.) (Oct. 1870-Nov. 1871) L. Reeve & Co.: London.
- STENZEL, H. B. 1959. *Cretaceous oysters of southwestern North America*. *Congr. Geol. Internac., XXa session, Mexico City, 1956*. *El sistema Cretacico*. 1:15-37, 19 figs.
- STENZEL, H. B. 1971. *Oysters*. Pp. i-iv, N953-N1224, 153 figs. In: R. C. Moore (ed.), *Treatise on invertebrate paleontology*. Part N, vol. 3, *Mollusca* 6, *Bivalvia*. *Geol. Soc. America*.
- SUTTER, H. 1917. *Descriptions of new Tertiary Mollusca occurring in New Zealand, accompanied by a few notes on necessary changes in nomenclature*. Pt. 1. *New Zealand Geol. Survey Paleont. Bull.* 5:vii + 93 pp., 13 pls.
- SWAINSON, W. 1835. *The elements of modern conchology briefly and plainly stated, for the use of students and travelers*. London. viii + 62 pp.

- THIELE, J. 1889. Die abdominalen Sinnesorgane der Lamellibranchier. Zeitschrift für Wissenschaftliche Zoologie 48(1): 47-59, pl. 4.
- THUNBERG, C. P. 1793. Techning och beskrifning pa en stor Ostronsort ifran Japan. K. Svenska Vetensk. Akad., Handlingar. 14:140-142.
- TORIGOE, K. 1981. Oysters in Japan. J. Sci. of Hiroshima Univ., Ser. B, Div. 1 (Zool.) 29(2):291-419, 36 pls.
- TORIGOE, K. 1983. Systematic position of *Ostrea sedea setoensis* Habe, 1957. Venus 41(4):291-295, pls. 1-2.
- VYALOV, O. S. 1936. Sur la classification des huîtres. Acad. Sci. USSR, Comptes Rendus (Doklady) New Ser., vol. 4 (13), No. 1:17-20.
- WADA, S. 1953. Larviparous oysters from the tropical West Pacific. Rec. Oceanogr. Works Japan, New Ser. 1(2):66-72. [not seen]
- WHITE, K. M. 1942. The pericardial cavity and the pericardial gland of the Lamellibranchia. Proc. Malacol. Soc. Lond. 25(2):37-88.

NOTE ADDED IN PROOF

While this paper was in press a paper was published with extensive descriptions, good photographs and many locality records of *Parahyotissa (Pliohyotissa) quercinus* (Sowerby, 1871), from the Gulf of California and southward to Manzanillo, Colima, Mexico: Gemmell, J., C. M. Hertz & B. W. Myers, 1985. A problem oyster in the Gulf of California ("*Ostrea*" *quercinus* Sowerby, 1871 rediscovered). Festivus (Publication of the San Diego, Calif., Shell Club) 17(5): 43-48.

Gonatus ursabrunae and *Gonatus oregonensis*, Two New Species of Squids from the Northeastern Pacific Ocean (Cephalopoda: Oegopsida: Gonatidae)

by

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Abstract. Two new species of gonatid squids are described from the northeastern Pacific. *Gonatus ursabrunae* spec. nov. is distinguished by the presence of greatly enlarged suckers in two locations: in the lateral rows of the middle portions of arms I-III, and in the proximal portion of the dactylus. This species has been taken off Oregon and west to the central Aleutian Islands. *Gonatus oregonensis* spec. nov. is characterized primarily by the number of club suckers, greater than in any other *Gonatus* (s.s.) species. This species has been taken only off Oregon. The status of systematics in the family is discussed and the species compared. Based on existing collections, up to three additional species of Gonatidae may remain undescribed in the North Pacific, and one in the Antarctic. *Gonatus phoebetriae* Imber, 1978, is shown to be a *nomen dubium*.

INTRODUCTION

THE FAMILY Gonatidae is of major importance to the ecology of the Subarctic Pacific; species of this group dominate the pelagic cephalopod fauna in this area (JEFFERTS, 1983; KUBODERA & JEFFERTS, 1984), and are important in the diets of seabirds, fishes, and marine mammals (LEBRASSEUR, 1966; SANGER & BAIRD, 1977; FISCUS, 1982). Greater knowledge of the taxonomy of gonatids is vital to an understanding of broader ecologic questions in the Subarctic Pacific.

Three genera are currently recognized in the family: *Gonatopsis* Sasaki, 1920, *Berryteuthis* Naef, 1921, and *Gonatus* Gray, 1849. *Gonatopsis* is distinguished by the loss of tentacles in the adults. The following species are recognized: *Gonatopsis octopedatus* Sasaki, 1920, *G. borealis* Sasaki, 1923, *G. makko* Okutani & Nemoto, 1964, *G. japonicus* Okiyama, 1969, and *G. okutani* Nesis, 1972. Another form of *Gonatopsis*, type A of KUBODERA (1978) has been described, but not named. *Berryteuthis* is characterized by the absence of club hooks, a septemdentate radula, and a carpal-locking zone that extends up onto the manus and dactylus as a "fixing apparatus" (BERRY, 1913). Two species are presently recognized: *Berryteuthis magister* (Berry, 1913) and *B. anonychus* (Pearcy & Voss, 1963).

The taxonomy of *Gonatus* has recently been in a state

of flux. The genus is characterized by a quinquedentate radula and a carpal-locking zone consisting of alternating ridges with large suckers medially and grooves with fleshy knobs medially. Prior to 1972 only two species were recognized: *G. fabricii* (Lichtenstein, 1818) and *G. antarcticus* Lönnerberg, 1898. *Gonatus berryi* Naef, 1923, had been forgotten until YOUNG (1972) revived usage of the name and redescribed the species. *Gonatus kamtschatica* Middendorff, 1849, was originally inadequately described on the basis of a specimen no longer extant, and has been declared a *nomen dubium* (KUBODERA & OKUTANI, 1981a). Since 1972 seven new species have been described: *G. onyx* Young, 1972, *G. pyros* Young, 1972, *G. californiensis* Young, 1972, *G. tinro* Nesis, 1972, *G. madokai* Kubodera & Okutani, 1977, *G. middendorffi* Kubodera & Okutani, 1981a, and *G. steenstrupi* Kristensen, 1981. Two others have been described, but not named: *Gonatus* type C of KUBODERA, 1978 (synonym, *Gonatus* type A of KUBODERA & OKUTANI, 1981b) and *Gonatus* sp. of BUBLITZ, 1980. A form that probably represents an additional species occurs in Antarctic waters (YOUNG, 1972). *Gonatus phoebetriae* Imber, 1978, was described on the basis of a single lower beak. Because variation in the form of beaks within species is frequently broad (Fiscus, 1983, personal communication), and complete specimens are absent, I consider *G. phoebetriae* to be a *nomen dubium*, as does KRISTENSEN (1981).

MATERIALS AND METHODS

The material examined (Table 1) was collected by two separate research programs: one conducted by the University of Washington aboard the R/V *Brown Bear* (ARON, 1958, 1962) and the other conducted by the Oregon State University (O.S.U.) Nekton group aboard the R/V's *Yaquina* and *Cayuse* (e.g., PEARCY, 1964). Both sampling programs employed Isaacs-Kidd Midwater Trawls (ISAACS & KIDD, 1953) of various sizes (1.83, 2.44, 3.05 m depressor width) and configurations. Several of the O.S.U. Nekton samples were taken with Isaacs-Kidd Midwater Trawls (IKMT) that had multiple plankton samplers (MPS) as closing cod ends. The MPS was developed by BÉ (1962) and modified by PEARCY & HUBBARD (1964), PEARCY & MESECAR (1971), and PEARCY *et al.* (1977) to fish three or five nets at discrete subsurface depth horizons. Mesh size in the *Brown Bear* IKMT was 7.6 cm, with a 1.3 cm liner in the aft portion; the O.S.U. Nekton sampling program used 5 mm mesh in all but the cod end, which was 0.571 mm Nitex.

The samples were preserved in 10% buffered formalin-seawater solution at sea and transferred to fresh 5% buffered formalin in the laboratory before examination. Samples were subsequently transferred to 50% isopropyl alcohol, although often as long as 24 years after collection. The specimens were examined, enumerated, and measured to the nearest mm (or 0.5 mm, depending on dimension of the structure in question). Initial drawings were made with a *camera lucida*. The following counts and measurements were made, although not all measurements were always possible on all specimens. Measurements not further defined here correspond to those of VOSS (1956).

DML, dorsal mantle length
 MW, mantle width
 FL, fin length
 FW, fin width
 HW, head width
 ED, eye diameter, maximum diameter of bulbous
 AL I, length of arm I, measured from the base between arms I to the tip
 AL II, length of arm II, measured from the base between arms II and III to the tip
 AL III, length of arm III, measured from the base between arms III and IV to the tip
 AL IV, length of arm IV, measured from the base between arms IV to the tip
 TL, tentacle length, total length of tentacle stalk and club
 CL, club length, measured from basal sucker of carpus to tip of dactylus
 AH, arm hooks (present/absent)
 CH, largest (central) club hook (present/absent)
 OCH, other (than central) club hooks (number present/absent)
 DH, hook distal to large central club hook (present/absent)

PH, hooks proximal to large central club hook (number present/absent)

CS, total number of club suckers, counted from basal sucker of carpus to tip of dactylus

HAC I-IV, half arm count (number of suckers or suckers/hooks on the proximal half of arms I-IV)

Other abbreviations:

MWI, mantle width index = MW/DML

FLI, fin length index = FL/DML

FWI, fin width index = FW/DML

EDI, eye diameter index = ED/DML

TLL, tentacle length index = TL/DML

CLI, club length index = CL/DML

CAS, California Academy of Sciences, Department of Invertebrate Zoology, Golden Gate Park, San Francisco

OSUI, Oregon State University Invertebrate reference collection; College of Oceanography, Corvallis

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Family GONATIDAE Hoyle, 1886

Characterized by a simple, straight funnel-locking cartilage; buccal connectives that attach ventrally to arms IV; tetraserial brachial armature, including two medial rows of hooks (except male *Berryteuthis anonychus*, which lack hooks).

Genus *Gonatus* Gray, 1849

Radula with five teeth in a transverse row; tentacles well developed, club with carpal-locking zone consisting of alternating ridges with large suckers medially and grooves with fleshy knobs medially.

Gonatus ursabrunae Jefferts, spec. nov.

(Figures 1, 2)

? *Gonatus fabricii* SASAKI, 1929 (*pars*):269-290, pl. 22, fig. 14; text fig. 128C.

Gonatus sp. A, JEFFERTS, 1983:88-93, including table 5 and fig. 31.

Material examined: **Holotype:** a juvenile of 24 mm DML; R/V *Brown Bear* cruise 235, haul 46; W. Aron and P. McCrery; south of Alaska Peninsula; 53°57'N, 157°39'W, 1.8 m IKMT fished open 0-225 m; 25 July 1959, 0129-0222 h; CAS 040163. **Paratype:** 1 juvenile, 20 mm DML; R/V *Brown Bear* cruise 235, haul 46; W. Aron and P. McCrery; south of Alaska Peninsula; 53°57'N, 157°39'W, 1.8 m IKMT fished open 0-225 m; 25 July 1959, 0129-0222 h; OSUI 701. **Paratype:** 1 juvenile, 19 mm DL; R/V *Yaquina* cruise YALOC 66, haul 849, south of Alaska Peninsula; 52°58.5'N, 162°48'W, 3.0 m IKMT-MPS fished open 0-2400 m; 6 July 1966, 0707-1330 h; USNM 816326. **Paratype:** 1 juvenile, 18 mm DML; R/V *Yaquina* cruise YALOC 66, haul 845; south of Alaska Peninsula; 54°58.2'N, 166°02'W, 1.8 m IKMT fished open

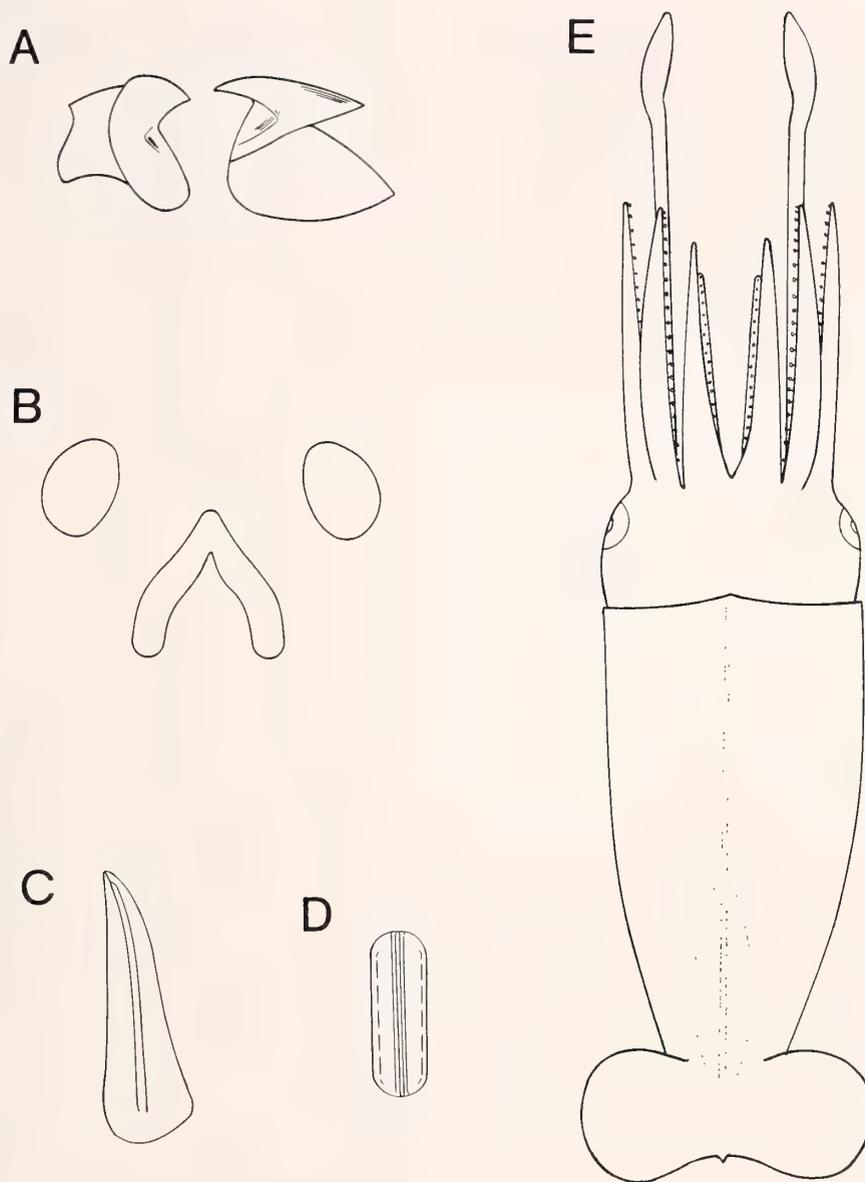


Figure 1

Gonatus ursabrunae spec. nov. A, lower and upper mandibles, CAS 057606, 17 mm DML. B-D, USNM 816236, 19 mm DML: B, funnel organ; C, funnel cartilage; D, nuchal cartilage. E, whole animal, dorsal aspect, OSUI 701, 20 mm DML.

0-200 m; 4 July 1966, 0240-0321 h; OSUI 696. **Paratype:** 1 juvenile, 17 mm DML; R/V *Yaquina* cruise YALOC 66, haul 849; south of Alaska Peninsula; 52°58.5'N, 162°48'W, 3.0 m IKMT-MPS fished open 0-2400 m; 6 July 1966, 0707-1330 h; CAS 057606. **Paratype:** 1 juvenile, 15 mm DML; R/V *Yaquina* cruise YALOC 66, haul 837; J. Donaldson; south of Adak Island; 50°32.3'N, 176°04.5'W, 1.8 m IKMT fished open 0-160 m; 22 June 1966, 0031-0107 h; CAS 057607. **Paratype:** 1 juvenile, 12 mm DML; R/V *Yaquina* cruise YALOC 66, haul 842; J. Donaldson; southeast of Adak

Island; 51°43.8'N, 175°20'W, 1.8 m IKMT fished open 0-200 m; 1 July 1966, 0309-0347 h; USNM 816325.

Additional material (all in the collections of Oregon State University): 2 juveniles, mantles missing; R/V *Yaquina* cruise YALOC 66, haul 843; J. Donaldson; south of central Aleutian Islands; 51°01.0'N, 171°32.0'W, 1.8 m IKMT fished open 0-200 m; 2 July 1966, 0305-0345 h; 1 juvenile, mantle missing; R/V *Yaquina* cruise YALOC 66, haul 850; J. Donaldson; south of Alaska Peninsula; 53°33.8'N, 160°08.0'W, 1.8 m IKMT fished open 0-160 m; 7 July 1966, 0125-0205 h; 3 juveniles, 23 mm DML,

2 missing mantles; R/V *Brown Bear* cruise 176, haul 34; Allen and P. McCrery; south of Alaska Peninsula; 52°29'N, 160°59'W, 1.8 m IKMT fished open 0–60 m; 1 August 1957, 0146–0222 h; 1 juvenile, 18 mm DML; R/V *Brown Bear* cruise 176, haul 85; P. McCrery, Semon, and Linger; south of Aleutian Islands; 51°26'N, 174°10'W, 1.8 m IKMT fished open 0–225 m; 24 August 1957, 0032–0124 h; 1 juvenile, 15 mm DML; R/V *Brown Bear* cruise 235, haul 23; W. Aron and P. McCrery; Gulf of Alaska; 52°49'N, 142°45.5'W, 1.8 m IKMT fished open 0–225 m; 20–21 July 1959, 2334–0028 h; 1 juvenile, 18 mm DML; R/V *Brown Bear* cruise 235, haul 44; W. Aron and P. McCrery; south of Alaska Peninsula; 53°55.5'N, 153°17'W, 1.8 m IKMT fished open 0–400 m; 24 July 1959; 0337–0454 h; 1 juvenile, 23 mm DML; R/V *Brown Bear* cruise 235, haul 45; W. Aron and P. McCrery; south of Alaska Peninsula; 53°56.5'N, 157°57.5'W, 1.8 m IKMT fished open 0–400 m; 25 July 1959, 0004–0119 h; 2 juveniles, 21, 25 mm DML; R/V *Brown Bear* cruise 235, haul 47; W. Aron and P. McCrery; south of Alaska Peninsula; 53°57'N, 157°49'W, 1.8 m IKMT fished open 0–60 m; 25 July 1959, 0223–0300 h; 1 juvenile, 22 mm DML; R/V *Yaquina* sta. NH-65; off Oregon coast; 44°43.3'N, 125°41.1'W, 1.8 m IKMT fished open 0–200 m; 14 February 1967, 0418–0500 h.

Description: Mantle plump, widest at anterior margin (MWI = 30–53, widest in small individuals; meristic indices summarized in Table 2), narrowing to pointed tip and adhering to gladius (Figure 1e). Mantle of soft consistency. Eyes large, occupying entire lateral surface of head (EDI = 18–21); anterior sinus small and broad. Ventral surface of mantle slightly emarginate at anterior edge. Fins relatively small, FWI = 41–58, FLI = 26–50, very thin, posteriorly attached just dorsal and anterior to the posterior tip of the gladius; posterior edge of fins united at midline, and projecting slightly posteriorly (Figure 1e). Funnel not extending as far as midpoint of eyes; in most specimens anterior tip of funnel not, or only just, visible at ventral margin of mantle (perhaps owing to contraction on preservation). Mantle-locking cartilage straight, slightly expanded posteriorly (Figure 1c). Dorsal component of funnel organ a broad inverted V, with expanded posterior lobes (Figure 1b). Ventral element of funnel organ a pair of small ovoid pads each about half the length of each branch of dorsal element. Funnel valve large and broad. Nuchal folds low and indistinct, no more than two folds observed on one side; the low and short olfactory papilla is just posterior to the eyes, in line with and anterior to the funnel-mantle locking cartilages.

Arm formula generally III ≥ II > I ≥ IV. Arms relatively short: ALI for longest arms (III or II) 42–56, ALI for shortest arms (IV) 25–44. Aboral keels well developed on arms IV. Trabeculate protective membranes very well developed on arms I–III, especially in larger individuals. Brachial armature quadriserial; suckers of the two medial rows small (0.18–0.20 mm diameter) in all individuals examined (largest individual examined, the holotype, was

24 mm DML). These medial suckers have about nine long, slender, blunt teeth on the inner distal margin (Figure 2c), those on the largest suckers reach about 0.024 mm in length, or approximately one-fifth of the diameter of the sucker opening. The two lateral rows of suckers are borne on trabeculae and consist of suckers that are greatly enlarged along the middle third of arms I–III (Figure 2f). The largest of these suckers are 0.50 mm in diameter and have 9–16 short, blunt teeth (much shorter than on suckers from the medial rows) on the distal inner margin (Figure 2d). Arms IV bear four rows of equally sized suckers (0.10–0.12 mm in diameter in holotype) which are smaller than the medial suckers of arms I–III. Half-arm counts for the two largest specimens are given in Table 3, but are not very consistent between the two specimens. It is extremely difficult to make accurate counts on smaller specimens. These counts of only two specimens are of little use by themselves; when a larger body of data becomes available such counts may show consistent differences between species.

Tentacles are of moderate length, TLI = 53–79, and the clubs are moderately short, CLI = 13–25 (Figure 2a). A dorsoaboral keel is present on the club from the level of the central hook (or enlarged sucker) to the tip of the dactylus. The medial zone of the manus contains a central hook in the holotype, and an enlarged central sucker in specimens of 19 and 20 mm DML, with three or four proximal suckers in all three specimens (Figure 2a). A carpal-locking zone consists of approximately five alternating ridges and suckers. The dorsal marginal zone contains suckers in four rows, and the ventral marginal zone bears four to five rows. The dactylus suckers are disposed in about six rows just distal to the central hook (or enlarged sucker), but these rapidly decrease to four regular rows which continue out the length of the dactylus to a circlet of small suckers at the tip. The suckers distal to the central hook number approximately 110 (full club sucker counts are impossible, as no mature specimens are available, and many of the proximal suckers remain as buds even in the larger specimens). The dactylus suckers just distal to the central hook reach a maximum diameter of 0.30 mm in the holotype, and decrease in size distally (Figure 2b). In other species of *Gonatus* (specimens of similar size were used where possible), dactylus suckers never approach this maximum size:

Species	DML	Sucker diameter
<i>californiensis</i>	112	0.25
<i>oregonensis</i>	46	0.20
<i>madokai</i>	40	0.14
<i>pyros</i>	35	0.14
<i>berryi</i>	30	0.13
<i>onyx</i>	26	0.08
<i>middendorffi</i>	35	buds
<i>madokai</i>	22	buds
sp. C of <i>Kubodera</i>	15	buds

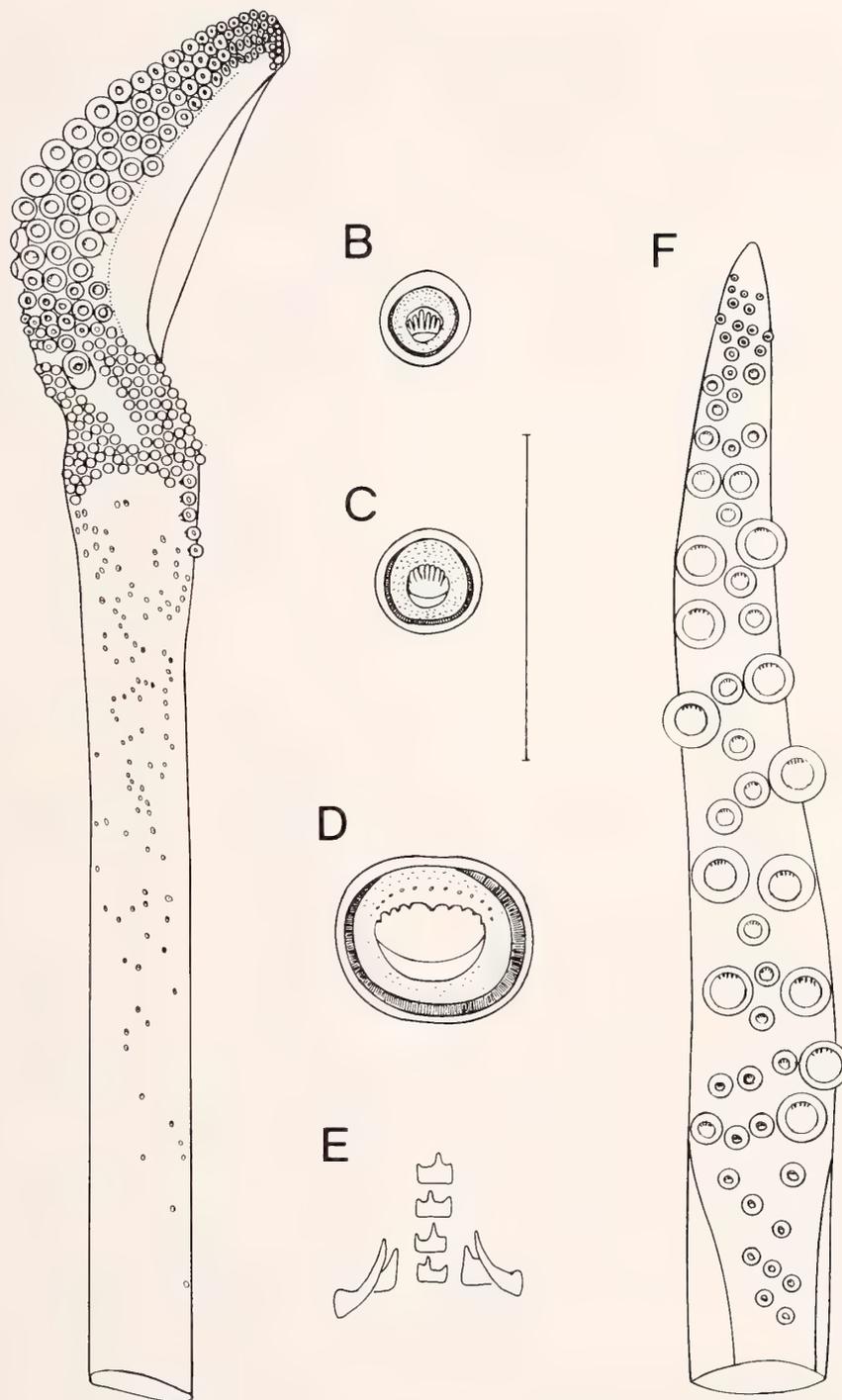


Figure 2

Gonatus ursabrunae. A-F, USNM 816326, 19 mm DML: A, tentacle; B, enlarged dactylus sucker; C, normal brachial sucker of medial row, A III; D, enlarged brachial sucker of lateral row, A III; E, radula; F, right arm III. Scale (B, C, D), 1 mm.

Table 1

Station data for the material examined, including type number (OSUI: 687-701. CAS: 040162-057608. USNM: 816325-816328. * indicates holotypes); station or haul number; date; latitude (N); longitude (W); gear depressor width of IKMT (m), or IKMT + MPS (hauls 2057#4, 2107#5, 2110#1 and #5); depth sampled (m); local time of sampling; and the vessel from which the sample was collected (Y, R/V *Yaquina*; B, R/V *Brown Bear*; C, R/V *Cayuse*).

Type no.	Haul no.	Latitude	Longitude	Gear	Date	Time	Depth	Vessel
<i>Gonatus ursabrunae</i>								
696	845	54°58.2'	166°02'	1.8	4 Jul 66	0240-0321	0-200	Y
700, 701	235-46	53°57'	157°39'	1.8	25 Jul 59	0129-0222	0-225	B
040163*	235-46	53°57'	157°39'	1.8	25 Jul 59	0129-0222	0-225	B
057606	849	52°58.5'	162°48'	3.0	6 Jul 66	0707-1330	0-2400	Y
057607	837	50°32.3'	176°04.5'	1.8	22 Jun 66	0031-0107	0-160	Y
816325	842	51°43.8'	175°20'	1.8	1 Jul 66	0309-0347	0-200	Y
816326	849	52°58.5'	162°48'	3.0	6 Jul 66	0707-1330	0-2400	Y
—	843	51°01.0'	171°32.0'	1.8	2 Jul 66	0305-0345	0-200	Y
—	850	53°33.8'	160°08.0'	1.8	7 Jul 66	0125-0205	0-160	Y
—	1016	44°44.4'	125°44.6'	1.8	14 Feb 67	0418-0500	0-200	Y
—	176-34	52°29'	160°59'	1.8	1 Aug 57	0146-0222	0-60	B
—	176-85	51°26'	174°10'	1.8	24 Aug 57	0032-0124	0-225	B
—	235-23	52°49'	142°46'	1.8	20 Jul 59	2334-0028	0-225	B
—	235-44	53°55.5'	153°17'	1.8	24 Jul 59	0337-0454	0-400	B
—	235-45	53°56.5'	157°57.5'	1.8	25 Jul 59	0004-0119	0-400	B
—	235-47	53°57'	157°49'	1.8	25 Jul 59	0223-0300	0-60	B
<i>Gonatus oregonensis</i>								
687	1011	44°46.2'	125°52.0'	1.8	13 Feb 67	1347-1728	0-1500	Y
690	2057#4	44°35.1'	125°32.5'	2.4	21 Jul 71	0314-0348	300-400	Y
692	2110#5	44°37.4'	125°41.3'	2.4	29 Nov 72	0327-0335	surface	Y
040162*	1692	44°39.1'	128°21.8'	1.8	21 Aug 69	0327-0414	0-240	C
057608	1563	44°40.2'	127°49.1'	1.8	30 Jun 69	2330-0020	0-220	Y
057609	2110#1	44°33.9'	125°39.2'	2.4	29 Nov 72	0105-0216	0-200	Y
816327	1091	44°40.9'	127°56.2'	1.8	3 Jun 67	2300-2343	0-185	Y
816328	2107#5	44°37.2'	125°42.3'	2.4	28 Nov 72	0641-0715	200-300	Y
—	884	44°54.2'	125°25'	1.8	25 Aug 66	0100-0540	0-2000+	Y
—	953	44°39.0'	125°41.4'	1.8	18 Dec 66	0042-0415	0-950	Y

Tentacle stalk suckers are small (about 0.04 mm diameter) and numerous. In a 19 mm individual, there are 25 suckers in the ventral row, 28 in the dorsal row, and 57 on the oral face between the two rows. In smaller individuals, the stalk suckers appear to be arranged in roughly six alternating rows. Measurements of the holotype and paratypes are given in Table 3.

Buccal connectives are attached dorsally to arms I and II and ventrally to arms III and IV. Seven short buccal lappets are present.

A spindle-shaped liver is present in smaller individuals, oriented obliquely to the body axis. Complete hook development is unknown, but the central hook develops at 20-24 mm DML; arm hooks and other club hooks may develop at sizes greater than 24 mm DML.

No trace of chromatophores remains on these specimens, most likely due to preservation. No photophores are present.

The radula (Figure 2e) is of the normal *Gonatus* type, with five rows of teeth: a tricuspid rhachidian, and simple admedian and lateral teeth on each side. No ridges are

visible on the teeth. The central tooth of the rhachidian is off-center, alternating sides with each row, *i.e.*, the teeth of the second and fourth rows are aligned, as are the teeth of the first and third rows.

The upper mandible is slightly curved and acutely pointed; both the upper and lower are pigmented only at the tips in a specimen of 19 mm DML (Figure 1a).

Type designation: The holotype is a juvenile of 24 mm DML. R/V *Brown Bear* cruise 235, station 46; W. Aron and P. McCrery; south of Alaska Peninsula, northeast Pacific; 53°57'N, 157°39'W; collected with a 1.8 m IKMT fished open 0-225 m; 25 July 1959, 0129-0222 h.

Location of type: California Academy of Sciences, Department of Invertebrate Zoology, Golden Gate Park, San Francisco. Catalogue number: CAS 040163.

Etymology: *ursabrunae*, after the vessel R/V *Brown Bear*, from which the holotype was collected.

Distribution: The known distribution is limited to the northeastern Pacific, but may extend into the northwest-

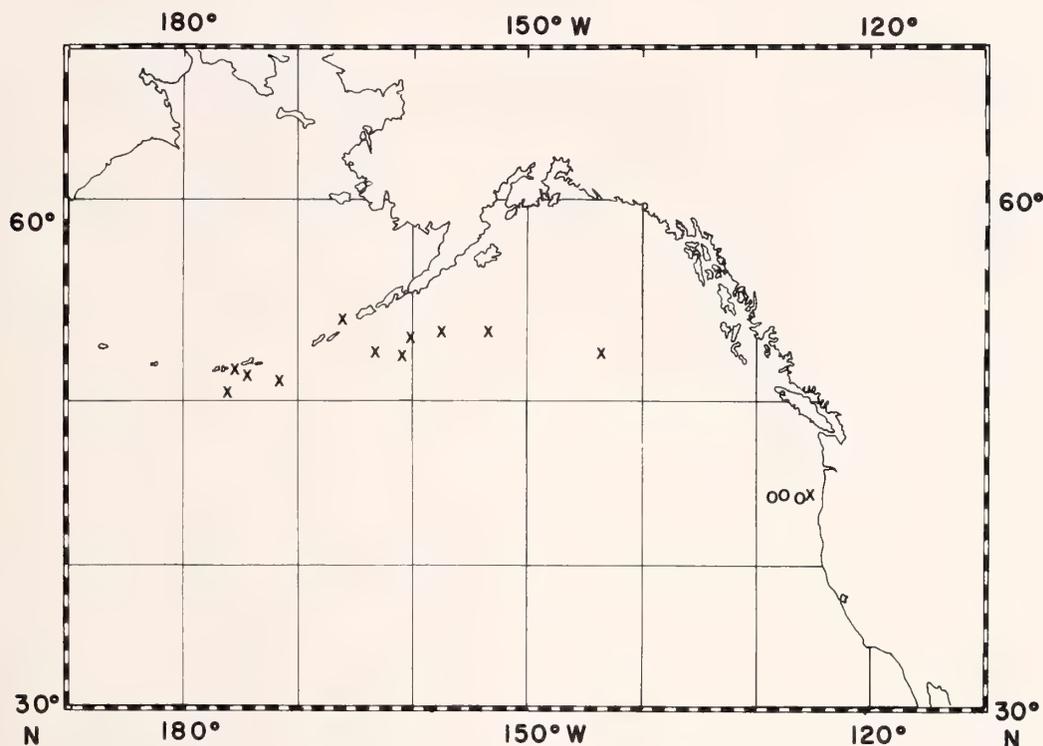


Figure 3

Location of hauls capturing *Gonatus ursabrunae* (x) and *Gonatus oregonensis* (o). For clarity, not all hauls are shown: three hauls captured *G. ursabrunae* in the area 53°56'–57'N, 157°39'–58'W; seven hauls captured *G. oregonensis* in the area 44°34'–54'N, 125°25'–52'W.

ern Pacific, considering Sasaki's specimen (see Discussion below). Twenty individuals have been collected in 14 mid-water hauls (all open; mostly 0–200 m; two hauls 0–400 m, one 0–2400 m; see Table 1) from the northern California Current and the Alaska Current as far west as 176°W (Figure 3). Okutani (*in litt.*, 1982) has seen three similar individuals in the collections of the University of Alaska. One was collected at Seward (60°N, 149°W), and the others in southeastern Alaska (56°N, 134°W; 58°N, 135°W).

Discussion: *Gonatus ursabrunae* clearly belongs in the genus *Gonatus* because of the structure of the radula and the development of a central hook on the tentacular club. Comparison of similarly sized specimens shows that it is not *G. pyros*, as it lacks an optic photophore, nor is it *G. berryi*, as no arm hooks are yet evident, as they are in juvenile *berryi*; neither can it be *G. tinro*, as it does have a club hook. Comparably sized individuals are known for *G. onyx*, *G. madokai*, *G. californiensis*, *G. middendorffi*, and *Gonatus oregonensis* (spec. nov., described and discussed below); none of these demonstrates the enlarged brachial and club suckers characteristic of this species. BUBLITZ (1980:76) stated that some of his specimens of *Gonatus* type A (which was described as *G. middendorffi*, KUBODERA

& OKUTANI, 1981a) showed slightly enlarged suckers in the lateral arm rows ("1.5–2 times as large as the corresponding median sucker"); however, his figure (pl. 30) clearly shows just the reverse, that the median sucker (transforming into a hook) is larger than the lateral sucker. These specimens otherwise agree with the description of *G. middendorffi*, which is separable from *Gonatus ursabrunae* by its MWI and the size at which club hooks develop. There are other differences, especially in club armature, which serve equally well to differentiate all of these species (Tables 4, 5). *Gonatus* type C of KUBODERA, 1978, is known from individuals as large as 16 mm DML; there is no indication of enlarged suckers in these, and this type is further characterized by a separated epidermis, which does not occur in *Gonatus ursabrunae*. BUBLITZ's (1980) new species also has no indication of enlarged suckers in the lateral rows: "each sucker of the median two rows is about 1.2 times as large as the corresponding lateral sucker" (BUBLITZ, 1980:61), and has five rows of sucker buds on the tentacular stalk as opposed to six in larvae of *G. ursabrunae*. The tentacles of Bublitz's species are shorter (TLI = 37–49) but have clubs of about the same size (CLI = 18–24); in addition, the ventral marginal zone comprises 3 or 4 rows of suckers in Bublitz's species, vs. 4 or 5 in *G. ursabrunae*. Several other differ-

Table 2

Meristic indices for *Gonatus ursabrunae*. Abbreviations as in methods section, with additions: ALIM, arm length index for longest arm (length of arm over DML \times 100); \bar{X} , mean; SD, standard deviation.

Index	Type no.							Range	\bar{X}	SD
	040163	701	816326	696	057606	057607	816325			
DML	24	20	19	18	17	15	12	12-24	17.9	3.80
MWI	33	30	42	44	53	40	42	30-53	40.6	7.52
FLI	21	20	21	22	18	20	17	17-22	19.9	1.77
FWI	46	45	53	56	41	53	58	41-58	50.3	6.32
HWI	29	36	26	33	29	33	33	26-35	31.1	3.18
EDI	21	20	21	19	18	20	21	18-21	20.0	1.15
ALIM	42	45	47	56	53	47	50	42-56	48.6	4.79
TLI	79	60	63	—	71	53	67	53-79	65.5	9.03
CLI	21	25	21	—	18	13	—	13-25	19.6	4.45

ences in tentacle sucker counts and disposition are evident: suckers distal to the central hook number approximately 85 in Bublitz's species (22 mm DML), but about 110 in *G. ursabrunae* (19 mm DML); suckers of the dorsal row, ventral row, and oral face of the tentacular stalk number about 15, 10, and 0 in Bublitz's species (22 mm DML), but 28, 25, and 57, respectively, in *G. ursabrunae* (19 mm DML).

SASAKI (1929) included one larva (pl. 22, fig. 14; text fig. 128C) in the description of *Gonatus fabricii* which appears to correspond to *Gonatus ursabrunae*. Measurements of this individual have been included here, in Table 3. SASAKI (1929:269) noted: "The suckers of the first three

pairs of arms, uniform, except in the largest larva referred to, where the suckers of the outer two series on these arms are much larger than those of the inner two series." In addition, he noted that the proximal suckers on arms IV were also enlarged, and numbered from two to seven, in the larvae of *G. fabricii*, although it is not clear from the description to which specimen(s) he was referring. No such condition has been noted for *Gonatus ursabrunae*. The geographical origin of Sasaki's specimen is unknown; it apparently came from collections of the *Albatross*, and SASAKI (1929:270) listed the following localities from which the *Albatross* collected *G. fabricii*: "Milne Bay, Simushir I., Kurile group; Bowers Bank, Bering Sea; near Near

Table 3

Measurements (in mm) of selected individuals of *Gonatus ursabrunae*. "Sasaki" refers to the specimen described by SASAKI (1929) which is discussed in the text. Type no.: 040163, 057606, 057607 are CAS; 696, 701 are OSUI; 816325, 816326 are USNM. ES, enlarged sucker.

Index	Type no.							Sasaki
	040163	701	816326	696	057606	057607	816325	
DML	24	20	19	18	17	15	12	14
MW	8	6	8	8	9	6	5	6.5
FL	5	4	4	4	3	3	2	—
FW	11	9	10	10	7	8	7	—
HW	7	7	5	6	5	5	4	—
ED	5	4	4	3.5	3	3	2.5	—
AL I	7	6	7	8	6	6	5	3.5
AL II	9	9	8	10	8	7	6	4
AL III	10	9	9	10	9	7	6	4
AL IV	8	6	6	8	6	5	3	2.5
TL	19	12	12	—	12	8	8	7
CL	5	5	4	—	3	2	?	?
AH	—	—	—	—	—	—	—	—
CH	—	ES	ES	—	—	—	—	—
OCH	—	—	—	—	—	—	—	—
HAC I	18	23	—	—	—	—	—	—
HAC II	25	19	—	—	—	—	—	—
HAC III	22	20	—	—	—	—	—	—
HAC IV	30	27	—	—	—	—	—	—

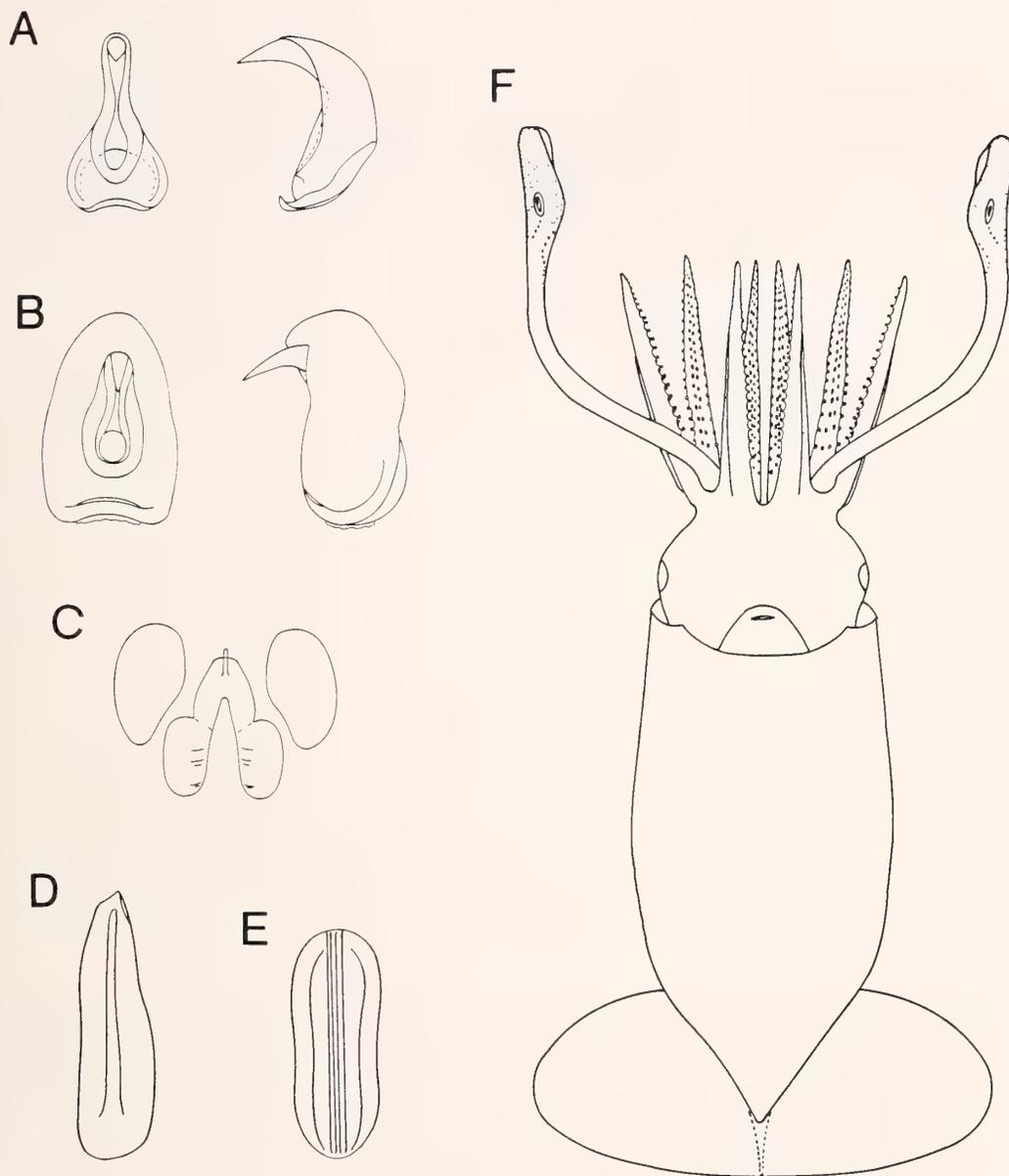


Figure 4

Gonatus oregonensis spec. nov. A-E, USNM 816327, 46 mm DML: A and B, hook of right arm III, with hood removed and with hood intact, front and lateral views; C, funnel organ; D, funnel cartilage; E, nuchal cartilage. F, whole animal, ventral aspect, CAS 057608, 31 mm DML.

Is., Aleutians; east of Kamchatka; south of Alaska; and near Commander Is."

Gonatus oregonensis Jefferts, spec. nov.

(Figures 4, 5)

Gonatus sp., E. JEFFERTS, 1983:94-98, including table 6 and fig. 31.

Material examined: **Holotype:** a juvenile of 39 mm DML; R/V *Cayuse* haul 1692; R. Findley; off the coast

of Oregon; 44°39.1'N, 128°21.8'W, collected with a 1.8 m IKMT fished open 0-240 m; 21 August 1969, 0327-0414 h; CAS 040162. **Paratype:** 1 juvenile, 46 mm DML; R/V *Yaquina* haul 1091; R. Eagle; off Oregon coast; 44°40.9'N, 127°56.2'W, 1.8 m IKMT fished open 0-185 m; 3 June 1967, 2300-2343 h; USNM 816327. **Paratype:** 1 juvenile, 35 mm DML; R/V *Yaquina* haul 1011; off Oregon coast; 44°46.2'N, 125°52.0'W, 1.8 m IKMT fished open 0-1500 m; 13 February 1967, 1347-1728 h; OSUI 687. **Paratype:** 1 juvenile, 31 mm DML; R/V

Table 4

Comparison of species of the family Gonatidae from the North Pacific. Adult characters (indices for animals over 40 mm DML), including known size range (DML in mm), number of teeth in transverse row of radula, shape of nuchal cartilage, photophores, mantle width index, maximum arm length index, size at which arm hooks develop (DML in mm), hook and sucker pattern on club (*e.g.*, hHhhh is one distal hook, a large central hook, and three proximal hooks), size (DML in mm) at which the central, distal, and proximal hooks develop, rows of suckers on the dactylus (from just distal to the hooks toward the end—in *Berryteuthis*, the manus is included; Irr, irregular), number of suckers on the club,

Species	Known size range	Teeth on radula	Nuchal cartilage	Photophores	MWI	ALIM	Arm hooks
<i>Gonatus</i>							
<i>ursabrunae</i>	12–30	5	rectangular	none	—	—	>24
<i>pyros</i>	7–66	5	rectangular	optic	26	64	17–22
<i>berryi</i>	6–119	5	rectangular	none	25–35	64–72	7–9
<i>tinro</i>	7–89	5	rectangular	none	20	64	19–21
<i>onyx</i>	2–98	5	rectangular	none	21–27	50–59	26–28 or 18–20
<i>madokai</i>	6–329	5	rectangular	none	23–30	90–103	16–19
<i>middendorffi</i>	6–296	5	rectangular	none	18–22	40–52	20–30 or 26–30
<i>oregonensis</i>	24–46	5	rectangular	none	26	63	24–30
<i>californiensis</i>	24–112	5	rectangular	none	19–33	46–55	26–29
sp. C of Kubodera	4–16	5	? rectangular	none	—	—	>16
sp. of Bublitz	7–80	5	rectangular	none	33–35	63–65	21–38
<i>Gonatopsis</i>							
<i>borealis</i>	4–290	7	panduriform	none	22–39	44–67	30–35
<i>Berryteuthis</i>							
<i>anonychus</i>	5–99	7	panduriform	none	21–29	30–33	? >30
<i>magister</i>	6–320	7	panduriform	none	27–29	62–68	>16 or 55–60

Yaquina haul 1563; P. Kalk and D. Stein; off Oregon coast; 44°40.2'N, 127°49.1'W, 1.8 m IKMT fished open 0–220 m; 30 June–1 July 1969, 2330–0220 h; CAS 057608. **Paratype:** 1 juvenile, 30 mm DML; R/V *Yaquina* haul 2057#4; W. Pearcy; off Oregon coast; 44°42.4'N, 125°32.5'W, 1.8 m IKMT fished open 0–600 m; 21 July 1971, 0314–0348 h; OSUI 690. **Paratype:** 1 juvenile, 30 mm DML; R/V *Yaquina* haul 2107#5; off Oregon coast; 44°37.2'N, 125°42.3'W, 3.0 m IKMT + MPS fished 300–200 m; 28 November 1972, 0641–0715 h; USNM 816328. **Paratype:** 1 juvenile, 30 m; R/V *Yaquina* haul 2110#1; off Oregon coast; 44°33.9'N, 125°39.2'W, 3.0 m IKMT + MPS fished 0–200–150 m; 29 November 1972, 0105–0216 h; CAS 057609. **Paratype:** 1 juvenile, 24 mm; R/V *Yaquina* haul 2110#5; off Oregon coast; 44°37.4'N, 125°41.3'W, 3.0 m IKMT + MPS fished at surface; 29 November 1972, 0327–0335 h; OSUI 692.

Additional material (all in the collections of Oregon State University): 1 juvenile, 26 mm DML; R/V *Yaquina* haul 953; station NH-50; Coleman; off Oregon coast; 44°38.8'N, 125°20.7'W, 1.8 m IKMT fished open 0–950

m; 18 December 1966, 0042–0415 h; 1 juvenile, 19 mm DML; R/V *Yaquina* haul 884; station WG-16; Coleman and Wyandt; off Oregon coast; 44°54.2'N, 125°25'W, 1.8 m IKMT fished open 0–2000 m; 25 August 1966, 0100–0540 h.

Description: Mantle plump, widest in the midsection (MWI = 29–43; meristic indices are summarized in Table 6). Ventral anterior margin of mantle emarginate (Figure 4f). The corners of this emargination project at the anterior ends of the mantle-locking cartilages. Head less wide than mantle, with at least two nuchal folds. Eyes are large, occupying the entire lateral surfaces of head (EDI = 15–23); an optic sinus is at the anterior end, between the bases of the tentacle and arm III.

Fins broad but relatively short: FWI = 80–90 for animals over 30 mm DML; FLI = 25–45. Fins united posteriorly, extending beyond the tip of the gladius. A cartilaginous end cone extends to the posterior limit of the fins. Posterior margin of fins essentially straight, anterior margin convex. Margins quite thin, fragile, especially anteriorly.

Table 4
Continued.

and the sucker distribution pattern on the tentacular stalk (*e.g.*, 1V, 1-2, 1D represents one row of suckers along ventral margin, 1-2 suckers on medial face, and 1 row along dorsal margin of the stalk). Abbreviations as in Table 3. From original data and NESIS (1972), YOUNG (1972), KUBODERA & OKUTANI (1977, 1981a, b), BUBLITZ (1980), BUBLITZ & NISHIYAMA (MS).

Club formula	C Hook	D Hook	P Hooks	Rows on dactylus	Club suckers	Stalk pattern
?H??	20-24	? (>24)	? (>24)	6->4	194+	1V, 57, 1D
hHhhhh	15-18	18-23	21-26	Irr->4	159-181	2V, 50-125, 1D
hHsshhhh	12-17	19-28	25-32	4	162-178	1V, 1-2, 1D
no hooks	—	—	—	5-6->18 >12->4-5	576-600	—
sHsssss or hHsssss	17-24	—	—	5-6->4	165-194	1V, <10, 1D
hHhhhhh	>72	>72	>72	5-6->4	215+	2V, few, 1D
hHsssss or hHshhss	>60	>60	>250	7-8->4	340	1V, few, 1D
hHhhhhss	24-30	24-30	35-39	7-8->5-6	295-370	1V, 63-74, 1D
hHhhhs	17-23	24-30	35-41	7-8->4	217-269	1V, 40-80, 1D
-S--	—	? (>16)	? (>16)	—	buds	—
hHhhhhh	13-15	>22	22-38	5-6->4	183	1V, none, 1D
—	—	—	—	—	55 max	—
no hooks	—	—	—	13->4	650-738	—
no hooks	—	—	—	16->4	1106-1273	—

Funnel reaching only slightly past the posterior extent of the eye. Funnel-locking cartilage slightly curved laterally, with a shallow medial groove which widens caudad, and with a distinct anterior fold, corresponding to a projection on the ventral surface of the mantle (Figure 4d). Funnel valve small and broad. Dorsal pad of funnel organ very broad, with an anterior papilla and narrow ovoid pads at the posterior ends of the arms (Figure 4c). General shape that of an inverted V, but with posterior portions of arms laterally offset from anterior portions. Ventral component of funnel organ consists of two broadly ovoid pads each nearly as long as the arms of the dorsal pad. Nuchal cartilage only slightly clavate, and slightly wider at anterior end. The cartilage has a narrow medial ridge with a medial groove, and broad lateral grooves (Figure 4e).

Arms of moderate length, ALI = 59-63 in 46 mm DML individual, 43-53 in 30 mm DML individual. Arm formula generally III \geq II > IV \geq I. Aboral keels are strong and nearly always evident on arms IV; they are occasionally discernible on arms I-III. Trabeculate protective membranes are exceedingly well developed on arms I-III;

the marginal rows of suckers are borne on the trabeculae. Arms I-III bear hooks in the medial rows (Figures 4a, b, 5); these develop at a mantle length of 24-30 mm. Arms IV bear four rows of suckers. Lateral suckers of arms I to III relatively small, with about eight closely set, elongate, blunt teeth (Figure 5d). Half-arm counts for two of the larger individuals are given in Table 7.

The tentacle is long, TLI = 60-105 (depending on preservational state), and bears a fairly large club (CLI = 21-20). A swimming keel is present on the dorsal surface of the dactylus, extending from the level of the distal hook to the tip of the dactylus (Figure 5g). Dorsal and ventral protective membranes are also present, but are very short and ill-developed. They originate on the stalk and extend along the club to its tip. The club bears a large central hook, a distal hook about half the size of the central one, and several proximal hooks. The central and distal hooks develop at a DML of about 24-30 mm, but the proximal hooks are not evident until a length of 35-39 mm is attained. In the proximal series (Figure 5f), the suckers next to the central hook are the first to transform into hooks, so that an animal of 39 mm may have two hooks proximal

Table 5

Comparison of early life history stages of species of the family Gonatidae. Characters for individuals under 40 mm DML, including size range of specimens included (mm DML), mantle width index, maximum arm length index, rows of suckers on tentacular stalk in larval forms (these suckers are lost as the club begins to develop), tentacle length index, and club length index. Information from original data and NESIS (1972), YOUNG (1972), KUBODERA & OKUTANI (1977, 1981a, b), BUBLITZ (1980), and BUBLITZ & NISHIYAMA (MS). (BUBLITZ, 1981, measured stretched mantle width).

Species	Size range	MWI	ALIM	Rows of stalk suckers	TLI	CLI
<i>Gonatus</i>						
<i>ursabrunae</i>	12-24	24-53	42-56	6	50-79	13-25
<i>pyros</i>	13-25	42	38-48	5-6	52	21
<i>berryi</i>	13-30	30-33	48	5-6	35-100	25
<i>tinro</i>	10-28	35-47	34-74	5-6	40	10-15
<i>onyx</i>	6-26	35-40	35-40	5	25-55	20-25
<i>madokai</i>	10-40	30-35	30-80	4-5	30-90	12-15
<i>middendorffi</i>	6-40	24-40	25-45	4	30	15
<i>oregonensis</i>	24-39	29-43	42-67	6	60-105	21-30
<i>californiensis</i>	29-38	29-32	41-47	?	66-82	21-24
sp. C of Kubodera	6-16	40-50	30	5-6	50-75	4-8
sp. of Bublitz	11-13	35-61	23-55	5	41-75	18-34
	16-22	42-45	37-59	5	37-49	18-24
<i>Gonatopsis</i>						
<i>borealis</i>	5-30	30-40	25-40	4-5	25-30	—
<i>Berryteuthis</i>						
<i>anonychus</i>	5-30	25-45	33-40	3-4	~50	7-18
<i>magister</i>	7-16	40-45	35-40	5-6	50	5-13

to the central, and three to four suckers, and an animal of 46 mm may have four hooks proximal to the central, and two suckers.

The carpal-locking zone consists of four to five ridges with accompanying suckers, alternating with five to six knobs. This series extends onto the stalk. The ventral marginal zone contains four rows of suckers and the dorsal marginal zone five. The tentacular stalk bears single rows of suckers on both the ventral and dorsal margin of its inner face. The space between the rows is beset with many

small suckers. The number of suckers in the ventral row is at least 74 in the 46 mm specimen, in the dorsal row, at least 63, and on the medial face, at least 70. In a 24 mm specimen, the stalk suckers appear to be arranged in six, somewhat irregular, alternating rows.

The dactylus bears many small but roughly equal-sized suckers (0.20 to 0.25 mm at DML 46 mm). These have narrow openings and four to six long, slender, peglike teeth on the distal border of the inner ring (Figure 5e) and are disposed in seven or eight rows just distal to the

Table 6

Meristic indices for *Gonatus oregonensis*. Abbreviations as in Table 2.

Index	Type no.								Range	\bar{X}	SD
	816327	040162	687	057608	690	816328	057609	692			
DML	46	39	35	31	30	30	30	24	24-46	33.1	6.77
MWI	35	31	29	42	33	43	33	38	29-43	35.5	5.07
FLI	48	44	34	32	40	40	40	33	32-48	38.9	5.59
FWI	89	82	80	81	83	83	83	58	58-89	79.9	9.23
HWI	22	28	31	29	30	23	30	25	22-31	27.2	3.45
EDI	16	22	—	19	23	15	20	17	15-23	18.9	3.02
ALIM	63	64	54	58	53	60	67	42	42-67	57.6	7.95
TLI	96	69	80	81	63	107	103	75	63-107	84.2	16.1
CLI	26	23	26	23	27	30	30	21	21-30	25.8	3.28

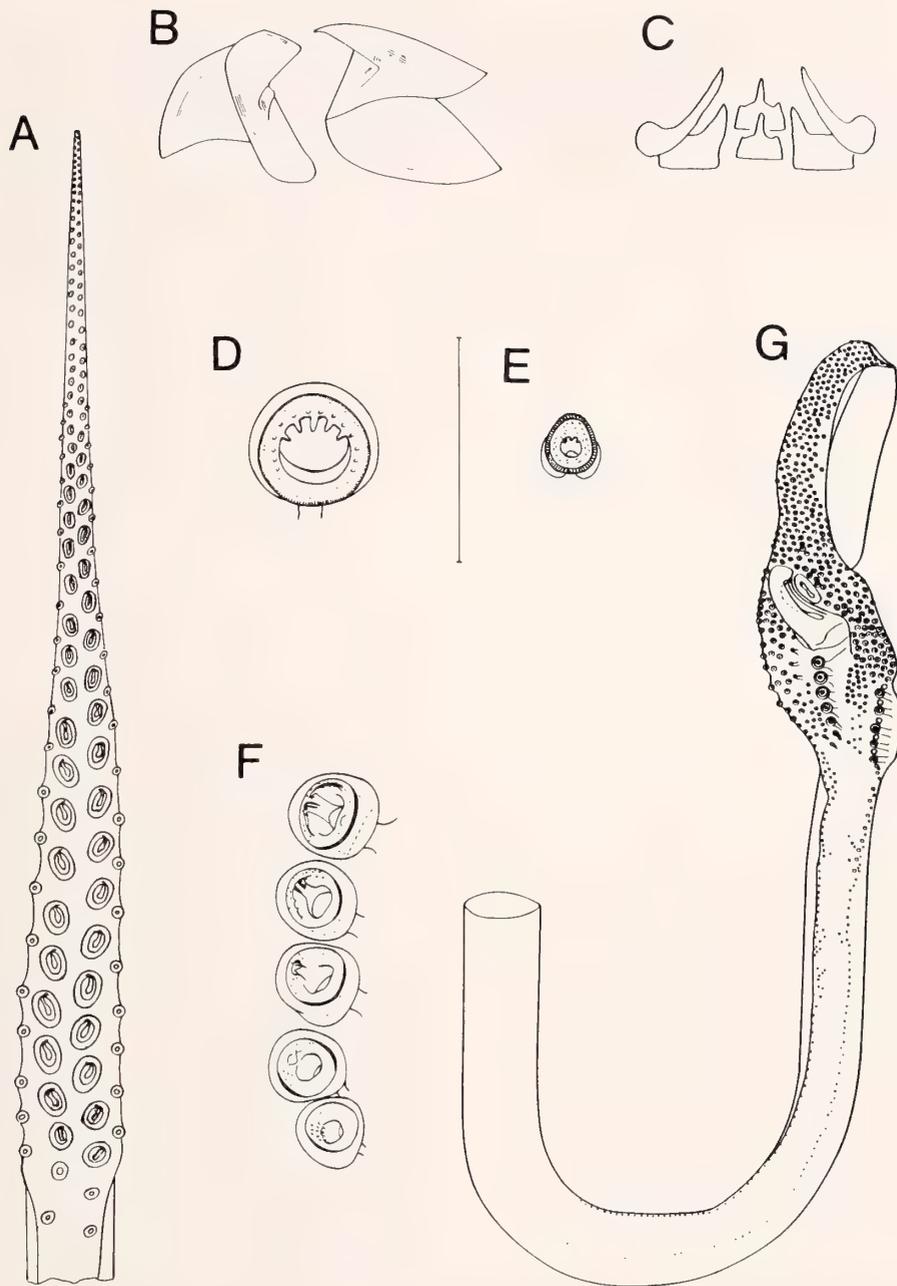


Figure 5

Gonatus oregonensis. A, right arm III, USNM 816327, 46 mm DML. B, C, OSUI 687, 35 mm DML: B, mandibles; C, radula. D–G, USNM 816327, 46 mm DML: D, brachial sucker, right arm III; E, dactylus sucker; F, proximal series of club; G, tentacle. Scale (D and E), 1 mm.

hooks, decreasing to five or six rows near the tip (Figure 5g). A cirlet of small suckers occupies the tip of the dactylus. The total number of suckers on the dactylus, ventral marginal zone, and dorsal marginal zone is 320 in the 46 mm specimen, and shows a range of 295 to 370 in the other specimens.

Buccal connectives are connected to dorsal borders of arms I and II and to the ventral borders of arms III and IV.

The radula is of the normal quinquedentate *Gonatus* type, with tricuspid rhachidian, unicuspid admedian, and unicuspid lateral. No ridges are apparent on the radular

Table 7

Measurements (in mm) and counts for selected individuals of *Gonatus oregonensis*. Type no.: 040162, 057608, 057609, CAS; 687, 690, 692, OSUI; 816327, 816328, USNM. D, damaged; +, present; -, absent or not applicable.

Haul: type no.:	1091 816327	1692 040162	1011 687	1563 057608	2057#4 690	2107#5 816328	2110#1 057609	2110#5 692
Index								
DML	46	39	35	31	30	30	30	24
MW	16	12	10	13	10	13	10	9
FL	22	17	12	10	12	12	12	8
FW	41	32	28	25	25	25	25	14
HW	10	11	11	9	9	7	9	6
ED	7.5	8.5	D	6	7	4.5	6	4
AL I	27	22	16	15	13	13	15	8
AL II	28	25	19	18	15	16	19	10
AL III	29	24	19	17	16	18	20	10
AL IV	28	18	17	14	13	14	18	9
TL	44	27	28	25	19	32	31	18
CL	12	9	9	7	8	9	9	5
AH	+	+	+	+	+	+	+	-
CH	+	+	+	+	+	+	+	-
DH	+	+	+	+	+	+	+	-
PH	4	2	-	-	-	-	-	-
CS	320	347	339	355	370	295	320	300
HAC I	20/14	-	17/5	-	-	-	-	-
HAC II	22/15	-	19/9	-	-	-	-	-
HAC III	19/15	-	17/9	-	-	-	-	-
HAC IV	47	-	35	-	-	-	-	-

teeth, and the central teeth of the rhachidian are aligned in each row (Figure 5c).

The upper mandible is long and acute; both upper and lower mandibles are darkly colored only on the tips in a specimen of 46 mm (Figure 5b).

Type designation: The holotype is a juvenile of 39 mm DML. R/V *Cayuse*, haul 1692; Findley; off the coast of Oregon; 44°39.1'N, 128°21.8'W; collected with a 1.8 m IKMT fished open 0-240 m; 21 August 1969, 0327-0414 h.

Location of type: California Academy of Sciences, Department of Invertebrate Zoology, Golden Gate Park, San Francisco. Catalogue number: CAS 040162.

Etymology: *oregonensis*, after the type locality; to emphasize the morphological similarity to another species localized in the California Current, *G. californiensis*.

Distribution: This species is currently known only from waters off Oregon. Ten individuals were collected in ten midwater hauls (all open, mostly 0-400 m; one 0-1500 m, one 0-2000 + m) in the northern portion of the California Current system (Figure 3). Measurements for eight of these are given in Table 7.

Discussion: This species is easily separable from all but one of the described species of *Gonatus* (Table 4, 5). The distribution of hooks on the club separates it from *G.*

berryi (in which the proximal hooks are separated from the central hook by one or two suckers), from *G. onyx* (no proximal hooks), and from *G. tinro* (no club hooks). *Gonatus pyros* has an optic photophore, and *G. madokai* has only eight to ten minute suckers on the oral face of the tentacular stalk (several other characters also serve to separate these species). *Gonatus middendorffi* develops all club hooks at a much larger size (over 60 mm DML), and has a more slender body. *Gonatus* sp. of BUBLITZ (1980) has fins which are somewhat less broad (FWI = 43-87 vs. 80-89 in *Gonatus oregonensis*), and shows significant differences in the number and disposition of club suckers (probably fewer than 100 club suckers in *Gonatus* sp. of BUBLITZ, 1980, arranged in four rows on the dactylus).

This species is less easily separable from *Gonatus californiensis*. The distribution of hooks on the club is the same in the two species, and the size at which all hooks develop is similar. There are, however, consistent differences in fin dimensions, in sucker counts on the club, and in distribution of suckers on the dactylus. My present collection does not contain mature individuals; these differences may be better characterized on examination of larger individuals. YOUNG's (1972) specimens of *Gonatus californiensis* (29-112 mm DML) showed a FWI = 54-70. Specimens of *G. oregonensis* 30 mm and over had a FWI = 80-89. The clubs are also somewhat larger in *G. oregonensis*: CLI = 21-30 vs. 17-24 in *G. californiensis*. Club sucker counts show no overlap in the two species:

G. oregonensis ranges from 295 to 370, and Young's *G. californiensis* from 217 to 269. In *Gonatus oregonensis*, suckers are arranged in seven to eight rows at the base of the dactylus, and decrease to five to six rows at the tip. In *G. californiensis*, the dactylus suckers are disposed in eight rows basally and "decrease to four rows about halfway out on the dactylus" (YOUNG, 1972:52). The arms are also noticeably longer in *G. oregonensis* than in *G. californiensis*: at 46 mm DML, the longest arms (III and II) are 23–24 mm in *G. californiensis* and 28–29 mm in *G. oregonensis*. Further comparison supports this difference (the data for *G. californiensis* are from YOUNG, 1972):

Arm length index for longest arms (II, III)

DML	<i>californiensis</i>	<i>oregonensis</i>
46 mm	50–52	61–63
38–39	47	62–64
34–35	47	54
29–30	41	50–67

This new form thus represents an intermediate condition between *Gonatus tinro*, which has a *Berryteuthis*-like club with no hooks but many (>400) suckers, and *G. californiensis*, *G. pyros*, and *G. madokai*, which have central, distal, and proximal hooks, but fewer (<270) suckers on the club. I believe that this form represents a distinct species, as several characters show no overlap with *G. californiensis*: fin dimensions, arm length, and sucker number and distribution on the club.

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LITERATURE CITED

- ARON, W. 1958. Preliminary report of midwater trawling studies in the north Pacific Ocean. Tech. Rept. 58. Univ. Wash. Dept. Oceanogr., Seattle.
- ARON, W. 1962. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. J. Fish. Res. Bd. Canada 19(2):271–314.
- BÉ, A. W. H. 1962. Quantitative multiple opening and closing plankton samplers. Deep-Sea Res. 9:144–151.
- BERRY, S. S. 1913. Notes on some west American cephalopods. Proc. Acad. Natur. Sci. Philadelphia 1913:72–77.
- BUBLITZ, C. 1980. Systematics of the cephalopod family Gonatidae from the southeastern Bering Sea. Master's Thesis, Univ. Alaska, Fairbanks. 177 pp.
- BUBLITZ, C. & T. NISHIYAMA. Manuscript. Developmental morphology of the gonatid cephalopods, with special reference to *Gonatus tinro*.
- FISCUS, E. H. 1982. Predation by marine mammals on squids of the eastern North Pacific Ocean and the Bering Sea. Mar. Fish. Rev. 44(2):1–10.
- GRAY, J. E. 1849. Catalogue of the Mollusca in the collection of the British Museum: I, Cephalopoda Antepedia. London. 164 pp.
- HOYLE, W. E., 1886. Report on the Cephalopoda collected by HMS *Challenger* during the years 1873–76. Rept. Voy. Challenger, Zool. 16(44):1–246.
- IMBER, M. J. 1978. The squid families Cranchiidae and Gonatidae (Cephalopoda: Teuthoidae) in the New Zealand region. New Zealand J. Zool. 5:445–484.
- ISAACS, J. D. & L. W. KIDD. 1953. Isaacs-Kidd midwater trawl. Scripps Inst. Oceanogr. Ref. 53-3. 21 pp.
- JEFFERTS, K. 1983. Zoogeography and systematics of cephalopods of the northeastern Pacific Ocean. Doctoral Thesis, Oregon State Univ., Corvallis. 291 pp.
- KRISTENSEN, T. K. 1981. The genus *Gonatus* Gray, 1849 (Mollusca: Cephalopoda) in the North Atlantic. A revision of the North Atlantic species and description of *Gonatus steenstrupi* n. sp. Steenstrupia, Zool. Mus. Univ. Copenhagen 7(4):61–99.
- KUBODERA, T. 1978. Systematics and morphological changes with growth in the early life stages of pelagic squids of the family Gonatidae in the Subarctic Pacific region. Master's Thesis, Fac. Fish., Hokkaido Univ. 107 pp.
- KUBODERA, T. & K. JEFFERTS. 1984. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific. Bull. Nat. Sci. Mus. Tokyo 10(3):91–106 *et seq.* in press.
- KUBODERA, T. & T. OKUTANI. 1977. Description of a new species of gonatid squid, *Gonatus madokai* n. sp., from the northwest Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). Jap. J. Malacol. (Venus) 36(3):123–151.
- KUBODERA, T. & T. OKUTANI. 1981a. A new species of gonatid squid, *Gonatus middenдорffi* n. sp., from the northern North Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). Bull. Nat. Sci. Mus., Tokyo, Ser. A 7(1):7–26.
- KUBODERA, T. & T. OKUTANI. 1981b. The systematics and identification of larval cephalopods from the northern North Pacific. Res. Inst. N. Pac. Fish. Hokkaido Univ., Spec. Vol.: 131–159.
- LEBRASSEUR, R. J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Bd. Canada 23(1):85–100.
- LICHTENSTEIN, K. M. H. 1818. *Onychoteuthis*, seprien mit kralen. Isis 1818:1591–1592.
- LÖNNBERG, E. 1898. On the cephalopods collected by the Swedish expedition to Tierra del Fuego, 1895–96. Svenska Expeditionen till Magellanslanderna 2(4):49–64.
- MIDDENDORFF, A. T. 1849. Beiträge zu einer Malacozoologia Rossica. II. Aufzählung und Beschreibung der zur Meeresfauna Russlands gehörigen Einschaler. Mém. Acad. Imp. Sci. St. Pétersbourg, 6me Sér., 6:329–516.
- NAEF, A. 1921. Das System der dibranchiaten Cephalopoden und die mediterranen Arten derselben. Mitt. Zool. Stn. Neapel 22:527–542.
- NAEF, A. 1923. Fauna und Flora des Golfes von Neapel und

- der angrenzenden Meeres-Abschnitte. Monograph 35. Cephalopoda. 2 vols. 863 pp. (Translated by Israel Progr. Sci. Trans., 1972, Jerusalem, 917 pp.)
- NESIS, K. N. 1972. Two new species of gonatid squids from the North Pacific. Zool. Zh. 51(9):1300-1307.
- OKIYAMA, M. 1969. A new species of *Gonatopsis* from the Japan Sea, with the record of a specimen referable to *Gonatopsis* sp. Okutani, 1967 (Cephalopoda: Oegopsida, Gonatidae). Publ. Seto Mar. Biol. Lab. 17(1):19-32.
- OKUTANI, T. & T. NEMOTO. 1964. Squids as the food of sperm whales in the Bering Sea and Alaskan Gulf. Scient. Rep. Whales Res. Inst. Tokyo 18:111-122.
- PEARCY, W. G. 1964. Some distributional features of mesopelagic fishes off Oregon. J. Marine Res. 22(1):83-102.
- PEARCY, W. G. & L. HUBBARD. 1964. A modification of the Isaacs-Kidd midwater trawl for sampling at different depth intervals. Deep-Sea Res. 11(2):263-264.
- PEARCY, W. G., E. E. KRYGIER, R. MESECAR & F. RAMSEY. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.
- PEARCY, W. G. & R. S. MESECAR. 1971. Scattering layers and vertical distribution of animals off Oregon. Proc. Int. Symp. Biol. Sound Scatt. Ocean. U.S. Naval Oc. Office MC Rept 005:381-394.
- PEARCY, W. G. & G. L. VOSS. 1963. A new species of gonatid squid from the northeastern Pacific. Proc. Biol. Soc. Wash. 76:105-112.
- SANGER, G. A. & P. A. BAIRD. 1977. The trophic relationships of marine birds in the Gulf of Alaska and the southern Bering Sea. Part 14. In: J. C. Bartonek, C. J. Lensink, P. J. Gould, R. E. Gill & G. A. Sanger (co-principal investigators), Annual Report, OCSEAP RU-341. U.S. Fish. Wildl. Serv. OBS-CE. Anchorage, Alaska, 1 April 1977.
- SASAKI, M. 1920. Report on the cephalopods collected during 1906 by the United States Bureau of Fisheries steamer "Albatross" in the northwestern Pacific. Proc. U.S. Natl. Mus. 57(2310):163-203.
- SASAKI, M. 1923. On a new eight-armed squid from Hokkaido, *Gonatopsis borealis* n. sp. Annot. Zool. Japon. 10:203-207.
- SASAKI, M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. J. Fac. Agric. Hokkaido Imp. Univ. 20 Suppl. 10:1-357.
- VOSS, G. L. 1956. A review of the cephalopods of the Gulf of Mexico. Bull. Mar. Sci. Gulf Carrib. 6(2):85-178.
- YOUNG, R. E. 1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithsonian Contrib. Zool. 97:1-150.

A New Species of *Eubranchus* Forbes, 1838, from the Sea of Cortez, Mexico

by

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Abstract. The nudibranch *Eubranchus cucullus* spec. nov. from the Sea of Cortez, Mexico is described. This description represents the second occurrence of the genus *Eubranchus* in the Sea of Cortez.

THE GENUS *Eubranchus* forms a group composed primarily of temperate species (EDMUNDS & KRESS, 1969). During the collection of opisthobranch mollusks in the Sea of Cortez a new species of aeolid nudibranch belonging to the genus *Eubranchus* Forbes, 1838, was discovered. To date the only other eubranchid nudibranch reported from the Sea of Cortez is *Eubranchus rustyus* (Marcus, 1961) (MCDONALD, 1983:186). The description of a new species is presented here.

Family EUBRANCHIDAE Odhner, 1934

Eubranchus Forbes, 1838

Eubranchus cucullus Behrens, spec. nov.

(Figures 1 to 5)

Material examined: (1) **Holotype:** One specimen approximately 5 mm long (preserved) collected in 10 m of water at Puerto Refugio, Isla Angel de La Guarda, Baja

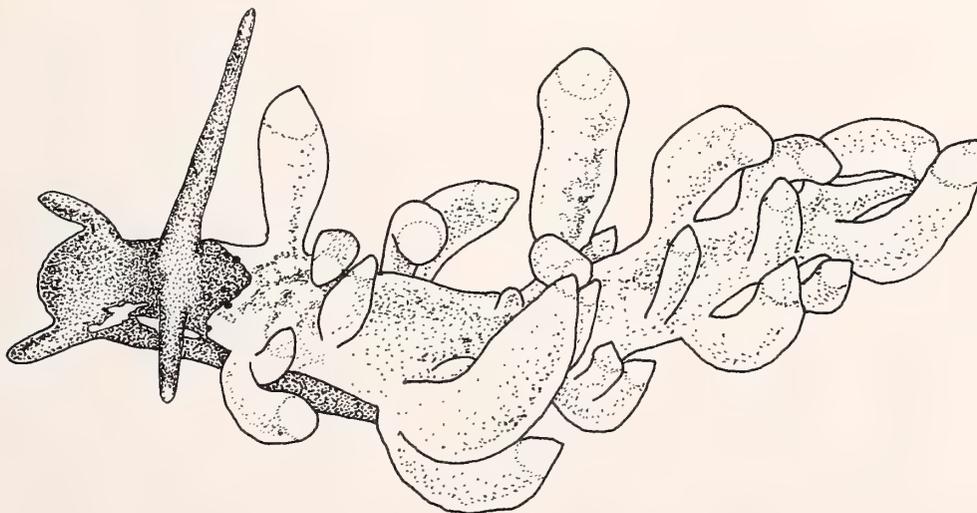


Figure 1

Dorsal view of *Eubranchus cucullus* spec. nov. Puerto Peñasco, Sonora, Mexico. April 21, 1978. Drawn from color transparency.



Figure 2

Eubranthus cucullus spec. nov. Puerto Refugio, Isla Angel de La Guarda, Baja California, Mexico. Approximately 10 mm. Photograph by Jeff Hamann.

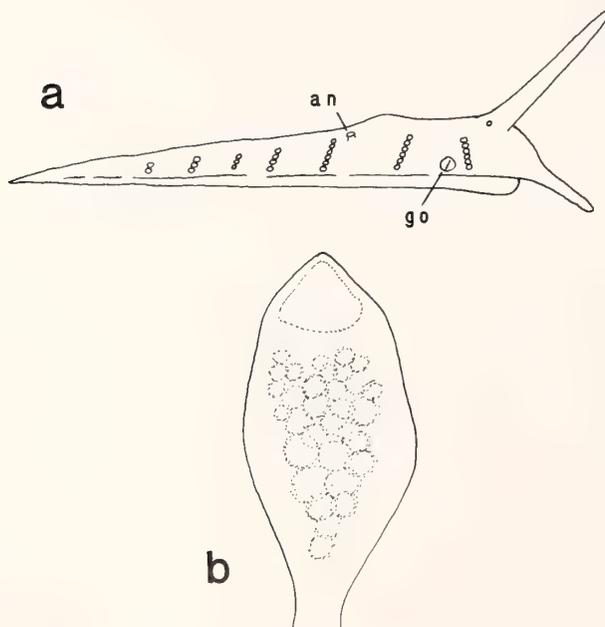


Figure 3

a. Diagrammatic right lateral view of body of *Eubranthus cucullus* spec. nov.; an = anus, go = genital orifice. b. Detail of ceras of *Eubranthus cucullus* spec. nov.

California, Mexico (Lat. 29°32'50"N; Long. 113°35'55"W) in August 1982 by Jeff Hamann. This specimen is deposited in the collection of the California Academy of Sciences, Department of Invertebrate Zoology and Geology (CAS), San Francisco, California, CAS Catalogue No. 055515.

(2) **Paratypes:** One specimen, 4 mm long (preserved) collected with the holotype is deposited in the CAS collection, Catalogue No. 055516.

(3) One specimen, 3 mm long (preserved) collected with the holotype is also deposited in the CAS collection (Catalogue No. 055517). A color transparency of a living specimen of *Eubranthus cucullus* is on file at CAS.

Description: The living animals were up to 10 mm long. The body is typically aeolidiform (Figures 1, 2). The foot is narrow, linear, and tapering posteriorly into a short blunt tail. The foot corners are triangular but not elongate. The cephalic tentacles are cylindrical with a blunt tip and slightly less than one-half the length of the rhinophores (Figures 1, 3a). The rhinophores are long, smooth, and tapering to a blunt tip (Figures 1, 3a). The cerata are cylindrical and irregularly inflated (Figure 3b). The liver diverticulum is nodular within each ceras. The cerata are arranged in 6 oblique rows dorsolaterally on either side of the dorsum. An example of the branchial half formula is I 5-8, II 6-7, III 6, IV 3-4, V 3, VI 2.

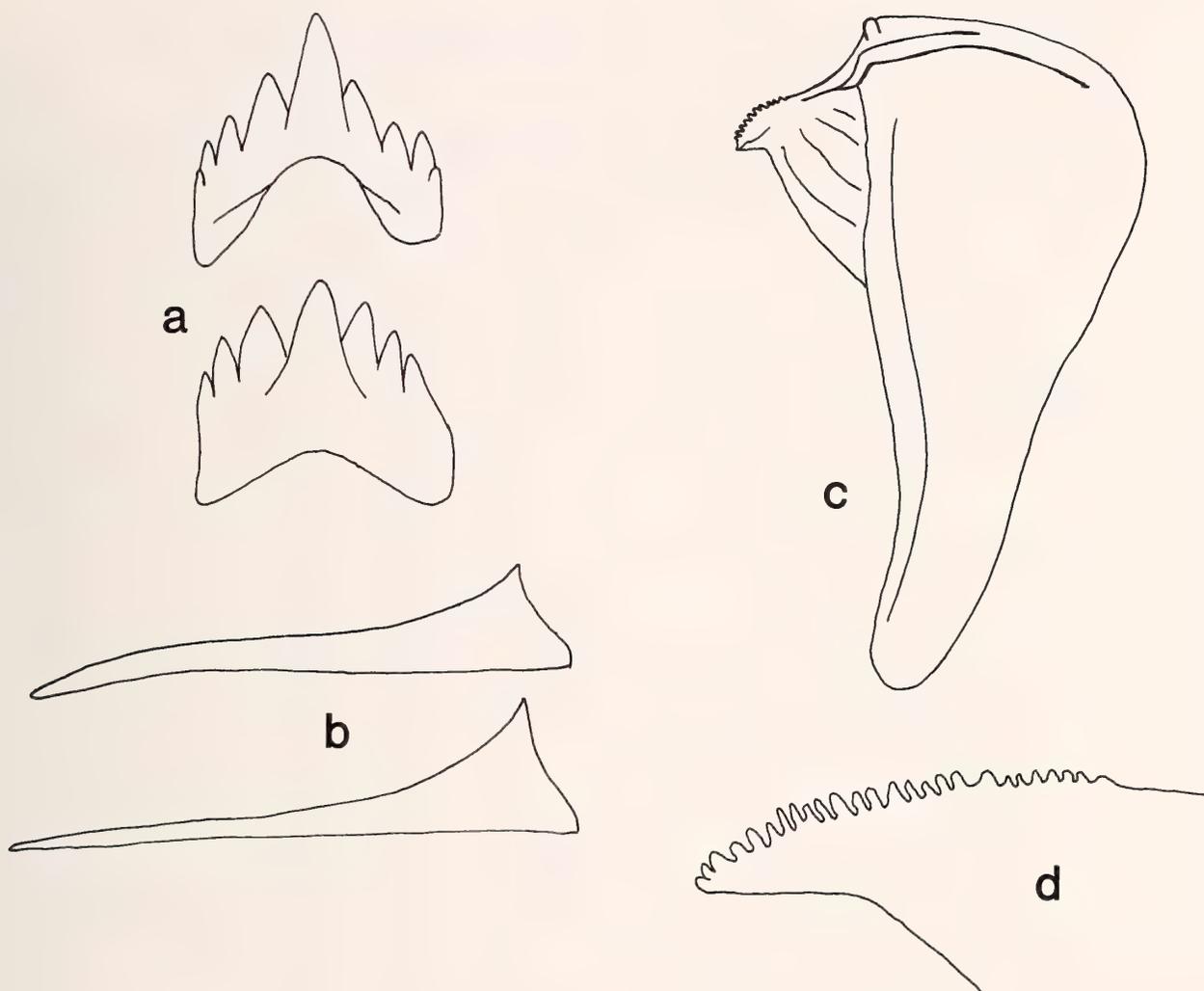


Figure 4

Radula and jaw of *Eubranchus cucullus* spec. nov. a. Rachidian tooth. b. Lateral tooth. c. Jaw plate. d. Masticatory edge of jaw.

The first two rows are anterior to the pericardial elevation (Figure 3a). The largest cerata are closest to the midline, those at the margins being smaller. The anal pore is anterior to the medial ceras of the third row and ventral to the pericardial elevation (Figure 3a). The genital orifice lies posteroventrally to the first ceratal row on the right side (Figure 3a).

Except for the head region, rhinophores, and anterior margins of the foot, the entire body is encrusted with an opaque white pigmentation (Figure 2). The head, cephalic tentacles, rhinophores, and the anterior half of the foot margins are deep rust-brown. On the rhinophores this pigmentation diminishes, leaving them transparent. In some specimens, opaque white marks occur on the sides of the head and cephalic tentacles. Variable numbers of rust-brown specks and spots occur dorsomedially on the

notum and subapically on the cerata. In some specimens the cnidosac appears cream colored, while in others it is transparent.

The radular formula is $82 \times 1.1.1$. The central cusp of the rachidian tooth projects above the 3 or 4 large lateral denticles per side (Figure 4a). The lateral teeth, thin rectangular plates with a single triangular cusp directed toward the rachidian (Figure 4b), are typical of *Eubranchus*. The basal leg of the lateral tooth is extremely long and tapering, measuring from 4–5 times the height of the cusp. The jaws are narrow, tapering posteriorly (Figure 4c). The masticatory border bears about 25 conical denticles (Figure 4d). The penis is conical and armed with a stylet (Figure 5a).

The egg mass is a white-cream colored coil of about $1\frac{1}{2}$ whorls attached to the substrate at the center of the whorl

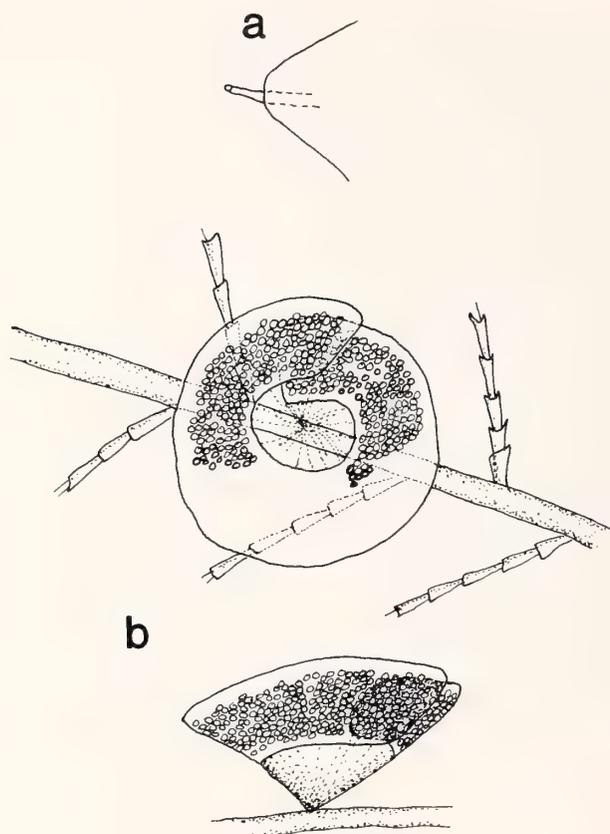


Figure 5

a. Penis of *Eubranthus cucullus* spec. nov. b. Egg mass of *Eubranthus cucullus* spec. nov. (All eggs not shown.)

(Figure 5a). This mass consists of more whorls than that described by HURST (1967) for *Eubranthus olivaceus*. The outer edge of the coil is free of egg capsules. The egg capsules are closely arranged, each containing a single egg. The egg masses collected in August 1982 averaged 2 mm in diameter and less than 0.5 mm in height. One coil was 2–3 eggs thick and 8–10 eggs wide. Egg ribbons were encountered attached to the perisarc of an unidentified plumularid hydroid.

Eubranthus cucullus is known intertidally and subtidally to depths of 10 m. Specimens are collected most commonly on plumularid hydroids. Localities within the northern and central Gulf of California where this species has been collected include Puerto Peñasco, Sonora, Mexico and Puerto Refugio, Isla Angel de La Guarda, and Loreto, Baja California, Mexico.

Discussion: The characteristics delineating the genus *Eu-*

branchus are concise and well defined (EDMUNDS & KRESS, 1969). In their review of the genus, EDMUNDS & KRESS (1969) listed 24 species. ROLLER (1972) added *Eubranthus sanjuanensis* from the northeastern Pacific fauna. BABA (1975) described two new species from the northwest Pacific, and ORTEA (1979) added the most recent species from the Canary Islands. Although some taxonomic problems have existed among European species, as chronicled by Edmunds & Kress, the northeastern Pacific members of the genus are clearly distinguishable. Of the 28 species known worldwide, none exhibit the striking white encrustation over the body or the dark rust-brown head. This characteristic alone establishes *Eubranthus cucullus* as a distinct species. Concerning the four west American species, the greater number of rows of teeth in the radula of *E. cucullus* (82) is distinctive. *Eubranthus misakiensis* Baba, 1960, has 40–46; *E. olivaceus* (O'Donoghue, 1922), has 32–35; *E. rustyus* (Marcus, 1961) has 50–60; and *E. sanjuanensis* has 50 (ROLLER, 1972; McDONALD, 1983). The shape of the lateral teeth and the denticulation of the masticatory edge of the jaw also separate this species as distinct. *Eubranthus cucullus* has a very long tapering tooth, and 25 denticles on the jaw edge, twice as many as occur in the four other west American species.

The specific name *cucullus*, from the Latin word for "hood" or "cowl," is chosen to call attention to its dark rust-brown cephalic hood.

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LITERATURE CITED

- BABA, K. 1975. On two new species of *Eubranthus* from Ayukawa, Echizen coast, Japan Sea side of middle Japan (Nudibranchia; Eolidoidea; Eubranthidae). *Jap. J. Malacol. (Venus)* 34(3–4):65–72.
- EDMUNDS, M. & A. KRESS. 1969. On the European species of *Eubranthus* (Mollusca: Opisthobranchia). *J. Mar. Biol. Assoc. U.K.* 49:879–912.
- HURST, A. 1967. The egg masses and veligers of thirty northeast Pacific Opisthobranchs. *Veliger* 9(3):255–288.
- MCDONALD, G. 1983. A review of the nudibranchs of the California coast. *Malacologia* 24(1–2):114–276.
- ORTEA, J. 1979. Una nueva especie de *Eubranthus* (Mollusca: Opisthobranchia) de Tenerife, Isla Canarias. *Rev. Fac. Cienc. Univ. Oviedo (Ser. Biología)* 20–21(1979–80):169–176.
- ROLLER, R. A. 1972. Three new species of eolid Nudibranch from the west coast of North America. *Veliger* 14(4):416–423.

The Role of Shell Geometry as a Deterrent to Predation in Terebrid Gastropods

by

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Abstract. High-spined gastropod shells vary in their susceptibility to attack by durophagous (shell-destroying) predators. Slender terebrid gastropods with small apertures are damaged significantly less often than less slender species when exposed to calappid crabs. When damaged, slender terebrids are killed significantly less frequently than less slender species. The actual cause of slender terebrids' lesser vulnerability is uncertain, but small aperture size, a geometric correlate of shell geometry, may be responsible for the observed differences. High-spined shells are probably less likely than other shell shapes to be attacked successfully by other durophagous predators.

Frequencies of repair marks have been interpreted by some authors as an index of a shell's effectiveness in deterring potential predators. In experiments conducted for this study, nonlethal attacks were as common on robust terebrids as on slender forms, despite the fact that a higher proportion of attacks on robust forms were successful. Comparison of repair mark frequencies obtained from laboratory experiments to those observed in local populations showed slender terebrids bore fewer repair marks than robust forms, although the differences were not statistically significant. These observations suggest that repair marks are not an adequate index of a turritelliform shell's vulnerability to durophagous predators.

INTRODUCTION

PREDATION by durophagous (shell-destroying) predators is a major source of mortality among temperate and, especially, tropical marine mollusks (VERMEIJ, 1977a, b, 1978, 1982a, 1983). Durophagous predators employ two fundamentally different tactics in attacking gastropod prey. One tactic is crushing and the second is peeling, where the shell is pared away leaving the snail exposed. Crushing is believed to predominate on hard substrates while peeling is understood to be more common on soft substrata (VERMEIJ, 1978, 1982a, 1983; PALMER, 1979), although both modes of predation are found in both types of habitats.

Marine gastropods have evolved a variety of morphological features which serve to deter durophagous predators, including spines (PALMER, 1979), axial ribs (BERTNESS & CUNNINGHAM, 1981; VERMEIJ, 1982a), shortened spires (KITCHING *et al.*, 1966), thickened apertural lips (VERMEIJ, 1977a, 1978, 1982a), and apertures constricted by teeth or very narrow apertures (VERMEIJ, 1977a, 1978, 1979, 1982a; HUGHES & ELNER, 1979; BERTNESS & CUNNINGHAM, 1981). This paper will ex-

plore further one possible consideration: the role of shell geometry as a defense against durophagous predators. More specifically, this study will focus on the interaction between terebrid gastropods and a predatory decapod crustacean, *Calappa hepatica* (Linnaeus).

The Terebridae (Coniacea) are a family of common sand-dwelling marine neogastropods. They are limited to tropical and temperate regions and are abundant in shallow waters throughout the Indo-Pacific region. The family first appeared in the Late Cretaceous (TAYLOR *et al.*, 1980) and now includes approximately 150 extant species (BOSS, 1971). The interrelationships of terebrid genera are not well understood but the family is believed to be derived from the Conidae or an intermediate between the Conidae and Turridae, from which the Conidae were also derived (RUDMAN, 1969). The evolution and diversification of this family are both part of a general Cenozoic radiation of predatory marine neogastropods (TAYLOR *et al.*, 1980) and a part of the Mesozoic Marine Revolution (VERMEIJ, 1977a), wherein a variety of predation-resistant taxa replaced older, less resistant taxa that dominated the Paleozoic and early Mesozoic faunas.

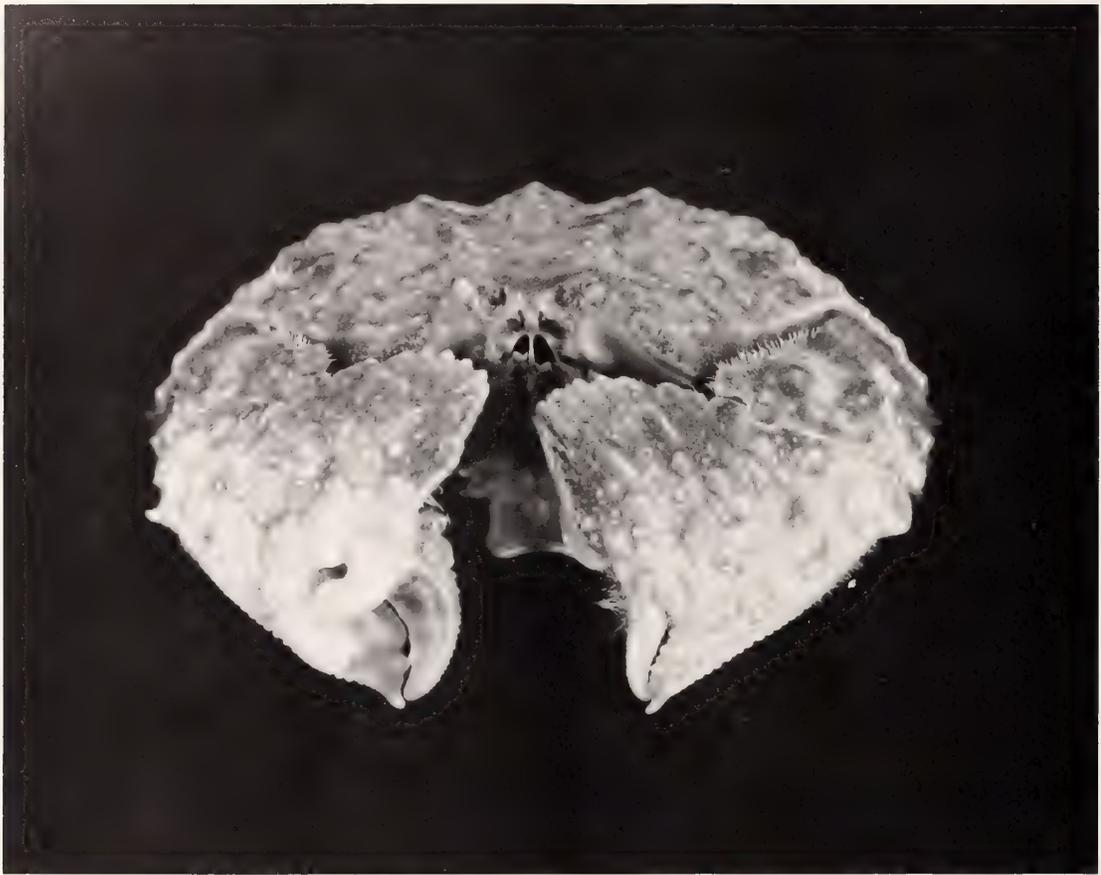


Figure 1

Calappa hepatica. Note the well-developed master cheliped and the large tooth on the dactyl that is used for peeling snails. Specimen was collected at Motupore Island, Papua New Guinea; carapace length is 65 mm.

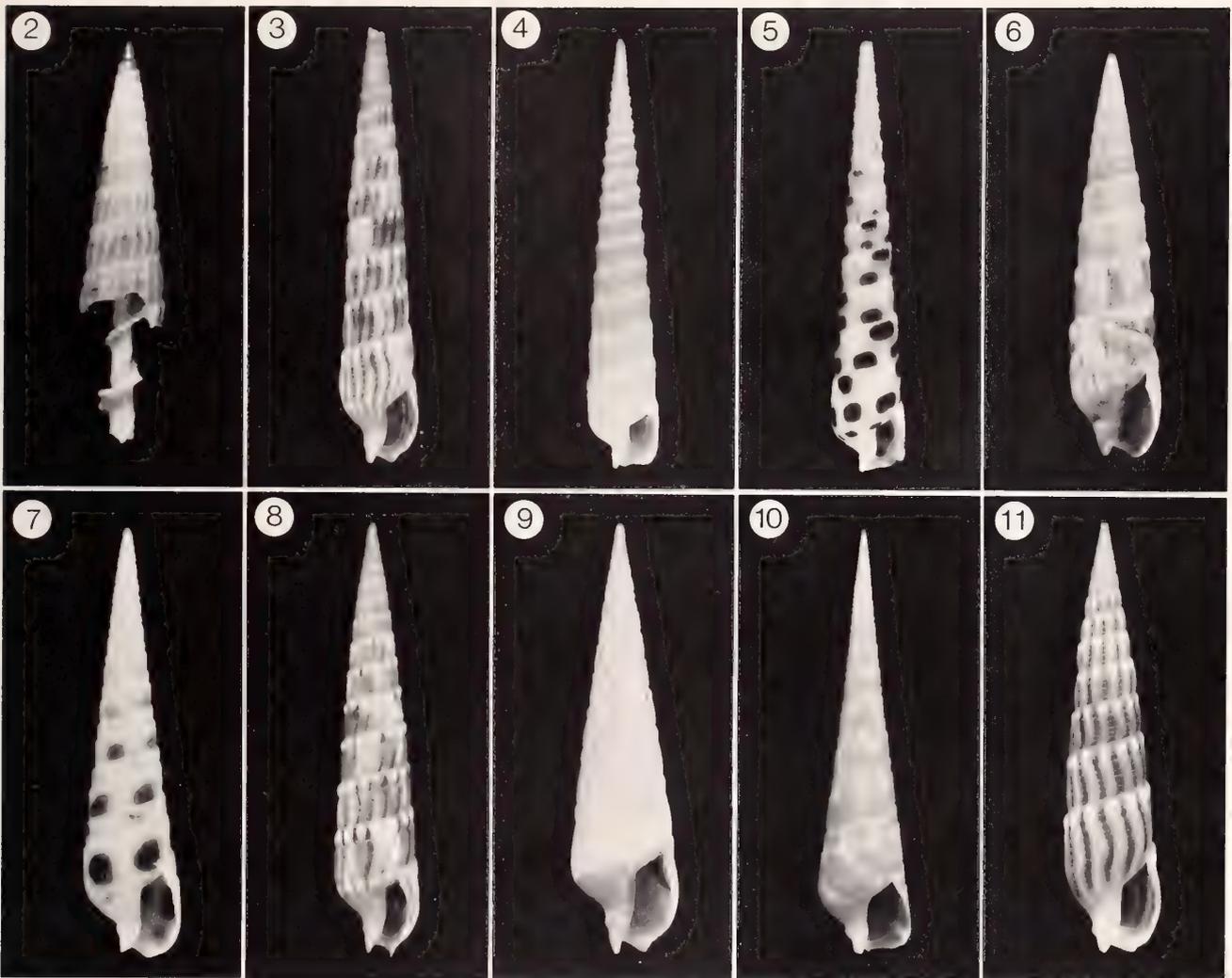
The natural history of terebrids is poorly known; only three species—*Hastula cinerea* (MARCUS & MARCUS, 1960), *Terebra gouldi* (MILLER, 1975), and *Hastula inconstans* (MILLER, 1979)—have been studied in any detail. Based on this limited information, it appears that durophagous predators, especially the sand crab *Calappa* (Figure 1) are important natural predators of small (<4 cm) terebrids.

Calappa is distributed throughout the tropical oceans of the world and commonly co-occurs with *Terebra*. It attacks its gastropod prey by peeling (Figure 2) (SHOUP, 1968; VERMEIJ, 1982a). The crab holds the prey with the small cheliped and uses its highly modified master cheliped (Figure 1) to peel away the shell. Unlike crabs from other families (e.g., *Cancer productus* Randall, *Eriphia sebana* [Shaw and Nodder] [ZIPSER & VERMEIJ, 1978]; *Ozius verreauxii* Saussure [BERTNESS & CUNNINGHAM, 1981]), *Calappa* does not employ peeling as a mode of attack complementary to others, such as clipping the spire. Instead, *Calappa* is exclusively a peeler.

Morphological features that inhibit peeling, such as a

thickened outer lip or varices, have been shown to reduce the likelihood of a successful attack by *Calappa* (VERMEIJ, 1982a). Another possibility is that shell geometry or a correlate of shell geometry may confer resistance to peeling. A high-spined shell is actually a very long, thin, tightly coiled and slowly expanding calcium carbonate tube. A calappid crab would need to attack the shell through a small aperture and peel a high-spined shell further than what would be necessary for shells with a more trochiform geometry. Gastropods with very slender shells can often retract deeply into their shells, as much as several whorls into the shell (VERMEIJ *et al.*, 1980; VERMEIJ, 1982a). The small aperture of turritelliform snails may prevent *Calappa* from inserting its dactyl process to begin the peeling process.

VERMEIJ *et al.* (1980) tested the hypothesis that slender gastropods are more resistant to peeling. They predicted that if frequencies of attack were constant among terebrid gastropods, then those shells most resistant to predation should have a higher frequency of repair marks on their shells. Surprisingly, they found that slender terebrids ac-



Explanation of Figures 2 to 11

Figure 2. *Duplicaria baileyi* peeled by *Calappa hepatica*. The shell exterior has been peeled away leaving the columella intact. Shell length (to end of columella) is 15 mm.

Figure 3. *Terebra kilburni*. This and specimens in Figures 4-11 are from Motupore Island, Papua New Guinea. Shell length is 24 mm.

Figure 4. *Terebra laevigata*. Shell length is 26 mm.

Figure 5. *Terebra subulata*. Shell length is 28 mm.

Figure 6. *Terebra affinis*. Shell length is 22 mm.

Figure 7. *Terebra areolata*. Shell length is 23 mm.

Figure 8. *Terebra columellaris*. Shell length is 22 mm.

Figure 9. *Terebra conspersa*. Shell length is 21 mm.

Figure 10. *Terebra dimidiata*. Shell length is 47 mm.

Figure 11. *Terebra undulata*. Shell length is 23 mm.

usually had a lower average number of repair marks, implying that slender shells were more, not less, susceptible to peeling. This conclusion was supported in part by VERMEIJ (1982a), who found that a low frequency of repair marks implied that durophages were not present in the local habitat or that most attacks were successful.

The objective of this project was to provide a more direct test of the hypothesis that shell geometry or a correlate of shell geometry inhibits predation by peeling crabs. Also, the experiments allow comparison of actual success,

under experimental conditions, in avoiding predation by a durophagous decapod to repair frequencies in natural populations, thus permitting direct evaluation of the accuracy of repair frequencies as an estimate of a shell's effectiveness in providing protection against shell-destroying predators.

MATERIALS AND METHODS

Specimens of *Terebra* were collected from shallow (3-15 m) subtidal sand patches on the northwestern side of Mo-

Table 1

Results of offering slender and robust species of terebrids to crabs (*Calappa hepatica*). n is the total number of individuals of a given terebrid species offered to the crabs. Attacks is the number of those individuals damaged by the crabs. P_a is the proportion of individuals damaged by the crabs (attacks/n). Successes is the number of snails killed by the crabs. P_s is the proportion of successful attacks (successes/attacks).

	n	Attacks	P_a	Successes	P_s
Slender species:					
<i>Terebra kilburni</i>	55	4	0.08	0	0.00
<i>Terebra laevigata</i>	69	5	0.07	1	0.20
<i>Terebra subulata</i>	45	1	0.02	0	0.00
Subtotal	169	10	0.06	1	0.01
Robust species:					
<i>Terebra affinis</i>	22	3	0.14	1	0.33
<i>Terebra areolata</i>	15	1	0.07	1	1.00
<i>Terebra columellaris</i>	53	10	0.19	6	0.60
<i>Terebra conspersa</i>	53	10	0.19	7	0.70
<i>Terebra dimidiata</i>	12	3	0.25	1	0.33
<i>Terebra undulata</i>	46	10	0.22	5	0.50
Subtotal	201	37	0.18	21	0.57
Total	370	47	0.13	22	0.46

tupore Island (9°32'S, 147°16'E), in Bootless Bay, on the southern coast of Papua New Guinea. Individuals of over 20 species could easily be collected by sieving sand through a 3 mm mesh screen. The specimens were returned to the Motupore Island Research Center and maintained in a large water-table.

Sixty-eight percent of the snails were carefully examined under low-power magnification and the number of repair marks and shell length were recorded for each animal. Only well-defined repaired breaks that crosscut growth lines were counted. Only data for individuals ranging in size from 10 to 39 mm were used for this study (several of the species reach sizes in excess of 100 mm), in order to minimize the size bias in the numbers of repairs expected on any one snail (VERMEIJ *et al.*, 1980).

Calappa hepatica (Linnaeus, 1758) is abundant on sand flats at the north end of Motupore Island. The crabs are active at high tide and can be collected by hand as the tide recedes. Six crabs ranging from 41 to 65 mm in carapace width were collected and each was transferred to a running seawater aquarium. Enough coarse sand was provided to cover the bottom of the tank and allow the crab to burrow completely.

The terebrids were divided into two shape classes: slender and robust. Species were assigned to the slender class according to the criteria suggested by VERMEIJ *et al.* (1980); slender species are those with 18 or more whorls when the shell is 20 to 29 mm in length, 20 or more whorls when the shell is 30 to 49 mm in length, or more than 21 whorls when the shell length exceeds 50 mm (Figures 3–5). Robust shells are those with fewer whorls than required for assignment to the slender class at specified

lengths (Figures 6–11). The slender species offered to *Calappa* were *Terebra kilburni* (Burch, 1965), *T. laevigata* (Gray, 1834), *T. subulata* (Linnaeus, 1767), and the robust species were *T. affinis* (Gray, 1834), *T. areolata* (Link, 1807), *T. columellaris* (Hinds, 1844), *T. conspersa* (Hinds, 1844), *T. dimidiata* (Linnaeus, 1758), and *T. undulata* (Gray, 1834) (Figures 3–11).

Each crab was simultaneously offered four or five (two slender and two or three robust) terebrids as potential prey. Rejected prey were not re-offered to the same crab, but undamaged individuals were occasionally re-offered to another crab. The prey were presented in the morning and remained in the crab's tank for 24 h. Twenty-four hours was selected as the test period because it was a substantially longer time than VERMEIJ (1982a) found necessary for crab attacks but minimized disturbance within the tanks. At the end of each trial the snails were recovered and the results recorded for each individual. The snails were classified as either not damaged, damaged but not killed (shell broken but animal not harmed), or killed (shell broken and some portion of the snail eaten). Representatives of each shape class were offered each day, but only one individual of each species was placed in the tank at a time.

VERMEIJ (1977b) has emphasized that there is an important size component to the outcome of any encounter between gastropods and predatory crabs. When the gastropod reaches a relatively large size in comparison to the crab it tends to become invulnerable to the crab's attack. Vermeij referred to this as the critical size. MILLER (1975) observed this effect in his study of *Terebra gouldi*, noting that individuals larger than a few centimeters were no

longer preyed upon by *Calappa*. To avoid a possible size bias in this experiment all the snails offered to the crabs were small in size, generally less than 35 mm. There was no apparent increase in susceptibility for small shells in the data.

Calappa attacks on the terebrids occurred infrequently, sometimes raising concerns that individual crabs might not be healthy. If a particular crab failed to damage any shells for several consecutive days, a juvenile *Strombus gibberulus* Linnaeus was added to that crab's tank. Healthy crabs attack *S. gibberulus* quickly and relatively easily (VERMEIJ, 1982a), and the snail's demise was taken as evidence of the crab's good condition. During the course of experiments reported here, none of the crabs became unresponsive.

RESULTS

Terebrids, 201 robust and 169 slender, were offered to the crabs (Table 1). Thirty-seven of the robust terebrids were damaged when exposed to *Calappa* and, of that number, 21 were killed. Likewise, 10 of the slender terebrids were damaged but only a single individual was killed. These data can be employed to answer two separate questions; first, are robust terebrids more likely than slender ones to be damaged and, secondly, once damage occurs is there a greater likelihood that damage to a robust terebrid will be fatal?

More than 18% of the robust species were damaged while only 6% of the slender species had the aperture lip peeled. The frequencies of damage differ strongly from those expected if the two groups were equally likely to be attacked and damaged ($\chi^2 = 10.13$, $P < 0.002$). Slender terebrids are much less likely than robust species to be damaged when exposed to *Calappa*.

Fewer than half of the terebrids damaged by *Calappa* were killed. Among the robust species, 57% of the attacks were successful. In contrast, only one of the ten (10%) slender individuals that were attacked was killed. Again, the two frequencies differ significantly from those expected if the two shapes were equally likely to be killed during an attack ($P < 0.02$, Fisher's Exact Test [SOKAL & ROHLF, 1981]).

The sum result of these two effects is that slender terebrids are not very likely to be attacked successfully by *Calappa*. Indeed, only one individual of the 169 slender terebrids offered was killed for a frequency of kills well below 1%. This frequency is far lower than that of robust terebrids or of other gastropod species reported by VERMEIJ (1982a).

Slender terebrids collected for this project averaged 0.64 repairs per individual while robust species averaged 0.78 (Table 2). This difference was not significant (Mann-Whitney test), nor was there any significant difference between the two groups in the proportions of individuals lacking repairs altogether (chi-square test).

Table 2

Repair mark frequencies on terebrids from the Motupore Island Research Center. All data are for snails between 10 and 39 mm in length.

	n	Repairs	Frequency
Slender species:			
<i>Terebra kilburni</i>	36	29	0.80
<i>Terebra laevigata</i>	92	60	0.65
<i>Terebra subulata</i>	26	10	0.38
Subtotal	154	99	0.64
Robust species:			
<i>Terebra affinis</i>	12	16	1.33
<i>Terebra areolata</i>	9	3	0.33
<i>Terebra columellaris</i>	45	31	0.76
<i>Terebra conspersa</i>	21	23	1.10
<i>Terebra dimidiata</i>	4	0	0.00
<i>Terebra undulata</i>	24	14	0.58
Subtotal	115	87	0.78
Total	269	186	0.69

DISCUSSION

While a pattern of increased probabilities of lethal and nonlethal damage for robust terebrids is evident, the underlying mechanism remains unknown. The disparity in frequencies of attack among slender and robust terebrids cannot be interpreted unambiguously. The differences could arise from the way *Calappa* locates its prey, from prey selection by the predator once potential prey are detected, or from how the snails are attacked once found.

Calappa searches for prey by moving over the sediment and probing for buried prey with its chelipeds (SHOUP, 1968; MILLER, 1975; personal observations). Prey with a smaller profile might be less likely to be detected. Because terebrids burrow with the long axis of the shell subparallel to the sediment-water interface (anterior end down), slender terebrids, by definition, will have a consistently smaller profile (see Figures 3-11). Nevertheless, this effect is too small to account for the tremendous difference observed in frequencies of attack. The slender species have a cross-sectional area parallel to the shell axis at least 70% as great as the most robust species used in the experiment. This difference is not sufficient to account for the threefold difference in frequencies of attack, although it might have some effect on the overall results. Furthermore, X-radiographic studies of burrowing terebrids show slender terebrids burrow less deeply than robust forms, and should be more readily detected by the crabs (Signor, unpublished data). (For example, the anterior end of an 8-cm *Terebra dimidiata* will be 2.4 cm below the sediment surface, whereas the anterior end of a similar size *T. subulata* will be only 1.4 cm below the surface. In both cases, the apex will lie just below the sediment surface.)

Another hypothesis is that slender terebrids are somehow less desirable food items, and are not attacked if discovered. This seems unlikely, as many durophagous crabs, including *Calappa*, are surprisingly unselective when attacking potential prey items, and freely attack gastropods they have virtually no chance of killing (VERMEIJ, 1982a, b). *Carcinus maenas*, while selective in its attacks on mussels (ELNER & HUGHES, 1978), attacks all *Nucella lapillus* it encounters regardless of size (HUGHES & ELNER, 1979). Crabs have even attacked plastic models of long-extinct bivalves introduced into shallow marine habitats (LABARBERA, 1981). *Calappa* will eat the soft parts of slender terebrids when removed from the shell (personal observations), so there is no reason to suspect the crabs find slender terebrids inedible. However, the possibility of selective feeding behavior by *Calappa* should not be discounted as no data are presently available to demonstrate that prey selection does or does not occur.

Aperture size is a likely cause of slender terebrids' relative invulnerability to attack. Other researchers have observed that narrow or occluded apertures inhibit attack by predatory crabs (e.g., VERMEIJ, 1977a, 1978, 1982a; HUGHES & ELNER, 1979; BERTNESS & CUNNINGHAM, 1981). The results presented here are consistent with, but do not demand, that hypothesis.

Calappa possesses a large tooth on the dactyl of the master cheliped that meshes with two protuberances on the propodus (SHOUP, 1968). *Calappa* uses this tooth to peel away portions of the shell lip. The small apertures of terebrids, especially the more slender species, probably restrict the insertion of the calappid peeling tooth, in much the same way that a narrow or occluded aperture restricts access. Interestingly, the only slender terebrid killed was one attacked by the smallest calappid used in the experiment.

Regardless of the mechanism, slender terebrids are damaged or killed significantly less often when exposed to *Calappa*. This pattern seems to extend to comparisons between terebrids and forms with low spires. Overall, the frequencies of successful (fatal) attacks on *Terebra* by *Calappa* were far below those reported for other species by VERMEIJ (1982a). Only 10% of the robust terebrids offered to *Calappa* were attacked successfully, a result close to that observed by Vermeij for *Terebra affinis* (9.1%) and well below frequencies obtained for *Rhinoclavis aspera* (16%), *R. fasciata* (25%) and *Strombus gibberulus* (33%).

Terebra is also susceptible to shell crushing, the other mode of durophagous predation. Small rays are common in many of the shallow subtidal sand patches around Motupore Island and prey on mollusks and crustaceans dug out of the sediments with jets of water. But shell geometry might also serve to inhibit predation by shell crushers. Shell crushing fish must take the gastropod into their mouth in order to crush the snail with their jaws or pharyngeal mill. A long, slender shell could likely be more difficult than other geometries for the fish to manipulate

into the mouth for crushing. The effect of shell geometry as a defense against shell crushers has not been examined and would provide a useful complement to the results presented here.

VERMEIJ (1982a, b) has argued forcefully that repair marks on gastropods can be employed as an index of a shell's effectiveness as a deterrent to predation. The results presented above indicate that this generalization does not extend to high-spired snails. Robust terebrids sustained by far the higher frequency of successful attacks but also had a (not significantly) higher frequency of unsuccessful attacks (7.9% vs. 5.3% for slender species). Likewise, robust species have a higher frequency of repair marks than slender species in local populations, although the differences are less marked than in the experimental results. (The discrepancy might reflect the activity of other durophagous predators in the natural environment.) The shells of slender terebrids exposed to *Calappa* usually escape damage. This phenomenon may explain why VERMEIJ *et al.* (1980) were unable to use repair marks to substantiate their hypothesis that slender terebrids are less susceptible to peeling predators.

CONCLUSION

When exposed to the durophagous predator *Calappa*, slender, many whorled terebrids are damaged significantly less frequently than robust species. When *Calappa* attacks and damages a terebrid, the damage is fatal significantly less often in slender species. Robust species also suffer non-lethal damage as often as slender terebrids. These results support the hypothesis that shell geometry, or a correlate of shell geometry, can be an effective escape from predators. Repair marks are not a valid index of shell vulnerability in terebrid gastropods.

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LITERATURE CITED

- BERTNESS, M.D. & C. CUNNINGHAM. 1981. Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Mar. Biol. Ecol.* 50:213-230.

- BOSS, K. J. 1971. Critical estimate of the number of Recent Mollusca. Occ. Pap. Mol. 3:81-135.
- ELNER, R. W. & R. N. HUGHES. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. J. Animal Ecol. 47:103-116.
- HUGHES, R. N. & R. W. ELNER. 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. J. Anim. Ecol. 48:65-78.
- KITCHING, J. A., L. MUNTZ & F. J. EBLING. 1966. The ecology of Lough Ine XV. The ecological significance of shell and body form in *Nucella*. J. Anim. Ecol. 35:113-126.
- LABARBERA, M. 1981. The ecology of Mesozoic *Gryphea*, *Exogyra*, and *Ilymatogyra*. Paleobiology 7:510-526.
- MARCUS, E. & E. MARCUS. 1960. On *Hastula cinerea*. Bol. Fac. Fil. Cien. Letr. Univ. S. Paulo (Zool.) 23:25-66.
- MILLER, B. A. 1975. The biology of *Terebra gouldi* Deshayes, 1859, with a discussion of life history similarities among other terebrids of similar proboscis type. Pacific Sci. 29:227-241.
- MILLER, B. A. 1979. The biology of *Hastula inconstans* (Hinds, 1844) and a discussion of life history similarities among other hastulas of similar proboscis type. Pacific Sci. 33:289-306.
- PALMER, A. R. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. Evolution 33:697-713.
- RUDMAN, W. D. 1969. Observations of *Pervicacia tristis* (Deshayes, 1859) and a comparison with other toxoglossan gastropods. Veliger 12:53-64.
- SHOUP, J. B. 1968. Shell opening by crabs of the genus *Calappa*. Science 160:887-888.
- SOKAL, R. R. & F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Co.: San Francisco. 859 pp.
- TAYLOR, J. D., J. N. MORRIS & C. N. TAYLOR. 1980. Food specialization and the evolution of predatory prosobranch gastropods. Palaeontology 23:375-409.
- VERMEIJ, G. H. 1977a. The Mesozoic marine revolution: evidence from snails, predators and grazers. Paleobiology 3: 245-258.
- VERMEIJ, G. J. 1977b. Interoceanic differences in vulnerability of shelled prey to crab predation. Nature 260:135-136.
- VERMEIJ, G. J. 1978. Biogeography and adaptation: patterns of marine life. Harvard Univ. Press: Cambridge. 332 pp.
- VERMEIJ, G. J. 1979. Shell architecture and causes of death of micronesian reef snails. Evolution 33:686-696.
- VERMEIJ, G. J. 1982a. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. Malacologia 23:1-12.
- VERMEIJ, G. J. 1982b. Unsuccessful predation and evolution. Amer. Natur. 120:701-720.
- VERMEIJ, G. J. 1983. Shell-breaking predation through time. Pp. 649-669. In: M. J. S. Tevesz & P. L. McCall. Biotic interactions in Recent and fossil benthic communities. Plenum. Publ. Co.: New York.
- VERMEIJ, G. J., E. ZIPSER & E. C. DUDLEY. 1980. Predation in time and space: peeling and drilling in terebrid gastropods. Paleobiology 6:352-364.
- ZIPSER, E. & G. J. VERMEIJ. 1978. Crushing behavior of tropical and temperate crabs. J. Exp. Mar. Biol. Ecol. 31: 155-172.

Gametogenesis in a Population of the Hard Clam, *Mercenaria mercenaria* (Linnaeus), in North Santee Bay, South Carolina¹

by

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Abstract. Adult hard clams, *Mercenaria mercenaria* (Linnaeus, 1758), were sampled monthly between December 1977 and February 1979 and semi-monthly from March to June 1981, from subtidal populations in North Santee Bay, South Carolina. Gonad development was monitored using standard histological methods and resulting slides were examined with light microscopy at 100 and 400 \times . Observed gametogenic progression was best categorized by five stages or phases of development: inactive, ripe, spawning, partially spent, and spent. Both male and female clams displayed a complex progression of gametogenesis. Gonadal tissue was not uniformly dominated by clearly defined, distinct stages. Instead, gonads routinely exhibited several stages simultaneously and progressed through slow shifts in domination of stages in gonad tissue. Spawning in the population occurred continuously for six months (May to October) with at least two apparent peaks of spawning activity in the summer months.

INTRODUCTION

HARD CLAM, *Mercenaria mercenaria* (Linnaeus, 1758), landings in South Carolina have increased substantially in recent years. An estimated 6809 acres (2756 ha), or roughly 1% of South Carolina marsh-estuarine area of 746,445 acres (302,086 ha), contain clams in various commercial densities (ANDERSON *et al.*, 1978). As the demand on the fishery and subsequent pressure on the resource continue to grow, it becomes important to determine recruitment potential of the stocks. The documentation of gametogenesis in a fishery resource is the first logical step in estimations of population recruitment. Although data are scant on the reproductive cycle in hard clam populations of South Carolina, a number of studies on the gonadal development of clams from other areas have been described. LOOSANOFF (1937a, b) determined the seasonal gonadal changes of *M. mercenaria* from Long Island Sound and showed that temperature is an environmental factor regulating the gonadal cycle in hard clams. PORTER (1964) studied clams from Core Sound, North Carolina, and suggested that gonadal differences in populations could be caused by racial differences or by phenotypic responses to

variable environmental factors. KECK *et al.* (1975) compared the gonadal cycles of *M. mercenaria* from Delaware Bay and Cape Henlopen for evidence of physiological races. They found that divergent developmental patterns did exist between the two areas. EVERSOLE *et al.* (1980) documented the gametogenic cycle of *M. mercenaria* seed from North Carolina planted in an estuary near Clark Sound, South Carolina. PLINE (1984) compared gametogenesis in two size classes of *M. mercenaria* in Georgia.

Differences in gonadal cycles between geographically separated populations are not limited to the hard clam (*Mercenaria mercenaria*) as shown by PFITZENMEYER (1962), ROPES & STICKNEY (1965), and SHAW (1962, 1965) for the soft clam, *Mya arenaria* (Linnaeus, 1758); HOLLAND & CHEW (1974) for the manila clam, *Venerupis japonica* (Deshayes); and JONES (1981) and THOMPSON *et al.* (1980) for the ocean quahog, *Arctica islandica* (Linnaeus, 1767).

Hard clam populations in South Carolina are subjected to environmental conditions that significantly differ from those characterizing the northeastern and Middle Atlantic states. Water temperatures are relatively moderate in winter (normally $\geq 10^{\circ}\text{C}$ monthly means) and very warm in summer ($\geq 28^{\circ}\text{C}$ monthly means). This study was initiated to determine the natural cycle of gonadal development in native populations of South Carolina clams and to compare the results with those of previous studies on hard clam populations from other areas.

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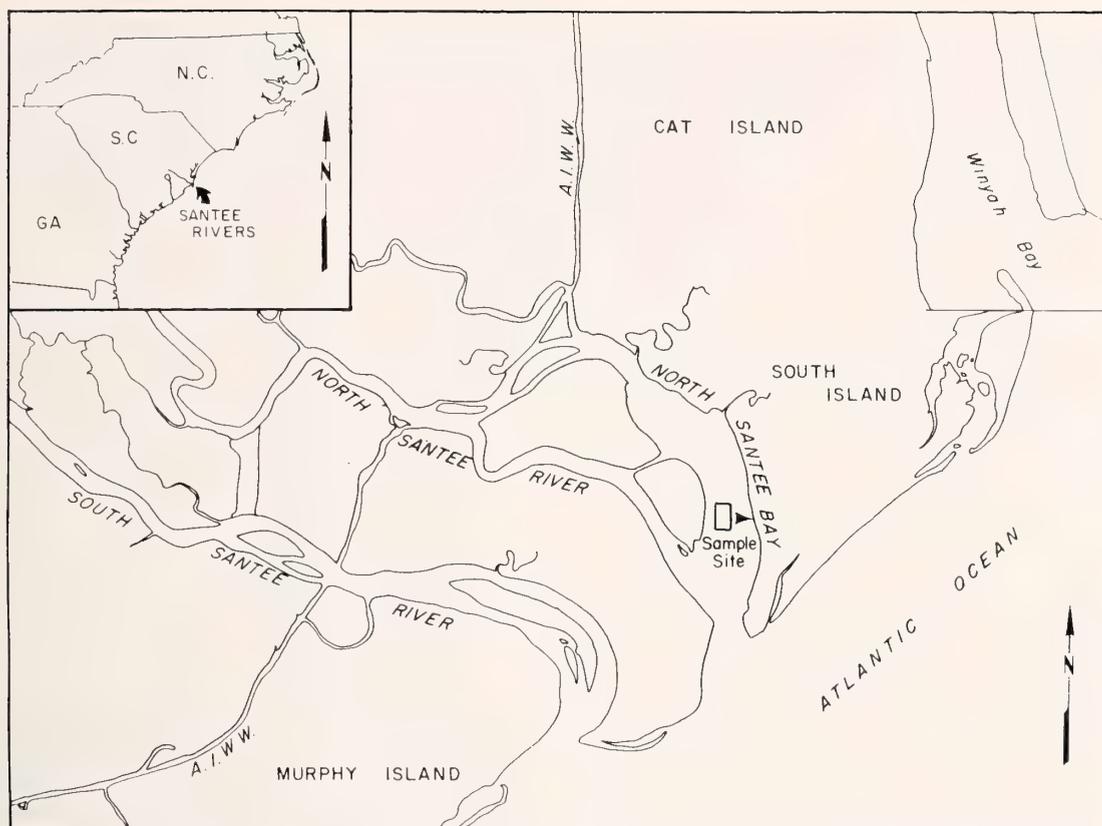


Figure 1

Sampling location in North Santee Bay, South Carolina.

MATERIALS AND METHODS

Twelve hard clams were collected monthly from December 1977 to February 1979 and biweekly from March to June 1981. All animals were from North Santee Bay, South Carolina (Figure 1). The bay is characterized by substrates of soft mud mixed with shell and an average depth of approximately 1–2 m at mean low water. The North Santee Bay was chosen as a study site because of its dense beds of hard clams and oysters (*Crassostrea virginica* Gmelin, 1791). ANDERSON *et al.* (1978) found the highest density hard clam populations in South Carolina in the North Santee delta system. Hard clams for this study were obtained with a 19-cm × 53-cm boxed-type oyster dredge. Hydrographic data were collected coincidentally with sampling and included measurements of air and water temperatures, and salinity. All clams were returned to the laboratory and stored under refrigeration at approximately 5°C. Tissue samples were always removed within 24 h of collection. Before dissection, shell lengths (anterior-posterior axis) were measured to the nearest millimeter with vernier calipers.

Whole clams were fixed in FAA (formalin-acetic acid-alcohol) for two to four weeks. Either a cross- or longi-

tudinal section was cut through the mantle, gonad, and underlying digestive gland. Dissected tissues were then placed in FAA for 24 h and washed in running tap water for approximately 4 h. Tissues were prepared for sectioning by dehydration in alcohol, clearing in toluene, and infiltration in 57°C paraffin (PREECE, 1972). After proper embedding in paraffin, the tissues were sectioned at 7 μm on a rotary microtome. Sections were made at three areas of each tissue block, approximately 20 μm apart. All sections were stained with Gill's hematoxylin and counterstained with alcoholic eosin. The sections were examined with a light microscope and photomicrographs of various stages of gametogenesis were taken at 40, 75, and 185×.

Examination of slides made it quite evident that a gametogenic index had to be devised to organize or categorize the developmental stages in this study. The slides were examined first under low power (100×) to scan the entire gonadal area and under high power (400×) to assess each follicle. Often, two or more stages occurred simultaneously within each section; therefore, stage criteria decisions were based upon the condition of the majority of the section. In most cases 80% or more of the section represented no more than one stage. This technique was

particularly useful in staging the spawning and partially spent categories which were segregated on the basis of percent lumen filled with ovocytes and spermatocytes (representing spawning activity) and the number of mature gametes remaining.

RESULTS

Initial surveys of collected gonadal tissues indicated that only five readily identifiable stages of gametogenesis were apparent in the populations of South Carolina *Mercenaria mercenaria* sampled. PORTER (1964) and KECK *et al.* (1975) used 14 and 10 developmental stages, respectively, to describe the gametogenic cycle of *M. mercenaria*. EVERSOLE *et al.* (1980), however, also classified the gonads of *M. mercenaria* into five developmental stages. In contrast to the latter, the degree of spawning that we observed in this study made classifying the gonads into the single stage of "ripe and spawning" difficult. Staging gonads as early active and active was also difficult. This necessitated the formulation of an index suitable for the prolonged ripe and spawning period and reduced inactive period characterized by these hard clams. The five developmental stages (spent, inactive, ripe, spawning, and partially spent) established were distinguished by the following characteristics.

Spent (Figures 2, 3): Follicles are nearly empty, and a thin band of spermatocytes or few small ovocytes may occur along the follicle wall. Few large undischarged ovocytes or spermatozoa and some spermatids are found free in the lumen of some follicles. Usually follicles are extended but may occasionally be compressed in shape or size. Undifferentiated cells may be present in a few follicles.

Inactive: Gonads are in a state of quiescence, and follicles are either absent or very few in number. A few follicles contained numerous undifferentiated cells, but no recognizable primary or secondary gametogonia are present.

Ripe (Figures 4, 5): Follicles are extended and full of darkly staining ova or spermatozoa with their tails pointing toward the center of the lumen. Large ovocytes have been freed from the follicle wall into the lumen, with the nucleus apparent in most cells and the nucleolus apparent in some. Some attached spermatocytes and ovocytes are located along the follicle wall. Spermatids, staining lighter than the spermatocytes or spermatozoa, lie in a layer or in groups outside the central core of the spermatozoa.

Spawning (Figures 6, 7): Generally large expanded follicles still contain many mature ova in the lumen or dense bands of ripe spermatozoa surrounding a partially empty lumen. Around the periphery of the follicles may be many spermatids, spermatocytes, or ovocytes still attached to the follicle wall.

Partially spent (Figures 8, 9): Most follicles are empty

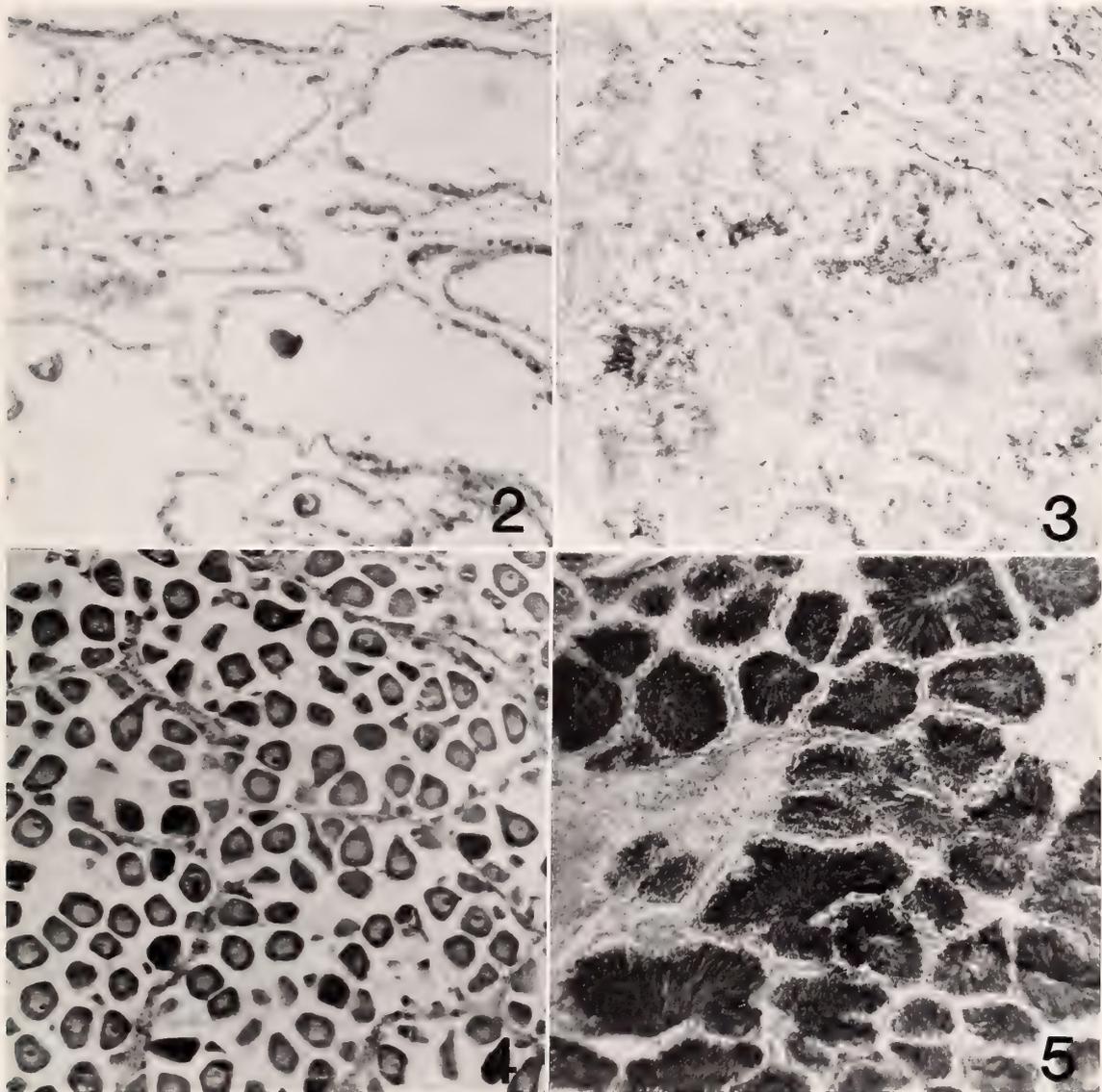
of spermatozoa or of large ovocytes but generally have a thin band of spermatocytes or small ovocytes along the follicle wall. Other follicles are still dense with spermatozoa or ripe ova scattered in the lumen.

The progression of gametogenesis in female clams as reflected by this study was not characterized by clearly defined, distinct stages. Instead, the gonads often exhibited several stages simultaneously and progression of the sexual cycle occurred in a gradual but complex manner. Figure 11 illustrates this progression in oogenesis throughout the study period. Approximately 80% of the female gonads examined from late December 1977 samples were spent. Gonads with partly discharged ovocytes and others with follicles filled with ripe ova in the largest part of the lumen appeared in February and continued until May. By the end of May, as the water temperature increased to 22°C, all females examined were ripe and normal oval-shaped ovocytes had reached a size of 65–70 μm .

Indications of spawning were evident in late June (water temperature, 26°C) with a distinct decrease in the number of ripe ova and an increase of gonads with partially spent lumen. This spawning condition continued through October showing a gradual shift from a ripe appearance to a partially spent condition. LOOSANOFF (1937b) suggested that the spawning of an individual hard clam is not completed in one attempt but is extended for a certain period of time, depending upon the individual and ecological peculiarities. Some follicles with few undischarged ovocytes free in the lumen were characteristic of all of the females examined in November. This completely spent condition was not evident in December when ripe ova reappeared in half of the gonads examined. The percentage increase in ripe females in December, January, and February could indicate that active gametogenesis occurred immediately after the spawning. The new ovocytes at this time varied considerably in size and averaged 55–60 μm . In most cases, the ova were oval in shape with the nucleus clearly apparent.

Samples taken biweekly, March through June 1981, are combined into monthly means in Figures 10–12. Most female gonads (Figure 11) were marked with a spawning or partially spent condition. The number of large unspawned ova found in the ovaries of these clams varied greatly with individuals. In some cases, almost all the ova were discharged with only a few ripe ovocytes remaining (Figure 8). In most, however, a comparatively large number of ova were retained (Figure 6). Ovocytes at this time averaged 55–60 μm in size. Some small ovocytes were observed in March but these were relatively sparse. Ovocytes greater than 68 μm in size had increased in number by May and June, but the majority of the ova were still between 55 and 60 μm .

Male clams reiterated the complex progression of gametogenesis exhibited by the females. Figure 12 illustrates, by percent of sample population in various sexual stages, this progression of the male sexual cycle. In Feb-



Explanation of Figures 2 to 5

Figure 2. Spent stage of oogenesis ($\times 40$).

Figure 3. Spent stage of spermatogenesis ($\times 75$).

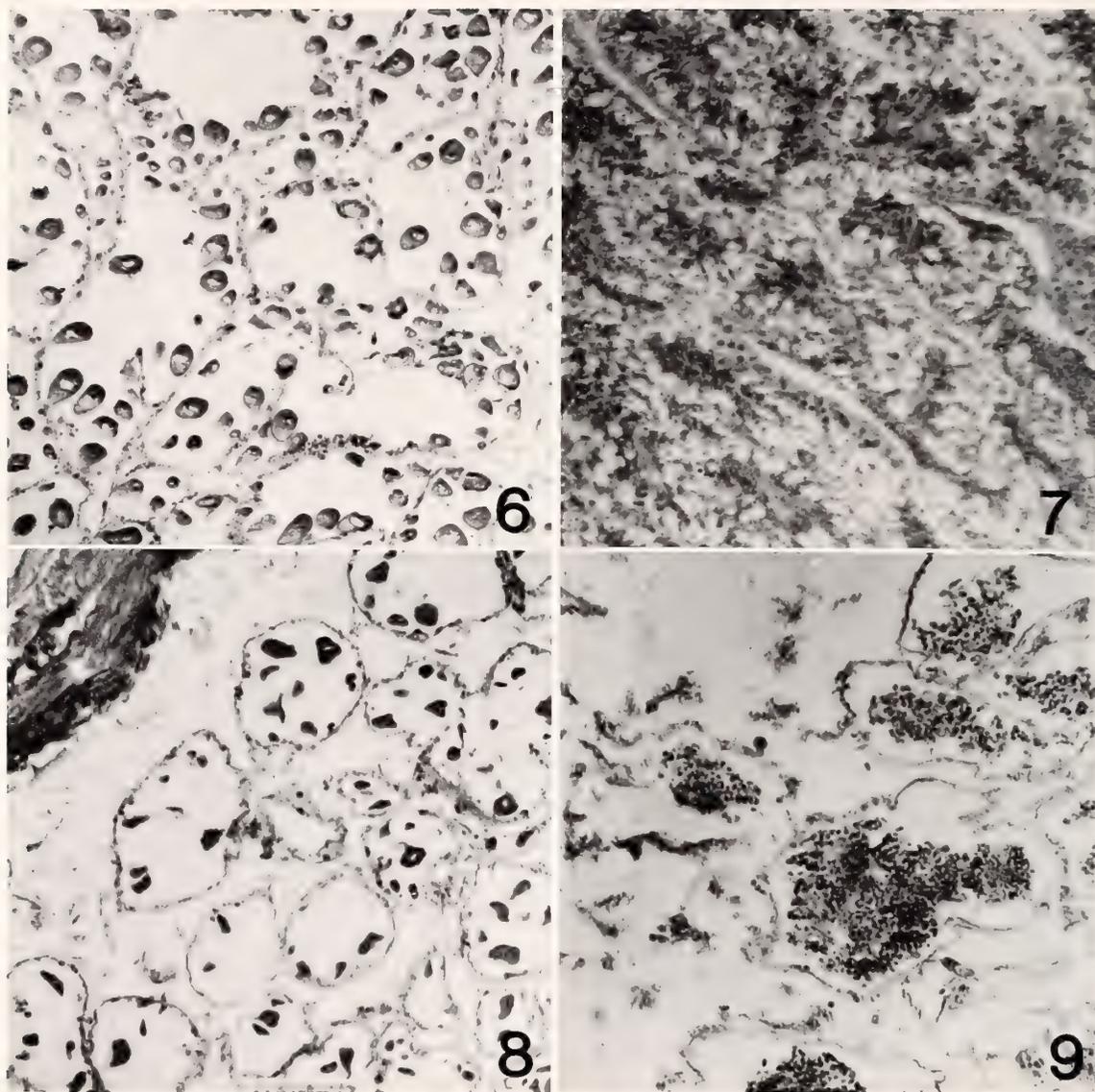
Figure 4. Ripe female ($\times 75$).

Figure 5. Ripe male ($\times 40$).

ruary, gonads in 85% of the males examined were ripe, with most follicles containing mature spermatozoa in the lumen. A decline in the percentage of ripe males occurred in March when approximately half of the gonads examined were ripe while all of the others were spawning. In April, all male gonads were ripe with follicles packed with darkly stained spermatozoa with their tails oriented inwards toward the center of the lumen. A mature condition continued in the majority of the males through October with only a small percentage in a spawning or partially spent condition. By November when water temperatures

were approximately 18°C, all male gonads examined had discharged their gametes and were in a generally spent condition. Males exhibiting extended follicles filled with ripe spermatozoa were apparent again in December, and a high percentage of ripe males remained through February.

Water temperatures recorded during the study were not significantly different from typical South Carolina coastal conditions. Water temperatures ranged from a low of 5.3°C in February 1978 to a high of 30.2°C in August 1978. Ambient water temperatures recorded at sample collection



Explanation of Figures 6 to 9

Figure 6. Spawning female, with many ova retained ($\times 75$).

Figure 7. Spawning male, with many sperm retained ($\times 40$).

Figure 8. Partially spent female ($\times 75$).

Figure 9. Partially spent male ($\times 185$).

are presented in Figure 10. Available salinity records indicate a salinity range of 24.0 to 34.0‰ over the collection period.

The seasonal variation of the gonadal cycle is presented in Table 1. Data are presented as percentage of individuals in each developmental stage per season. The table indicates that during the winter of 1977–1978 clams were undergoing all stages of gametogenesis, although a high percentage (36%) were ripe. The largest percentage (27%) of inactive clams were observed during this season. By the summer, ripe gonads were present in 69% of the population examined. All other clams were spawning or par-

tially spent. The fall season of 1978 was characterized by the greatest percentage of spent individuals. Follicles containing ripe gametes were apparent in most clams examined during the winter of 1978–1979. The spring and early summer of 1981 were represented by a high proportion of ripe clams, reiterating the observations of 1978.

DISCUSSION

Temperature is a major environmental factor regulating gametogenesis in a variety of marine bivalves (LOOSANOFF, 1937a, b; GIESE, 1959; ANSELL, 1961; GALTISOFF, 1964;

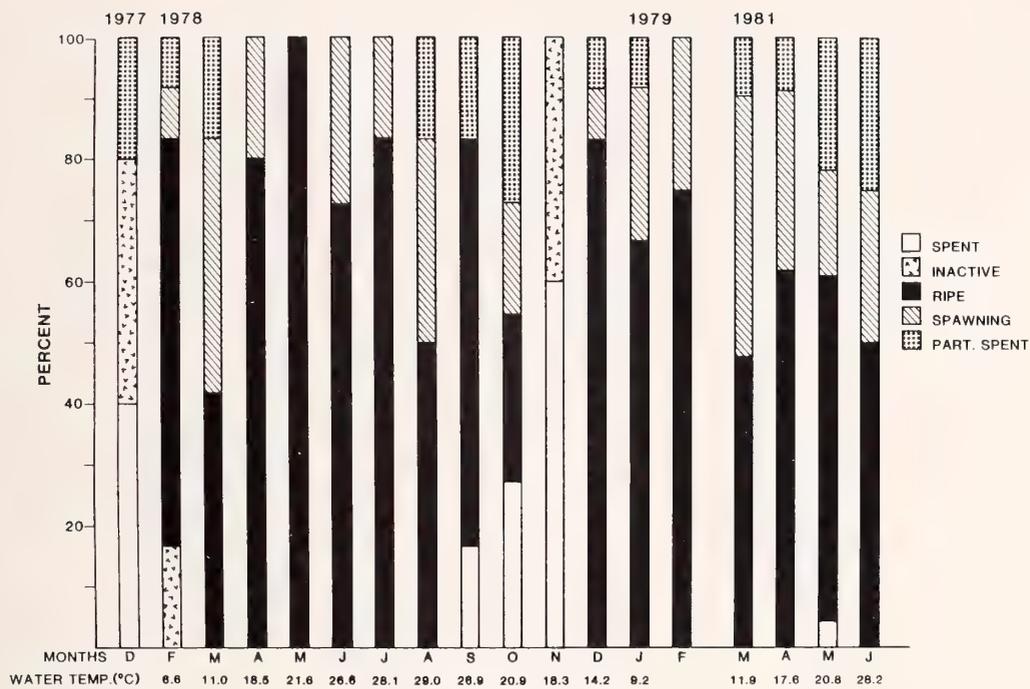


Figure 10

Stages of gonad development in *Mercenaria mercenaria* from North Santee Bay, South Carolina. Shaded areas represent percent frequency of clams in each stage from December 1977 to February 1979 (see legend). March to June 1981 data represent composites of biweekly samples. Temperatures are ambient recorded water temperatures at time of sampling.

PORTER, 1964; KECK *et al.*, 1975; EVERSOLE *et al.*, 1980; PLINE, 1984). The seasonal temperature differences that exist between Long Island Sound, Delaware Bay, Georgia, and North and South Carolina coastal waters would

naturally lead to differences in their respective bivalve population reproductive cycles. Local environmental conditions can also influence and confound gametogenesis in bivalves. CARRIKER (1961) showed that depth of water

Table 1

Seasonal variation (as percentiles) in developmental stages of gonads from a hard clam, *Mercenaria mercenaria*, population in North Santee Bay, South Carolina.

Seasons	Number examined	Stage				
		Spent	Inactive	Ripe	Spawning	Partially spent
Winter (1977-1978)						
Dec.-Feb.	22	18	27	36	5	14
Spring						
Mar.-May	34			74	21	6
Summer						
Jun.-Aug.	35			69	26	6
Fall						
Sep.-Nov.	33	33	12	30	9	15
Winter (1978-1979)						
Dec.-Feb.	36			75	19	6
Spring/Summer (1981)						
Mar.-Jun. -	90	1		56	29	14

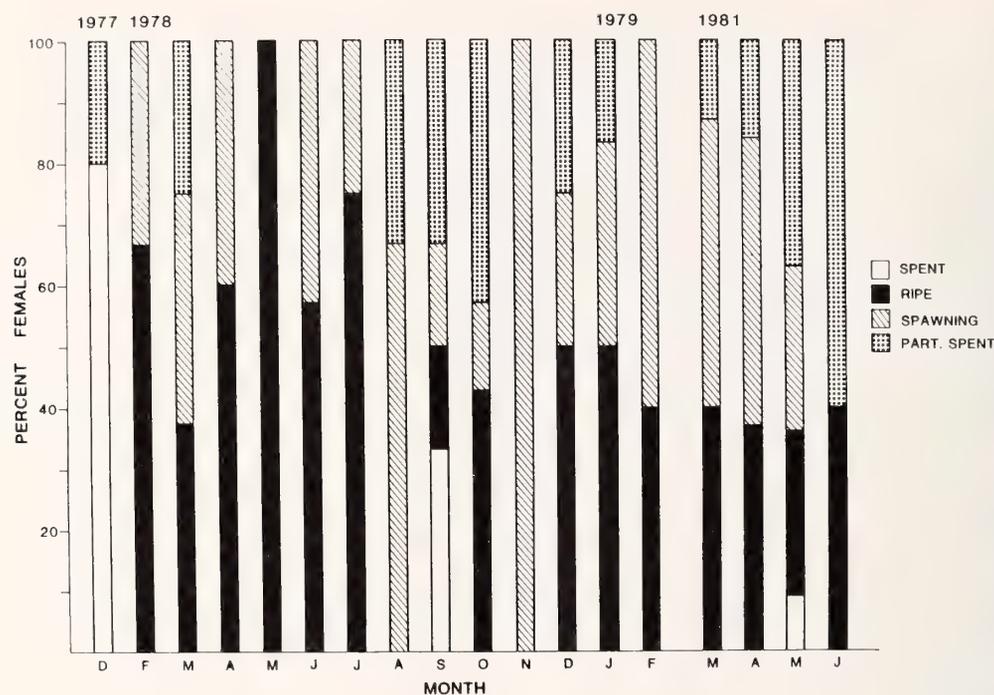


Figure 11

Stages of gonad development in female *Mercenaria mercenaria* from North Santee Bay, South Carolina, between December 1977 and June 1981. Shaded areas represent percent frequency of each stage of development for each month (see legend).

and local circulation patterns can, together with temperature, greatly influence the onset of spawning activity in hard clams. ANSELL *et al.* (1964) showed that thermal effluents produced marked temporal alterations in hard clam gametogenesis.

EVERSOLE *et al.* (1980) indicated that *Mercenaria mercenaria* had a prolonged spawning period with two breeding peaks per year in Clark Sound, South Carolina. Hard clams from Wassaw Sound, Georgia, exhibited a true bimodal cycle with two distinct periods of gametogenesis and two spawning periods (PLINE, 1984). PORTER (1964) found a similar pattern in North Carolina. This bimodal pattern, however, was not found in hard clam populations in Delaware Bay (KECK *et al.*, 1975) or in Long Island Sound (LOOSANOFF, 1937b). A similar pattern of changing reproductive strategies along a latitudinal gradient has been noted for *Mya arenaria* (PFITZENMEYER, 1962; ROPES & STICKNEY, 1965; SHAW, 1962, 1965). EVERSOLE *et al.* (1980) suggested that breeding seasons of *M. mercenaria* change with respect to latitude, becoming prolonged and containing more synchronized polymodal breeding patterns with decreasing latitude. This phenomenon has been observed in other temperate marine invertebrates (GIESE, 1959).

Spawning in this study was apparent only by declines in the percent lumen filled with ripe gametes. Spawning apparently is a long, rather continuous process beginning

in April or May and continuing to September or October. EVERSOLE *et al.* (1980), PORTER (1964), KECK *et al.* (1975), and PLINE (1984) found similar protracted spawning seasons. KECK *et al.* (1975) noted that the rate of temperature change probably provides a stronger spawning stimulus than absolute temperature. PLINE (1984) noted that the rapid rise and fluctuation of the water temperatures over the intertidal hard clam beds in Wassaw Sound was probably the factor that induced spawning as early as March. Normal spawning temperatures are slightly different in the areas mentioned above: 27–30°C in North Carolina (PORTER, 1964), 25–27°C in Delaware (KECK *et al.*, 1975), 23–25°C in Long Island (LOOSANOFF, 1937b), above 20–23°C in Clark Sound (EVERSOLE *et al.*, 1980), 22–26°C in Wassaw Sound (PLINE, 1984), and above 20°C in North Santee Bay (present study).

The period of inactivity and/or early active gametogenesis could be rapid because of the moderate winter water temperatures in South Carolina, thus making it difficult to observe and document this stage of gametogenesis. PLINE (1984) observed a low percentage of recuperative (inactive) clams which he attributed to the short duration of this phase. EVERSOLE *et al.* (1980) indicated that undifferentiated (inactive) clam gonads and gonads showing early stages of gametogenesis occurred more frequently among smaller size classes of hard clams. This might also explain the low percentage of inactive and early active

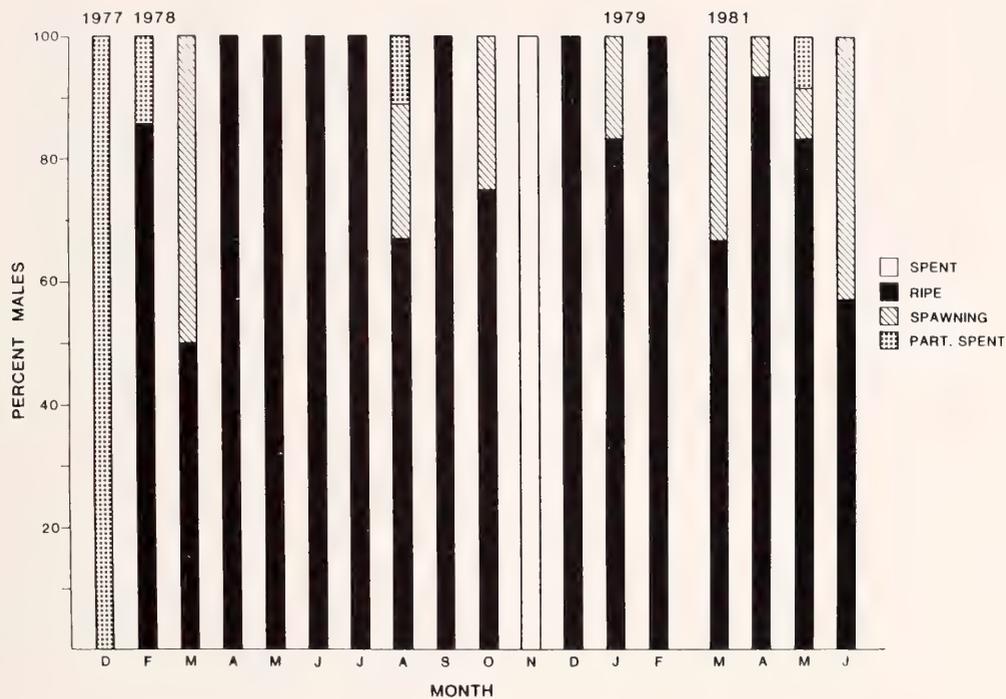


Figure 12

Stages of gonad development in male *Mercenaria mercenaria* from North Santee Bay, South Carolina, between December 1977 and June 1981. Shaded areas represent percent frequency of each stage of development for each month (see legend).

stages observed in the present study which used, for the most part, specimens in the large chowder size class (>75 mm SL). KECK *et al.* (1975) found no case where it was impossible to determine sex, indicating a paucity of inactive specimens in their survey. LOOSANOFF (1937b) did not report any undifferentiated gonads for Long Island male clams and mentions the presence of undifferentiated cells along the inner walls of the ovarian follicles only immediately after spawning. PLINE (1984), comparing littlenecks (38–68 mm SL) to chowders (>78 mm SL), indicated that there was evidence that chowders ripen more quickly than littlenecks. He also observed that chowders had longer and more extensive spawning periods and a shorter redevelopment period than littlenecks.

Active gametogenesis also appears to continue after spawning since so many ripe gonads were found in December and January. LOOSANOFF (1937b) reported major redevelopment immediately after spawning in Long Island waters, and observed many ripe gonads in December and January. PORTER (1964) reported that at least 50% of his clams retained a ripe appearance through the fall and winter. EVERSOLE *et al.* (1980) reported an increase in the number of ripe and spawning clams in December, March, and April collections, and suggested that this indicated that regeneration occurred after fall spawning and continued into spring.

EVERSOLE *et al.* (1980) observed differences in shell length between sexes in a young population of *Mercenaria mercenaria*. Females appeared larger than males and males were larger than undifferentiated clams. However, they speculated that as clams in a cohort continued to grow and entered subsequent breeding periods, these size differences should become less apparent. ANSELL (1961) found no significant size difference between male and female clams. There was no evidence of a size-sex relationship among the North Santee Bay chowders examined. Shell lengths ranged from 54 to 109 mm with approximately equal numbers of males and females in all size classes.

Ova, approximately 55–60 μm in diameter, were observed in the follicles of female clams during most of the sampling period. Although this dimension appeared to be the average size of the oocytes, smaller and less numerous oocytes (25–30 μm) appeared in small numbers during late winter and early spring. Occasionally, during the summer, large ova reaching the previously reported (LOOSANOFF & DAVIS, 1963) maximum size of 70–73 μm were seen. LOOSANOFF (1937b) found large oocytes measuring 55–60 μm in almost every gonad studied. He indicated that they represented cells of previously developed gonad tissue. PLINE (1984) also noticed large oocytes (50–60 μm), which he suggested were residual egg cells from previous ovogenic cycles, in gonads that were in an early

active phase. BRICELJ & MALOUF (1980) indicated that mature oocytes can vary widely in size, from about 50 to 97 μm .

Hard clams from North Santee Bay, South Carolina exhibited no progression of well-defined stages of gonad development. Instead, there were gradual shifts in gametogenesis with two or more stages usually present in the same gonad simultaneously. PLINE (1984) found many male littlenecks showing a considerable overlap of developmental phases among follicles within a single gonad. There also appeared to be no time at which the hard clams in the North Santee Bay population were truly "inactive." Samples contained some clams in various stages of gametogenesis throughout the year, although the percent of the population undergoing active gametogenesis changed significantly. This condition is not unique to South Carolina adult clams. LOOSANOFF (1937b) found no undifferentiated gonads in hard clams from Long Island Sound, and KECK *et al.* (1975) and PLINE (1984) found only small percentages of hard clams in a recuperative phase in Delaware Bay and Wassaw Sound, Georgia, respectively. The occurrence of morphologically ripe sperm and ova throughout most of the year in North Santee Bay is an interesting feature of the sexual behavior of local *Mercenaria mercenaria*. LOOSANOFF (1937b) commented that the sexual cycle of the hard clam was not in phase with other bivalve mollusks in Long Island Sound. Results from this study substantiate the suggestion that *M. mercenaria* exhibits an unusual cycle of gonadal development. In South Carolina the cycle is further confounded by an extremely long spawning season and abbreviated periods of early active gametogenesis.

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LITERATURE CITED

- ANDERSON, W. D., W. J. KEITH, F. H. MILLS, M. E. BAILEY & J. L. STEINMEYER. 1978. A survey of South Carolina's hard clam resources. South Carolina Wildlife and Marine Resources Dept., S.C. Marine Resources Center Tech. Rep. #32. Charleston, S.C. 32 pp.
- ANSELL, A. D. 1961. Reproduction, growth and mortality of *Venus striatula* (da Costa) in Kames Bay, Millport. J. Mar. Biol. Assoc. U.K. 41:191-215.
- ANSELL, A. D., K. F. LANDER, J. COUGHLAN & F. A. LOOSMORE. 1964. Studies on the hard shell clam, *Venus mercenaria*, in British waters. Growth and reproduction in natural and experimental colonies. J. Appl. Ecol. 1(1):63-82.
- BRICELJ, V. M. & R. E. MALOUF. 1980. Aspects of reproduction of hard clams (*Mercenaria mercenaria*) in Great South Bay, New York. Proc. Natl. Shellfish. Assoc. 70:216-229.
- CARRIKER, M. R. 1961. Interrelation of functional morphology, behavior, and autecology in early stages of the bivalve, *Mercenaria mercenaria*. J. Elisha Mitchell Sci. Soc. 77(2): 168-241.
- EVERSOLE, A. G., W. K. MICHENER & P. J. ELDRIDGE. 1980. Reproductive cycle of *Mercenaria mercenaria* in a South Carolina estuary. Proc. Natl. Shellfish. Assoc. 70:22-30.
- GALTSOFF, P. S. 1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Fish & Wildl. Serv. Fish. Bull. 64:1-480.
- GIESE, A. C. 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. Ann. Rev. Physiol. 21:547-576. V. E. Hall (ed.). Ann. Rev., Inc.: Palo Alto, Calif.
- HOLLAND, D. A. & K. K. CHEW. 1974. Reproductive cycle of the manila clam (*Venerupis japonica*), from Hood Canal, Washington. Proc. Natl. Shellfish. Assoc. 64:53-58.
- JONES, D. S. 1981. Reproductive cycles of the Atlantic surf clam *Spisula solidissima*, and the ocean quahog *Arctica islandica* off New Jersey. J. Shellfish Res. 1:23-32.
- KECK, R. T., D. MAURER & H. LIND. 1975. A comparative study of the hard clam gonad developmental cycle. Biol. Bull. (Woods Hole) 148:243-258.
- LOOSANOFF, V. L. 1937a. Development of the primary gonad and sexual phase in *Venus mercenaria* Linnaeus. Biol. Bull. (Woods Hole) 72:389-405.
- LOOSANOFF, V. L. 1937b. Seasonal gonadal changes of adult clams, *Venus mercenaria* (L.). Biol. Bull. (Woods Hole) 72: 406-416.
- LOOSANOFF, V. L. & H. C. DAVIS. 1963. Rearing of bivalve molluscs. Pp. 1-236. In: F. S. Russell (ed.), Advances in marine biology, Vol. 1. Academic Press: New York.
- PFITZENMEYER, H. T. 1962. Periods of spawning and setting of the soft-shelled clam *Mya arenaria*, at Solomons, Maryland. Chesapeake Sci. 3:114-120.
- PLINE, M. 1984. Reproductive cycle and low salinity stress in adult *Mercenaria mercenaria* L. of Wassaw Sound, Georgia. Master's Thesis, Georgia Institute of Technology.
- PORTER, H. J. 1964. Seasonal gonadal changes of adult clams, *Mercenaria mercenaria* (L.), in North Carolina. Proc. Natl. Shellfish. Assoc. 55:35-52.
- PREECE, A. 1972. A manual for histologic technicians. Little, Brown and Co.: Boston. 428 pp.
- ROPES, J. W. & A. P. STICKNEY. 1965. Reproductive cycle of *Mya arenaria* in New England. Biol. Bull. (Woods Hole) 128(2):315-317.
- SHAW, W. N. 1962. Seasonal changes in female soft-shell clams, *Mya arenaria*, in the Tred Avon River, Maryland. Proc. Natl. Shellfish. Assoc. 53:121-132.
- SHAW, W. N. 1965. Seasonal gonadal cycle of the male soft-shell clam, *Mya arenaria*, in Maryland. U.S. Fish & Wildl. Serv., Spec. Sci. Rept., Fish. No. 508:1-5.
- THOMPSON, I., D. S. JONES & J. W. ROPES. 1980. Advanced age for sexual maturity in the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). Mar. Biol. 57:35-39.

Surficial Shell Resorption in *Nautilus macromphalus* Sowerby, 1849

by

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Abstract. Like many prosobranch gastropods, *Nautilus macromphalus* Sowerby, 1849, resorbs a thin layer of shell material from the surface of its penultimate whorl prior to extending the edge of the black layer during growth. The resorption occurs along a millimeter wide band skirting the edge of the black layer and apparently is accomplished by the mantle edge. The depth of resorption is uneven within and between individuals. This is the first report of shell resorption among the extant Cephalopoda. Surficial resorption in cephalopods must have evolved independently from the gastropods but is postulated to serve a common function in both groups: to provide a fresh surface to which new shell material may be attached.

INTRODUCTION

RESORPTION is a normal component of shell growth in many marine gastropods. In addition to the well-known examples of resorption to remove obstacles to further growth, such as varices on muricid gastropods (CARRIKER, 1972), or to enlarge the shell interior, as occurs in *Conus* (KOHN *et al.*, 1979), more subtle patterns of resorption are common. Many prosobranch gastropods resorb a thin sheet of shell material from the surface of the penultimate whorl (GRAY, 1833; SIGNOR, 1982). The resorption is limited to an area in the parietal region as wide as, or slightly wider than, the shell surface the body whorl will cover after further growth. Surficial resorption removes very little shell material; in *Terebra dimidiata* (Linnaeus, 1758) (Neogastropoda: Terebridae) the total thickness of the resorbed material is only a few micrometers. One hypothesized function of surficial resorption is to provide a fresh surface upon which new shell material can be deposited (SIGNOR, 1982).

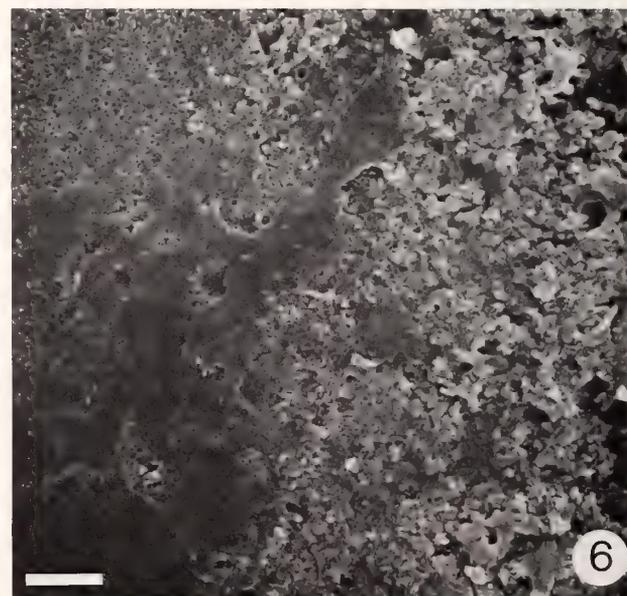
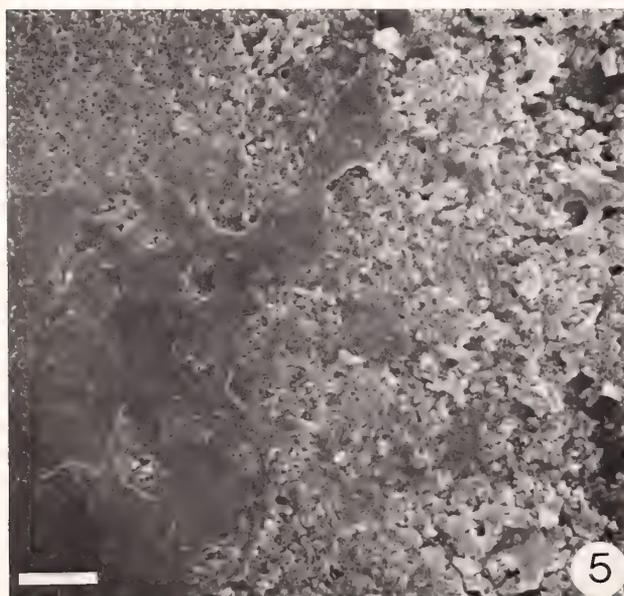
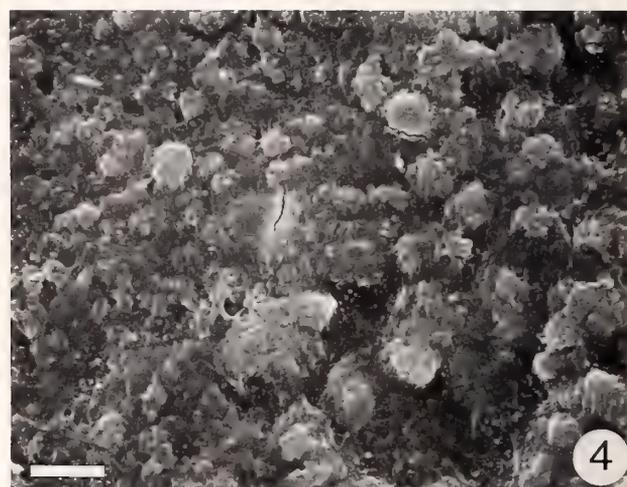
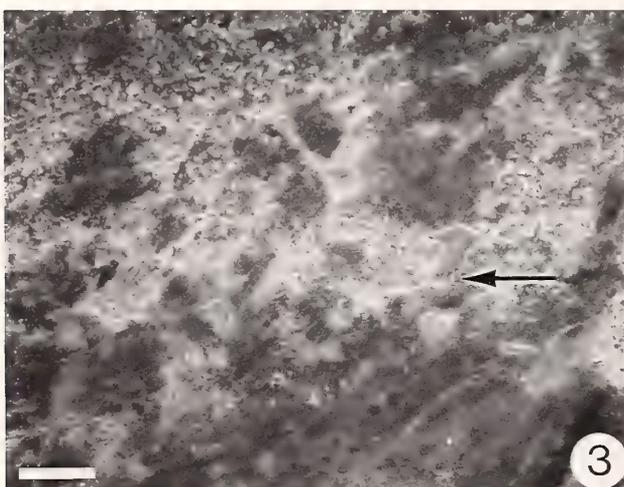
If the foregoing hypothesis is correct, one should expect surficial resorption to occur in the other extant group of multiwhorled mollusks with conjoined whorls, the Nautiloidea. In secreting its shell, *Nautilus* must contend with the same constructional problems encountered by gastropods. Both must securely attach new shell material to the surface of the conch without detracting from the shell's structural integrity. Furthermore, because the first nautiloids were cyrtconic, surficial resorption must, if present, have evolved independently from the Gastropoda or

any common ancestor. In this perspective, *Nautilus* is an ideal comparison group for testing the structural integrity hypothesis for the functional significance of surficial resorption.

Shell resorption has not been described previously in *Nautilus*, and surficial resorption has not, to my knowledge, been observed among extant Cephalopoda. Shell resorption in the Nautiloidea has been postulated previously (TASNÁDI-KUBACSKA, 1962) but only in the context of decollation of primitive nautiloids.

The *Nautilus* shell is planispiral, involute, and consists of about three whorls in mature specimens (Figure 1). Microstructurally, the outer shell wall is comparatively simple, consisting of three aragonitic layers (BØGGILD, 1930; GRÉGOIRE, 1962; STENZEL, 1964; ERBEN *et al.*, 1969; MUTVEI, 1972). The outer shell layer (often referred to as the porcellaneous layer) is composed of irregular prismatic crystals while the thicker, middle layer is nacreous. The thin inner prismatic layer consists of small prisms oriented perpendicular to the shell surface (ERBEN *et al.*, 1969). The septal microstructure is more complex but is also primarily nacreous (BØGGILD, 1930; GRÉGOIRE, 1962; STENZEL, 1964; ERBEN *et al.*, 1969; MUTVEI, 1972). Growth is determinate (COWEN *et al.*, 1973); the animal ceases to deposit the characteristic irregular color bands in the last half whorl of growth and the final septa are closely approximated.

Nautilus deposits a dull black organic film above the dorsal region of the aperture (Figure 1). The origin of this layer is uncertain but it is apparently deposited by



the mantle edge (Joubin, 1892; Stenzel, 1964). Once deposited, the black layer remains unbroken until it is covered by nacre. Shell resorption, if present, must occur along the dorsal perimeter of the black layer, where the mantle edge rests during life.

MATERIALS AND OBSERVATIONS

Live specimens of *Nautilus macromphalus* Sowerby, 1849, were collected by Peter D. Ward near Noumea, New Caledonia. The animals were removed from the shells and the clean shells returned to the University of California, Davis, for further study. Only immature specimens were examined in the scanning electron microscopy phase of this study. If surficial resorption exists in *Nautilus* and occurs in conjunction with growth, as in gastropods, there would be no reason to expect evidence of resorption in adults, where growth has ceased. Immature individuals were initially identified by size and color pattern; this characterization was later confirmed by a lack of approximated terminal septae when specimens were sectioned. The specimens were prepared for examination by scanning electron microscopy (SEM) by cutting free centimeter-square size pieces of the shell exterior. Most pieces were cut so as to center the boundary between the black layer and the unmodified surface of the penultimate whorl but other areas of the shell surface were also examined. The specimens were cleaned with ethanol and an ultrasonic bath, mounted on SEM stubs, and then sputter-coated with gold/palladium and examined under SEM.

Visual examination of *Nautilus macromphalus* reveals that the edge of the black layer is usually slightly lower than the unmodified shell surface. (This is often most easily detected by running a fingernail over the boundary between the black layer and the unmodified shell surface.) The degree of offset varies from individual to individual, in some cases appearing flush and in others having the black layer visibly below the unmodified shell surface. The offset cannot reflect the presence of a low growth line, because the edge of the black layer is not congruent with growth lines. The only possible explanation for the black layer lying below the level of the shell surface over

which it is extending is that shell resorption occurs before the advance of the black layer.

Examination of specimens cut perpendicular to the boundary of the black layer shows that the thin outer shell layer, the porcellaneous layer, extends under the black layer. Therefore, resorption cannot remove more than about 0.18 mm of shell material, the approximate thickness of the porcellaneous layer. Measurement of the thickness of the outer shell layer, using an ocular micrometer, shows the portion under the black layer is approximately 0.12 mm, or averages about two-thirds the thickness of the uncovered portion of the outer shell layer. Resorption prior to deposition of the black layer is the only plausible explanation for this reduction in the thickness of the porcellaneous layer.

Under low-power optical magnification the normal shell surface appears vitreous. Along the edge of the black layer the shell surface has a hazy luster, suggesting that some modification of the shell surface has occurred.

Under scanning electron microscopy, the shell surface of *Nautilus macromphalus* has an irregular, pitted appearance (Figure 2). Fine growth lines are visible as uneven cuestas, apparently formed when new growth extends the shell from beneath the previous shell edge. Small pits are scattered unevenly over the surface and are densely concentrated in some areas. These concentrations usually fall along growth lines or where the shell apparently was damaged. The pits can approach one micrometer in size but most are less than half that diameter. The origin of the pits is unknown; one possibility is that they are produced by an endolithic organism, perhaps a boring fungus.

At the edge of the black layer the shell is irregularly eroded to a depth of several micrometers (Figure 3). The erosion occurs only along a band, about 1 mm in width, between the black layer and the unmodified shell surface. The depth of resorption is extremely variable, from a few micrometers up to several hundred micrometers. The eroded area is rough in appearance, with irregular hummocks of shell material separated by more deeply eroded areas (Figure 4). The advancing black layer eventually covers the eroded region and is itself later overgrown by further deposits of nacreous shell material.

Explanation of Figures 1 to 6

Figure 1. Immature *Nautilus macromphalus* from New Caledonia. Photo courtesy of P. Ward. Scale bar is 3.4 cm.

Figure 2. Shell surface of *Nautilus macromphalus*. Illustrated area is from flank of body chamber. Arrow indicates position of small, irregular cuesta interpreted here as growth line. Scale bar is 5 μm .

Figure 3. Boundary between unmodified shell surface and resorbed area on flank of penultimate whorl. Arrow indicates po-

sition of boundary. Direction of growth is to top. Scale bar is 50 μm .

Figure 4. Resorbed area at boundary of black layer. Note uneven, hummocky appearance. Scale bar is 5 μm .

Figures 5 and 6. Stereo pair of the boundary between the resorbed area and the unmodified shell surface. Direction of growth is to the right. Scale bars are 4 μm .

The morphology of the resorbed area is shown in Figures 5 and 6, a stereoscopic pair of micrographs taken of a single specimen. (The two pictures show the same region but are taken from two different angles, 6 degrees apart.) Perceived depth-of-field in SEM images can often be deceiving, because electron shadowing in SEM micrographs is quite different from patterns of illumination normally encountered in the human environment. In Figures 5 and 6, the resorbed area to the right of the micrographs sometimes appears to overlie the unmodified shell surface shown at the left of the picture. When examined through a stereoscopic viewer, it is immediately obvious that resorption has cut down into the shell surface shown at right.

Shell resorption in *Nautilus macromphalus* occurs along the entire margin of the black layer, from umbilicus to umbilicus. No portion of the shell's surface is covered by the black layer before the surface is modified by resorption.

DISCUSSION

Surficial resorption in *Nautilus macromphalus* is generally similar in form to that observed in many prosobranch gastropods, although the precise pattern of resorption differs somewhat in detail. In *N. macromphalus* the resorption is relatively deep and irregular, whereas the shallow, even resorption in the prosobranch *Terebra dimidiata* produces a smooth, flat surface (SIGNOR, 1982). Unlike most prosobranch gastropods, *N. macromphalus* alters the entire surface of the penultimate whorl, less narrow bands at the umbilici, but this reflects differences in shell geometry and not function. Despite these small differences, the effects of the resorption are identical: to remove the surface of the penultimate whorl as growth proceeds.

Surficial resorption is so widespread among different taxa of prosobranch gastropods that it is difficult to imagine resorption serving a function relating to the specific ecology of each given species. The convergent evolution of surficial resorption in *Nautilus macromphalus* greatly strengthens this argument. The ecology of *Nautilus* is very different from any prosobranch gastropod; what *Nautilus* and prosobranch gastropods have in common is a coiled shell where fresh growth surfaces contact and overlie older shell. The function of surficial resorption most likely lies in the few commonalities shared by prosobranch gastropods and *Nautilus*. The hypothesis that the function of surficial resorption is constructional, and that the mantle edge prepares a suitable surface to which the black layer and new shell material can be attached, meets the foregoing criterion. Alternatively, the function, if any, of surficial resorption could be to remove small epibionts or boring micro-organisms which might infest the shell's surface.

Relatively large calcareous epibionts are demonstrably too large to be removed by surficial resorption. Serpulid tubes not removed by the *Nautilus* during growth are simply plastered over by the black layer and, later, by na-

creous deposits (JOUBIN, 1892; STENZEL, 1964). LANDMAN (1983) documents the occurrence of a barnacle that grew on a live, juvenile *Nautilus*. The side of the barnacle was plastered with alternating layers of black organics and aragonite.

Surficial resorption in *Nautilus macromphalus* must be a convergently evolved character, because the most primitive and earliest orders of nautiloids, the Plectronocerida, Ellesmerocerida and others, consist of orthoconic and breviconic forms (SWEET *et al.*, 1964; YOCHELSON *et al.*, 1973; DZIK, 1981; CHEN & TEICHERT, 1983). Since growth in these straight or slightly curved forms would not involve overgrowth or extension of the mantle over previously deposited shell, surficial resorption would not have occurred. Surficial resorption must have appeared later in the evolution of the nautiloids, along with or after the evolution of coiled conchs where successive whorls were in contact with each other.

It would be interesting to determine whether the other great clade of fossil cephalopods, the Ammonoidea, exhibited surficial resorption. Answering this question would require extremely well-preserved fossil specimens. Thus far, I have not been able to obtain sufficiently well-preserved material to allow detection of surficial resorption, if present, in this group.

While resorption of shell material is commonplace among the Gastropoda, to my knowledge this is the first report of shell resorption among the extant Cephalopoda. Resorption may have occurred among extinct cephalopods, however. For example, the decollate nautiloids (*e.g.*, *Sphooceras truncatum* [Barrande, 1868]) might have resorbed a portion of the conch, allowing separation of the deciduous portion (TASNÁDI-KUBACSKA, 1962), in much the same way as the gastropods *Caecum* (BERNER, 1942) or *Rumina decollata* (KAT, 1981) weaken their shells by resorption prior to shedding the deciduous portion. The mechanism by which this resorption, if present, would have occurred is uncertain. Resorption requires direct application of the mantle to the area where shell material is to be removed. Although authors have postulated the presence of "cameral mantle" to account for the formation of cameral deposits in some nautiloids (TEICHERT, 1933, in FISCHER & TEICHERT, 1969; FLOWER, 1939; KOLEBABA, 1974), there is no compelling evidence for the presence of living tissues within the camerae, except the siphuncle, of any nautiloid (for recent reviews of the debate over formation of cameral deposits, see FISCHER, in FISCHER & TEICHERT, 1969; DZIK, 1981; CRICK, 1982). Thus, it is uncertain if resorption did occur in conjunction with decollation in primitive nautiloids and, if so, how that resorption might have occurred.

An important and unresolved question is how gastropods and *Nautilus* accomplish shell resorption, and what happens to shell material secondarily removed by the animal. It is not certain that uptake of ions removed from the shell occurs in the mantle, nor is it certain what part of the mantle might be responsible for the resorption.

Lacking this information, the term "resorption," while well established in the literature for this process, must be applied with caution. Based on current knowledge, it can only be used in the sense of "localized secondary dissolution." The experiments necessary to demonstrate uptake of secondarily dissolved ions through the mantle are tractable, however, and would permit resolution of this question.

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LITERATURE CITED

- BERNER, L. 1942. La croissance de la coquille chez les Gastropodes. Bull. Inst. Ocean. Monaco 816, 16 pp., 1 pl.
- BØGGILD, O. B. 1930. The shell structure of the mollusks. K. Danske Vidensk. Selsk. Skrifter, Naturvidensk og Mathem. 2:232-326, 15 pls.
- CARRIKER, M. R. 1972. Observations on removal of spines by muricid gastropods during shell growth. *Veliger* 15:69-74, 1 pl.
- CHEN, J. & C. TEICHERT. 1983. Cambrian cephalopods. *Geology* 11:647-650.
- COWEN, R., R. GERTMAN & G. WIGGETT. 1973. Camouflage patterns in *Nautilus*, and their implications for cephalopod paleobiology. *Lethaia* 6:201-214.
- CRICK, R. E. 1982. The mode and tempo of cameral deposit formation: evidence of orthoconic nautiloid physiology and ecology. Proc. Third North Amer. Paleont. Conf. 1:113-118.
- DZIK, J. 1981. Origin of the Cephalopoda. *Acta Palaeontologica Polonica* 26:161-191.
- ERBEN, H. K., G. FLAJS & A. SIEHL. 1969. Die Fruhontogenetische Entwicklung der Schalenstruktur ectocochleater Cephalopoden. *Palaeontographica Abh. A.* 132:1-54.
- FISCHER, A. G. & C. TEICHERT. 1969. Cameral deposits in cephalopod shells. *Univ. Kansas Paleont. Contr. Paper* 37, 30 pp.
- FLOWER, R. H. 1939. Study of the Pseudoorthoceratidae. *Palaeontographica Americana* 2:1-219.
- GRAY, J. E. 1833. Some observations on the economy of molluscous animals, and on the structure of their shells. *Phil. Trans. R. Soc. Lond.* 123:771-819.
- GRÉGOIRE, C. 1962. On submicroscopic structure of the *Nautilus* shell. *Bull. Inst. Roy. Sci. Nat. Belg.* 38:1-71.
- JOUBIN, L. 1892. Recherches sur la coloration du tégument chez les cephalopodes. 4me partie. Gland sécrétant le vernis noir chez le Nautilé. *Arch. Zool. Exper. Gen. Ser.* 2, 10: 319-324.
- KAT, P. W. 1981. Shell shape changes in the Gastropoda: shell decollation in *Rumina decollata*. *Veliger* 24:115-119, 1 pl.
- KOHN, A. J., E. R. MEYERS & V. R. MEENAKSHI. 1979. Internal remodeling of the shell by a gastropod mollusc. *Proc. Natl. Acad. Sci. U.S.A.* 76:3406-3410.
- KOLEBABA, I. 1974. A new orthocerid with a cameral mantle. *Vest. Ústř. Úsat. Geol.* 49:293-297.
- LANDMAN, N. H. 1983. Barnacle attachment on live *Nautilus*: implications for *Nautilus* growth rate. *Veliger* 26:124-127.
- MUTVEI, H. 1972. Ultrastructural studies on cephalopod shells. Part I. The septa and siphonal tube of *Nautilus*. *Bull. Geol. Inst. Univ. Upsala. N.S.* 3, 8:237-261.
- SCHINDEWOLF, O. H. 1967. Analyse eines Ammoniten-Gehäuses. *Akad. Wiss. und Literatur (Mainz), Math.-Naturwiss. Kl., Abh. Jahrg.* 1967, no. 8:137-188, pls. 1-16.
- SIGNOR, PHILIP W., III. 1982. Growth-related surficial resorption of the penultimate whorl in *Terebra dimidiata* (Linnaeus, 1758) and other marine prosobranch gastropods. *Veliger* 25:79-82, 1 pl.
- STENZEL, H. B. 1964. Living Nautilus. Pp. K59-K93. In: R. C. Moore (ed.), *Treatise on invertebrate paleontology, Part K, Mollusca 3.* The Geological Society of America and the University of Kansas Press.
- SWEET, W. C., C. TEICHERT & B. KUMMEL. 1964. Phylogeny and evolution. Pp. K106-K114. In: R. C. Moore (ed.), *Treatise on invertebrate paleontology, Part K, Mollusca 3.* The Geological Society of America and the University of Kansas Press.
- TASNÁDI-KUBACSKA, A. 1962. Pathologie der vorzeitlichen tiere. *Paläopathologie* 1:1-269.
- TEICHERT, C. 1933. Der Bau der actinoceroiden Cephalopoden. *Palaeontographica Abt. A* 78:111-130, 8 pls.
- YOCHELSON, E. L., R. H. FLOWER & G. C. WEBERS. 1973. The bearing of the new Late Cambrian monoplacophoran genus *Knighthoconus* upon the origin of the Cephalopoda. *Lethaia* 6:275-310.

Egg Capsules and Veligers of the Whelk *Bullia digitalis* (Gastropoda: Nassariidae)

by

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Abstract. The sandy beach whelk *Bullia digitalis* can package its eggs in two different ways. Clumps of eggs may be contained in a single large sheath and deposited in the sand, or each clump of 150 eggs or more may be contained in its own capsule and held on the ventral surface of the maternal foot. In the latter case up to 40,000 eggs may be produced at one time. The eggs and capsules are described for the first time, as is the veliger stage, which is passed within the egg. The reproductive strategy of *B. digitalis* is contrasted with that of *B. tenuis*.

INTRODUCTION

Bullia digitalis (Dillwyn) is a nassarid whelk which is abundant on medium to high energy sandy beaches along the west and south coasts of southern Africa. Its biology, together with that of other species of the genus, has been reviewed by BROWN (1982). On beaches in the Eastern Cape Province of South Africa, gametogenesis occurs between March and May, vitellogenesis and egg storage taking place from June to December or January, after which the females spawn (MCGWYNNE, 1980). We believe that the timing of events on the west coast may be both different and more variable than in the Eastern Cape (BROWN, 1971) and in recent years we have discovered females with eggs from early July to late January at Van Riebeeck Strand (Ou Skip), just north of Table Bay.

Females of several intertidal species of *Bullia* tend to migrate offshore before producing their egg capsules (BROWN, 1982). *Bullia digitalis* appears to be no exception (MCGWYNNE, 1980), although this migration of females is more marked in some areas than in others. The gravid females found at Van Riebeeck Strand were all buried just below low water mark, the migratory tendency thus being poorly developed.

Egg cases of *Bullia digitalis* were first described by Professor J. Omer-Cooper in a letter to one of us (A.C.B.), this description being subsequently confirmed by BROWN (1971). A case measured about 2 cm in length and 1.2 cm in width and contained more than 1500 eggs arranged in clumps of 50 to 100 or more. Such egg cases were found 4 to 12 cm below the surface of the sand, usually in the presence of an adult female.

The present work was undertaken due to the discovery of *Bullia digitalis* eggs, from Van Riebeeck Strand, that were packaged differently, being held in numerous small capsules under the maternal foot, and also to the acquisition for the first time of eggs containing veligers.

MATERIALS AND METHODS

Of the several females of *Bullia digitalis* discovered carrying egg capsules beneath their feet, four were returned to the laboratory from Van Riebeeck Strand. The capsules and the eggs within them were counted and measurements made using a graduated eyepiece in a binocular microscope. In addition we had on loan from the South African Museum a female with capsules collected on Fish Hoek beach, False Bay, by Mrs. C. M. Connolly on 5 January 1961; in these capsules all the eggs had hatched or were on the point of hatching, as miniature adults.

More recently, a whelk collected at Van Riebeeck Strand produced a full batch of egg capsules in the laboratory. These were discovered on 19 January 1984, well over a month after the animal had been captured. It is almost certain that this whelk had copulated in the field, the sperm being stored in the spermatheca. A number of capsules shed from the parental foot were held over sand in flowing seawater at 14°C. In each egg a veliger larva could be observed, which swam actively in the water if mechanically released from the egg. Several such veligers were examined and photographed under light microscopy, using various types of illumination, first while they were swimming freely and later while held immobile under a coverslip.



Figure 1

Egg capsules of *Bullia digitalis* removed from the foot of a gravid female ($\times 12$). The cases are typical except for one near the center of the picture, which contains few eggs.

RESULTS

Eggs and Egg Capsules

The number of capsules per female varied from 150 to 203, each capsule typically containing 150 to 200 eggs, although an occasional capsule had only 30 or 40. Each capsule measured $3.00 \pm 0.05 \times 1.5 \pm 0.15$ mm, had an extremely thin, transparent, membranous wall, and possessed an attachment thread at either end, one thread being more coiled than the other. The capsules were attached loosely to the undersurface of the maternal foot and to one another by a sparse but viscous mucous secretion and were further anchored to one another by their coiled attachment threads. A group of such egg capsules, removed from the foot and comprising about a quarter of those present, is shown in Figure 1. Each egg was about $220 \mu\text{m}$ in diameter, as were the eggs and newly hatched young collected by Mrs. Connolly on Fish Hoek beach.

Gravid whelks in the laboratory protected their capsules by curling the foot over them to form a tubular brood pouch, in the manner described from *Bullia melanoides* by ANSELL & TREVALLION (1970), while during crawling only the margins of the foot were used. These protective behavior patterns did not appear to be entirely adequate, however, as the whelks tended to shed capsules.

The Veligers

Each veliger carried a very thin, transparent protoconch consisting of $1\frac{1}{2}$ whorls. The veligers measured $205 \pm 25 \mu\text{m}$ between the apex of the protoconch and the leading edge of the head. At its widest the shell diameter was $98 \pm 7 \mu\text{m}$. The head was bordered by a bilobed velum, which was heavily ciliated with cilia of two types; the longer ($10 \mu\text{m}$ in length) exhibited metachronal rhythm, while the shorter cilia, only about half that length, showed a more random pattern of movement. Two well-defined tentacles

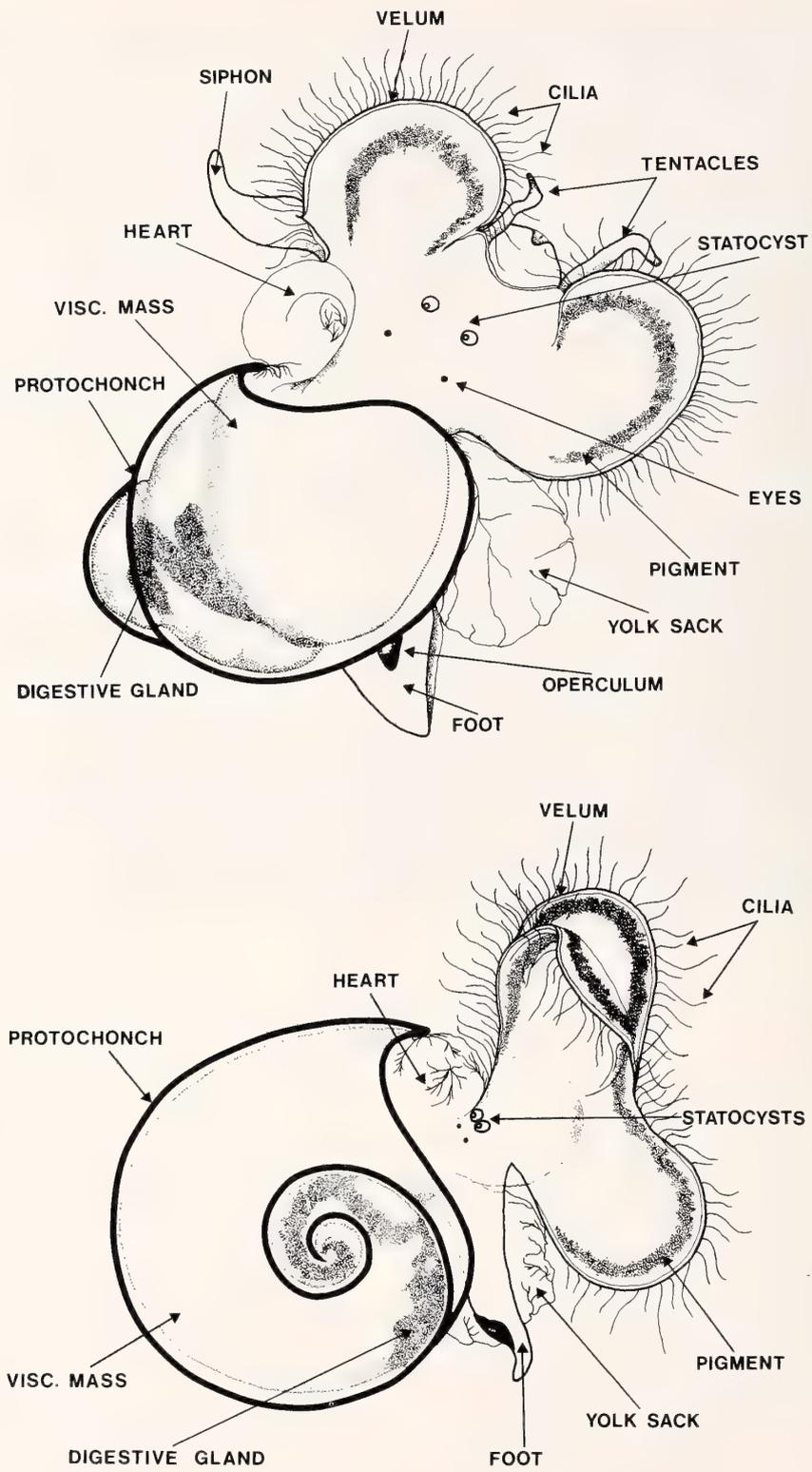


Figure 2

Veliger larva of *Bullia digitalis*. Above, dorsal view. Below, lateral view.

and a siphon were present, as was a ridge of dark orange pigment on the velum that probably represents the respiratory complex of the adult. A pair of eyes was apparent, despite the fact that the adults lack eyes (BROWN, 1982). Laterally and slightly anterior to the eyes, a pair of statocysts lay close to the actively pumping heart. Torsion had already occurred but it could not be determined whether torsion was complete. A small foot and operculum were present. A sac lying on the outside of the body and attached near the base of the visceral mass was tentatively identified as a yolk sac, as its contents dissolved rapidly on contact with acetone, indicating the presence of lipids. A veliger of *Bullia digitalis* is shown in Figure 2.

Attempts to rear the eggs failed, the veligers becoming lethargic and darkly pigmented; within five days they had become infested by larvae of a digenic trematode and died soon thereafter. Eggs in capsules that remained attached to the feet of other individuals also failed to develop.

DISCUSSION

Although the literature on planktonic prosobranch larvae is voluminous, descriptions of veliger stages passed within the egg are rare and no *Bullia* veliger has previously been described. THIRIOT-QUIÉVREUX (1980) described the planktonic veligers of *Nassarius*, a genus closely related to *Bullia*, but these differ considerably from the veligers described here. On the other hand, veligers of *Littorina littorea* are quite similar to those of *Bullia digitalis*, both in size and at least superficially in morphology (FISH & FISH, 1977), with the exceptions that the cilia on the velum of *Littorina* are 3 to 5 times longer and no tentacles are visible.

The eggs of all species of *Bullia* so far investigated produce crawling young, the larval stages being passed within the egg (BROWN, 1982). *Bullia digitalis* is no exception and the small size of the eggs of this species may thus be remarked upon, as one might have expected eggs of little more than 0.2 mm in diameter to hatch at a much earlier stage. It is also of interest that every egg we examined had within it a living veliger and that every egg in the capsule collected by Mrs. Connolly contained a miniature adult; there are thus no nurse eggs in this species, despite tentative previous suggestions (BROWN, 1971, 1982).

The numbers and size of young *Bullia digitalis* contrast with those of *B. tenuis*, a subtidal species whose egg cases and young have recently been described (BROWN, 1985). The adults of these two species are of similar size and appearance, but *B. tenuis* produces only about 60 egg capsules at a time and each capsule contains only one developing egg, although nurse eggs are also apparently pres-

ent. By contrast, *B. digitalis* appears capable of producing up to 40,000 young at one time, but these are minute compared with the young of *B. tenuis*, which may attain a shell length of 5.3 mm before emerging from their capsules (BARNARD, 1959; BROWN, 1985). It is clear that these extremes represent very different strategies and it must be supposed that juvenile mortality is high in *B. digitalis* as compared with *B. tenuis*.

Finally, *Bullia digitalis* can package its eggs in two different ways—either with each clump of eggs contained in its own capsule, as reported here, or with all the clumps in a single all-embracing case or sheath, as described by Professor Omer-Cooper and subsequently by BROWN (1971). In the former circumstance, the tiny capsules are loosely attached to the undersurface of the foot, while if contained in a single large case they are deposited in the sand. It is clear that such a large case must be formed outside the body of the parent and it is logical to suppose that it is molded by the foot after the eggs have been extruded; its size and shape certainly support this explanation. Differences in egg packaging according to circumstances of food availability are not unknown among the Nassariidae (MCKILLUP & BUTLER, 1979) but the present example would appear to be the most extreme so far reported for any of the Prosobranchiata.

LITERATURE CITED

- ANSELL, A. D. & A. TREVALLION. 1970. Brood protection in the stenoglossan gastropod *Bullia melanoides* (Deshayes). *J. Natur. Hist.* 4:369-374.
- BARNARD, K. H. 1959. Contributions to the knowledge of South African marine Mollusca. Part II: Gastropoda: Prosobranchiata: Rhachiglossa. *Ann. S. Afr. Mus.* 45:1-237.
- BROWN, A. C. 1971. The ecology of the sandy beaches of the Cape Peninsula, South Africa. Part 2: the mode of life of *Bullia* (Gastropoda: Prosobranchiata). *Trans. Roy. Soc. S. Afr.* 39:281-320.
- BROWN, A. C. 1982. The biology of whelks of the genus *Bullia* (Nassariidae). *Oceanogr. Mar. Biol. Ann. Rev.* 20:309-361.
- BROWN, A. C. 1985. Egg capsules and young of *Bullia tenuis* (Nassariidae). *J. Moll. Stud.* (in press).
- FISH, J. D. & S. FISH. 1977. The veliger larva of *Hydrobia ulvae* with observations on the veliger of *Littorina littorea* (Mollusca: Prosobranchiata). *J. Zool. (Lond.)* 182:495-503.
- MCGWYNN, L. E. 1980. A comparative ecophysiological study of three sandy beach gastropods in the Eastern Cape. Master's Thesis, University of Port Elizabeth. 144 pp.
- MCKILLUP, S. C. & A. J. BUTLER. 1979. Modification of egg production and packaging in response to food availability in *Nassarius pauperatus*. *Oecologia* 43:221-231.
- THIRIOT-QUIÉVREUX, C. 1980. Identification of some planktonic prosobranch larvae present off Beaufort, North Carolina. *Veliger* 23:1-9.

The Ecology and Local Distribution of Non-marine Aquatic Gastropods in Viti Levu, Fiji

by

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Abstract. Freshwater habitats throughout the island of Viti Levu, Fiji were investigated for gastropods, water conductivity, water hardness, temperature, substrate, and current speed from August 1982 to February 1984. In general the values of conductivity, hardness, and temperature increased toward the sea; but this was not true of all river systems and these factors were not as important in influencing the distribution of the 32 gastropod species as were physical factors, specifically distance from the sea, substrate, and current speed. Using these physical factors the running water gastropods were classified into five groups. Gastropods were absent from long stretches of all rivers where the water was deep and turbid and the bottom unstable.

INTRODUCTION

DURING 1971 STARMÜHLNER (1976) sampled the gastropods at stations near the town of Suva and near the forestry station of Nadarivatu on the island of Viti Levu, Fiji. However, no further sampling of gastropods in the remaining extensive network of rivers and streams on Viti Levu has been reported.

The aim of this study was to find the distribution of the freshwater gastropods on the island of Viti Levu, Fiji and to establish the factors that were most important in influencing the distribution of the various species.

STUDY AREA

Viti Levu is an oval-shaped island, reaching about 150 km long and 100 km wide (Figure 1). The interior is mountainous and the highest peak, Mt. Victoria (Tomanivi), is 1312 m high. Because Viti Levu is in the path of the southeast trade winds, the southeastern side and the interior receive heavy rainfall and are covered in rain forest, while the northwestern side is comparatively dry and much of it is used for growing sugar cane. The mean annual temperature is 29–30°C and the annual rainfall is about 3000 mm.

The two longest rivers are the Rewa and Sigatoka, which rise in the central high country and flow southward. The Rewa River system drains nearly one-third of the island. Recently two artificial lakes have been formed. The construction of a hydroelectric dam on the upper Rewa River

resulted in Lake Monasavu, and a dam to impound water to supply the towns of Lautoka and Nadi has produced Lake Vaturu (Figure 1).

MATERIALS AND METHODS

Gastropods were collected from rivers, streams, and lakes from July 1982 to February 1984. The collecting stations 1–47 are shown on the map of Viti Levu (Figure 1). They were chosen to be as representative as possible while being accessible by road or track.

The river bed and plants at each station were searched for 30 min. The upper and lower surfaces of stones and boulders were searched, leaf litter and water-weed were inspected, and sand and gravel were sieved. Representatives of all gastropod species were collected and taken to the laboratory for identification. Shell, operculum, radula, and reproductive organs were used in the identification of the snails following several authors: MOUSSON (1870), RIECH (1937), BENTHEM-JUTTING (1956), FRANC (1956), STARMÜHLNER (1970, 1976).

Water speed was estimated by timing a float between two fixed points, the water temperature was taken to the nearest 0.5°C, and in some cases a water sample was collected from the station. At the Institute of Natural Resources, University of the South Pacific, water samples were analyzed for conductivity (μs), which indicates the total ion concentration, and for hardness ($\text{mg CaCO}_3/\text{L}$) by titration with EDTA (ethylene-diaminetetraacetic acid).

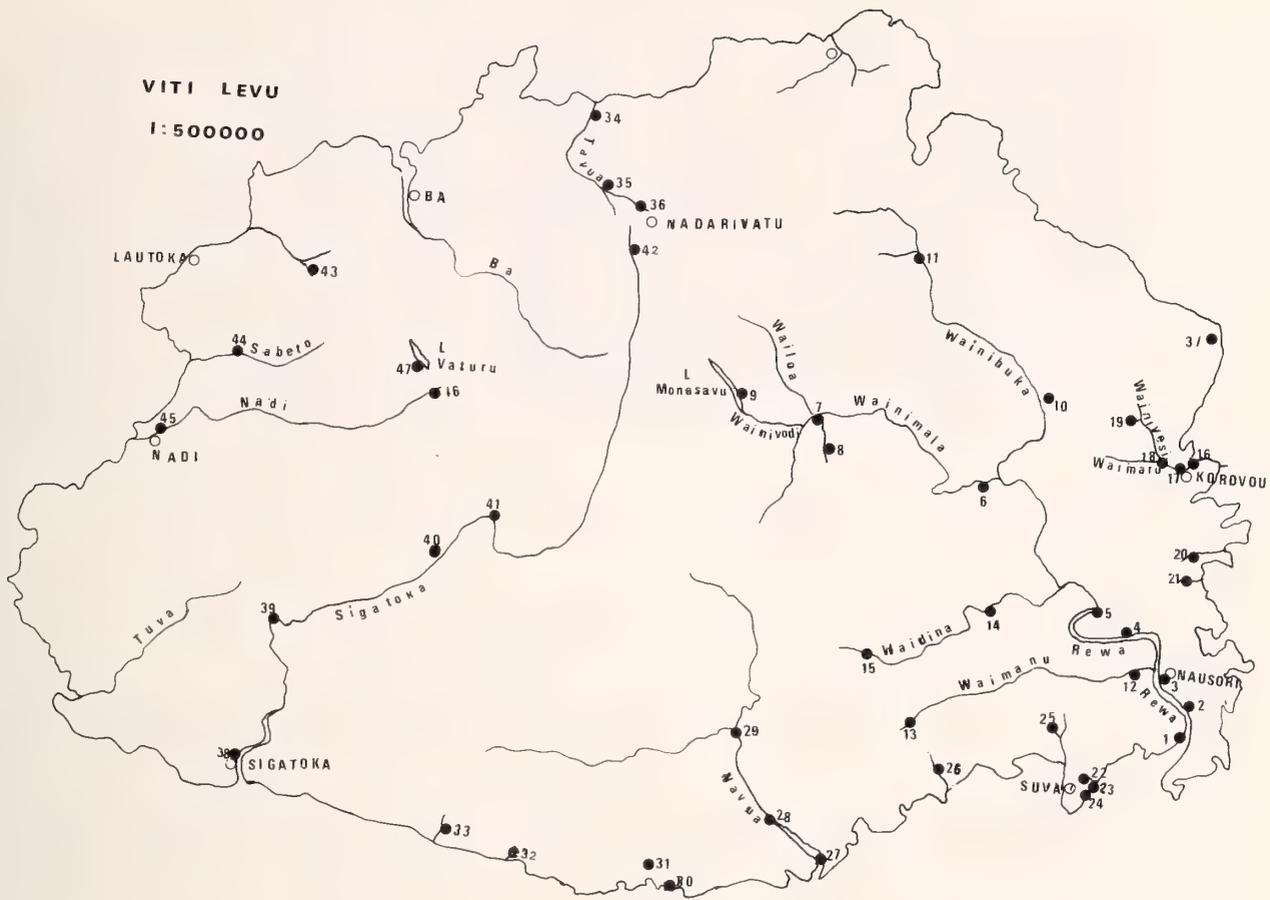


Figure 1

A map of the main river systems of Viti Levu, Fiji showing the localities of sampling stations 1-47.

RESULTS

Species Found

Thirty-two species were found and identified (Table 1). The nomenclature of STARMÜHLNER (1976) has been used where possible.

The gastropods found in still water were the pulmonates *Planorbarius corneus* (Linnaeus, 1758), *Physastra nasuta* (Morelet, 1856), *Ferrissia noumeensis* (Crosse, 1871), *Gyraulus montrouzieri* (Gassies, 1863), and the prosobranch *Melanoides tuberculata* (O. F. Müller, 1774). The European snail *Planorbarius corneus* was probably introduced into station 24 from a freshwater aquarium. *Melanoides tuberculata* was the most widespread species; it was found at 22 of the 47 stations. *Physastra nasuta* was the next most widespread species, being found at 14 stations. Both species lived in ditches and dalo patches on gravel and mud as well as on stones in water currents as fast as 80 cm/s (Table 1). *Ferrissia noumeensis* was present on stones, gravel, and water plants at seven stations—two ponds, two small streams (stations 21, 23), one slowly

flowing river (station 17), and two fast flowing inland rivers (stations 11, 19). This suggests that it is also widespread but often overlooked because of its small size (<5.0 mm). *Gyraulus montrouzieri* was found on water-weed in still and slowly flowing water at two stations (23, 30).

The remaining gastropod species lived in running water. Using the parameters of distance from the sea, current speed, and bottom substrate of the river or stream in which they lived, these gastropods can be divided into 5 groups:

- (1) 200 m-2 km from the sea in currents from 0 to 10 cm/s, substrate of mud or sand with some rocks and water plants: *Assiminea crosseana* (Gassies, 1858) on plants, *Clithon oualaniensis* (Lesson, 1831) on sand or mud, *Neritina turrata* (Gmelin, 1790) on mud, *Clithon spinosus* (Budgin, 1845), and *Neritina auriculata* Lamarck, 1816, on rocks.
- (2) 300 m-8 km from the sea in a current up to 40 cm/s, substrate of stones and rocks: *Clithon corona* (Linné, 1758), *Clithon diadema souleyetana* (Récluz, 1841), and *Melanoides arthurii* (Brot, 1871).

Table 1

The physical conditions, results of water analysis, and gastropods present at the sampling stations. ND = not determined.

Sam- pling station number	River & map reference (1:50,000 Viti Levu)	Substrate	Distance from sea (km)	Water speed (cm/s)	Temper- ature (°C)	Total ion concentra- tion (µs)	Hardness (mg CaCO ₃ /L)	Gastropods present
1	Rewa R. (tidal), Lokia landing, XE644983	sand, rocks & plants	2	0-10	25	190	78	<i>Neritina turtoni</i> , <i>N. squamipicta</i> , <i>Septaria porcellana depressa</i> , <i>Thiara bellicosa</i> , <i>Assimineia crosseana</i>
2	Rewa R. (tidal), Nausori airport, XF622060	mud	8	0-10	26	111.6	51	<i>Neritina turtoni</i> , <i>N. squamipicta</i> , <i>Thiara belliosa</i> , <i>Cithon corona</i>
3	Rewa R., Nausori bridge, XF651041	mud, sand & plants	11	0-10	27	99	43	<i>Neritina turtoni</i> , <i>N. squamipicta</i> , <i>Septaria lineata</i> , <i>Melanoides aspirans</i>
4	Rewa R., XF552110	mud, weed & wood	22	0-10	27	ND	ND	<i>Neritina turtoni</i> , <i>N. squamipicta</i>
5	Rewa R. at Baulevu, XF530135	mud & shingle	38	0-10	26.5	98.6	39	(<i>Batissa violacea</i> , a freshwater clam)
6	Waimimala R. at Serea, XF380265	shingle	72	30-50	26.5	50.3	25.5	—
7	Waimimala R., 2 km below Laselevu, XF202367	shingle & boulders	90	30-40	24	82.2	31	<i>Fijidoma maculata</i> , <i>Physastra nasuta</i>
8	Stream into Waimimala R., 1.5 km above Matainisau, XF190339	shingle & boulders	97	40-60	23	75.5	35	<i>Fijidoma maculata</i> , <i>Fluviopupa pupoidea</i> , <i>Melanoides tuberculata</i> , <i>Physastra nasuta</i>
9	Lake Monasavu, XF115377	mud & stones	110	0	25	ND	ND	<i>Physastra nasuta</i>
10	Stream into Wainibuka R., 1 km south Wailotaui, XF340479	boulders	77	0-60	25	68.5	28	<i>Melanoides tuberculata</i> , <i>Septaria porcellana depressa</i>
11	Wainibuka R., 1.8 km south of Rokovuaka, XF340479	stones & boulders	100	50-80	29	132.8	66	<i>Fijidoma maculata</i> , <i>Fluviopupa pupoidea</i> , <i>Melanoides tuberculata</i> , <i>Physastra nasuta</i> , <i>Thiara scabra</i> , <i>Ferrissia noumeensis</i>
12	Waimanu R. pumphouse, XE552059	stones	21	20-30	25	80	35	—
13	Stream into Waimanu R., Namosi road, XE274997	stones & boulders	46	30-50	23	73.7	34	<i>Melanoides tuberculata</i>
14	Waidina R., Monasavu road, XF470155	stones	43	30-50	23	42.6	19.5	<i>Physastra nasuta</i>
15	Waidina R. at Namosi, XF212055	stones & boulders	82	0-30	23.5	63.2	31	<i>Fluviopupa pupoidea</i> , <i>Melanoides lutosus</i> , <i>M. tuberculata</i>
16	Waimara R. at end of road, XF668315	mud, sand & stones	2	0	28	131.4	55	<i>Cithon diadema souleyetana</i> , <i>Neritina auriculata</i>
17	Waimara R. at Korovou, XF630325	mud & water- weed	5	0-10	28.5	91.3	38.8	<i>Ferrissia noumeensis</i> , <i>Neritina rubida</i>
18	Junction of Wainivesi & Waimara R., XF630325	gravel & stones	10	20-30	29.5	99	44.9	<i>Melanoides tuberculata</i>
19	Stream into Wainivesi R., XF595375	gravel, stones & boulders	15	0-30	28	89.5	39.1	<i>Ferrissia noumeensis</i> , <i>Fluviopupa pupoidea</i> , <i>Melanoides lutosus</i> , <i>M. tuberculata</i> , <i>Physastra nasuta</i> , <i>Neritina pulligera</i>

Table 1
Continued.

Sam- pling station number	River & map reference (1:50,000 Viti Levu)	Substrate	Distance from sea (km)	Water speed (cm/s)	Temper- ature (°C)	Total ion concentra- tion (μ s)	Hardness (mg CaCO ₃ /L)	Gastropods present
20	Waidalice R. at end of road, XF645250	mud & stones	5	0-10	29	ND	ND	<i>Clithon corona</i> , <i>Neritina squamipicta</i> , <i>Septaria lineata</i>
21	Stream at forestry, XF635170	rock & weed	4	0-20	30	ND	ND	<i>Ferrissia noumeensis</i> , <i>Melanooides tuberculata</i>
22	Uluituni Cr., mangroves, Suva, XE534926	mud & leaves	0.2	0	29	ND	ND	<i>Clithon oualaniensis</i> , <i>Neritina auriculata</i> , <i>N. turrita</i> (marine: <i>Melampus striatus</i> , <i>Pythia scarabaeus</i> , <i>Littorina undulata</i>)
23	Uluituni Cr., USP campus, stream, XE532928	mud, gravel & weed	0.3	10	29	ND	ND	<i>Ferrissia noumeensis</i> , <i>Gyraulus montrouzieri</i> , <i>Melanooides tuberculata</i> , <i>M. arthurii</i> , <i>Physastra nasuta</i>
24	Lily pond, Suva Grammar School, XE532922	mud & plants	0.3	0	28	ND	ND	<i>Ferrissia noumeensis</i> , <i>Melanooides tuberculata</i> , <i>Physastra nasuta</i> , <i>Planorbis corneus</i>
25	Vago Cr., Wailuku, XF529007	shingles, boulders & rocks	5	40-80	24	62.8	31	<i>Melanooides tuberculata</i> , <i>M. aspirans</i> , <i>Neritina pulligera</i> , <i>N. pettii</i> , <i>N. macgillivrayi</i> , <i>Septaria suffreni</i> , <i>S. porcellana depressa</i> , <i>Thiara terpsichore</i> , <i>T. amarula</i>
26	Creek beside Nabukavesi-Namosi road, XE312925	gravel & shingle	4	30-40	26	49.6	19.5	<i>Melanooides arthurii</i> , <i>M. tuberculata</i>
27	Navua R. at bridge, XE224856	mud, rocks & plants	4	0-10	25	68.8	33	<i>Neritina rubida</i> , <i>N. squamipicta</i> , <i>N. turtoni</i>
28	Navua R. at Waiyanitu, XE185888	gravel & stones	15	30	25	68.5	34.5	—
29	Navua R. at Namuamua, XE129990	shingle & boul- ders	28	30-50	25	ND	ND	<i>Neritina pulligera</i>
30	Lily ponds, Pacific Harbour, XE138819	mud & plants	0.3	0	28	ND	ND	<i>Ferrissia noumeensis</i> , <i>Gyraulus montrouzieri</i> , <i>Melanooides tuberculata</i>
31	Sago swamp, Pacific Harbour, XE134847	mud & dead leaves	2	0	28	ND	ND	<i>Melanooides tuberculata</i> , <i>Physastra nasuta</i>
32	Stream on Coral coast, WE825855	sand, gravel & boulders	0.3	10-30	29	ND	ND	<i>Clithon corona</i> , <i>Neritina pettii</i> , <i>Melanooides tuberculata</i>
33	Korolevu Cr., upstream from air- strip, WE780878	stones	2	30-40	28	ND	ND	<i>Neritina pulligera</i> , <i>Septaria porcellana depressa</i>
34	Tavua R. town bridge, WF925720	mud & stones	2	0-10	30	601	237.9	<i>Clithon diadema souleyetana</i> , <i>Neritina turtoni</i> , <i>N. squamipicta</i> , <i>Septaria porcellana depressa</i>
35	Waikubakuba R. at village, WF988920	shingle & boul- ders	14	40-60	25	135.2	64.2	<i>Melanooides tuberculata</i> , <i>Physastra nasuta</i>
36	Stream into Waikubakuba R. at Nadarivatu, XF029579	boulders	18	0-50	22	55.1	26.6	<i>Fluviopupa pupoidea</i>

Table 1
Continued.

Sam- pling station number	River & map reference (1:50,000 Viti Levu)	Substrate	Distance from sea (km)	Water speed (cm/s)	Temper- ature (°C)	Total ion concentra- tion (μ s)	Hardness (mg CaCO ₃ /L)	Gastropods present
37	Stream between Lodonu & Natovi, XF676440	stones	0.5	20-40	27	ND	ND	<i>Cithon diadema souleyetana</i> , <i>C. corona</i> , <i>Melano-</i> <i>anoides aspirans</i> , <i>Septaria porcellana depres-</i> <i>sa</i>
38	Sigatoka R. at town bridge, WE545948	mud, wood & stones	2	0-10	28	164	91	<i>Cithon spinosa</i> , <i>Neritina turtoni</i> , <i>N. auricula-</i> <i>ta</i> , <i>N. turrita</i> , <i>Septaria luzonica</i>
39	Sigatoka R., 20 km upstream from bridge, WF635130	stones	22	30-50	28	151.9	103	—
40	Stream into Sigatoka R., near Tuva, WF790214	gravel, stones & rocks	50	0-60	26.5	267	131	<i>Melanooides tuberculata</i> , <i>Thiara scabra</i>
41	Sigatoka R., 2 km upstream from Keyasi, WF835230	stones	65	50-60	26.0	161.7	71	<i>Fluviopupa pupoidea</i> , <i>Melanooides tuberculata</i>
42	Nadala Cr. into Sigatoka R. at Na- darivatu, XF023566	shingle & boul- ders	110	20-40	23	43.1	21.2	<i>Melanooides lutosus</i> , <i>M. tuberculata</i> , <i>Physastra</i> <i>nasuta</i>
43	Stream at Vakabuli, WF595525	stones	8	20-40	28	ND	ND	<i>Melanooides aspirans</i> , <i>M. tuberculata</i> , <i>Physastra</i> <i>nasuta</i> , <i>Septaria suffreni</i>
44	Sabeto R., near power station, WF525410	stones & rocks	6	50-80	27	ND	ND	<i>Melanooides tuberculata</i> , <i>Neritina pulligera</i> , <i>Septaria porcellana depressa</i> , <i>S. suffreni</i>
45	Nadi R. at town bridge, WF445322	mud & stones	4	0-10	32	229	90	<i>Cithon diadema souleyetana</i> , <i>Melanooides pli-</i> <i>caria</i> , <i>Neritina squampicia</i> , <i>Septaria luzoni-</i> <i>ca</i> , <i>S. porcellana depressa</i> , <i>Thiara terp-</i> <i>sichore</i>
46	Nadi R. at Natawa, WF711349	gravel, stones & boulders	35	30-60	25	231	99	<i>Fluviopupa pupoidea</i> , <i>Melanooides lutosus</i> , <i>M.</i> <i>tuberculata</i> , <i>Physastra nasuta</i>
47	Lake Vaturu, WF705375	mud & stones	38	0	28	53.5	32	<i>Melanooides tuberculata</i> , <i>Physastra nasuta</i>

- (3) 2–11 km from the sea in currents from 0 to 10 cm/s, substrate of mud and sand with some rocks and water plants: *Melanoides plicaria* (Born, 1780) on mud and sand, *Neritilia rubida* (Pease, 1867) on plants, *Septaria lineata* (Lamarck, 1816) and *Neritina squamipicta* Récluz, 1843, on plants and rocks, *Neritina turtoni* (Récluz, 1843) on mud and rocks, and *Thiara bellicosa* (Hinds, 1844) on mud. *Neritina squamipicta* and *N. turtoni* were found 22 km from the sea (station 4).
- (4) 300 m–11 km from the sea in currents from 20 to 80 cm/s, substrate of rocks and boulders with patches of stones and gravel: *Melanoides aspirans* (Hinds, 1847), *Thiara amarula* (Linné, 1758), and *Thiara terpsichore* (Gould, 1847) on gravel and stones in slower currents, and *Neritina macgillivrayi* (Reeve, 1855), *Neritina petiti* Récluz, 1843, *Neritina pulligera* (Linné, 1767), *Septaria porcellana depressa* (Linné, 1758), and *Septaria suffreni* (Récluz, 1841) on rocks. *Septaria porcellana depressa* was found 77 km (station 10) and *N. pulligera* 28 km (station 29) from the sea.
- (5) 15–110 km from the sea in currents from 30 to 80 cm/s, substrate of stones, boulders, and rocks: *Fijidoma maculata* (Mousson, 1865) on stones, *Fluviopupa pupoidea* Pilsbry, 1911, *Melanoides lutosus* (Gould, 1847), and *Thiara scabra* (O. F. Müller, 1774) on stones, boulders, and rocks (Table 1).

Characteristics of the River Systems

When the physical data from all the river systems were pooled, an inverse correlation was found between distance from the sea and temperature ($P < 0.05$), hardness ($P < 0.05$), and total ions ($P < 0.01$) (Spearman's rank correlation coefficient r_s , ELLIOTT, 1977). Generally, however, the number of gastropod species did not follow this inverse correlation. More often there were more species near the mouth of the rivers and in the headwaters than in the middle reaches.

The pattern of decreasing temperature, total ions, and hardness with increasing distance from the sea was not apparent in all rivers. However, this was the trend in the short, steep Waikubakuba-Tavua river system (Figure 1, stations 34, 35, 36) where temperature (30, 25, 22°C), total ions (601, 135.2, 55.1 μs), and hardness (237.9, 66.2, 26.6 mg CaCO_3/L) decreased as distance (2, 14, 36 km) increased.

The lowland Wainivesi-Waimara system illustrated the lack of correlation between distance from the sea and the number of species found. Here, there were two gastropod species 2 km from the mouth, two other species 5 km from the sea at station 17, one species 10 km inland at station 18, and six species in the headwaters at station 19 (Figure 1). In this river system there was little variation in water hardness (55, 38.8, 44.9, 39.1 mg CaCO_3/L), or temperature (28, 28.5, 29.5, 28°C) from mouth to headwater (Table 1).

All of the rivers and streams studied contained sufficient

dissolved ions to support a gastropod population. The lowest conductivity, 43.1 μs , was obtained at Nadala Creek, station 42 (Figure 1), where the three gastropods *Melanoides tuberculata*, *M. lutosus*, and *Physastra nasuta* were frequently found. The total ion concentration here was low compared with that in the water of the English Lake district where the main ions are sodium and calcium in equal proportions and the conductivity is 112 μs , or with those in a limestone stream such as the river Avon (Wiltshire, England) which has a conductivity of about 450 μs , or with those in water of salinity 3‰ which has a conductivity of 6000 μs (MACKERETH *et al.*, 1978; HAYNES, 1982).

The concentration of calcium ions necessary for the presence of mollusks varies but if the quantity of water is great enough they will tolerate low concentrations. For example, *Planorbis carinatus* is common in Lake Windermere, England where the calcium concentration is 5 mg/L (MACAN, 1974). The lowest values for hardness in this study were 21.1 mg CaCO_3/L at station 42 and 19.5 mg CaCO_3/L at station 26 (Figure 1). *Melanoides arthurii*, *M. tuberculata*, *M. lutosus*, and *Physastra nasuta* were present at one or both of these stations.

The water temperature varied from 22 to 32°C. Although generally the water was warmer nearer the river mouth, inland species such as *Fijidoma maculata* and *Fluviopupa pupoidea* were found in temperatures up to 29°C (station 11). It is possible that they were restricted to inland streams because they require a low temperature (22–23°C) for reproduction.

Gastropods were absent from long stretches of the larger rivers (stations 6, 12, 28, 22) due to unstable bottom substrates and to the depth of the often turbid water. The freshwater clam *Batissa violacea* Lamarck was often present under such conditions.

DISCUSSION

All the species found have been reported from other Pacific islands (RIECH, 1937; STARMÜHLNER, 1970, 1976). However, four species, *Gyraulus montrouzieri*, *Planorbis corneus*, *Clithon spinosus*, and *Neritina squamipicta*, have not been reported previously from Fiji. In addition, *Fijidoma maculata* has been previously recorded only from swift flowing parts of the Rewa and Lami river systems, Viti Levu (MORRISON, 1954). In this survey it was found in the headwaters of the Rewa, at stations 7 and 8 in the Wainimala River, and at station 11 in the Wainibuka River where it reached a density of 2250/m².

Decreases in total ion concentration and temperature in the mountain streams of Madagascar, Sri Lanka, and New Caledonia similar to those observed in the Waikubakuba-Tavua river system were reported by STARMÜHLNER (1979). These trends were absent in some of the longer river systems of Fiji.

When Starmühlner sampled the Vago Creek (station 25) in 1971 (STARMÜHLNER, 1976) he reported a water

speed of 0.5–1 m/s, a temperature of 23.6°C, a total ion concentration of 45 μ s, and the following species present: *Neritina pulligera*, *Septaria porcellana depressa*, *Thiara amarula*, *Melanoides aspirans* and *M. tuberculata*. This is not dissimilar to the findings of the present study when the water speed was 40–80 cm/s, the temperature 24°C, the total ion concentration 62.8 μ s, and the same species were found as in 1971 plus *Septaria suffreni*, *Thiara terpsichore*, *Neritina macgillivrayi*, and *N. petiti*. Starmühlner also sampled at Nausori (station 3) where he found the temperature was 27.4°C compared with 27°C in this study. The species that he found were *Neritina turtoni*, *Septaria lineata* and *Thiara bellicosa*. In this study *T. bellicosa* was absent but *Neritina squamipicta* and *Melanoides aspirans* were present.

Starmühlner sampled at 8 stations in the Suva area and J. A. McLean sampled at 4 stations in the interior near Nadarivatu (STARMÜHLNER, 1976). Starmühlner found 18 species, three of these were not discovered in this survey. These were *Clithon olivaceus* (Récluz), *Neritina canalis* (Sowerby), and *Septaria macrocephala* (Le Guillou). All three were found during 1983 in clear torrential streams on the relatively undeveloped Fiji islands of Ovalau, Taveuni, Kadavu, and Gau. It is possible that they have become rare on Viti Levu due to the increase in road building and logging. Both activities disturb the soil which is then washed into the rivers and streams during heavy rains and increases the turbidity of the water. Mud is deposited on rocks and stones where it inhibits the growth of algae, the main food source of these gastropods.

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LITERATURE CITED

- BENTHEM-JUTTING, W. S. S. VAN. 1956. Systematic studies on the non-marine Mollusca of the Ind-Australian Archipelago. *Treubia* 23(2):259–427.
- ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater Biological Association Scientific Publication No. 25*. 156 pp.
- FRANC, A. 1956. Mollusques terrestres et fluviatilis de L'Archipel Néocalédonien. *Mém. Mus. Natl. Hist. Natur., Sér. A Zool.* 3(1):200 pp.
- HAYNES, A. 1982. Ecological and behavioural studies on the water snail *Potamopyrgus jenkinsi* (Smith) in the Upper Avon. Doctoral Thesis, The Open University. 336 pp.
- MACAN, T. T. 1974. *Freshwater ecology*. 2nd ed. Longman Group Ltd.: London. 343 pp.
- MACKERETH, F. J. H., J. HERON & J. F. TALLING. 1978. Water analysis: some revised methods for limnologists. *Freshwater Biological Association Scientific Publication No. 36*. 20 pp.
- MORRISON, J. P. E. 1954. The relationships of old and new world melanians. *Proc. U.S. Natl. Mus.* 103(3325):357–394.
- MOUSSON, A. 1870. Faune malacologique terrestre et fluviatile des Îles Viti, publiée d'après les envois de M. le Dr. E. Graeffe. *J. Conchol.* 18(2):179–236.
- RIECH, E. 1937. Systematische, anatomische, ökologische und tiergeographische Untersuchungen über die Süßwassermollusken Papuasiens und Melanesiens. *Arch. Naturgesch. (N.F.)* 6(36):40–101.
- STARMÜHLNER, F. 1970. Études Hydrobiologiques en Nouvelle-Calédonie. *O.R.S.T.O.M., Ser Hydrobiol.* 4(3/4):3–127.
- STARMÜHLNER, F. 1976. Beiträge zur Kenntnis der Süßwasser-Gastropoden pazifischer Inseln. *Ann. Naturhist. Mus. Wien* 80:473–656.
- STARMÜHLNER, F. 1979. Distribution of freshwater molluscs in mountain streams of tropical Indo-Pacific Islands (Madagascar, Ceylon, New Caledonia). *Malacologia* 18:245–256.

A Bibliography and List of Molluscan Names of Josiah Keep

by

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Abstract. A list of the books and papers by the early west coast malacologist Josiah Keep and a list of the 12 molluscan names that he introduced are presented. Two neotypes are designated.

JOSIAH KEEP was an early malacologist on the west coast of the United States whose particular contribution was as a popularizer of the study of shells. The several editions of his *West Coast Shells* were responsible for recruiting the interest of many a student and amateur.

Josiah Keep was born in Paxton, Massachusetts, on May 11, 1849. He received a Bachelor's degree from Amherst College in 1874 and a Master's from the same institution in 1877. That year he also married and moved to California. There he taught at the Golden Gate Academy for one year, then Alameda High School for seven years, where he was principal from 1881 to 1885.

In 1885, he became Professor of Natural Sciences at Mills College in Oakland, California, with which he was associated for the rest of his life. He came to specialize in courses in geology and astronomy, but his real love was the Mollusca. Between 1881 and 1910 he published several editions of his handbook on the shells of the west coast (KEEP, 1881, 1887d, 1888c, 1892, 1893, 1904, 1910b; 1935, posthumous edition by KEEP & BAILY). The interest that they elicited was one of the cornerstones of malacology in the western states.

He died in Pacific Grove, California, on July 27, 1911, where he is buried. (For more information on his life, see ANONYMOUS, 1911; DALL, 1911a, b.)

Here I present what is intended to be a complete bibliography of his papers on the Mollusca. In addition, careful examination of the 1887 edition of *West Coast Shells* reveals that he inadvertently introduced several Carpenter manuscript names, some of which have escaped previous detection. These probably got onto collection labels in California through identified specimens returned by Philip Carpenter to Henry Hemphill, another early west coast collector. As evidence of this, there are three lots identified by Carpenter in the California Academy of Sciences from

the Hemphill collection with three of these manuscript names on them. This material is cited below, but there is no evidence that Keep ever saw these particular lots. In each case, Keep probably had specimens in his own collection labeled with these names. In addition, Keep introduced three Hemphill manuscript names.

After his death, Keep's personal collection was sold by his family to the Institute of Geology & Paleontology of Tohoku University in Sendai, Japan, in 1915, where it is housed today.¹ The collection has some 3000 lots that belonged to him. The larger portion of the separate Mills College Collection went to the Department of Paleontology at the University of California at Berkeley. A smaller part went to the Department of Invertebrate Zoology at the California Academy of Sciences. I have examined these last two collections, as well as spot-checked the collection of the United States National Museum of Natural History, where Keep sent some specimens. Aside from the already isolated syntype of *Alvania aequisculpta* in the NMNH, I could not find Keep type material in any of them. Drs. Tamio Kotaka and Kenshiro Ogasawara of the Institute of Geology & Paleontology at Tohoku University have thus far been unsuccessful in finding type specimens of these 12 taxa in the Keep collection there.

Class Bivalvia

marginata, *Crassatella*—KEEP 1887d:179, *ex* Carpenter MS. No locality given.

Type material—USNM 15578, neotype (COAN, 1984:

¹ Some workers were evidently misled into believing that Keep's collection went to Tokyo and was lost during World War II (for example, A. G. Smith, in ANONYMOUS, 1968).

233), the same specimen that is the lectotype of *Psephis salmonea* CARPENTER, 1864:539; 611; 641. San Diego, San Diego Co., Calif.

Remarks—A synonym of *Halodakra (Stohleria) salmonea* (Carpenter, 1864). There is a specimen identified by Carpenter with this name on it from the Hemphill collection in the California Academy of Sciences (CASIZ 036681), but there is no evidence that Keep ever saw it.

Class Gastropoda

aequisculpta, *Alvania*—KEEP, 1887d:65, ex Carpenter MS.

No locality given.

Type material—USNM 219564, syntype. San Diego, San Diego Co., Calif.; “on mossy rocks at low tide”; H. Hemphill; sent to the USNM by Keep in 1910. According to a letter from Bartsch to Keep (16 Aug. 1910) in the Archives at Mills College, four additional specimens were returned to Keep. The USNM syntype was figured by BARTSCH (1911:358–359; 362; pl. 32, fig. 7).

Remarks—*Manzonina (Alvinia) aequisculpta* (Keep, 1887, ex Carpenter MS), according to PONDER (1985:48; 150, figs. 101G–I).

castanea, *Chemnitzia*—KEEP, 1887d:52; fig. 33, ex Carpenter MS. No locality given.

Type material—Not located. DALL & BARTSCH (1909:101) say that they borrowed the “types” from Keep, but BARTSCH (1912:322) later claimed to have examined only a single specimen. In any event, the type lot came from San Diego, San Diego Co., Calif.

Remarks—*Turbonilla (Pyrgiscus) castanea* (Keep, 1887, ex Carpenter MS), according to PALMER (1958:252). Figured by DALL & BARTSCH (1909:pl. 9, figs. 1, 1a), a specimen from San Pedro, Los Angeles Co., Calif. If workers become worried by the brevity of Keep’s description, a neotype could be designated.

A lot of four specimens from the Hemphill collection is in the California Academy of Sciences with this name on it identified by Carpenter (CASIZ 049331), but there is no evidence that Keep ever saw it.

Coincidentally, DALL & BARTSCH (1907:509–510; 534; pl. 47, fig. 7) named a different and new species *Turbonilla (Pyrgiscus) castanea*, and DALL (1908:131) renamed it *T. (P.) castanella* because of its homonymy with Keep’s taxon.

columbiana, *Fluminicola nuttalliana* var.—KEEP 1887d:63, ex Hemphill MS. Rivers of Oregon and Washington.

Type material—Not located.

Remarks—Should apparently be *Lithoglyphus columbianus* (Keep, 1887), according to TAYLOR (1975:60), or *Fluminicola columbiana* Keep, 1887, according to BURCH (1982:22; 93, fig. 145). It has often been dated from PILSBRY, 1899:121; 123; 125.

columbiana, *Physella*—KEEP, 1887d:120, ex Hemphill MS. Columbia River, Oregon/Washington.

Type material—Not located.

Remarks—Should evidently be *Physella columbiana* Keep, 1887, according to BURCH (1982:53; 159, fig. 639). It has often been dated from HEMPHILL (1890:27), and it was misspelled as *Physella “columbella”* by KEEP (1904:152).

gracilente, *Evalea*—KEEP, 1887d:52–53, ex Carpenter MS.

No locality given; presumably California.

Type material—Not located. **Neotype** (herein), USNM 842108, designated from USNM 46152. Bahia Todos Santos, Baja California Norte. Figured by DALL & BARTSCH (1909:pl. 18, figs. 7, 7a).

Remarks—Should apparently be *Odostomia (Chrysalida) gracilentis* (Keep, 1887, ex Carpenter MS). (Since *Odostomia* is treated as a feminine noun, an *-is* ending would be appropriate.) It is **not** a secondary homonym of *O. interstincta gracilenta* MONTEROSATO, 1878:93; Keep’s species has an “-ie” in the stem, whereas Monterosato’s has only an “-e,” and the two adjectives are placed into different termination groups (ICZN Code Art. 57e, f). However, DALL & BARTSCH (1909:160–161; 243; pl. 18, figs. 7, 7a) named *O. (C.) virginialis* as a replacement name for Keep’s taxon. They thought the two names were homonyms, misspelling both as *gracilienta*. (They incorrectly dated Monterosato’s taxon as 1884.) They also inappropriately selected a type for their taxon which, as a replacement name, should retain the same type specimen as the replaced homonym.

Although Keep’s taxon is virtually a *nomen dubium* because of its scanty description, Dall & Bartsch have essentially given it status. I think that the most nomenclaturally stable solution is to make their “type” of *O. virginialis* the neotype of Keep’s *Evalea gracilente*; this then simultaneously makes it the neotype of Dall & Bartsch’s unnecessary replacement name.

insculpta, *Oscilla*—KEEP, 1887d:52, ex Carpenter MS. No locality given, but presumably southern California.

Type material—Not located. **Neotype** (herein), USNM 106501. Punta Abreojos, Baja California Norte. Figured by DALL & BARTSCH (1909:pl. 20, figs. 8, 8a).

Remarks—A secondary homonym of *Odostomia insculpta* DE KAY, 1844:115–116; 263; pl. 31, fig. 297. DALL & BARTSCH (1909:183; 244; pl. 20, figs. 8, 8a) proposed *O. (Iolaea) eucosmia* expressly as a replacement name, but they inappropriately designated a “type” for their taxon.

As with the preceding, the most nomenclaturally stable solution is to make their “type” a neotype of Keep’s taxon, which in turn makes it a neotype of theirs. The correct name for the species is *Odostomia (Iolaea) eucosmia* Dall & Bartsch, 1909.

interclathrata, *Clathurella*—KEEP, 1887d:65, ex Carpenter MS. No locality given, but presumably California.

Type material—Not located.

Remarks—Because this has not been cited since its first appearance and because of its ambiguous description, it should probably be regarded as a *nomen dubium*.

subquadrata, *Amphisphyr*a—KEEP, 1887d:125, *ex* Carpenter MS. No locality given, but presumably California.

Type material—Not located. There are three specimens in the California Academy of Sciences identified by Carpenter from the Hemphill collection (CASIZ 049330), but there is no evidence that Keep ever saw them.

Remarks—Workers on opisthobranchs may want to consider whether this should be regarded as the earliest name for *Diaphana californica* DALL, 1919:299.

tincta, *Tegula gallina*—KEEP, 1887d:84. No locality given, but presumably southern California.

Type material—Not located.

Remarks—A synonym of *Tegula gallina* (FORBES, 1852:271). This varietal name has sometimes been dated from PILSBRY, 1889:169–170, *ex* Hemphill MS. Keep probably also got the name from Hemphill, but he didn't credit it to him.

Class Polyplacophora

decoratus, *Callistochiton*—KEEP, 1887d:112, *ex* Carpenter MS. No locality given, but presumably southern California.

Type material—Not located.

Remarks—An overlooked introduction of this name, according to Ferreira (*in litt.*, 26 March 1984), which has generally been dated from PILSBRY, 1893:269–270. See also FERREIRA (1979:448–449).

fimbriatus, *Callistochiton*—KEEP, 1887d:112, *ex* Carpenter MS. No locality given, but presumably southern California.

Type material—Not located.

Remarks—An overlooked introduction of this name, making it a senior synonym of *Callistochiton crassico-status* PILSBRY, 1893:264–265, according to Ferreira, *in litt.*, 26 March 1984. See also FERREIRA (1979:447–448). This name is not preoccupied by *Chiton fimbriatus* SOWERBY, 1840:293–294, a Peruvian chiton.

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BIBLIOGRAPHY AND LITERATURE CITED

All works cited in the text, relevant works about Keep, and papers by Keep that pertain to biology are listed here. Volume, bulletin, and monograph numbers are in bold face; series numbers, in parentheses, precede volume numbers; issue numbers, in parentheses, follow volume numbers; supplemental information, such as second methods of listing volumes, part numbers, and parenthetical statements are given in brackets. Plates and portraits are listed, but not text figures, maps, charts, and tables. Exact publication dates are given when possible.

ANONYMOUS. 1904. West American shells [concerning Keep's new book]. *Nautilus* **18**(5):59–60 (6 Sept. 1904).

ANONYMOUS. 1911. In memory of Professor Josiah Keep. Pamphlet from memorial service, Sept. 3, 1911. With Mills Bull. (1)**4**:35 pp.; 1 port. (Dec. 1911).

ANONYMOUS. 1968. [About the acquisition of Mills College collection by Calif. Acad. Sci.]. *Calif. Acad. Sci., Casual Crier* **2**(1):1–2 (1 July 1968).

BARTSCH, PAUL. 1911. The recent and fossil mollusks of the genus *Alvania* from the west coast of America. *U.S. Natl. Mus., Proc.* **41**(1863):333–362; pls. 29–32 (15 Nov. 1911).

BARTSCH, PAUL. 1912. Additions to the west American pyramidellid mollusk fauna, with descriptions of new species. *U.S. Natl. Mus. Proc.* **42**(1903):261–289; pls. 35–38 (17 May 1912).

BURCH, JOHN BAYARD. 1982. Freshwater snails (Mollusca: Gastropoda) of North America. U.S. Environmental Protection Agency, Off. Resh. & Develop., Evtl. Monitoring & Support Lab., EPA-600/3-82-026:vi + 294 pp.; 775 figs. (April 1982).

CARPENTER, PHILIP PEARSALL. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. *Brit. Assoc. Adv. Sci., Rept.* **33** [for 1863]:517–686 (post-1 Aug. 1864).

COAN, EUGENE V. 1984. The Bernardinidae of the eastern Pacific (Mollusca: Bivalvia). *Veliger* **27**(2):227–237; 10 figs. (5 Oct. 1984).

DALL, WILLIAM HEALEY. 1908. Note on *Turbonilla castanea* and *Odostomia montereyensis*. *Nautilus* **21**(11):131 (7 March 1908).

DALL, WILLIAM HEALEY. 1911a. Professor Josiah Keep. *Science* **34**(873):371 (22 Sept. 1911).

DALL, WILLIAM HEALEY. 1911b. Professor Josiah Keep. *Nautilus* **25**(6):61–62; frontis. (19 Oct. 1911) [a reprint of the preceding].

DALL, WILLIAM HEALEY. 1919. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. *U.S. Natl. Mus., Proc.* **56**(2295):293–371 (30 Aug. 1919).

DALL, WILLIAM HEALEY & PAUL BARTSCH. 1907. The pyramidellid mollusks of the Oregonian faunal area. *U.S. Natl. Mus., Proc.* **33**(1574):491–534; pls. 44–48 (31 Dec. 1907).

DALL, WILLIAM HEALEY & PAUL BARTSCH. 1909. A monograph of west American pyramidellid mollusks. *U.S. Natl. Mus., Bull.* **68**:xii + 258 pp. (13 Dec. 1909).

DE KAY, JAMES ELLSWORTH. 1844. Natural history of New York. Zoology of New-York, or the New-York fauna; . . . pt. V: Mollusca. Albany (State Geol. Surv.) viii + 271 pp.; 40 pls.

FERREIRA, ANTONIO J. 1979. The genus *Callistochiton* Dall, 1879 (Mollusca: Polyplacophora) in the eastern Pacific, with the description of a new species. *Veliger* **21**(4):444–466; 3 pls.; 9 figs. (1 April 1979).

FORBES, EDWARD. 1852. On the marine Mollusca discovered

- during the voyage of the *Herald* and *Pandora*, by Capt. Kellett, R.N., and Lieut. Wood, R.N. Zool. Soc. London, Proc. for 1850 [pt. 18] (217):270-272 (24 Jan. 1852); (218):273-274; pls. 9, 11 (post-24 Jan. 1852).
- HEMPHILL, HENRY. 1890. New forms of western limniades. *Nautilus* 4(3):25-27 (6 July 1890).
- KEEP, JOSIAH. 1881. Common sea-shells of California. Upton Bros.: San Francisco. 64 pp.; 16 pls.
- . 1886a. Eminent naturalists. I. [Thomas Say]. *West Amer. Sci.* 2(18):85-86 (Sept. 1886).
- . 1886b. Eminent naturalists.—II. Rafinesque. *West Amer. Sci.* 2(19):99-102 (Oct. 1886).
- . 1886c. Eminent naturalists.—III. Augustus A. Gould, M.D. *West Amer. Sci.* 3(20):6-8 (Dec. 1886).
- . 1887a. Eminent naturalists.—IV. Isaac Lea, LL.D. *West Amer. Sci.* 3(21):25-28 (Jan. 1887).
- . 1887b. Eminent naturalists. V. Hugh Miller. *West Amer. Sci.* 3(22):47-49 (Feb. 1887).
- . 1887c. Eminent naturalists. VI. Linnaeus. *West Amer. Sci.* 3(25):118-119 (May 1887).
- . 1887d. West coast shells. A familiar description of the marine, fresh water, and land mollusks of the United States, found west of the Rocky Mountains. Bancroft Bros.: San Francisco. 230 pp.; 182 figs.; frontis. (July 1887).
- . 1887e. Beauties of the sea. *West Amer. Sci.* 3(28):153-155 (Aug. 1887).
- . 1888a. Cabinet notes. *Conchologists Exchange* 2(8):107-108 (Feb. 1888).
- . 1888b. George W. Tryon, Jr. *West Amer. Sci.* 4(35):37-38 (March 1888).
- . 1888c. West coast shells. A familiar description of the marine, fresh water, and land mollusks of the United States, found west of the Rocky Mountains. Samuel Carson: San Francisco. 230 pp.; 182 figs.; frontis.
- . 1889. Summer studies in conchology. *Nautilus* 3(5):54-56 (1? Oct. 1889).
- . 1890a. A word to young collectors. *Nautilus* 3(10):115-117 (12 March 1890).
- . 1890b. The *Haliotis*. *Nautilus* 4(2):13-15; 3 figs. (27 June 1890).
- . 1890c. The Tryons' Handbook for young conchologists. San Francisco. 8 pp.; 2 figs.
- . 1891. Mollusks of the San Francisco markets. *Nautilus* 4(9):97-100 (11? Jan. 1891).
- . 1892. West coast shells. A familiar description of the marine, fresh water, and land mollusks of the United States, found west of the Rocky Mountains. S. Carson: San Francisco. 230 pp.; 182 figs.; frontis.
- . 1893. West coast shells. A familiar description of the marine, fresh water, and land mollusks of the United States, found west of the Rocky Mountains. H. S. Crocker: San Francisco. 230 pp.; 182 figs.; frontis.
- . 1895. A study of fossil shells. *Nautilus* 9(1):7-10 (2 May 1895).
- . 1896. West Coast species of *Haliotis*. *Nautilus* 9(11):129-132 (10 March 1896).
- . 1897. A tray of shells from Denmark. *Nautilus* 10(11):124-127 (7 March 1897).
- . 1899a. Caring for shells. *Nautilus* 12(11):132 (5 March 1899).
- . 1899b. *Pomatia aspersa* in California. *Nautilus* 13(5):60 (31 Aug. 1899).
- . 1900. To West Coast conchologists. *Nautilus* 14(1):10 (2 May 1900).
- . 1901a. Conchology. *Conchologist* 1(1):1-2 (Jan. 1901) [concerning this journal, see ROTH & CARLTON (1970)].
- . 1901b. Exotic mollusks in California. *Nautilus* 14(10):114-115 (1 Feb. 1901).
- . 1901c. Shells and sea-life. *Western Series Readers* 8. Whitaker & Ray: San Francisco. 200 pp.; 87 figs.; frontis.; 12 photos.; 1 etching (post-6 Feb. 1901).
- . 1902. *Helix aspersa* increasing in California. *Nautilus* 15(10):119 (5 Feb. 1902).
- . 1904. West American shells. A description in familiar terms of the principal marine, fresh water and land mollusks of the United States found west of the Rocky Mountains, including those of British Columbia and Alaska. Whitaker & Ray: San Francisco. 360 pp.; 303 figs.; frontis. (post-11 July 1904).
- . 1905. Edible mollusks of the Pacific. *Pacific Fisherman* 3(1):19-21; 6 figs. (Jan. 1905).
- . 1907. [On the loss of copies of *West American Shells* in the San Francisco fire.] *Nautilus* 20(12):144 (12 April 1907).
- . 1910a. List of the most common mollusks found around Monterey Bay. Hancock Bros.: San Francisco. 20 pp. (July 1910).
- . 1910b ["1911"]. West coast shells (revised edition). A description of the principal marine mollusks living on the west coast of the United States, and of the land shells of the adjacent region. Also a chapter on the fresh water mollusks of the Pacific slope by Harold Hannibal. Whitaker & Ray-Wiggin: San Francisco, Calif. 346 pp.; 3 pls.; frontis.; 300 figs. (Dec. 1910, according to TAYLOR, 1975:298).
- . 1935 [posthumous]. The story of the pecten as told by himself. Whimsical reprints number 4 from *Shells and Sea Life*, a book for children, written by Josiah Keep in 1901. Eucalyptus Press: Mills College, Calif. 13 pp. (Oct. 1935).
- . 1946 [posthumous]. The story of the pecten as told by himself. A chapter from *Shells and Sea Life*, written for children by Josiah Keep in 1901. Eucalyptus Press: Mills College, Calif. 10 pp. (Dec. 1946).
- . 1949 [posthumous]. The poetry of shells. Eucalyptus Press: Mills College, Calif. 25 pp. (Oct. 1949).
- KEEP, JOSIAH [POSTHUMOUS] & JOSHUA L. BAILY, JR. 1935. West Coast shells: a description in familiar terms of the principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Stanford Univ. Press: Stanford, Calif. & Oxford Univ.: London. xii + 350 pp.; 334 figs. (post-1 Feb. 1935).
- MONTEROSATO, TOMMASO DI MARIA ALLERI [MARCHESE DI]. 1878. Eumerazione e sinonimia delle conchiglie Mediterranee. *Palermo, Giorn. di Scienz. Natur. ed Econ.* 13:61-115.
- PALMER, KATHERINE EVANGELINE HILTON (VAN WINKLE). 1958. Type specimens of marine Mollusca described by P. P. Carpenter from the West Coast (San Diego to British Columbia). *Geol. Soc. Amer., Mem.* 76:viii + 376 pp.; 35 pls. (8 Dec. 1958).
- PILSBRY, HENRY AUGUSTUS. 1889. [Trochidae, pt. 2]. *Manual Conchology* (1)11(42):65-128; pls. 15-32 (5 July 1889).
- PILSBRY, HENRY AUGUSTUS. 1893. Polyplacophora. Lepidopleuridae, Ischnochitonidae, Chitonidae, Mopaliidae. *Man. Conch.* (1)14(56, 56a):209-350 + i-xxxiv; pls. 41-68 (1 July 1893).
- PILSBRY, HENRY AUGUSTUS. 1899. Catalogue of the Amnic-

- lidae of the western United States. *Nautilus* **12**(11):121-127 (5 March 1899).
- PILSBRY, HENRY AUGUSTUS. 1904. West American Shells [a review]. *Nautilus* **18**(8):95-96 (17 Dec. 1904).
- PONDER, WINSTON F. 1985. A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Australian Mus., Rec. Suppl.* **4**:221 pp; 153 figs. (12 Feb. 1985).
- ROTH, BARRY & JAMES T. CARLTON. 1970. A forgotten periodical of West American conchology. *Nautilus* **84**(1):31-32 (16 July 1970).
- SOWERBY, GEORGE BRETtingham, II. 1840. Descriptions of some new chitons. *Mag. Natur. Hist. (n.s.)* **4**(42):287-294; pl. 16 (June 1840).
- TAYLOR, DWIGHT WILLARD. 1975. Index and bibliography of late Cenozoic freshwater Mollusca of western North America. *Univ. Michigan, Mus. Paleo., Claude W. Hibbard Mem. Vol. 1* [Papers on Paleo. no. 5]:284 pp.

NOTES, INFORMATION & NEWS

Concerning Carpenter's "First Duplicate Series" of Mazatlán Shells

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It has evidently not come to the attention of many workers on the marine molluscan fauna of the tropical eastern Pacific that an important collection of the mollusks studied by Philip P. Carpenter in the preparation of his Mazatlán catalogue (CARPENTER, 1857b), formerly at the New York State Museum, is now housed in the Division of Mollusks of the U.S. National Museum of Natural History (NMNH). Although this transfer, which occurred in September 1955, was mentioned by BRANN (1966:12), many workers have overlooked the material because it is stored in special cases apart from both the main and the type collections.

This collection, which Carpenter called the "first duplicate series" of the Reigen collection, is of special significance in part because it contains syntypes of many of Carpenter's new taxa from Mazatlán (or paralectotypes if lectotypes have already been selected). In general, workers have properly chosen to select lectotypes from among the primary collection of Mazatlán mollusks in the British Museum (Natural History) in London. However, there are some instances in which the BM(NH) specimens are lost, broken, or have disintegrated. When this has occurred, the material in the NMNH may have intact syntypes for lectotype designation. For some species, there are more specimens in the NMNH than there are in the British Museum (Natural History) holdings.

The collection in the NMNH was listed by CARPENTER (1860), and later discussed and listed by PALMER (1951). After its transfer to the NMNH, it was arranged and catalogued by Florence Ruhoff just before she left that institution. It is now housed in two cabinets near the end of the mollusk collection. As Carpenter originally requested when he turned the material over to the New York

State Museum, the collection is stored as an intact unit containing both the type material of his new species as well as specimens of other species. Most of the specimens originally mounted on Carpenter's glass slides have been removed and stored in regulation containers like those used for the balance of the NMNH collection. The original species and tablet numbers were carefully recorded on new specimen labels, as these data are of great importance in recognizing types.

Bibliography and Literature Cited

- BRANN, D. C. 1966. Illustrations to "Catalogue of the collection of Mazatlan shells" by Philip P. Carpenter. *Paleo. Res. Inst.*: Ithaca, New York. 111 pp.; 60 pls. (1 April 1966).
- CARPENTER, P. P. [For a complete bibliography of Carpenter's papers on the Mollusca, see COAN (1969); however, the most relevant to understanding his work on Mazatlán are included here.] 1855. List of four hundred and forty species of shells from Mazatlan. *British Assn. Adv. Sci., Rept.* 24 [for 1854]:107-108.
- CARPENTER, P. P. 1857a. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. *British Assn. Adv. Sci., Rept.* 26 [for 1856]: 159-368 + 4 pp.; pls. 6-9 (pre-22 April 1857). [Many of the names Carpenter validated in the following work are listed here first as *nomina nuda*; see especially pp. 241-281.]
- CARPENTER, P. P. 1857b. Catalogue of the collection of Mazatlan shells, in the British Museum: collected by Frederick Reigen, . . . London (British Museum) i-iv + ix-xvi + 552 pp. (1 Aug. 1857) [Warrington ed., i-viii + i-xii + 552 pp., published simultaneously] [repr.: *Paleo. Res. Inst.*, 1967].
- CARPENTER, P. P. 1860. Catalogue of the Reigen collection of Mazatlan Mollusca, presented to the State Cabinet . . . , being the first duplicate of the collection presented to the British Museum. *Regents Univ. State of New York, 13th Ann. Rept. on the Condition State Cabinet Natur. Hist.* [for 1859]:21-36 (post-10 April 1860).
- CARPENTER, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. *British Assn. Adv. Sci., Rept.* 33 [for 1863]:517-686 (post-1 Aug. 1864) [see especially pp. 542-548].
- COAN, E. V. 1969. A bibliography of the biological writings of Philip Pearsall Carpenter. *Veliger* 12(2):222-225 (1 Oct. 1969).
- KEEN, A. M. 1968. West American mollusk types at the British Museum (Natural History) IV. Carpenter's Mazatlan collection. *Veliger* 10(4):389-439; pls. 55-59 (1 April 1968).
- PALMER, K. E. H. (VAN WINKLE). 1951. Catalogue of the first duplicate series of the Reigen collection of Mazatlan shells in the State Museum at Albany, New York. *New York State Mus., Bull.* 342:79 pp.; 1 pl. (Jan. 1951).

Two Little-Known Italian Papers on Galápagos
Intertidal Zonation and Mollusks

by

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Berkeley, California 94720

Two papers that resulted from a 1971–1972 Italian expedition to the Galápagos Islands were kindly brought to my attention by Dr. E. V. Coan. These papers are not likely to be known to workers interested in the marine biota of the Galápagos because they were published in Italian and in a journal not often encountered in libraries.

The first paper, published in 1974, is by Francesco Cinelli and Paolo Colantoni (CINELLI & COLANTONI, 1974) and deals with some observations on the marine benthic zonation of the rocky coast of the Galápagos Islands. The authors describe the specific organisms, both invertebrates and algae, that were found in the supralittoral, midlittoral, and infralittoral zones at nine stations on six islands. This zonation information is compared to the littoral zonation pattern known to occur in the Mediterranean Sea. In addition to documenting the spatial distribution, Cinelli and Colantoni comment on the biogeographic affinities of the organisms (including several molluscan taxa) found within the three zones. The supralittoral and midlittoral organisms are considered to have tropical affinities, while the infralittoral organisms are considered to have temperate or cold-temperate affinities.

The second paper, published in 1979, is by Marco Taviani (TAVIANI, 1979), and concerns the chitons, gastropods, and bivalves collected by the Italian expedition. Taviani documents the occurrence of 3 chitons, 52 gastropods, and 9 bivalves from 14 stations on 10 islands. The text provides information and observations about each species, and the plates have good illustrations. No new species are described. In addition, Taviani discusses the origin and composition of the molluscan fauna from geological, paleontological, and geographic perspectives.

Both papers are recommended to anyone interested in the Galápagos marine invertebrate biota, particularly mollusks. The bibliographies of both papers contain many useful Galápagos references and also five references to additional papers resulting from the same Italian expedition, including one on chitons. An address for Marco Taviani, to whom reprint requests for both papers can be sent, is: Laboratorio di Geologia Marina del C.N.R., Via Zamboni 65, 40127 Bologna, Italia.

Literature Cited

CINELLI, F. & P. COLANTONI. 1974. Alcune osservazioni sulla zonazione del bentos marino sulle coste rocciose delle Isole Galápagos (Oceano Pacifico). Museo Zoologico dell'Università di Firenze [Florence]: Galápagos, Studi e

ricerche. Spedizione 'L. Mares-G.R.S.T.S.' Gruppo Ricerche Scientifiche e Tecniche Subacquee. 22 pp., 17 figs.
TAVIANI, M. 1979. I molluschi marini raccolti dalla spedizione "L. Mares-G.R.S.T.S." alle Isole Galapagos 1. Gastropoda e Bivalvia. Museo Zoologico dell'Università di Firenze [Florence]: Galápagos, Studi e ricerche. Spedizione 'L. Mares-G.R.S.T.S.' Gruppo Ricerche Scientifiche e Tecniche Subacquee. 61 pp., 90 figs.

Some Additional Notes on the Distributions
of Eastern Pacific Donacidae

by

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In redistributing the research materials from the office of the late Dr. Joseph P. E. Morrison, curators at the U.S. National Museum of Natural History came across a number of lots of eastern Pacific *Donax*. Morrison had evidently planned to work on this group and had isolated some interesting specimens for examination, specimens that I did not have a chance to see during my study of that group (COAN, E. 1983. The eastern Pacific Donacidae. *Veliger* 25(4):273–297).

Two of these lots provide new distributional records:

Donax caelatus caelatus—Occurs as far south as Isla San José, Panama (8°15'N, 79°8'W) (USNM 598877a). I had previously seen specimens only from as far south-east as Golfito, Costa Rica.

Donax dentifer—Occurs as far north as Tapachula, Chiapas, Mexico (14°43'N, 92°26'W) (USNM 591610). This extends the known distribution from Guatemala northward into Mexico.

An Extension of the Known Depth Range for
Sepia elegans Blainville, 1827

(Cephalopoda: Sepioidea)

by

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Muelle de Bouzas s/n, Vigo, Spain

The cuttlefish *Sepia elegans* Blainville, 1827, has a geographical distribution extending in the eastern Atlantic from 15° to 55°N, and throughout the Mediterranean Sea. The total depth range of the species was listed as 60 to 450 m in the Atlantic Ocean, and from 20 to 250 m in the Mediterranean Sea (MANGOLD-WIRZ, 1963). ROPER *et al.* (1984) have pointed out that *Sepia elegans* is a small, demersal species with a depth range from 30 to 430 m.

The purpose of this note is to show that the shallow limit of the bathymetric distribution of *Sepia elegans* must be changed. We frequently have captured this species from 2 to 45 m depth in the Ria de Vigo (Vigo estuary) (42°15'N–8°48'W).

The Ria de Vigo is a drowned tectonic valley. Its water circulation is estuarine. Interchanges with Atlantic water are very important. *Sepia elegans* occupies habitats in the central and outer parts of the estuary but is not found in the inner reaches of the estuary. *Sepia officinalis* is more euryhaline and lives and spawns throughout the estuary including its inner part, where there are large fluctuations in salinity (GUERRA, 1984; in prep.).

Literature Cited

- GUERRA, A. 1984. Cefalópodos de la Ría de Vigo. Resultados preliminares. Cuadernos de Area de Ciencias Marinas. Seminario de Estudios Galegos 1:333–348.
- MANGOLD-WIRZ, K. 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. Vie et Milieu (Suppl.) 13:1–285.
- ROPER, C. F. E., M. J. SWEENEY & C. E. NAUEN. 1984. FAO species catalogue. Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of the species of interest to fisheries. FAO Fish. Synop., No. 125, Vol. 3, 277 pp.

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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*. 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, 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.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on October 19, 1984, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 28 of *The Veliger*. For affiliate members of the Society, the subscription rate for Volume 28 will remain unchanged at US\$22.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will increase very slightly to US\$44.00, also now with postage to domestic addresses included. An additional US\$3.00 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

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Erratum: Volume 27, Number 3 (January 2, 1985)

Due to an oversight by the author, an error occurred in the article by Paul S. Mikkelsen, 1985, A comparison of two Florida populations of the coquina clam, *Donax var-*

iabilis Say, 1822 (Bivalvia: Donacidae). II. Growth rates. *Veliger* 27(3):308-311. Because the error is in a result, and thus may cause problems for future investigators, we make it known here.

On page 308, eighth line of "Results," change "7.3" to "3.7."

Opinions: 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 42, Part 2, on 27 June 1985:

Opinion No. 1306 (p. 146). *Ledella bushae* Warén, 1978, is the type species of *Ledella* Verrill & Bush, 1897 (Mollusca, Bivalvia).

Opinion No. 1315 (p. 165). *Eolis alderi* Cocks, 1852, is the type species of *Aeolidiella* Bergh, 1867 (Mollusca, Gastropoda).

Sale of C. M. S. Publications

All back volumes still in print, both paper-covered and cloth-bound, are available only through "The Shell Cabinet," 12991 Bristow Road, Nokesville, VA 22123. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Morgan Breeden at the above address.

Volumes 1 through 13, 24, 26, and 27 are out of print.

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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 back-

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Literature cited

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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.

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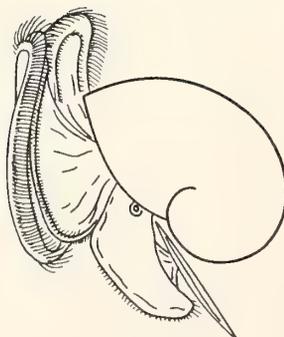
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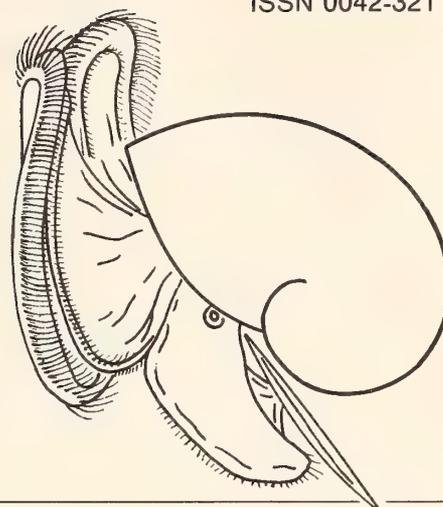
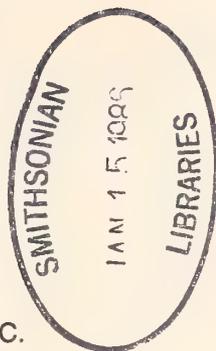
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A Revision of the Genus *Acanthopleura* Guilding, 1829 (Mollusca: Polyplacophora)

by

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Abstract. Fifteen species of *Acanthopleura* Guilding, 1829 (= *Corephium* Gray, 1847a; *Enoplochiton* Gray, 1847a; *Maugeria* Gray, 1857; *Sclerochiton* Dall, 1881; *Francisia* Dall, 1882; *Rhopalopleura* Thiele, 1893; *Mesotomura* Pilsbry, 1893a; *Amphitomura* Pilsbry, 1893a; *Liolophura* Pilsbry, 1893a; *Squamopleura* Nierstrasz, 1905a; *Clavarizona* Hull, 1923; *Acanthozostera* Iredale & Hull, 1926; *Planispina* Taki, 1962) are here recognized, two of which are new to science. The fifteen species are *A. granulata* (Gmelin, 1791), *A. spinosa* (Bruguière, 1792), *A. echinata* (Barnes, 1824), *A. nigra* (Barnes, 1824), *A. gemmata* (Blainville, 1825), *A. hirtosa* (Blainville, 1825), *A. gaimardi* (Blainville, 1825), *A. loochooana* (Broderip & Sowerby, 1829), *A. brevispinosa* (Sowerby, 1840a), *A. japonica* (Lischke, 1873), *A. curtisiana* (Smith, 1884), *A. miles* (Carpenter in Pilsbry, 1893c), *A. araucariana* (Hedley, 1898), *A. arenosa* Ferreira, spec. nov., and *A. rehderi* Ferreira, spec. nov. Despite large specimen size, intertidal habitat, and world-wide, mostly tropical distribution, *Acanthopleura* is not represented in the fossil record.

The genus-name *Acanthopleura* Guilding, 1829, began as a grouping of seven heterogeneous "sections," each defined by the girdle characteristics of a given species. Although subsequent authors (SWAINSON, 1840; GRAY, 1847a, 1857; SHUTTLEWORTH, 1853; Carpenter in DALL, 1882) altered GUILDING'S (1829) concept, it was left to PILSBRY (1893c:213-218) to restrict *Acanthopleura* to the "section" characterized by "zona [=girdle] spinosa," and typified by *Chiton spinosus* Bruguière, 1792. Assigning species without teeth in the posterior valve to a new genus, *Liolophura*, PILSBRY (1893c) divided *Acanthopleura* into four subgenera based upon the characteristics of the insertion plate of the posterior valve: (1) *Acanthopleura s.s.* (type, *C. spinosus* Bruguière), with "a very long insertion plate cut into numerous teeth by short slits," (2) *Maugeria* Gray, 1857 (restricted) (type, *C. piceus* Gmelin), with "the pectinated insertion plate cut into numerous teeth by slits similar to those of the head-valve," (3) *Amphitomura* Pilsbry, 1893a (type, *C. borbonica* Deshayes), with "the insertion-plate very short, with blunt, crenulated edge, interrupted only by a single mopaloid slit on each side," and (4) *Mesotomura* Pilsbry, 1893a (type, *C. echinatum*

Barnes), with "the long insertion plate deeply pectinated outside, its edge interrupted only by a single median-posterior slit."

Yet, *Acanthopleura* (*sensu* PILSBRY, 1893c), a widespread, tropical to subtropical group of large, accessible (intertidal to emergent), and abundant specimens, has remained problematical in regard to the biological species involved and their taxonomic arrangement. Complicated by the appearance of several ill-defined nominal genera, subgenera, species, and subspecies much before clear understanding of the whole group had been attained, *Acanthopleura* has been sorely in need of revision. But, likely, the difficulties in assembling sufficient material from exotic areas have been such as to stifle earlier attempts to study the group.

This revision rests upon the examination of material in the museum collections of the California Academy of Sciences, San Francisco (CAS); Los Angeles County Museum of Natural History (LACM); University of Colorado Museum, Boulder, Colorado (UCM); Academy of Natural Sciences of Philadelphia (ANSP); U.S. National Museum of Natural History, Washington, D.C. (USNM); British Museum (Natural History) (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Uppsala Universitets Zoologiska Museum, Sweden (UuzM); The Australian Museum, Sydney (AMS); Western Australian

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Museum, Perth (WAM); National Museum of Victoria, Melbourne (NMV); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (IRScnB); Musée d'Histoire Naturelle, Bucarest, Romania (MHNb); Istituto di Zoologia dell'Università di Firenze, Italy (MF); and in the personal collections of Dr. John S. Pearse, University of California, Santa Cruz, California; Salle Crittenden, Oakland, California; Clay Carlson and Patty Jo Hoff, Merize, Guam; Ian Loch, Sydney, Australia; Richard A. Van Belle, Sint-Niklaas, Belgium; J. R. Penprase, West Hobart, Tasmania; and J. R. Penniket, Warkworth, New Zealand. Additional material and field observations were obtained by, and are presently in the collection of, A. J. Ferreira (AJF collection station numbers on file at CAS).

An effort was made to study all available type specimens deemed necessary to resolve or clarify taxonomic problems; where type material is mentioned in the literature but no attempt was made here to verify its existence or repository, reference is made only to information at hand regarding types "not examined"; where there is no information in the literature about type specimens and no attempt was made here to examine or locate type material, the types are said to remain "unascertained."

SYSTEMATIC TREATMENT

Polyplacophora Gray, 1821

Neoloricata Berghayn, 1955

Ischnochitonina Berghayn, 1930a

Chitonidae Rafinesque, 1815

Acanthopleura Guilding, 1829

Description: Mostly large, oval, depressed, round-backed chitons. Valves thick, heavy, beaked. Tegmental sculpture coarsely granular to wrinkled, often obliterated by erosion; tegmentum broadly inflexed at posterior margin of intermediate valves. Mucro central to posterior. Ocelli scattered throughout anterior valve, anterior $\frac{1}{3}$ to $\frac{2}{5}$ of lateral areas of intermediate valves, and postmucro area of posterior valve. Gills mostly holobranchial (*i.e.*, extending along 90–100% of foot [SIMROTH, 1894:247]). Articulamentum whitish to blue, brown, or black. Strong sutural laminae. Insertion plates markedly pectinate on outside; on posterior valve insertion teeth may be absent in part or in total, often buttressed by transverse callus; slits 8–12 on anterior valve, 1 (2 in one species) on intermediate valves, 0–10 on posterior valve. Girdle thick, muscular, densely covered with calcareous elements, variable in length and in shape from spikes to spines, spinelets, or scales. Radula major lateral teeth with discoid heads (with 4 cusps in one species).

All species of *Acanthopleura* are confined to the intertidal zone. Specimens are often found on the surface of rocks, often exposed at low tide.

Type-species: *Chiton spinosus* Bruguière, 1792, by subsequent designation (GRAY, 1847b).

Synonyms:

Corephium Gray, 1847a (not Browne, 1789)

Type: *Chiton echinatus* Barnes, 1824, by subsequent designation (GRAY, 1847b).

Enoplochiton Gray, 1847a

Type: *Chiton niger* Barnes, 1824, by monotypy.

Maugeria Gray, 1857

Type: *Chiton piceus* Gmelin, 1791 (= *Chiton granulatus* Gmelin, 1791), by subsequent designation (PILSBRY, 1893c).

Sclerochiton Dall, 1881 (not Kraatz, 1859)

Type: *Chiton miles* Carpenter in Pilsbry, 1893c, by monotypy.

Francisia Dall, 1882

Type: *Chiton spinosus* Bruguière, 1792, by original designation.

Rhopalopleura Thiele, 1893

Type: *Chiton aculeatus* Linnaeus, 1758 (?= *Chiton echinatus* Barnes, 1824), by monotypy.

Mesotomura Pilsbry, 1893a

Type: *Chiton echinatus* Barnes, 1824, by monotypy.

Amphitomura Pilsbry, 1893a

Type: *Chiton borbonicus* Deshayes, 1863 (= *Chiton brevispinosus* Sowerby, 1840a), by original designation.

Liolophura Pilsbry, 1893a

Type: *Chiton japonicus* Lischke, 1873, by original designation.

Squamopleura Nierstrasz, 1905a

Type: *Chiton miles* Carpenter in Pilsbry, 1893c, by subsequent designation (Pilsbry, 1893c).

Clavarizona Hull, 1923

Type: *Chiton hirtosus* Blainville, 1825, by original designation.

Acanthozostera Iredale & Hull, 1926

Type: *Chiton gemmatus* Blainville, 1825, by original designation.

Planispina Is. Taki, 1962

Type: *Acanthopleura* (*Amphitomura*) *planispina* Berghayn, 1933 (= *Acanthopleura gemmata* [Blainville, 1825]), by original designation.

Remarks: The arrangement of species here allocated to *Acanthopleura* differs significantly from that of PILSBRY (1893c). It is based on the appreciation of over-all similarities among species rather than on modifications of any single character. Most generic names here synonymized under *Acanthopleura* had been defined solely in terms of changes in the girdle elements or in the insertion plate of the posterior valve, ignoring similarities in body plan among species. As a result, species that in most respects appear extremely close, such as *Chiton gemmatus* Blainville, 1825, and *C. gaimardi* Blainville, 1825, had been placed in different genera (even in different subfamilies) on account of modifications in the posterior valve, notwithstanding extreme closeness in all other features. Such situations are here corrected, and 15 species of *Acanthopleura* recognized:

Acanthopleura granulata (Gmelin, 1791)
Acanthopleura spinosa (Bruguère, 1792)
Acanthopleura echinata (Barnes, 1824)
Acanthopleura nigra (Barnes, 1824)
Acanthopleura gemmata (Blainville, 1825)
Acanthopleura hirtosa (Blainville, 1825)
Acanthopleura gaimardi (Blainville, 1825)
Acanthopleura lochooana (Broderip & Sowerby, 1829)
Acanthopleura brevispinosa (Sowerby, 1840a)
Acanthopleura japonica (Lischke, 1873)
Acanthopleura curtisiana (Smith, 1884)
Acanthopleura miles (Carpenter in Pilsbry, 1893c)
Acanthopleura araucariana (Hedley, 1898)
Acanthopleura arenosa Ferreira, spec. nov.
Acanthopleura rehderi Ferreira, spec. nov.

Acanthopleura has no fossil record. The paleontological literature contains only two possible references to the genus as here understood: SMITH (1960:67) mentioned (but did not cite) *Acanthopleura* in "Pleist., S. Am. (Bol.)"; and COSSMAN (1888:20) allocated one posterior valve from the Eocene of the Paris Basin to *Enoplochiton*, as *E. rochebrunei*, which "is probably no chiton at all" (VAN BELLE, 1983:128).

Acanthopleura spinosa (Bruguère, 1792)

Figures 1 to 6, and 112-S

Chiton spinosus BRUGUIÈRE, 1792:25, pl. 2, fig. 1; LAMARCK, 1819:321; BURROW, 1815:185, pl. 26, fig. 4; MAWE, 1823:1, 3-4, pl. 1, fig. 3; WOOD, 1825:4, pl. 1, fig. 38; BLAINVILLE, 1825:550; SOWERBY, 1840b:1, 10, sp. no. 2, fig. 151; REEVE, 1842:12, pl. 134, fig. 151; 1847, pl. 9, fig. 51; ADAMS & ADAMS, 1858:475; CHENU, 1859:381, fig. 2868; PAETEL, 1869:66, 1873:80; FISCHER, 1885:881 (in subgen. *Acanthopleura*); ARNOLD, 1901:322 (fig. only) (reprinted, 1968); LAMY, 1923:260.

Maugeria spinosa: GRAY, 1857:184.

Francisia spinosa: TRYON, 1883:343, pl. 85, fig. 81; HADDON, 1886:30.

Acanthopleura spinosa: PILSBRY, 1893c:220, pl. 45, figs. 80-87; THIELE, 1893:373, pl. 30, fig. 3; HIDALGO, 1905:272; NIERSTRASZ, 1905a:101, 1905b:152; HORST & SCHEPMAN, 1908:526; HEDLEY, 1910:352; IREDALE, 1910b:158, 1914b:668; ASHBY, 1918:86, 1922a:31-32, 1926:384, 388-389; IREDALE & HULL, 1926:264-265, pl. 38, figs. 1-2 (reprinted, 1927:127-128, pl. 16, figs. 1-2); THIELE, 1929:22; BERGENHAYN, 1930a:32-33; LELOUP, 1933a:24-25, 1933b:2-3; KURODA, 1941:71; LELOUP, 1952:59-61, text fig. 20, pl. 6, fig. 4; ALLAN, 1959:239, fig. 6b; Is. TAKI, 1962:47; IW. TAKI, 1964:412; ANG, 1967:415-416, pl. 7, figs. 1-4; WU, 1969:103-104, figs. 1, 7-15; WELLS, 1981:253.

Acanthopleura spinosa montebelloensis ASHBY, 1922a:32.

Type material and type locality:

Chiton spinosus Bruguère, 1792: Type specimens (2) at MNHN (*vide* LAMY, 1923), not examined; locality, not originally stated but presumed to be "isle Maria, baye

de l'Est," Australia, according to label accompanying types (LAMY, 1923).

Acanthopleura spinosa montebelloensis Ashby, 1922a: Types' (Ashby coll. No. 5888) whereabouts unknown (not at WAM [WELLS, 1977]); locality "Monte Bello Island," Western Australia (20°25'S, 115°32'E).

Material examined:

AUSTRALIA: Yardie Creek, North West Cape, 2 specimens (WAM 56-74); Monte Bello Is., 1 specimen (WAM 69-74); Roseman Id., Dampier Arch., 2 specimens (WAM 65-74); Kendrew Is., Dampier Arch., 7 specimens (WAM 1341-78); Port Hedland, 1 specimen (WAM 66-74); Flaccout Bay, 1 specimen (WAM 618-67); Walsh Point, Admiralty Gulf, 3 specimens (WAM 79-78; WAM 1107-78); Pt. Gantheaume, near Broome, 2 specimens (WAM 10884); Riddal Beach, Broome, 2 specimens (WAM 60-74); Broome, 1 specimen (NMV); Kuri Bay, 1 specimen (WAM 55-74); Yampi Sound, 4 specimens (WAM 64-74); Augustus Id., Bonaparte Arch., 2 specimens (WAM 58-74); "N.W. Australia," 4 specimens (WAM 1106-78; NMV); Darwin, 1 specimen (NMV); Nightcliff, Darwin, 1 specimen (WAM 61-74); Fanny Bay, N.T., 5 specimens (NMV); Rainbow Cliffs, Gove, N.T., 1 specimen (I. Loch coll.).

NEW GUINEA: Soweik Soepiori, Schouten Is., 1 specimen, 75 mm long (ANSP 207130).

SULAWESI (=Celebes): 32 km E of Manado, 3 specimens (CAS 009806; CAS 012252).

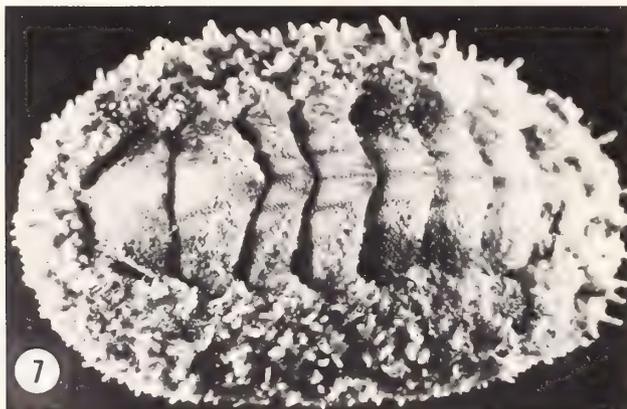
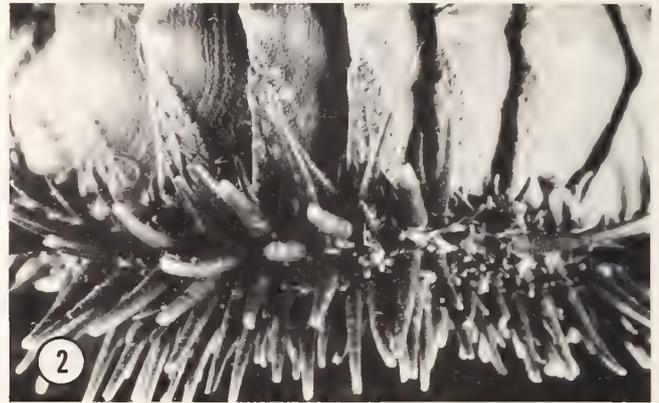
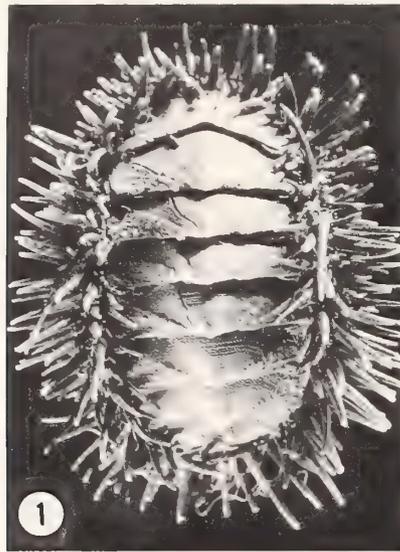
TAIWAN: Wan-li-tong, Ping-tung Co., 1 specimen (UCM 27522).

PHILIPPINES: Hundred Islands, Lingayen Gulf, Luzon, 16 specimens (AJF 464; AJF 465).

Description: Excellent accounts of *Acanthopleura spinosa* were given by PILSBRY (1893c), IREDALE & HULL (1926), and WU (1969).

Among 60 specimens of *Acanthopleura spinosa* here examined, largest 80 mm long (in alcohol) (WAM 1107-78). Body width/length mean 0.66. Tegmentum uniform dark chestnut in color. Lateral areas hardly defined, not raised (Figures 1, 2). Tegmental sculpture of minute granules on anterior valve, postmucro area of posterior valve, and lateral areas of intermediate valves. Central areas almost smooth except for discrete transverse, concentric growth rugae. Mucro obtuse, moderately posterior; postmucro convex with marked slope. Width of tegmental surfaces of valves i/viii, 1:22. Ocelli round to oval, 40-50 μ m in diameter, scattered throughout anterior valve, anterior $\frac{2}{3}$ to $\frac{4}{5}$ of lateral areas of intermediate valves, and postmucro area. Gills with 50-70 plumes per side.

Articulamentum reddish-brown in middle, lighter to almost white at periphery. On valve viii, tegmentum length/width mean 0.60; articulamentum wider than tegmentum (width of articulamentum/width of tegmentum on valve viii, mean 1.49). Sutural laminae wide; sinus well defined. Insertion plates relatively long, strongly pectinate on outside; on valve i, length of insertion plate/length of tegmentum, mean 0.36. On valve viii (Figures 3, 4), insertion teeth in part ($\frac{2}{3}$) fused to somewhat rounded, transverse callus; in specimen 50 mm long, insertion teeth (at midline



of valve) 1.3 mm long on outside but extend only 0.4 mm beyond transverse callus on inside of valve. Slit formula 12/16-1-8/12; some intermediate valve(s) (particularly valve II) show 2 slits on one or both sides. Sinus plate often pectinate on valve ii, but not so on other valves; on valve viii, relative width of sinus (width of sinus/width of sutural plates), mean 1.0.

Girdle upper surface with abundant, dark red, slender spines, sharply pointed, up to 16 mm long, 0.7 mm thick, in large specimens (Figure 5); girdle covered otherwise with dark red elements, translucent to opaque, as small as 30–50 μm long, variable in length and shape, representing all stages of growth from scalelike to spine. Girdle bridges (see Ferreira, 1983a) empty, *i.e.*, without significant elements. Undersurface paved with juxtaposed rows of transparent, squarish scales, 50 \times 50 μm , roughly striated, inner edge somewhat convex as if articulating upon concave outer edge of adjacent scale.

Radula averaging 55% of specimen length (range 50–63%, SD = 7.9, n = 5) and 96 rows of teeth (range 80–110, SD = 11.9, n = 5). In specimen 75 mm long (AJF 464: Lingayen Gulf, Philippines), median tooth (Figure 6) 100 μm wide at anterior blade; first lateral teeth somewhat rectangular, outer edge deeply concave, about 220 μm at anterior blade; major lateral teeth with discoid head, 360 μm wide; outer marginal teeth 320 μm long, 350 μm wide (length/width, 0.9).

Distribution: *Acanthopleura spinosa* has been reported from Poulo Dama, Gulf of Thailand (LELOUP, 1952), Taiwan (WU, 1969), Philippines (HIDALGO, 1905; ANG, 1967), Java, Timor (HORST & SCHEPMAN, 1908), Pisang Islands (LELOUP, 1933b), Amboine Id. [=Ambon] (HORST & SCHEPMAN, 1908), New Guinea (NIERSTRASZ, 1905b; HORST & SCHEPMAN, 1908; LELOUP, 1933b), and New Caledonia (IREDALE & HULL 1926). In Australia it has been reported along the northwestern coast from the Monte Bello Islands (IREDALE, 1914b) to Cape York (HADDON, 1886). From the data, *A. spinosa* appears to be confined to the central Indo-Pacific from 25°N to 22°S, and from 105°E to 142°E. The northernmost verified record is Wanli-tong, Taiwan (25°11'N, 121°41'E) (UCM 27522); the southernmost and westernmost verified record, North West

Cape, Western Australia (21°45'S, 114°10'E) (WAM 1107-78); and the easternmost verified record, Gove (12°18'S, 136°55'E). The report of *A. spinosa* in New Caledonia (IREDALE & HULL, 1926) requires corroboration; collecting trips to New Caledonia (A. J. Ferreira, July 1980) and eastern New Guinea, Trobriand Is., and New Britain Id. (A. J. Ferreira, August 1981) failed to find the species.

Acanthopleura spinosa is confined to the intertidal zone, with specimens often exposed at low tide.

Remarks: *Acanthopleura spinosa* is very distinct from all other species of *Acanthopleura*, posing no problems in identification. The dark reddish color and the long, thin, sharp girdle spines are diagnostic. It is the only *Acanthopleura* with two slits, though inconstant, on intermediate valves.

Acanthopleura spinosa occurs sympatrically with *A. gemmata* and *A. miles* throughout its range. Field observations show that where *A. spinosa* and *A. gemmata* coexist (AJF 464-465: Gulf of Lingayen, Luzon, Philippines), estimated population sizes are in the proportion of 1:100.

Acanthopleura gemmata (Blainville, 1825)

Figures 7 to 23, and 113-C

Chiton gemmatus BLAINVILLE, 1825:544.

Acanthopleura gemmata: IREDALE, 1914b:668; ASHBY, 1918: 86 (in subgen. *Amphitomura*), 1922b:29–31, 1923b:230, 1926:384, 388–389, 1928:171–172, pl. 12, figs. 6, 7; WAY & PURCHON, 1981:313; WELLS, 1981:253; CHELAZZI *et al.*, 1983:115–125; FERREIRA, 1983b:278–282, fig. 30.

Acanthopleura gemmata queenslandica ASHBY, 1922a:30, 1926: 384, 1928:171–172.

Acanthopleura gemmata maudensis ASHBY, 1928:172, pl. 12, figs. 8, 9.

Amphitomura gemmata: ASHBY, 1920:291; HULL, 1925:114–115.

Acanthozostera gemmata: IREDALE & HULL, 1926:263, pl. 37, figs. 33, 34 (reprinted, 1927:126–127, pl. 15, figs. 33–34); IS. TAKI, 1947:1269, fig. 3607, 1960:197, pl. 90, fig. 3, 1962:46–47; ANG, 1967:418–421, pl. 14, figs. 1–5; WU, 1975:70–71, figs. 14–28.

Chiton spiniger SOWERBY, 1840a:287–288, Suppl. pl. 16, fig.

Explanation of Figures 1 to 4 and 7 to 10

Figure 1. *Acanthopleura spinosa* (Bruguière, 1792). Gove, N.T., Australia (AJF coll.); specimen 16 mm long.

Figure 2. *Acanthopleura spinosa* (Bruguière, 1792). Same specimen as in Figure 1. Close-up of lateral areas and girdle.

Figure 3. *Acanthopleura spinosa* (Bruguière, 1792). Same specimen as in Figure 1. Posterior aspect of posterior valve.

Figure 4. *Acanthopleura spinosa* (Bruguière, 1792). Same specimen as in Figure 1. Ventral aspect of posterior valve.

Figure 7. *Acanthopleura gemmata* (Blainville, 1825). Bunaken

Id., North Sulawesi, Indonesia (AJF 711); specimen 20 mm long.

Figure 8. *Acanthopleura gemmata* (Blainville, 1825). Koror, Palau, Western Caroline Islands (AJF 409); specimen 55 mm long. Dorsal aspect of posterior valve.

Figure 9. *Acanthopleura gemmata* (Blainville, 1825). Same specimen as in Figure 8. Posterior aspect of posterior valve.

Figure 10. *Acanthopleura gemmata* (Blainville, 1825). Same specimen as in Figure 8. Ventral aspect of posterior valve.

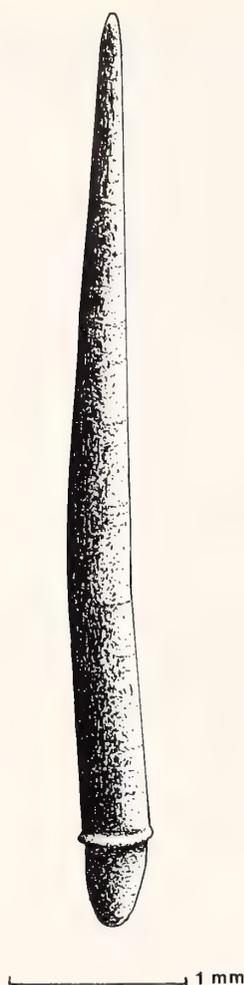


Figure 5

Acanthopleura spinosa (Bruguière, 1792). Hundred Islands, Lingayen Gulf (AJF 464); specimen 35 mm long. Girdle spine.

2, 1840b:1, 10, sp. no. 3, fig. 68, 1841:61; REEVE, 1847, pl. 14, fig. 75; JAY, 1850:99; ADAMS & ADAMS, 1854:475; CHENU, 1859:381-382, fig. 2871; TILLIER & BAVAY, 1905:176, 179.

Maugeria spinigera: GRAY, 1857:184.

Chiton (Acanthopleura) spiniger: SMITH, 1884:81; 1891:420; FISCHER, 1885:881; MARTENS, 1887:199.

Acanthopleura spiniger: DALL, 1879:298, fig. 28; TRYON, 1883:343, pl. 86, fig. 94; MOSELEY, 1884:145; 1885:18, pl. 6, figs. 1-3, 6-9; HADDON, 1886:23-25; PILSBRY, 1893c:221-226, pl. 48, figs. 22-32, pl. 49, figs. 33, 34; PELSENEER, 1899:8, 24-25; STURANY, 1904:267, 280; HIDALGO, 1905:272; IREDALE, 1910b:158; ODHNER, 1919:21, 42; ASHBY, 1922a:31; DAUTZENBERG, 1923:58, 1929:552; BUCKNILL, 1930:529, fig. 10; LELOUP, 1933a:19-23, 1933b:1-2, 1952:41, text fig. 15, pl. 2, 1981:9-10, fig. 3.

Acanthopleura spinigera: HORST & SCHEPMAN, 1908:526-527; THIELE, 1893:372, pl. 3, fig. 30; MELVILL &

STANDEN, 1899:180; THIELE, 1909:8, 1911:398-399; NIERSTRASZ, 1905a:99-101, 1905b:151-152 (in part), 1906:511-513; SYKES, 1907:34; SMITH, 1910:211; ASHBY, 1923a:226; PALLARY, 1926:28, pl. 4, figs. 4a, 4b; TOMLIN, 1927:291; BERGENHAYN, 1930a:32-33, pl. 8, fig. 75, pl. 9, fig. 84, 1930b:39-42, pl. 3, figs. 55-61, 70-74; LAMY, 1938:88; SOLEM, 1953:215; GREENFIELD, 1972:37-47.

Chiton aculeatus Gmelin" QUOY & GAIMARD, 1835:373-376; (Atlas, 1833), pl. 74, figs. 1-5.

Chiton (Acanthopleura) macgillivrayi ADAMS, 1855:120; PILSBRY, 1893c:224-225 (as syn. of *A. spiniger*).

Acanthopleura [sic] *vallantii* ROCHEBRUNE, 1882:192.

Acanthopleura rawakiana ROCHEBRUNE, 1882:195-196.

Acanthopleura balansae ROCHEBRUNE, 1882:197; LAMY, 1923:265.

Acanthopleura glareosa SMITH, 1884:81, *nomen nudum* (as syn. of *A. spiniger*).

Acanthopleura haddon: WINCKWORTH, 1927:206, pl. 28, figs. 1-4; LELOUP, 1937a:172-176, figs. 17-19; REES & STUCKEY, 1952:185; LELOUP, 1960:38-39; BOSCH & BOSCH, 1962:145; PEARSE, 1978:92-101, 1979:50, fig. 9; LELOUP, 1980b:6.

Acanthopleura planispina BERGENHAYN, 1933:36-38, text fig. 12, pl. 1, fig. 11, pl. 3, figs. 51-52, 54-59 (in subgen. *Amphitomura*).

Planispina planispina: IS. TAKI, 1962:47.

Acanthopleura bergenhayni LELOUP, 1937b:3, 1980c:1-5, figs. 1-3.

Acanthozostera virens ANG, 1967:421-422, pl. 15, figs. 1-5. "*Acanthopleura brevispinosa* (Sowerby)" ANG, 1967:416-417, pl. 13, figs. 1-5.

Type material and type locality:

Chiton gemmatus Blainville, 1825: Type material from "New Holland" presumed lost (ASHBY, 1928, *loc. cit.*); neotype, designated by ASHBY, 1928:172, pl. 12, fig. 6 (=holotype of *Acanthopleura gemmata queenslandica* Ashby, 1922a), "in coll. Ashby" (*vide* IREDALE & HULL, 1926:264), not examined; locality of neotype, Dunk Island, Queensland, Australia (17°56'S, 146°06'E).

Chiton spiniger Sowerby, 1840a: Lectotype (BMNH 1842.5.10.1654) and paralectotype (BMNH 1842.5.10.1652) designated herein; locality "Cagayan . . . Misamis, Island Midinao" and "island Siquijor," Philippines (SOWERBY, 1841:61), here restricted to Siquijor Id. (9°10'N, 123°33'E).

Chiton macgillivrayi Adams, 1855: Types unascertained; locality Fiji Islands.

Acanthopleura vallantii Rochebrune, 1882: Lectotype and paralectotype (at MHNH) designated herein; locality "Canal de Suez," Egypt.

Acanthopleura rawakiana Rochebrune, 1882: Lectotype (at MHNH) designated herein; locality "Rawak. Terre des Papous" (? Rawak, Sumba Id., Lesser Sunda Islands, 9°55'S, 119°50'E).

Acanthopleura balansae Rochebrune, 1882: Lectotype and 3 paralectotypes (at MHNH) designated herein; locality "Australie . . . Nouvelle Caledonie," here restricted to New Caledonia.

Acanthopleura gemmata queenslandica Ashby, 1922a: Holotype, "in coll. Ashby" (*vide* IREDALE & HULL, 1926:264), not examined; locality Dunk Island, Queensland, Australia (17°56'S, 146°06'E).

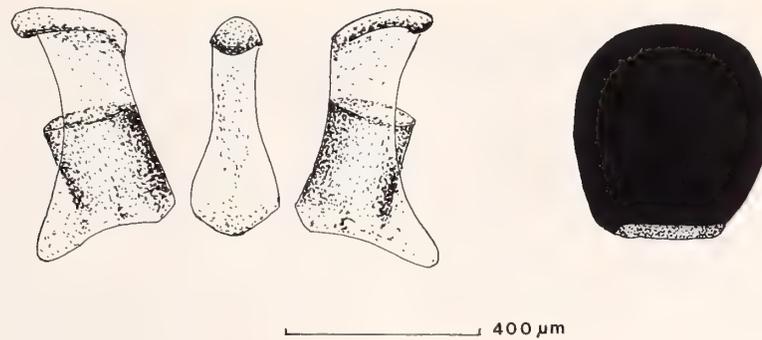


Figure 6

Acanthopleura spinosa (Bruguère, 1792). Hundred Islands, Lingayen Gulf, Philippines (AJF 464); specimen 75 mm long. Radula median and first lateral teeth, and head of major lateral tooth.

Acanthopleura haddoni Winckworth, 1927: Types unascertained; locality Aden (12°45'N, 45°12'E).

Acanthopleura gemmata maudensis Ashby, 1928: Holotype, "Ashby Coll." (fide ASHBY, 1928), not examined; locality Maud's Landing, Western Australia (23°06'S, 113°48'E).

Acanthopleura planispina Bergenhayn, 1933: Holotype (UuzM no. 114a) and 4 paratypes (UuzM no. 114b); locality Bonin Islands (27°00'N, 142°10'E).

Acanthopleura bergenhayni Leloup, 1937b: Holotype (BMNH 19823); locality "N. C. Australia."

Acanthozostera virens Ang, 1967: Holotype (University of the Philippines, U.P. Am.-112), not examined; locality, Philippines, but exact "locality, collector, date not recorded" (ANG, 1967:422).

Material examined:

AUSTRALIA, W.A.: Dorre Id., Shark Bay, 8 specimens (WAM 469-74); Maud's Landing, 3 specimens (AMS 112352; WAM 9326); Ningaloo, Point Cloates, 1 specimen (WAM 34-74); Yardie Creek, North West Cape, 7 specimens (WAM 23-74; WAM 1743-78; WAM 1749-78); Exmouth Gulf, 1 specimen (WAM 26-74); Hermite Id., Monte Bello Is., 5 specimens (WAM 19-74; WAM 27-74); Long Id., near Onslow, 1 specimen (AMS C69355); "West Australia," 1 specimen, 65 mm long (AMS C44883); Monte Bello Id., 5 specimens (WAM 5887); Kendrew Id., Dampier Arch., 1 specimen (WAM 74-7); Barrow Id., 2 specimens (WAM 24-74; WAM 605-67); Whitnell Bay, Dampier Penins., 1 specimen (WAM 1111-78); Wood Id., 2 specimens (WAM 36-74); Cockatoo Is., 3 specimens (WAM 18-74); Broome, 8 specimens, largest 50 mm long (AMS C69100; WAM 8987; NMV); Buccaneer Arch., 36 specimens (AMS C42222); Lacepede Is., 1 specimen (WAM 30-74).

AUSTRALIA, N.T.: 1 specimen (AMS C77617); Anson Bay, 3 specimens, largest 54 mm long (AMS C31532); Fannie Bay, Darwin, 1 specimen (WAM 29-74); "N.C.," holotype of *A. bergenhayni* (BMNH 19823); Darwin, 14 specimens (WAM 38-74; NMV; AMS C112353; AMS C10722); Cape Wessel, 1 specimen (AMS C77821); Port Essington, 3 specimens, largest 70 mm long (AMS C85096; AMS C90471); Cape Arnhem, 1 specimen, 50 mm long (AMS C135475).

AUSTRALIA, Qld.: Swears Id., South Wellesby Is., Gulf of Carpentaria, 3 specimens (AMS C15820); Albatross Bay, Weipa, 1 specimen (AMS C109287); Darnley Id., 1 specimen (AMS C517900); Bamfield Point, Prince of Wales Id., Torres Strait, 1

specimen, 36 mm long (AMS C110626); Murray Id., Torres Strait, 9 specimens (AMS C29619; AMS C112345); Cape York, 1 specimen (Penprase coll.); Campwin Beach, 2 specimens, largest 45 mm long (AMS C135481); Lizard Id., 1 specimen (AMS C135478); Darnby Is., 1 specimen (AMS C51790); Cooktown, 1 specimen (C109286); Two Isles, 2 specimens (AMS C109286); Hope Id., 1 specimen (WAM 27990); Port Douglas, 3 specimens (Van Belle coll.; AMS C76027); Low Isles, 3 specimens (AJF 603); Michaelmas Cay, off Cairns, 1 specimen (AMS C53575); Alma Bay, Magnetic Id., 2 specimens (NMV); Armit Is., 5 specimens (NMV); Bowen, 1 specimen (AMS C109288); Palm Id., 4 specimens (AMS C9303); Brampton Id., Whitsunday Passage, 4 specimens (AMS C109290); Linderman Id., Whitsunday Passage, 13 specimens (AMS C109293); Heron Id., Capricorn Group, 3 specimens (AMS C109189; AMS C109292; CAS 012261); Wilson Id., Capricorn Group, 2 specimens, largest 110 mm long (AMS C135519); Hillsborough Channel, 1 specimen (AMS C125472); Gatecombe Head, 3 specimens, largest 75 mm long (AMS C18778); Keppel Bay, 2 specimens (AMS C109191; AMS C109295); Fairfax Id., Bunker Group, 1 specimen (AMS C69053); Port Curtis, 1 specimen (AMS C109294).

PAPUA NEW GUINEA: Manubada Id., Port Moresby, 6 specimens (AJF 608); Madang, 1 specimen (AJF 623); Kaibola, Kiriwina Id., Trobriand Is., 2 specimens (AJF 611); Rabaul, New Britain Id., 2 specimens (AJF 615); Blanche Bay, New Britain Id., 1 specimen, 35 mm long (AMS C3160); Gigira Id., Louisiade Arch., 6 specimens (AMS C82857); Misima Id., Louisiade Arch., 9 specimens (AMS 112348); Schouten Is., 16 specimens, largest 40 mm long (ANSP 207593; ANSP 207128); Yule Id., 3 specimens, largest 70 mm long (ANSP 84007).

INDONESIA NEW GUINEA: Padaido Is., 2 specimens, largest 30 mm long (ANSP 206192; ANSP 205047); Japen Id., 7 specimens, largest 53 mm long (ANSP 205227; ANSP 208964); Biak Id., 7 specimens, largest 30 mm long (ANSP 206295).

SULAWESI (=Celebes): Utara, 3 specimens, 48 mm long (CAS 009875; CAS 012252); Bunaken Id., 58 specimens (AJF 706; AJF 711); Manado Tua Id., 23 specimens (AJF 708); Manado Bay, 10 specimens, largest 48 mm long (AJF coll., leg. S. Motley).

THAILAND: Lower Siam, Butang Arch., 1 specimen (NMV); Hey Id., S of Phuket, 3 specimens (AJF 865).

MALAYSIA: Telor Id., 22 specimens (AJF 719); Kedah, 1 specimen (Penprase coll.).

SUMATRA: Padang, 1 specimen, ca. 50 mm long (ANSP 84316); Pagai, Mentavi Is., 1 specimen (NMV 4055; NMV 4056).

BALI: 5 specimens (AMS C60813).
 BORNEO: Marudu Bay, 2 specimens (ANSP 255743; ANSP 255742); Sapi Id., 1 specimen, 62 mm long (ANSP 275040).
 SOLOMON IS.: 1 specimen (Van Belle coll.); Tulagi, 9 specimens (AMS C30640); Florida Id., 2 specimens (AMS C11109); Skutland Id., 1 specimen, ca. 60 mm long (ANSP 310058).
 NEW CALEDONIA: 23 specimens (AMS C112346; AMS C112347; NMV); Ihiu, 1 specimen (NMV); "Hargraves Coll.," 1 specimen (AMS 11314); Noumea, 4 specimens (AJF 530; AJF 534); Baie des Citrons, Noumea, 2 specimens (AMS C72643); Roche al la Voile, Noumea, 1 specimen (AMS C72650); Bourrail, 4 specimens (AJF 539); Poindimie, 5 specimens (AJF 537); Faden Reef, Heinghene, 1 specimen (AMS C112344); Ile des Pins, 22 specimens (AJF 532; AMS C4343).
 PHILIPPINES: Rita Id., Ulugan Bay, Palawan (South China Sea), 3 specimens (AJF 822); "Auson" Id., off Port Barton, Palawan (South China Sea), 8 specimens, largest 56 mm long (AJF 820); Binumsalian Bay, Palawan, 4 specimens (AJF 814); Tawitani, Sulu Arch., 6 specimens (CAS 002383; CAS 009881); Laminusa Id., Siasi Group, Sulu, 3 specimens (CAS 009877); Luuk, Sulu, 2 specimens (CAS 0122200); Juruck Bay, Cagayan Sulu Id., Sulu, 7 specimens (CAS 012245); Cebu, 1 specimen (Van Belle coll.); Nonoc, 25 specimens (CAS 012795); Siquijor Id., 1 specimen disarticulated (AMS C135473); Maloh, Negros Id., 36 specimens (AJF 451); Sumillon Id., 10 specimens (AJF 453); Liloan Point, Cebu Id., 7 specimens (AJF 454); Apo Id., 2 specimens (AJF 455); San Jose, Negros Id., 6 specimens (AJF 456); Punta Cruz, Bohol Id., 14 specimens (AJF 459); Loon Id., off Bohol Id., 20 specimens (AJF 460); Inamora Id., off Bohol Id., 1 specimen (AJF 461); Mactan Id., off Cebu Id., 21 specimens (AJF 462); Sulpha Id., off Cebu Id., 10 specimens (AJF 463); Ambulong Id., Mindoro, 15 specimens (AJF 791; AJF 793); Ilin Point, Ilin Id., Mindoro, 4 specimens (AJF 797); Hundred Islands, Lingayen Gulf, Luzon, 34 specimens (AJF 464; AJF 465).
 TAIWAN: Orchid Id., near Hungtou Rock Formation, Taitung Co., 2 specimens, largest 41 mm long (UCM 28842); Keelung, 17 specimens (CAS 009880; CAS 016698).
 OKINAWA, Japan: Cape Ata, 32 specimens (CAS 002383; CAS 012253); Buckner Bay, 1 specimen, 25 mm long (CAS 002163); Okuma, 3 specimens (CAS 012221; S. Crittenden coll.); Meijo, 1 specimen (CAS 012242); White Beach, 2 specimens, largest 62 mm long (AMS C135474).
 BONIN IS., Japan: Holotype and 4 paratypes of *Acanthopleura planispina* Bergenhayn (UUZM Nos. 104, 104a); 2 specimens (CAS-SU 2871).
 PALAU: Koro, 55 specimens (AJF 409); Ngesil, 5 specimens (Carlson & Hoff coll.).
 YAP: 4 specimens (NMV; Crittenden coll.).
 GUAM: Pago Bay, 2 specimens (Carlson & Hoff coll.); Bile Bay, 4 specimens (Carlson & Hoff coll.).
 FIJI: 1 specimen, 50 mm long (AMS C135477); Tai Id., Nadi Bay, Viti-levu, 2 specimens (AJF 284); Naindi Bay, near Savusavu, Vanua-levu, 5 specimens (AJF 528); 1 specimen (NMV); Yasawa Is., 1 specimen (Van Belle coll.); Namuya Levu, Yasawa Group, 1 specimen (Penprase coll.); Vambia, Ono, 5 specimens (AMS C112349).
 TONGA: Tongatapu, N coast, 16 specimens, largest 55 mm long (CAS 046669; AJF coll., leg. M. Wolterding, Apr. 1984); Fanga Tavi Beach, Eva Id., 5 specimens (CAS 046670); Pangaimotu Id., 3 specimens, largest 48 mm long (AJF 766); Fafa Id., 5 specimens, largest 55 mm long (AJF coll., leg. M. Wolterding, May 1984); Afa Id., 1 specimen, 58 mm long (AJF 768); Tongatapu Id. and Valitua Id., 2 specimens (CAS 009883); Vava'u Id., 2 specimens (Penprase coll.).

MARQUESAS: Eiao, 1 specimen (AJF coll., ex C. Richard, École Pratique des Hautes Études, Paris).
 ISRAEL: Elat, Gulf of Aqaba, 2 specimens (Van Belle coll.); Na'ama Bay, Sinai Peninsula, 31 specimens (AJF 434).
 EGYPT: Wadi-el-Dom, Gulf of Suez, 6 specimens (AJF coll., leg. Dr. J. Pearse).
 OMAN: Masqat, 11 specimens, largest 45 mm long (K. Gudnason coll.).
 AFARS ET ISSAS: Djibouti, 4 specimens (MHNB; CAS 009874).
 SOMALIA: Gesira, 5 specimens, largest 50 mm long (MF 4106); Sar Uanle, 4 specimens, largest 50 mm long (MF 4107).
 COMORO IS.: Grand Comore Id., 1 specimen (CAS 001263).
 KENYA: Mombasa Beach, 5 specimens (AJF 593); Malindi, 17 specimens (AJF 594); Wamatu, 10 specimens (AJF 595); Twiga, 15 specimens (ANSP 276916; ANSP 287347); Wassini Id., 7 specimens (AJF 597).
 TANZANIA: Mbudya Id., 6 specimens (MHNB); Chumbe Id., 4 specimens (ANSP 213823); Tumbatu Id., 1 specimen (ANSP 212991); Zanzibar Is., 19 specimens (ANSP 212326; ANSP 213024; ANSP 213319; ANSP 214527); Dar-es-Salaam, 19 specimens (Van Belle coll.; CAS 9882; ANSP 283100).
 MADAGASCAR: Pointe de Tafondro, 3 specimens (ANSP 258101); Nossi Be, 136 specimens (ANSP 257344; ANSP 257601; ANSP 258553; ANSP 258627; ANSP 258911; ANSP 25864; ANSP 258965); Nossi Iranja, 35 specimens (ANSP 257084; ANSP 257085).

Description: BLAINVILLE's (1825) original description of *Chiton gemmatus* would have been quite sufficient to identify the species were it not for uncertainties developed on account of its considerable intraspecific variation, very wide geographic distribution, and the presence of several other closely related species. Even PILSBRY's (1893c) and IREDALE & HULL's (1926) accounts, good as they are, fail to characterize the species unequivocally.

Among over 1,210 specimens of *Acanthopleura gemmata* here examined, largest 110 mm long (dry) (AMS C135519; Wilson Id., Capricorn Group, Australia) (largest reported, 120 mm long [live] [IREDALE & HULL, 1926]). Specimens (Figures 7–10) depressed, round-backed, large; live specimen 82 mm long observed to shrink to 70 mm after two week preservation in 10% formalin in seawater followed by three months in isopropyl alcohol. Body width/length, mean 0.66. Intermediate valves beaked; posterior edge of valve ii forming 100–120° angle. Tegmentum grayish-green to grayish-brown, usually extensively eroded. Lateral areas poorly defined, hardly raised, sculptured with low-profile, irregular, round to elongate granules, sometimes coalesced into arched wrinkles; anterior valve and postmucro area of posterior valve similarly sculptured. Central areas almost featureless except for smaller to obsolete granules in pleural areas, and thin, ill-defined, transverse lamellae appressed across jugal areas. Mucro central (in small specimens) to somewhat posterior (in larger ones); postmucro strongly convex, at 45–90° slope. Ocelli round to oval, 50–70 μ m in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, and anterior $\frac{1}{3}$ to $\frac{1}{2}$ of lateral areas of intermediate valves. On valve i, tegmentum length/width,

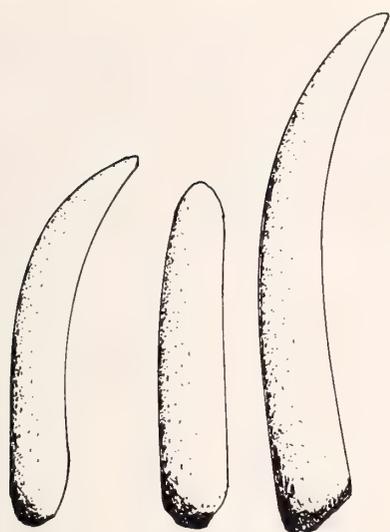


Figure 11

Acanthopleura gemmata (Blainville, 1825). Yeppoon, Qld., Australia; specimen 40 mm long. Girdle spines.

mean 0.5. On valve viii, articulamentum often wider than tegmentum; tegmentum length/width, mean 0.5. Widths of tegmental surfaces of valves i/viii, mean 1.1. Gills with 40–60 plumes per side.

Articulamentum color fairly constant for specimens from a given locality, but varying with locality from bluish-white to brown. Sutural laminae well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate mostly smooth; relative width of sinus (width of sinus/width of sutural lamina) on valve viii, 0.9. Insertion plates strongly pectinate on outside. On valve i, insertion teeth irregularly spaced, sometimes fused together; in midline, length of insertion plate/length of tegmentum, mean 0.2. On valve viii, pectinations extremely variable, resulting in incomplete slitting and poor definition of teeth, particularly towards midline; teeth often recurved forward, anteriorly fused to but extending beyond buttressing, transverse, round callus. Slit formula (not always clearly determinable), 8/11-1-6/10. Eaves thick (0.5 mm on midline of valve viii of specimen 50 mm long), moderately spongy.

Girdle thick, muscular, wide, often banded, shrinking appreciably with preservation; at level of valve iv, girdle may measure 75% of width of valve in live specimens, 50% of valve in alcohol preserved specimens, 30% in dry specimens. Upper surface crowded with white to dark gray, brown, or black spinelets (Figure 11), pointed to blunt, straight to curved, somewhat conical, about 3 × 0.6 mm in average-sized specimen (up to 7 × 1 mm in large specimens), with smaller to minute spinelets in between;

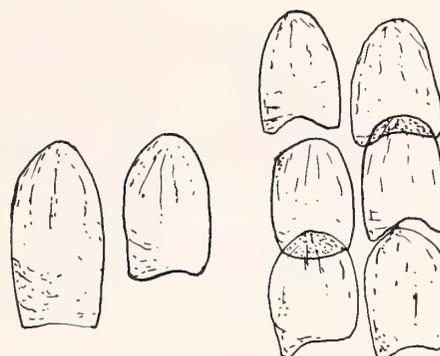


Figure 12

Acanthopleura gemmata (Blainville, 1825). Same specimen as in Figure 11. Scales of girdle undersurface.

in some specimens, pointed, crystalline, needle-like elements (up to 200 × 30 μm) may be seen, isolated or in clusters interspersed amidst spinelets. Girdle bridges, empty. Undersurface paved with imbricate, transparent, squarish scales (Figure 12), about 40 × 40 μm (becoming elongate towards outer margin), with 8–10 coarse striations radiating from outer edge of scale.

Radulae averaging 45% of specimen length (range 37–57%, SD = 7.2%, n = 13) and 63 rows of mature teeth (range 45–85, SD = 11.5, n = 13). Radular features (Figure 13) rather constant in 23 specimens examined: in specimen 52 mm long (AJF 594: Malindi, Kenya) median tooth 80 μm wide at anterior blade; first lateral teeth about 450 μm long, 230 μm wide at anterior blade; major lateral teeth with tubercle 170 μm long at anterior part of inner edge, and discoid head 350 μm wide; outer marginal teeth 300 μm long, 210 μm wide (length/width, 1.5).

Distribution: Among intertidal chiton species, *Acanthopleura gemmata* seems to have the widest range (Figure 113-C). It has been recorded, albeit by synonymous names, from about 32°E to 140°W, an east-west range of some 20,000 km. In the western Indian Ocean, it has been reported from the gulfs of Aqaba and Suez in the Red Sea (ROCHEBRUNE, 1882; NIERSTRASZ, 1905b; TILLIER & BAVAY, 1905; SYKES, 1907; HORST & SCHEPMAN, 1908; LELOUP, 1933a; PEARSE, 1978) down the east coast of Africa, from Djibouti (LELOUP, 1933a) through Somalia, Kenya, to Dar-es-Salaam, Tanzania (FERREIRA, 1983b), the Comoros Is. (NIERSTRASZ, 1905a, 1906), and the west coast of Madagascar (ODHNER, 1919; DAUTZENBERG, 1923, 1929), as well as at Aden and Barim Id., Yemen (WINCKWORTH, 1927), and Oman (LELOUP, 1937a; BOSCH & BOSCH, 1962). It has been reported at the Andaman Is. (LELOUP, 1952), west coast of Malaysia (WAY & PURCHON, 1981), Sumatra (BERGENHAYN, 1930a; LELOUP, 1952), Java (HORST & SCHEPMAN, 1908; BERGENHAYN,

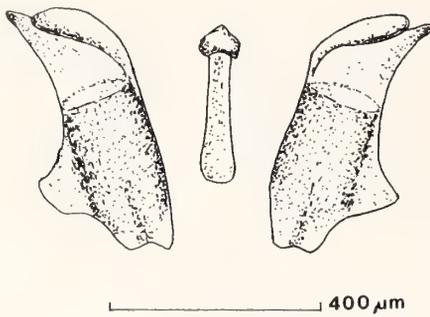


Figure 13

Acanthopleura gemmata (Blainville, 1825). Same specimen as in Figure 11. Radula median and first lateral teeth.

1930a; LELOUP, 1933a), Sunda Is. (BERGENHAYN, 1930a; LELOUP, 1933a), Lombok, Flores, Borneo (NIERSTRASZ, 1905a), Timor (LAMY, 1923), Amboine, Morotai, Sangi Is. (HORST & SCHEPMAN, 1908), Sulawesi (NIERSTRASZ, 1905a; LELOUP, 1933a, b), Halmahera Id., New Guinea (QUOY & GAIMARD, 1835; NIERSTRASZ, 1905a; HORST & SCHEPMAN, 1908; LELOUP, 1933a), New Ireland and Tonga (QUOY & GAIMARD, 1835); Philippines (SOWERBY, 1841; HIDALGO, 1905; LELOUP, 1933b; ANG, 1967), Taiwan (Is. TAKI, 1947, 1962; WU, 1975), Yaeyama Is. (Is. TAKI, 1938), Bonin Is. (BERGENHAYN, 1933, as *Acanthopleura planispina*), Solomon Is. (LELOUP, 1933a), Fiji (ADAMS, 1855; PILSBRY, 1893c; BERGENHAYN, 1930a; LELOUP, 1933a, 1952), and New Caledonia (ROCHEBRUNE, 1882; PILSBRY, 1893c; LAMY, 1923). In Australia, *A. gemmata* was reported from the "Torresian Region, . . . the whole coastline from Darwin east and south to Port Curtis, and west and south to Bunbury" (IREDALE & HULL, 1926:264); but ASHBY (1928:171) pointed out that, on the west coast, the species occurs southward not to Bunbury but to "a point between Carnarvon and Maud's Landing, north of Shark Bay." Reports of the species at the Society Is. (LELOUP, 1933a) and Hong Kong (BERGENHAYN, 1930a) have not been corroborated (VAN BELLE, 1980, 1982; A. J. Ferreira, field trips to Society Is. [Moorea, Sept. 1974, Tahiti, Aug. 1980 and Dec. 1983, Bora-Bora, Dec. 1983], and Hong Kong, Sept. 1982, Jan. 1983). The report of *A. gemmata* at Cape of Good Hope, South Africa (NIERSTRASZ, 1905b, 1906) is obviously in error.

In the Indian Ocean, the northernmost verified record is Elat, Gulf of Aqaba, Red Sea (29°33'N, 34°57'E); the southernmost verified record is Nossi Iranja, 50 km SW of Nossi Be, Madagascar (13°20'S, 48°15'E). Reported records from Mahakamby (=Mahajamba) and Tulear, Madagascar (23°21'S, 43°40'E) (ODHNER, 1919, as *A. spiniger*) require confirmation (KAAS, 1979). On the mainland of Africa, the species has been found as far south as Dar-es-Salaam, Tanzania (6°48'S, 39°17'E) (FERREIRA, 1983b, and herein).

There seems to be a wide distributional gap between the Red Sea and western Indian Ocean population on one side, and the Indo-Pacific population on the other. *Acanthopleura gemmata* has not been reported between Oman and the Andaman Is.; the species was not found on South Male Atoll, Maldives, or the southwest coast of Sri-Lanka (A. J. Ferreira, field trip, Feb. 1983). The recording gap, approximately between 58°E and 92°E, does not seem to be a collecting artifact due to inadequate sampling but a distributional disjunction, perhaps intermittent, for which no reasonable explanation is at hand.

In the central and eastern Indo-Pacific, *Acanthopleura gemmata* ranges from the Andaman Islands (92°45'E) to Tonga (175°W). It seems to be absent (another distributional gap?) in the Society Is. (A. J. Ferreira, above) and Samoa Is. (A. J. Ferreira, field trips to Tutuila Id. and Upolu Id., March 1976 and Dec. 1983), reappearing in the Marquesas Islands (9°S, 139.5°E), its easternmost record. The northernmost verified record is the Bonin Islands (27°00'N, 142°10'E). In Australia, the southernmost verified record on the east coast is Port Curtis, Qld. (24°00'S, 151°30'E); on the west coast, Dorre Island, Shark Bay, W.A. (25°09'S, 113°07'E).

Acanthopleura gemmata is confined to the intertidal and low subtidal zones, 0–2 m, with specimens often exposed at low tide. Reports of the species at subtidal depths (HADDON, 1886, at 11 m; NIERSTRASZ, 1905a, at 27 m) are obviously in error.

Remarks: As should be expected from a species with such a wide geographical distribution, *Acanthopleura gemmata* shows considerable intraspecific variation, particularly in the color of the tegmentum (from lighter grays to darker browns), color of the articulamentum (from blue to brown), tegmental sculpture (from granules to wrinkles, variable in shape and disposition), and in the girdle spinelets (from white to gray, brown, or black; from short and stubby to long and pointed). In regard to the latter, there seems to be some positive correlation between the length of the spinelets of a given specimen and the degree of erosion of the valves; specimens with the tegmentum uneroded tend to have longer spinelets, a phenomenon which seems to vary with locality but not necessarily with habitat (*i.e.*, exposure to surf).

The type material of *Chiton spiniger* consists of 2 syntype specimens, well preserved, dry, and flat. The specimen here designated lectotype (Figures 14–16) is accompanied by a pink museum label which says, in part, "Figured Syntype / Loc. — ? [Philippines] / Coll. — ? Purch. of H. Cuming." The specimen, dirty brown, 58 mm long, 35 mm wide; tegmentum clean, not encrusted or significantly eroded, shows abundant coarse, irregular granules in both central and lateral areas as well as in the anterior valve and postmucro of the posterior valve where they are arranged in concentric rows. Ocelli round to oval, 40–60 μ m in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior $\frac{1}{2}$ to $\frac{3}{5}$ of

lateral areas of intermediate valves. Mucro central, prominent; postmucro convex, with sharp, near vertical slope. Girdle with abundant calcareous spinelets up to 2.4 mm long, 0.4 mm thick. Soft parts absent; articulamentum dark brown; the number "42.5.10.1654" is written in black ink on underside of girdle. The other syntype specimen (BMNH 1842.5.10.1652), here designated paralectotype, 73 × 58 mm, has very similar features. Two other specimens, dry, flat, well preserved, part of the H. Cuming collection, were examined. The larger specimen (BMNH 19824/1), 80 × 47 mm, with yellow museum label, corresponds to the figured specimen in REEVE (1847: pl. 14, sp. & fig. 75); the smaller specimen (BMNH 19825/1), 35 × 19 mm, carries yellow museum label stating in part "Loc. Island of Siquijor [Philippines] found under stones at low water."

Pilsbry (in ASHBY, 1922a:29) recognized *Acanthopleura gemmata*, apparently as senior synonym of *A. spiniger*; but ASHBY (1922a) recommended retaining the name *spiniger* for the Sumatra specimens he had examined, reserving *gemmata* for the Australian population. Further, ASHBY (*loc. cit.*) postulated that specimens from Dunk Id., on account of differences in the tail valve, belonged to "a distinct geographical race" for which he proposed the name *A. gemmata queenslandica* (not *queenslandica* Pilsbry, 1894b) (see Remarks on *A. arenosa*).

As noted by HADDON (1886), the specimen(s) cited by QUOY & GAIMARD (1835) as "*Chiton aculeatus*" are of *A. gemmata*.

The type material of *Acanthopleura vaillantii* Rochebrune, 1882, consists of two specimens, dry, curled, soft parts removed, 45 and 40 mm in (estimated) length, showing remnants of glued paper. Accompanying label reads "rec. Vaillantii—Types [on red background] / *Acanthopleura vaillantii* Rochbr. / = *A. spinigera* Sow. / Mer rouge / Bull. Soc. Philom. 1882:192." The specimens agree with ROCHEBRUNE's (1882) description of the species; the larger is here designated lectotype, the smaller (Figure 17) paralectotype.

The type material of *Acanthopleura rawakiana* Rochebrune, 1882, consists of a single specimen (Figure 18). The label reads, in part, "Syntype [on red background] / *Acanthopleura rawakana* [sic] ROCH. 1882 / Terre des Papous / Bull. Soc. Philom. Paris 1882 p. 195." The specimen, here designated lectotype, agrees with ROCHEBRUNE's (1882) description, but the alleged locality, Rawak, could not be found on maps of New Guinea, new or old (Judy Kelly, National Library Service, Boroko, Papua New Guinea, *in litt.* 4 Dec. 1981), and is presumed to refer to a village of that name at Sumba Id., Lesser Sunda Islands.

The type material of *Acanthopleura balansae* Rochebrune, 1882, comprises 4 specimens, dry, somewhat curled, estimated lengths from 40 to 50 mm, showing bits of glued paper. Accompanying label reads, "rec. Balansa 1872. XIV-221 — Types [on red background] / *Acanthopleura balansae* Roch. / = *A. Spinigera* Sow. / rec.: Caledonie /

Bull. Soc. Philom. Paris 1882:197." The specimens, with soft parts intact, agree with ROCHEBRUNE's (1882) description of the species, the published dimensions corresponding to those of the largest specimen in the lot, here designated as lectotype; the 3 other specimens in the lot, one illustrated (Figure 19), are here designated paralectotypes.

The holotype of *Acanthopleura bergenhayni* Leloup, 1937b (BMNH 19823), is poorly preserved in alcohol; somewhat curled, estimated 60 mm long, 45 mm wide (including girdle); valves iii, v, vi, and vii in place, others missing except for part of valve viii showing pectinate teeth; valves bluish-gray, extremely eroded; girdle almost denuded of spinelets; spinelets white or grayish-black. Accompanying museum label reads, in part, "Holotype / *Acanthopleura bergenhayni* / 1 specs. Acc. no.: / Leloup, 1937 / Loc. N. C. Australia / Coll. Antarctic Exped., the Admiralty." The specimen (Figures 20, 21) agrees with LELOUP's (1937b:3) description, except in dimensions (Leloup [*loc. cit.*] described it as 53 × 40 mm), and corresponds to the current concept of *A. gemmata*.

The type material of *Acanthopleura planispina* Bergenhayn, 1933 (at UZM) consists of holotype and 4 paratypes, well preserved in alcohol. With holotype, type-written label reads, "Uppsala Univ. Zool. Mus. / Typesamlingen / nr. 144a / Mollusca"; three other handwritten labels add, ". . . Type—ex. J. R. M. Bergenhayn 1933 . . . Prof. Sixten Bocks Japan—Ex. 1914 / Bonin Islands (Ogasawara) / Taki ura Ebbestrand 28.7 / formal konserv . . ." Holotype (Figure 22), well preserved, flat, 36 mm long, 22 mm wide (including girdle); pulling down girdle (which, obviously, had been done before) shows pectinate insertion plate and single, well defined slit in midline. Contrary to BERGENHAYN's (1933) assertion, girdle spinelets do not appear distinct in any particular way. Paratypes, the anterior valve of one here illustrated (Figure 23), very similar to holotype; largest about 44 mm long, disarticulated, missing valve viii; second largest 39 mm long, with valves v, vi, and vii in place, but others missing; third largest curled, estimated 25 mm long, missing valve i; smallest 16 mm long, with all valves in place. The material corresponds to that described and illustrated by BERGENHAYN (1933) and to specimens of *A. gemmata* from other localities.

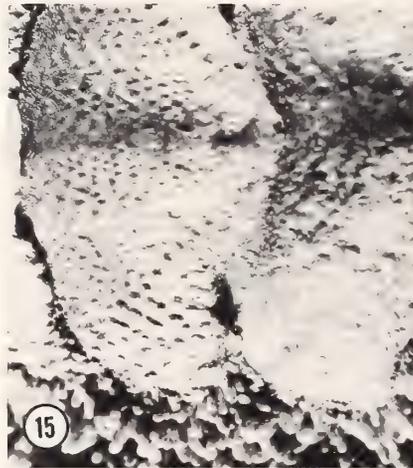
From the description and illustrations, *Acanthozostera virens* Ang, 1967, agrees clearly with the present understanding of *Acanthopleura gemmata*.

A number of other species regarded by authors as synonyms of *Acanthopleura gemmata* are here cast aside as insufficiently characterized:

(1) *Chiton aculeatus* LINNAEUS, 1758:667, no. 3, from "Asia," is unrecognizable (HANLEY, 1855; DODGE, 1952).

(2) *Chiton magnificus* SOWERBY, 1840b:2, sp. 11, fig. 52 (not Deshayes, 1827), is a *nomen nudum*.

(3) *Chiton granatus* REEVE, 1847: pl. 5, sp. & fig. 24, of unknown locality, is inadequately described. Carpenter (in PILSBRY, 1893c:224–225, pl. 48, figs. 29, 30) stated of



the tail-valve of the type "should be examined in order to tell whether it is a specimen of spiniger or of borbonica . . ." It is a *nomen dubium*.

(4) *Chiton piceus* REEVE, 1847: pl. 13, sp. & fig. 70, from "New Holland" (=Australia) (not Gmelin, 1791, from St. Thomas, West Indies) may apply to several similar species of *Acanthopleura* in Australia. Carpenter (in PILSBRY, 1893c:226, pl. 49, figs. 37, 38) examined "four specimens from Australia" regarded as types, but left no diagnostic clues. It remains a *nomen inquirendum*.

(5) *Chiton obesus* SHUTTLEWORTH, 1853:61, 69, is a *nomen nudum*.

(6) *Chiton cunninghami* REEVE, 1847, is here regarded as a *nomen inquirendum*. The holotype (BMNH 1951.1.25.6) (Figures 24–27), accompanied by a pink museum label which reads, in part, ". . . Loc. Australia, on the rocks / leg. Cunninghami / Coll. Cuming Acc. 1829," comprises 8 disarticulated valves which, reassembled, suggest a living specimen (with girdle) about 110–120 mm long, 70–80 mm wide. Valves thick, beaked; tegmentum dark brown with whitish midline band; anterior valve with irregular, round granules about 300–400 μm in diameter, in concentric rows; lateral areas hardly defined, with similar granules; central areas with similar granules in pleural regions, somewhat fused into antero-posterior riblets; jugum smooth, almost shiny; valve viii moderately inflated, posterior edge slightly sinused in middle third; mucro not prominent, somewhat posterior; postmucro convex; ocelli round to oval, 60 μm in diameter; articulamentum bluish-gray, darker in middle; sutural laminae subtriangular (on ii) to subrectangular (on viii); sinus well defined, sinusal plate coarsely pectinate; insertion teeth on valve viii, teeth very underdeveloped, as if sunken in middle third; slit formula 10-1-6. Radula and girdle not available. Carpenter (in PILSBRY, 1893c:225) described the specimen's girdle (apparently still available at the time) as "dried in around the valves, and the hairs are worn off except in the sutures, where they are short, crowded and black." The species was regarded by Carpenter (in PILSBRY, 1893c) as a synonym of *A. spiniger*

(= *A. gemmata*), a possibility that may be seriously considered if a pathologic posterior valve is assumed; IREDALE & HULL (1926) and KAAS & VAN BELLE (1980) considered it a synonym of *A. brevispinosa*, a supposition that goes contrary to the objective evidence.

In the western Indian Ocean, *Acanthopleura gemmata* is sympatric through much of its range with *A. brevispinosa*. In the central Indo-Pacific, *A. gemmata* is sympatric with *A. spinosa*, *A. araucariana*, *A. miles*, *A. curtisiana*, and *A. loochooana*; and is parapatric in the north with *A. japonica*, in the south with *A. gaimardi*, *A. arenosa*, and *A. hirtosa*.

In some localities, as personally observed in Fiji, Philippines, Palau, and at the Trobriand Islands, Papua New Guinea, specimens of *Acanthopleura gemmata* are often the object of human predation, and are so actively searched by the natives as a delicacy that entire populations have been nearly wiped out.

Acanthopleura brevispinosa (Sowerby, 1840)

Figures 28 to 34, and 112-B

Chiton brevispinosus SOWERBY, 1840a:287, Suppl. pl. 16, fig. 1, 1840b:1, 10, sp. no. 4, fig. 136; REEVE, 1847, pl. 9, sp. & fig. 52.

Acanthopleura brevispinosa: PLATE, 1898:167, pl. 11, figs. 111–112; PILSBRY, 1893c:231–232, pl. 47, figs. 18–21 (in subgen. *Amphitomura*); NIERSTRASZ, 1905a:102, 1906:511–515; ASHBY, 1931:49, pl. 7, fig. 82; (?) FISCHER, 1939:36; BARNARD, 1963:344; KAAS, 1979:868; LELOUP, 1980c:8–11, figs. 5, 7, map 1 (in part); CHELAZZI *et al.*, 1983:115–125.

[*Non*: ROCHEBRUNE, 1882:240; LAMY, 1936:267 (= *Plaxiphora mercatoris* Leloup, 1936); FISCHER, 1978:49 (in part); ANG, 1967:416–417, pl. 13, figs. 1–5 (= *A. gemmata*).]

Chiton borbonicus DESHAYES, 1863:37, figs. 12–13; MARTENS, 1880:300 (in subgen. *Acanthopleura*); VIADER, 1937:58.

Acanthopleura borbonica: PILSBRY, 1893a:105, 1893c:230–231, pl. 45, figs. 76–79 (in subgen. *Amphitomura*); THIELE, 1893:372, pl. 30, fig. 31; NIERSTRASZ, 1905a:102–103;

←

Explanation of Figures 14 to 22

Figure 14. *Acanthopleura gemmata* (Blainville, 1825): *Chiton spiniger* Sowerby, 1840a; lectotype (BMNH 1842.5.10.1654). Dorsal aspect of valves i and ii.

Figure 15. *Acanthopleura gemmata* (Blainville, 1825): *Chiton spiniger* Sowerby, 1840a; lectotype (BMNH 1842.5.10.1654). Dorsal aspect of valves iii and iv.

Figure 16. *Acanthopleura gemmata* (Blainville, 1825): *Chiton spiniger* Sowerby, 1840a; lectotype (BMNH 1842.5.10.1654). Dorsal aspect of valves vii and viii.

Figure 17. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura vaillantii* Rochebrune, 1882; paralectotype (MNHN).

Figure 18. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura rawakiana* Rochebrune, 1882; lectotype (MNHN).

Figure 19. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura balansae* Rochebrune, 1882; paralectotype (MNHN).

Figure 20. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura bergenhayni* Leloup, 1937b; holotype (BMNH 19823). Dorsal aspect of specimen with only valves iii and v in place.

Figure 21. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura bergenhayni* Leloup, 1937b; holotype (BMNH 19823). Fragment of posterior aspect of posterior valve.

Figure 22. *Acanthopleura gemmata* (Blainville, 1825): *Acanthopleura planispina* Bergenhayn, 1933; holotype (UJZM).



Melville, 1909:119; LELOUP, 1941:9 (in subgen. *Amphitomura*), 1980c:5–8, figs. 4–6, map 1 (in part).
Acanthopleura afra ROCHEBRUNE, 1882:192.

Type material and type locality:

Chiton brevispinosus Sowerby, 1840: Types unascertained; locality "Ins. Johanna [=Anjouan Id., Comoro Is.], E. Africa" (12°13'S, 44°29'E).

Chiton borbonicus Deshayes, 1863: Types unascertained; locality Reunion Id. (21°06'S, 55°38'E).

Acanthopleura afra Rochebrune, 1882: Lectotype and paralectotype (MNHN) here designated; locality Madagascar (Rochebrune [1882:192] gave "Cap de Bonne Espérance . . . ; Madagascar," as localities, but the first is clearly in error).

Material examined:

SOMALIA: Mogadiscio, 5 specimens, largest 35 mm long (MF 4108); Gesira, 7 specimens, largest 60 mm long (MF 4109).

KENYA: Mombasa Beach, 10 specimens, largest 67 mm long (AJF 593); Malindi, 6 specimens (AJF 594); Wamata, 13 specimens (AJF 595); Wassini Id., 5 specimens (AJF 597).

TANZANIA: Fumba, Zanzibar, 3 specimens (ANSP 213319); Mbody Id., 3 specimens (M. Bacescú coll.).

SEYCHELLES: 2 specimens (ANSP 310686); Port Ternary, Mahé Id., 1 specimen, 53 mm long (ANSP 311232); Anse Étoile, Mahé Id., 1 specimen, 50 mm long (ANSP 310382); North West Bay, Mahé Id., 10 specimens (AJF 564).

COMOROS: 1 specimen (ANSP 220840); Pamandzi Id., 2 specimens (*ex* Van Belle coll.); Grand Comore Id., 4 specimens (CAS 000489, CAS 001253, CAS 009876).

MADAGASCAR: Syntypes (2) of *Acanthopleura afra* Rochebrune, 1882 (MNHN); 1 specimen disarticulated, estimated 50 mm long, valves and radula (IRScNB I.G. 9247); 1 specimen, ca. 70 mm long, cited by Leloup (1980c) (IRScN I.G. 9247).

MAURITIUS: 3 specimens (ANSP 35915; ANSP 35952); Souillac, 3 specimens 26–32 mm long (ANSP 274063); Gris-Gris, 4 specimens, 18–33 mm long (ANSP 274088); Pte. Fayette, 8 specimens, 25–45 mm long (ANSP 273693); Vacoas Pt., 5 specimens (ANS 274168); Pointe-aux-Roches, 9 specimens (*ex* B. Smith, March 1979), 26 specimens (AJF 586).

REUNION: St. Gilles-les-Bains, 3 specimens (*ex* Van Belle coll.).

Description: SOWERBY (1840a) described specimens of *Chiton brevispinosus* as "rather flat, oval, narrowed in front;

the valves are rounded and smooth at the beaks, and granulated at the sides, in undulating, concentric ridges; . . . the numerous short black spines studding (the girdle) are tipped with light yellow points . . . a pretty relief to the general black colour of the shell" (p. 287). PILSBRY (1893c) pointed out "the valves concentrically wrinkled-grained at the sides of the central areas, and the ill-defined lateral areas . . . cut into granules by concentric and radiating grooves. End valves finely grooved radially, finely wrinkled concentrically; mucro posterior, prominent and rather acute. [Articulamentum] blackish-brown or purple-brown except [for white] sutural and insertion plates . . . Sinus broad, deep, rounded. [Slits 7/8-1-2]; anterior teeth moderately long, finely pectinated outside; posterior teeth very short, blunt, obsolete pectinated . . . [Girdle] narrow, clothed with white-tipped black spinelets . . ." (p. 231).

Among 138 specimens of *Acanthopleura brevispinosa* here examined, largest 67 mm long (in alcohol) (AJF 593: Mombasa Beach, Kenya). Body width/length, mean 0.61 (SD = 0.05; n = 25). Specimens (Figures 28–31) oval, depressed, round-backed. Intermediate valves beaked; posterior edge of valve ii forming 120–160° angle. Tegmentum purple-brown to dark brown or black, often with two parajugal cream-white bands. Tegmental sculpture of coarsely round granules, larger (up to 250 μm in diameter) and better defined at periphery, arranged in radial rows. Anterior valve with 30–50 rows of granules. Central areas featureless except for dull shagreened surface and, occasionally, some fine transverse, concentric rugae. Lateral areas not elevated, poorly defined except for 6–10 rows of granules. Mucro central to slightly posterior; postmucro convex, at 45–90° slope. Ocelli round to oval, 50 μm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, and anterior 1/2 to 2/5 of lateral areas of intermediate valves. Ratio of tegmental surfaces of valves i/viii, mean 1.06. On valve viii, length of tegmentum/width of tegmentum, mean 0.37 (SD = 0.04; n = 11).

Articulamentum dark brown to black, or bluish-white with dark brown area in middle of valve. Sutural laminae

←

Explanation of Figures 23 to 31

Figure 23. *Acanthopleura gemmata* (Blainville, 1825); *Acanthopleura planispina* Bergenhayn, 1933; paratype (UUZM). Anterior aspect of anterior valve.

Figure 24. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Anterior aspect of anterior valve.

Figure 25. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Dorsal aspect of intermediate valve.

Figure 26. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Dorsal aspect of posterior valve.

Figure 27. *Chiton cunninghami* Reeve, 1847; holotype (BMNH 1951.1.25.6). Ventral aspect of posterior valve.

Figure 28. *Acanthopleura brevispinosa* (Sowerby, 1840a). Wamata, Kenya (AJF 595); specimen, 23 mm long.

Figure 29. *Acanthopleura brevispinosa* (Sowerby, 1840a). Malindi, Kenya (AJF 594); specimen, 43 mm long. Dorsal aspect of posterior valve.

Figure 30. *Acanthopleura brevispinosa* (Sowerby, 1840a). Same specimen as in Figure 29. Posterior aspect of posterior valve.

Figure 31. *Acanthopleura brevispinosa* (Sowerby, 1840a). Same specimen as in Figure 29. Ventral aspect of posterior valve.

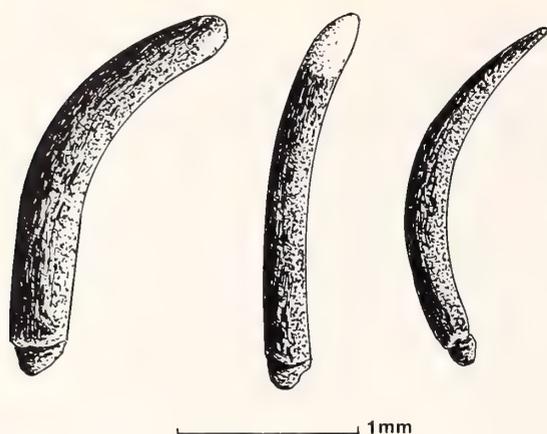


Figure 32

Acanthopleura brevispinosa (Sowerby, 1840a). Wamatu, Kenya (AJF 595); specimen 26 mm long. Girdle spines.

well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Insertion plates strongly pectinate on outer surface. On valve i, length of insertion plate/length of tegmentum, mean 0.17; insertion teeth irregularly spaced. On valve viii, relative width of sinus, 0.8; teeth poorly defined by incomplete and irregular slitting and underdevelopment of middle third of insertion plate; often only 2 slits, symmetrically placed; insertion teeth supported anteriorly by buttressing transverse, round, variably developed callus. Slit formula 7/11-1-2/6. Eaves moderately spongy. Gills with some 50 plumes per side.

Girdle wide, muscular, mostly black, usually not banded. Upper surface profusely beset with calcareous, dark brown to black, blunt spinelets (Figure 32), often tipped with yellowish-white, up to 3 mm long, 0.3 mm thick, amidst much smaller to minute ones. Girdle bridges empty. Undersurface covered with transparent, rectangular scales, about 50 μm long, 35 μm wide, with few, coarse longitudinal striations.

Radulae averaging 62% of specimen length (range 53–68%, SD = 6.6%, n = 6) and 93 rows of mature teeth (range 80–110, SD = 12.3, n = 6). In specimen 42 mm long (M. Bacescü coll.: Mbody Id., Tanzania) median tooth 130 μm wide at anterior blade; first lateral teeth 170 μm at anterior blade, outer edge deeply concave, outer posterior angle sharply pointed, inner posterior angle very elongate (Figure 33); major lateral teeth with discoid head 210 μm in diameter; outer marginal teeth 170 μm long, 250 μm wide (length/width, 0.7).

Distribution: *Acanthopleura brevispinosa* is confined to the western Indian Ocean (Figure 112-B). Its range, as here verified, extends from the east coast of Africa to the Seychelles, Comoros, Madagascar, Reunion, and Mauritius; and from Gesira, Somalia (1°58'N) to Santa Carolina Id. (KAAS, 1979) and Bazaruto Id., Mozambique (21°40'S)

(BARNARD, 1963). FISCHER's (1939) report of the species at "mer d'Oman" (? Gulf of Oman) and Aden requires confirmation. Reports of the species at Cabo Verde Arch. (ROCHEBRUNE, 1882; PILSBRY, 1893c; LELOUP, 1980c), Cape of Good Hope (ROCHEBRUNE, 1882; PILSBRY, 1893c; NIERSTRASZ, 1905a, 1906; ASHBY, 1931), Philippines (ANG, 1967; FISCHER, 1978), Indochina and Hong Kong (FISCHER, 1978), as well as at Rio de Janeiro (Brazil), Ile du Prince (Gulf of Guinea), Poulo Condor (Con Son Is., Vietnam), Moluccas (Indonesia), and Fiji (LELOUP, 1980c) are not credible and must be considered in error. Possibly in error, too, is the report of the species in the Red Sea (NIERSTRASZ, 1905a).

Acanthopleura brevispinosa is confined to the intertidal zone, with specimens often exposed up to 2 m above low tide level.

Remarks: The type material of *Acanthopleura afra* Rochebrune, 1882 (MNHN), is accompanied by a museum label which reads, in part, "rec. Verreaux. XIV 230 Types [on red background] / *Acanthopleura afra* Rchb. 1882 / = *A. borbonica* / Cap de Bonne Espérance . . ." It consists of 2 specimens, dry, curled, estimated length 60 and 50 mm, soft parts removed, showing indications of having been glued to cardboard. Girdle spinelets of smaller specimens mostly fallen off. The specimens agree with ROCHEBRUNE's (1882) description of the species. The larger specimen is here designated lectotype, the smaller, paralectotype (Figure 34). Of the two given localities, Cape of Good Hope is in error, and Madagascar, therefore, must be regarded as type locality.

Chiton nebulosus WOOD, 1828, figured (pl. 1, fig. 4), from "Isle of France," but undescribed, is here considered a *nomen dubium*; on subjective grounds, KAAS & VAN BELLE (1980) suggested the figured specimen might be of *Acanthopleura borbonica* (= *A. brevispinosa*).

Throughout its range, *Acanthopleura brevispinosa* is sympatric with *A. gemmata* from which it must be, therefore, carefully differentiated. Distinctions based on size, color, shape, tegmental sculpture, or girdle elements are potentially deceiving, given the intraspecific variation of the two species. The study of the radula is indispensable, particularly in questionable specimens. The radula of *A. brevispinosa* differs from that of *A. gemmata*, as well as from all other species of *Acanthopleura*, in (1) relatively longer size, (2) much greater number of rows of mature teeth, (3) wide, parallel-sided median teeth, (4) narrow, posteriorly pointed first lateral teeth with sharper outer edge protuberance, (5) relatively smaller head of major lateral teeth, and (6) proportionally shorter outer marginal teeth. Ratio between width (at anterior blade) of median tooth and width of head of major lateral teeth in *A. brevispinosa*, mean = 0.83 (n = 8; SD = 0.11; range 0.73–1.00); in specimens of 12 other species of *Acanthopleura* pooled together, mean = 0.32 (n = 33; SD = 0.08; range 0.21–0.43) ($P < 0.001$).

Acanthopleura araucariana (Hedley, 1898)

Figures 35 to 40, and 115-K

Ischnochiton araucarianus HEDLEY, 1898:100–101, figs. 3–6; NIERSTRASZ, 1905a:21, 1908:145 (in subgen. *Heterozona*); IREDALE & HULL, 1926:261–262 (as syn. of *Squamopleura miles*) (reprinted, 1927:123–124); LELOUP, 1939b:1–6 (as syn. of *S. miles*); KAAS & VAN BELLE, 1980:19 (as syn. of *S. miles*).

Sclerochiton araucarianus: THIELE, 1910a:96.

Type material and locality:

Ischnochiton araucarianus Hedley, 1898: Holotype (AMS C.4344); locality "Isle of Pines, New Caledonia" (22°37'S, 167°30'E).

Material examined:

NEW CALEDONIA: Pines Id., holotype of *Ischnochiton araucarianus* Hedley, 1898 (AMS C.4344); Pines Id., Kuto Beach, 55 specimens, largest 52 mm long (AJF 532).

LOYALTY IS.: Lifou Id., 1 specimen (NMV).

TONGA: Ha'alafu Beach, Tongatapu, 1 specimen, 25 mm long (AJF 767, *leg.* A. J. Ferreira & M. Wolterding, 3 Dec. 1983); Eua Id., intertidal zone up to 0.8 m above mid-tide water level, 16 specimens, largest 27 mm long (AJF coll., *leg.* M. Wolterding, 9 May 1984).

Description: HEDLEY (1898) gave an excellent description of *Ischnochiton araucarianus*: "Shell oval, depressed, valves rounded posteriorly, but the anterior ones more pointed. Colour greenish-grey, each valve shading posteriorly into cream, with a median wedge of black, which is sometimes split with a central white stripe. Interior dull purple, shading posteriorly into brown. Girdle . . . chequered black and cream. Lateral areas elevated with about three obscure, diverging lines of granules, more prominent on the anterior valves. Central areas finely and evenly corded transversely. Anterior valve radiately tuberculated. Posterior valve . . . with subcentral mucro, anterior area concentrically striated, posterior concentrically tuberculated, the mucro is eroded in specimens studied. Anterior and posterior valves with eight slits, median with one; teeth finely pectinated and roughened with minute grains. Scales of girdle radiately furrowed, somewhat apart, large and small intermingled, with a series of very small next the valves and along the margin. Gills extending along five-sixths of the foot. Length 38, breadth 22 mm" (HEDLEY, 1898:100–101).

The holotype (AMS C.4344), is accompanied by a pink museum label that reads, in part, ". . . Loc.: Isle of Pines, New Caledonia / Ref.: Fig'd. P. L. S., NSW, 1898, pt. 1, pg. 100 / Oct. 1897, Coll. C. Hedley." The specimen (Figures 35–38)—preserved dry, soft parts in place, partly disarticulated, valves ii, iii, and iv in place, others loose, plus fragment of girdle—agrees with HEDLEY's (1898) description and illustration of the species.

Among 74 specimens of *Acanthopleura araucariana* here examined, largest 52 mm long. Body width/length, mean

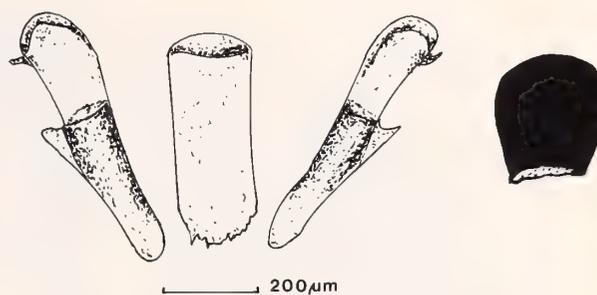


Figure 33

Acanthopleura brevispinosa (Sowerby, 1840a). Same specimen as in Figure 32. Radula median and first lateral teeth, and head of major lateral tooth.

0.60 (SD = 0.05; n = 10). Specimens depressed, round-backed, often markedly eroded. Shell in tones of light grays. Lateral areas of intermediate valves markedly raised, with few, robust, coarse granules, up to 350 μ m in diameter. Anterior valve and postmucro area of posterior valve similarly sculptured. Central areas with appressed, transverse lamellae, featureless otherwise. Mucro somewhat posterior; postmucro convex. Ocelli round to oval, 50–60 μ m in diameter, on anterior $\frac{1}{2}$ of lateral areas, anterior valve, and postmucro area of posterior valve. Gills holobranchial, 40–50 plumes per side.

Articulamentum white with dark brown discolorations at apex of valves. Sutural laminae well developed; sinus well defined. Insertion plates pectinate on outside. On valve viii, sinus relative width, 0.7; pectinations appreciably reduced in middle third, and 2 symmetrical slits at outer thirds; well developed transverse callus. Slit formula 8/9-1-2.

Girdle thick, muscular, light gray, often with few symmetrical black bands. Upper surface covered with coarsely striated scales (Figure 39), quite variable in size, up to 1300 μ m long, lightly imbricated or, more often, separated from each other by "nude" girdle; occasional hyaline spicules, single or bunched, amidst scales. Girdle bridges empty. Undersurface paved with transparent, squarish scales, 40 \times 40 μ m, outer edge convex, inner edge concave, arranged as if articulated in rows.

In specimen 32 mm long (AJF 532: Pines Id., New Caledonia), radula 10 mm in length, comprises 50 rows of mature teeth. Median tooth (Figure 40) 60 μ m wide at anterior blade; first lateral teeth, 120 μ m wide at anterior blade; head of second major lateral teeth, discoid, 200 μ m wide; outer marginal teeth, 200 μ m long, 180 μ m wide (length/width, 1.1).

Distribution: *Acanthopleura araucariana* is known only from Pines Id., adjacent Lifou Id., New Caledonia, and Eua Id. and Tongatapu Id., Tonga (21°10'S, 175°10'W) (Figure 115-K).

It is confined to the upper intertidal zone, having been



observed up to 2 m above water level, often exposed to the sun, immediately above the area occupied by the sympatric *Acanthopleura gemmata* (A. J. Ferreira, field observations at Kuto Beach, Pines Id., New Caledonia, 22–24 July 1980).

Remarks: The irregularity in the size of the girdle scales in *Acanthopleura araucariana* was noted by HEDLEY (1898), NIERSTRASZ (1905a) (who proposed a subgenus, *Heterozona*, on that account), and LELOUP (1939b).

IREDALE & HULL (1926), having examined the type of *Acanthopleura miles* and specimens of *A. araucariana* from New Caledonia, regarded them as conspecific. Yet, differences between *A. araucariana* and *A. miles* are apparent in (1) the lateral areas (markedly elevated in *A. araucariana*; hardly raised in *A. miles*), (2) the granules in lateral areas and end valves (large, elevated, coarse in *A. araucariana*; small, subdued, well defined in *A. miles*), and (3) the girdle scales (irregular in size, up to 1300 μm long, often separated by naked girdle in *A. araucariana*; relatively regular in size, up to 700 μm long, often imbricated in *A. miles*). These differences seem sufficient to justify separation at the species level.

Acanthopleura miles (Carpenter in Pilsbry, 1893)

Figures 41 to 47, and 115-M

Chiton (*Sclerochiton*) *miles* Carpenter in PILSBRY, 1893b: 189, pl. 46, figs. 1–5; SMITH, 1903:619; HEDLEY, 1910: 352.

Sclerochiton miles: ASHBY, 1923d:231, pl. 18, fig. 3.

Squamopleura miles: LELOUP, 1939c:1–6, figs. 1–4, 1940:1–7 (in part).

Chiton (*Squamopleura*) *miles*: SMITH, 1960:66.

Squamopleura imitator NIERSTRASZ, 1905a:102–103, pl. 8, figs. 212–218, 1905b:153–154; HORST & SCHEPMAN, 1908:527; LELOUP, 1933a:19, pl. 1, fig. 4, 1939d:4–8, figs. 3, 4, 10, 11, 20–27.

Sclerochiton imitator: THIELE, 1910:95, pl. 10, figs. 24–28.

Sclerochiton thielei ASHBY, 1923e:233.

Squamopleura carteri IREDALE & HULL, 1926:260, pl. 27, figs. 18, 20, 28 (reprinted, 1927:123, pl. 15, figs. 18, 20, 28).

Squamopleura stratiotes LELOUP, 1939d:9–12, figs. 5–7, 12–15, 28.

Squamopleura salisburyi LELOUP, 1939d:9–12, figs. 8, 9, 16–19, 29.

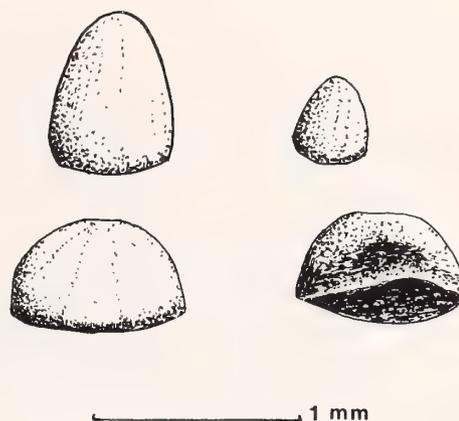


Figure 39

Acanthopleura araucariana (Hedley, 1898). Kuto Beach, Pines Id., New Caledonia (AJF 532); specimen 35 mm long. Girdle scales, outer side and inner side.

“*Sclerochiton curtisianus* (Smith)” ASHBY, 1922a:34 (*vide* ASHBY, 1923d:232); ANG, 1967:412–414, pl. 9, figs. 1–5.

“*Squamopleura curtisiana* (Smith)” LELOUP, 1933a:18–19, pl. 1, figs. 1, 2 (in part: specimen from Mansfield Id., *vide* LELOUP, 1939d:1–2, footnote); WU, 1975:69–70, figs. 1–13.

Type material and type locality:

Chiton (*Sclerochiton*) *miles* Carpenter in Pilsbry, 1893b: Holotype (BMNH 198017); locality “Torres Strait” (Australia).

Squamopleura imitator Nierstrasz, 1905a: Types unascertained, in Zoologischen Museum zu Amsterdam (*vide* NIERSTRASZ, 1905a); locality “Insel Remarksaja [? Sumatra, Indonesia, 4°52'N, 95°22'E] and Java.”

Sclerochiton thielei Ashby, 1923: Types unascertained; locality Sumatra.

Squamopleura carteri Iredale & Hull, 1926: Holotype (WAM 11662); locality Point Cloates, Western Australia (22°43'S, 113°40'E).

Squamopleura stratiotes Leloup, 1939d: Types unascertained; locality Trincomalee, Ceylon (8°34'N, 81°41'E).

Squamopleura salisburyi Leloup, 1939d: Types unascertained; locality Hambantota, Ceylon (6°07'N, 81°07'E).

Explanation of Figures 34 to 38

Figure 34. *Acanthopleura brevispinosa* (Sowerby, 1840a): *Acanthopleura afra* Rochebrune, 1822; paralectotype (MNHN).

Figure 35. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Side view of valves ii, iii, and iv.

Figure 36. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Dorsal view of valves ii, iii, and iv.

Figure 37. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Dorsal view of valves i, v, and viii.

Figure 38. *Acanthopleura araucariana* (Hedley, 1898): *Ischnochiton araucarianus* Hedley, 1898; holotype (AMS C-4344). Ventral view of valves i, v, and viii.

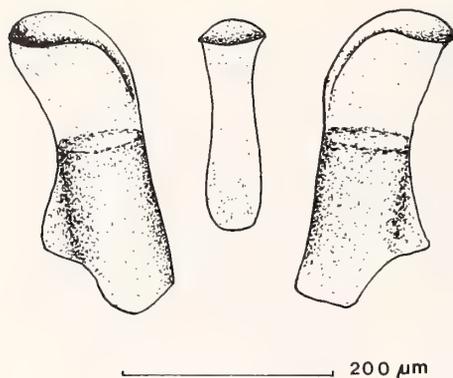


Figure 40

Acanthopleura araucariana (Hedley, 1898). Same specimen as in Figure 39. Radula median and first lateral teeth.

Material examined:

AUSTRALIA, W.A.: Maud's Landing, N of Carnarvon (24°53'S, 113°40'E), 2 specimens, ca. 30 mm long each (NMV); Point Cloates, holotype of *Squamopleura carteri* Iredale & Hull, 1926, ca. 35 mm long (WAM 11662); Dampier Arch., Kendrew Is., 8 specimens, largest 31 mm long (WAM 75-78; WAM 77-78; WAM 1340-78); Broome Bay, 1 specimen (NMV).

NEW GUINEA: Japen Id., Cape Tekopi, 1 specimen, 20 mm long (ANSP 272165).

BORNEO (Sabah, Malaysia): Layang-Layangan, Labuan Id., 19 specimens, largest 36 mm long (AJF 759); Tanjong-Kubong, Labuan Id., 48 specimens, largest 40 mm long (AJF 760).

TAIWAN: Coral reef southeast of Kungting, Pingtung Co., 18 specimens, largest 32 mm long (UCM 28885); Orchid Is., Taitung Hsien, 3 specimens, largest 30 mm long (UCM 28845); Hsiao-liu-chiu Id., Penghu Village, 2 specimens, largest 40 mm long (UCM 28864); Pingtung Hsien, 4 specimens, largest 32 mm long (UCM 28885).

PHILIPPINES: Hundred Islands, Lingayen Gulf, Luzon, 75 specimens, largest 35 mm long (AJF 464; AJF 465); "Auson" Id., off Port Barton, Palawan, 1 specimen, 26 mm long (AJF 820).

JAVA, Indonesia: Udjong Kuton, 1 specimen, 28 mm long (WAM 478-74).

SRI-LANKA (=Ceylon): Trincomalee, 4 specimens, largest 31 mm long (CAS 001203); Dondra Head, 22 specimens, largest 22 mm long (AJF 734); Dondra, 21 specimens, largest 22 mm long (AJF 735); Tangala, 58 specimens, largest 26 mm long (AJF 736; AJF 738); Galle, 22 specimens, largest 21 mm long (AJF 740).

Description: The original description of *Chiton (Sclerochiton) miles* is quite adequate to identify the species: "Shell . . . rugose, oval, depressed . . . dorsal ridge rounded . . . mucro [posterior], nearly flat; apices of the valves prominent, obtuse . . . Central areas transversely pretty regularly rugulose, the wrinkles appressed; lateral areas hardly elevated, moderately well defined, conspicuously rugose, rugae subradiating, granose; the end valves similarly sculptured . . . [slits, 11-1-9/11] . . . Teeth of posterior valves directed forward, strongly callosed inside above the slits, sulcate outside; the rest of the valves having the teeth sulcate outside and pectinated at the margins

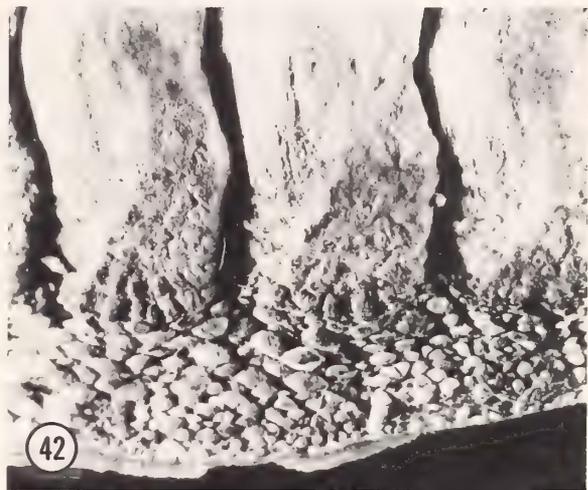
. . . Eaves moderate, solid . . . Sinus deep, wide, wavy, smooth . . . Girdle [with] large, solid, more or less separated scales which are striated outside . . ." (Carpenter in PILSBRY, 1893b:189).

Holotype (BMNH 198017), dry, in excellent condition, flat, 30 mm long, 18 mm wide, 5 mm high, shows evidence of having been glued to cardboard; soft parts removed, posterior valve disarticulated; girdle scales variable in size, up to 600 μ m long, discretely striated. Accompanying label reads, in part, "*Chiton (Sclerochiton) miles* (Carpenter MS) Pilsbry / HOLOTYPE / Torres Straits / H. Cumming coll. No. 42 / 1 specs Acc. no: 1829 . . ." The specimen (Figures 41-44) agrees with Carpenter's (in PILSBRY, 1893b) description and illustrations.

Among 176 specimens of *Acanthopleura miles* here examined, largest 40 mm long (live) (AJF 760: Labuan Id., Borneo). Body width/length, mean 0.63 (SD = 0.05; n = 30). Specimens round-backed, often depressed; valves moderately beaked, posterior edge angled (130-150° on valve ii). Tegmentum brownish-gray usually with dark jugal stripe. Lateral areas variably raised, from flat (in Sri-Lanka specimens) to elevated (in Taiwan specimens), with relatively small, round, well defined granules; diagonal line of lateral areas often defined by row of granules; tegmental surface between granules coarsely microgranular. Central areas featureless except for some 30 transverse, appressed trabeculae, 60-100 μ m thick, often interrupted on pleural areas by 4-6 poorly defined oblique riblets. Similar granules on end valves. Mucro central to slightly posterior; postmucro convex, at 30-45° slope. Widths of tegmental surfaces of valves i/viii, mean 1.2. On valve i, tegmentum length/width, mean ratio 2.1. On valve viii, tegmentum's length/width, mean 1.9. Eaves thick (0.5 mm at midline of valve viii of specimen 30 mm long), relatively solid. Ocelli round to oval, 50-60 μ m in diameter, randomly distributed amidst granules of anterior valve, postmucro area of posterior valve, and anterior $\frac{1}{3}$ to $\frac{2}{5}$ of lateral areas of intermediate valves. Gills with 40-50 plumes per side.

Articulamentum brown to white. Insertion plates strongly pectinate on outside. On valve i, length of insertion plate/length of tegmentum, mean 0.14; insertion teeth irregularly spaced. On valve viii, insertion plate with irregular pectinations becoming smaller to obsolete in middle $\frac{1}{3}$, often with only 2 symmetrical slits (but in some specimens with as many as 5); well defined transverse round callus. Slit formula 5/10-1-1/5. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Sinus well defined; sinusal plate, smooth; relative width of sinus (width of sinus/width of sutural lamina) on valve viii, 0.5.

Girdle thick, muscular, often all black. Upper surface covered with calcareous, opaque, oval, strongly convex scales (Figure 45), more or less separated (evident in live or wet preserved specimens) to somewhat imbricate, variable in size, often up to 600-700 μ m long (largest measured, 1100 μ m long), with 6-15 discrete striations; amidst



Explanation of Figures 41 to 44, and 47

Figure 41. *Acanthopleura miles* (Carpenter in Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter in Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Dorsal aspect of valves i and ii.

Figure 42. *Acanthopleura miles* (Carpenter in Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter in Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Side view of valves iii, iv, and v.

Figure 43. *Acanthopleura miles* (Carpenter in Pilsbry, 1893c):

Chiton (Sclerochiton) miles Carpenter in Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Dorsal aspect of posterior valve.

Figure 44. *Acanthopleura miles* (Carpenter in Pilsbry, 1893c): *Chiton (Sclerochiton) miles* Carpenter in Pilsbry, 1893c; holotype (BMNH 1951.2.1.2). Ventral aspect of posterior valve.

Figure 47. *Acanthopleura miles* (Carpenter in Pilsbry, 1893c): *Squamopleura carteri* Iredale & Hull, 1926; holotype (WAM 11662).

scales, occasional bunches of hyaline spicules, up to $100 \times 30 \mu\text{m}$. Girdle bridges empty. Undersurface covered with transparent, rectangular scales, $50 \times 30 \mu\text{m}$, with slightly convex outer edges, slightly concave inner edges; at outer

margin, fringe of translucent spicules, up to $150 \times 40 \mu\text{m}$, vaguely striated longitudinally.

In a specimen 25 mm long (AJF 464: Lingayen Gulf, Philippines), radula measures 10 mm in length (40% of

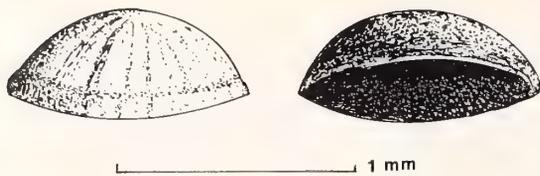


Figure 45

Acanthopleura miles (Carpenter in Pilsbry, 1893c). Hundred Islands, Lingayen Gulf, Philippines (AJF 464); specimen 25 mm long. Girdle scales, outer side and inner side.

specimen length), comprising 40 rows of mature teeth; median tooth, 40 μm wide at anterior blade, bulging posteriorly to 60 μm wide (Figure 46); lateral teeth 75 μm wide at anterior blade, with outer edge deeply concave, outer-posterior corner protruding almost to a knob; major lateral teeth with discoid head, 160 μm in width; outer marginal teeth 140 μm long, 100 μm wide (length/width, 1.4).

Distribution: Widely distributed in the central Indo-Pacific (Figure 115-M), from 25°S to 27°N, and from 73°E to 142°E, *Acanthopleura miles* has been recorded, albeit by synonymous names, at Atu Atoll, Maldives Is. (SMITH, 1903), Ceylon (LELOUP, 1939c, as *Squamopleura stratiotes* and *S. salisburyi*), Andaman Is. and Nicobar Is. (LELOUP, 1939c), Raja Id., Java, and Timor (NIERSTRASZ, 1905a, b; THIELE, 1909), Sumatra (THIELE, 1909; ASHBY, 1923d, as *S. thielei* Ashby, 1923d), Bali (LELOUP, 1933a, as *S. imitator*), Philippines (ANG, 1967, as *S. curtisiana*), Lanshu Id., Taiwan (WU, 1975, as *S. curtisiana*), Mansfield Id. (LELOUP, 1933a, as *S. curtisiana*), Torres Strait, Australia (Carpenter in PILSBRY, 1893b, type locality), Carnarvon, W. Australia (ASHBY, 1923d), Point Cloates, W. Australia (IREDALE & HULL, 1926, as *S. carteri*). The species is here recognized also at Taiwan, Philippines (Lingayen Gulf), Borneo, and New Guinea (AJF coll.).

Acanthopleura miles is confined to the intertidal zone, 0–0.5 m, often on rocks exposed at low tide.

Remarks: The identity of *Acanthopleura miles* has been much confused in the literature. IREDALE (1914b:125), noting that “Nothing like . . . *miles* has yet been seen from Torres Straits,” assumed the locality in error, a gratuitous assumption later echoed by ASHBY (1923) and IREDALE & HULL (1926). LELOUP (1939c) introduced *Squamopleura stratiotes* and *S. salisburyi*, from Ceylon, which he immediately (in the same paper!) synonymized as geographic forms of a single species, later (LELOUP, 1940) regarded simply as a variety (“*forma*”) of *S. miles*.

As observed here, *Acanthopleura miles* differs from *A. araucariana* in (1) lateral areas (very elevated in *A. araucariana*; hardly raised in *A. miles*), (2) tegmental granules (coarse, large in *A. araucariana*; well defined, small in *A. miles*), and (3) girdle scales (larger and separated in *A. araucariana*; smaller and often imbricated in *A. miles*).

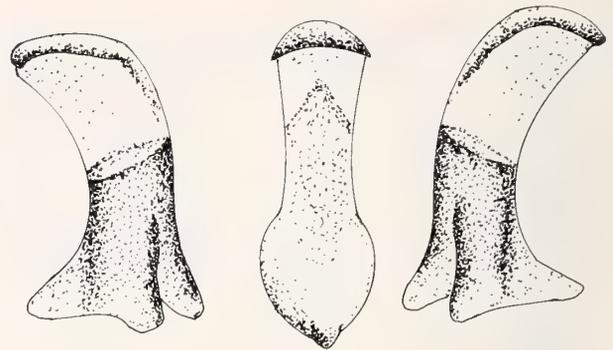


Figure 46

Acanthopleura miles (Carpenter in Pilsbry, 1893c); same specimen as in Figure 45. Radula median and first lateral teeth.

In the field, *Acanthopleura miles* was observed sharing the intertidal zone with *A. gemmata*, and *A. spinosa* (AJF 464, AJF 465, Lingayen Gulf, Philippines).

Acanthopleura curtisiana (Smith, 1884)

Figures 48 to 54, and 115-T

Chiton (Ischnochiton) curtisianus SMITH, 1884:78, pl. 6, fig. D. *Ischnochiton curtisianus*: PILSBRY, 1892b:97, pl. 24, fig. 6.

Liolophura curtisiana: PILSBRY, 1893c:242; HEDLEY & HULL, 1909:265.

Sclerochiton curtisianus: THIELE, 1910:96, pl. 10, figs. 29–35; IREDALE, 1910a:103–104, 1914b:125; ASHBY, 1922a:34.

Squamopleura curtisiana: HULL, 1923:160, 1925:114; IREDALE & HULL, 1926:259–260, pl. 37, figs. 5, 26–27 (reprinted, 1927:122–123, pl. 15, figs. 5, 26–27); MACKAY, 1930:292–295; LELOUP, 1933b:17–19, pl. 1, fig. 3 (in part: specimens from Aru Id.), 1939d:1–4, figs. 1–2.

[Non: LELOUP, 1933a:17–19, pl. 1, figs. 1–2; ANG, 1967:412–414; WU, 1975:69–70, figs. 1–13.]

Enoplochiton torri BASTOW & GATLIFF, 1907:27–30, pls. 3–4, figs. 1–12.

Sclerochiton aruensis THIELE, 1910:96, pl. 10, figs. 36–41.

Type material and locality:

Chiton (Ischnochiton) curtisianus Smith, 1884: Holotype (BMNH 1881.11.10.32); locality Port Curtis, Queensland, Australia (24°00'S, 151°30'E).

Enoplochiton torri Bastow & Gatliff, 1907: Types unascertained; locality Queensland, Australia.

Sclerochiton aruensis Thiele, 1910: Types unascertained; locality Aru Is., Indonesia (6°00'S, 134°30'E).

Material examined:

AUSTRALIA, Qld.: Utinga, Cape York, 15 specimens, largest 23 mm long (NMV); Port Curtis, holotype of *Chiton (Ischnochiton) curtisianus* Smith, 1884 (BMNH 1881.11.10.32); Port Curtis, 9 specimens, largest 23 mm long (NMV); Cid Id., W of

Whitsunday Id., 1 specimen, 18 mm long (CAS 044790); Shelly Beach, near Townsville, 10 specimens, largest 25 mm long (NMV); Gill's Beach, Hinchinbrook Id., 5 specimens (*ex* J. R. Penprase coll.); Broad Sound, 17 specimens, largest 18 mm long (NMV); Moreton Bay, 8 specimens, largest 24 mm long (NMV). AUSTRALIA, N.T.: Port Darwin, 2 specimens (CASG-SU 3389).

AUSTRALIA, W.A.: Point Cloates, 4 specimens, largest 40 mm long (cited by ASHBY, 1922a) (WAM 9336); Bay of Rest, Exmouth Gulf, 3 specimens, largest 25 mm long (WAM 1746-78); Dampier Arch., 2 specimens, largest 16 mm long (WAM 82-78; WAM 1079-75; Barrow Id., 1 specimen, 19 mm long (WAM 605-67); Cape Preston, 1 specimen, 17 mm long (WAM 1113-78); Broome, 1 specimen, 19 mm long (NMV).

Description: SMITH (1884) described *Chiton (Ischnochiton) curtisianus*, based on a specimen 16 × 9 mm (excluding girdle), as "Shell . . . dark greyish . . . [with] black broadish line from end to end down the middle of the back . . . with strong, concentric lines of growth . . . [Girdle] alternately light and dark . . . Valves arched, not carinate . . . very indistinct lateral areas . . . mucro probably near the centre . . . [Articulamentum] greenish blue, stained dark brown in the middle . . . [slits 10-1-0] . . . [Anterior valve insertion teeth] different-sized . . . striated on both sides but more strongly externally, their edges being sharp, but not smooth . . . [Posterior valve] much thickened within along the posterior edge, which is roughened by fine cross striae, there being no prominent teeth, and of course no notches . . . [Girdle] covered with small sub-imbriating oval [scales] . . . The granules of the surface have an irregular disposition, following to some extent the lines of growth" (SMITH, 1884:78-79).

The holotype (BMNH 1881.11.10.32) consists of 8 disarticulated valves; no girdle, no radula. Reassembled, the valves add up to 18 mm, indicating a live specimen (with girdle) about 20 mm long (larger than, but compatible with length given by SMITH [1884]). Museum pink label reads, in part, ". . . Holotype / *Chiton (Ischnochiton) curtisianus* Smith, 1884 . . . / Loc. Port Curtis . . . / leg. Coppinger / Pres. The Admiralty." The specimen (Figures 48, 49) agrees with SMITH's (1884: pl. fig. D) description and illustration: light brown, with darker jugal band flanked by lighter bands. Valves considerably eroded, round-backed; beak distinct on valve ii, indistinct on others; posterior edge angulate at 130° on valve ii, less so on valve iii, almost straight on valves iv-vii. Tegmentum on valve i sculptured with concentric rows of round to oval granules, 100-150 μm in diameter, often coalesced into minute ridges. Lateral areas of intermediate valves slightly raised, poorly defined otherwise; sculpture with similar granules. Central areas with similar granules, more noticeable in pleural areas (particularly on valve ii) where they align into longitudinal rows; jugal areas with similar granules, though less well defined, and few coarse, transverse growth rugae. Posterior valve somewhat flattened, much eroded; mucro central (?). Width of valve i/width of valve viii, 1.15. Ocelli round to oval, 70-90 μm in

diameter, throughout anterior valve, lateral areas of intermediate valves, and postmucro area of posterior valve.

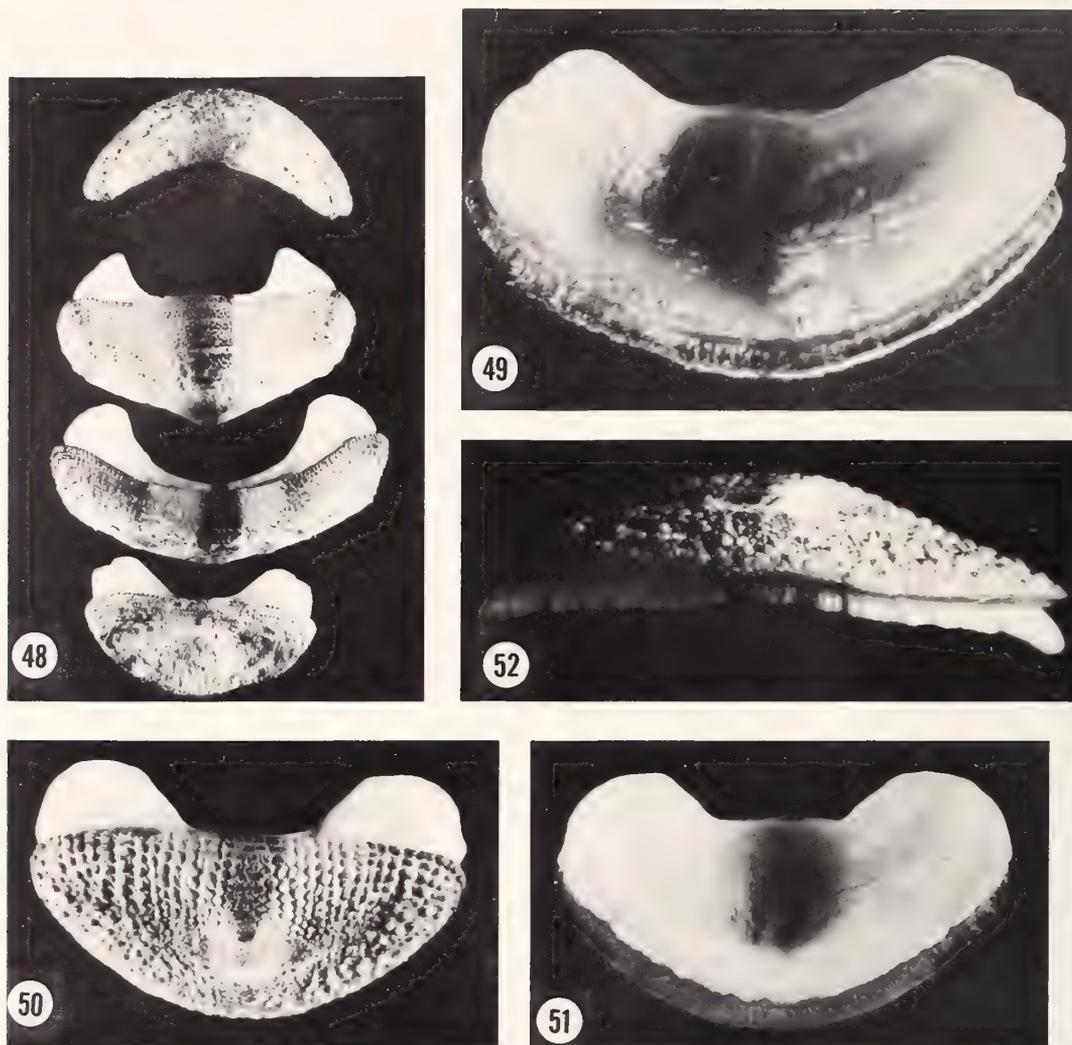
Articulamentum white with intense, large, brown discoloration in the middle. Sutural laminae, subtriangular on all intermediate valves, more so on ii; sinus very wide in all valves; on valve viii, width of sinus/width of sutural laminae, 0.9. Insertion plates pectinate on outside. On valve i, 10 slits, teeth 0.4 mm long. Intermediate valves uni-slit. On valve viii, insertion teeth almost obsolete, reduced to small pectinations on posterior aspect of round, transverse callus; only 2 (? 3) vestigial slits. Eaves relatively compact, 0.3 mm wide.

Among 78 specimens examined, largest 40 mm long (dry) (WAM 9336: Pt. Cloates, Australia). Body width/length, mean 0.66 (n = 20). Tegmentum grayish-green to grayish-brown, often with wide dark brown band at jugum. Lateral areas poorly defined, hardly elevated, with round to elongate granules, 100-200 μm in diameter, often in concentric rows. Central areas with smaller granules, 80-150 μm in diameter in pleural areas, often aligned in 10-15 longitudinal rows, much less apparent at jugum. Intermediate valves clearly beaked on valve ii, less so posteriorly; posterior edge of valve ii forming 130-140° angle. Mucro central; postmucro moderately convex (Figure 50). Ocelli round to oval, 60-80 μm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, and anterior 1/3 to 1/2 of lateral areas of intermediate valves. Widths of tegmental surfaces of valves i/viii, mean 1.08. On valve i, tegmentum length/width, mean 0.48. On valve viii, tegmentum length/width, mean 0.48. Eaves thick (0.4 mm in midline of valve viii), relatively solid. Gills 25-30 plumes per side.

Articulamentum white with diffuse light brown discolorations in middle. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Sinus wide. Insertion plates pectinate on outside. On valve i, length of insertion plate/length of tegmentum, mean 0.13. On valve viii (Figures 51, 52), insertion plate markedly underdeveloped to obsolete, often reduced to weak pectinations on posterior aspect of thick, smooth, transverse callus; 2 slits symmetrically placed at outer fourth of plate, weakly defined to obsolete. Slit formula 8/10-1-0/2.

Girdle thick, muscular, wide, often banded. Upper surface with oval, vaguely striated, opaque, calcareous scales (Figure 53), up to 300-400 μm in length in middle of girdle, progressively smaller to minute at margins; in living and alcohol preserved specimens, girdle scales are clearly separated from each other by about half of their width; occasional bunches of small, translucent spicules, up to 70 × 15 μm, amidst the scales. Girdle bridges empty. Undersurface covered with transparent, rectangular scales, 40 × 20 μm, with coarse striations.

In a specimen 17 mm long (NMV: Utinga, Cape York, Australia), radula 6 mm in length (35% of specimen length), comprising 35 rows of mature teeth. Median tooth (Figure 54), 35 μm wide at anterior blade, parallel-sided,



Explanation of Figures 48 to 52

Figure 48. *Acanthopleura curtisiana* (Smith, 1884): *Chiton curtisianus* Smith, 1884; holotype (BMNH 1881.11.10.32). Dorsal aspect of valves i, ii, v (?), and viii.

Figure 49. *Acanthopleura curtisiana* (Smith, 1884): *Chiton curtisianus* Smith, 1884; holotype (BMNH 1881.11.10.32). Ventral side of posterior valve.

Figure 50. *Acanthopleura curtisiana* (Smith, 1884). Cape York,

N.T., Australia (NMV); specimen 17 mm long. Dorsal aspect of posterior valve.

Figure 51. *Acanthopleura curtisiana* (Smith, 1884). Same specimen as in Figure 50. Ventral aspect of posterior valve.

Figure 52. *Acanthopleura curtisiana* (Smith, 1884). Same specimen as in Figure 50. Posterior aspect of posterior valve.

globose posteriorly; first lateral teeth 65 μm wide at well developed anterior blade; second lateral teeth with discoid head 130 μm in diameter; outer marginal teeth, 130 μm long, 80 μm wide (length/width, 1.6).

Distribution: *Acanthopleura curtisiana* is confined to tropical northern Australian waters (Figure 115-T). It has been recorded in Queensland at Port Curtis (SMITH, 1884; IREDALE, 1910a; HULL, 1923), Gladstone (HEDLEY & HULL, 1909), Keppel Bay, Broad Sound, Magnetic Id.

(MACKAY, 1930), Cape York (LELOUP, 1939c), Thursday Id. (IREDALE, 1910a), and (herein) at Moreton Bay (27°20'S), its southernmost record; in the Northern Territory, at Port Darwin (ASHBY, 1922a; and herein); in Western Australia at Point Torment, and Point Cloates (22°43'S), its southernmost record on the western coast. Reports of the species at Aru Is., Indonesia (6°S) (THIELE, 1909; LELOUP, 1933a), may constitute northernmost records. LELOUP's (1933a) report of the species at Mansfield Id. was later retracted (LELOUP, 1939d). Reports of *A.*

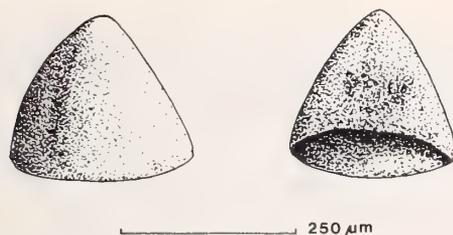


Figure 53

Acanthopleura curtisiana (Smith, 1884). Exmouth Gulf, W.A., Australia (WAM 1746-78); specimen 23 mm long. Girdle scales, outer and inner sides.

curtisiana in the Philippines (ANG, 1967) and Taiwan (WU, 1975) are presumed in error for *A. miles*.

Bathymetric range 0-1 m, on rocks often exposed at low tide.

Remarks: *Acanthopleura curtisiana* has often been confused with *A. miles*. The two species, hitherto assigned to *Squamopleura*, are identical in size, shape, color, and habitat, but they differ in (1) size of girdle scales (up to 400 μm long in *A. curtisiana*; up to 800 μm long in *A. miles*), (2) central areas (with longitudinal rows of granules on pleural areas in *A. curtisiana*; without granules, featureless except for fine, appressed, transversal lamellae at jugal areas in *A. miles*), (3) radula (median tooth parallel-sided in *A. curtisiana*; bulging posteriorly in *A. miles*).

THIELE's (1910) illustration of the median tooth of the radula of *Acanthopleura curtisiana* shows a two-pointed posterior end, instead of a globose end as here illustrated (Figure 54); the discrepancy may reflect intraspecific variation or the difficulties in properly visualizing radular teeth under ordinary microscopy.

Acanthopleura loochooana (Broderip & Sowerby, 1829)

Figures 55 to 61, and 114-L

Chiton loochooanus BRODERIP & SOWERBY, 1829:368.

Liolophura loochooana: PILSBRY, 1893c:244; (?) IS. TAKI, 1938: 411, 1962:46 (with *Liolophura gaimardi platispinosa* Leloup, 1939a, as syn.); KAAS & VAN BELLE, 1980:76.

Type material and locality:

Chiton loochooanus Broderip & Sowerby, 1829: Neotype (CAS 044306) here designated; locality "shore of Loo Choo Is." (=Ryukyu Islands, Japan), here restricted to Buckner Bay, Okinawa, Japan (26°17'51.5"N, 127°54'26"E), intertidal zone.

Other material examined:

OKINAWA, Japan: Buckner Bay, at rocky intertidal zone, neotype lot, 14 specimens, largest 26 mm, smallest 8 mm long, *leg.* E. V. Iverson, 23 Apr. 1975 (CAS 001627); Nagahama, 2 specimens, largest 25 mm long (CAS 019919; CAS 040204); Okuma, 1 specimen, ca. 50 mm long (S. Crittenden coll.).

TAIWAN: Penghu Is., south of Chienshan Village, Penghu Co.,

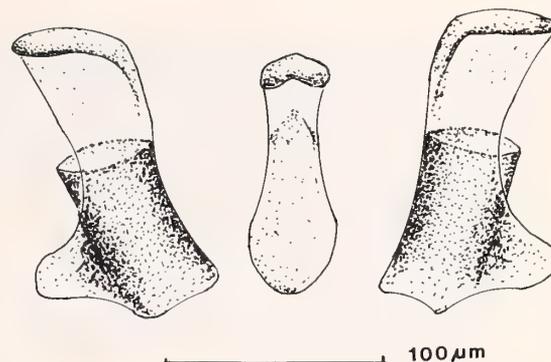


Figure 54

Acanthopleura curtisiana (Smith, 1884). Same specimen as in Figure 53. Radula median and first lateral teeth.

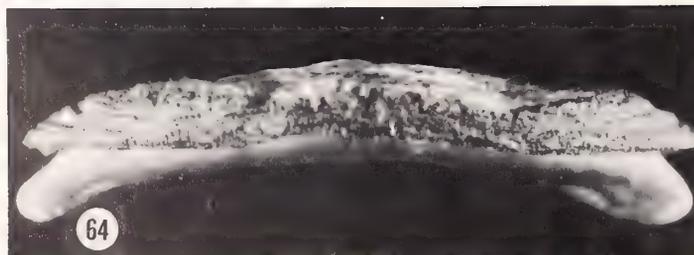
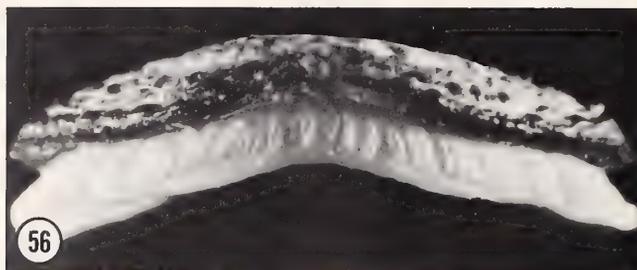
4 specimens, largest 28 mm long (UCM 28893); Keelung, 18 specimens, largest 26 mm long, *leg.* F. B. Steiner, Oct. 1963 & Sept. 1968 (CAS 009880; CAS 016698).

HONG KONG: Repulse Bay, Hong Kong Id., 2 specimens, largest 18 mm long (AJF 686); Cheung-Sha, Lantau Id., 7 specimens, largest 34 mm long (AJF 685).

Description: *Chiton loochooanus* was described as "*Ch. valvis subscabrosis, areis marginalibus radiatim granosis, margin coriaceo superne granoso, granielevatis; long. 15/20, lat. 3/10 poll. Hab. in mari Sinensi, ad littora Insulae Loo-Choo. A very pretty little Chiton, whose margin is covered with small grains resembling very short, blunt spines*" (BRODERIP & SOWERBY, 1829:368).

Among 48 specimens here referred to *Acanthopleura loochooana*, largest 50 mm long (in alcohol) (S. Crittenden coll.: Okuma, Okinawa). Body width/length, mean 0.65. Round-backed; intermediate valves beaked; posterior edge of valve ii forming 140-160° angle. Tegmentum grayish-white to brown, often with dark gray jugal stripe. Lateral areas elevated, well defined, crowded with low, round granules which tend to align radially and coalesce; anterior valve and postmucro area of posterior valve similarly sculptured. Central areas with ill-defined sculpture of appressed transverse lamellae, often broken into irregular granules or rugosities which, on pleural areas, tend to form forward-converging riblets. Mucro central (in small specimens) to posterior (in larger ones); postmucro slightly to markedly convex, slope varying with size of specimen (Figure 55). Ocelli round to oval, 60-70 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior half of lateral areas. On valve i, tegmentum length/width, mean 0.48. On valve viii, tegmentum length/width, mean 0.42. Widths of tegmental surfaces of valves i/viii, mean 1.2. Gills with 35-40 plumes per side.

Articulamentum brown with white discoloration at sutural laminae and insertion plates. Sutural laminae well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate



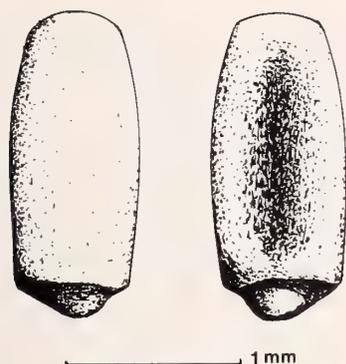


Figure 58

Acanthopleura lochooana (Broderip & Sowerby, 1829). Keelung, Taiwan (CAS 009880); specimen 29 mm long. Girdle scales, outer and inner sides.

smooth; relative width of sinus on valve viii, 0.8. Insertion plates pectinate on outside. On valve i, insertion teeth irregularly spaced; in midline, length of insertion teeth/length of tegmentum, mean 0.13. On valve viii, pectinations and teeth underdeveloped to obsolete in middle third, hardly extending beyond transverse round callus in outer third; slits of posterior valve not always clearly determinable (Figures 56, 57). Slit formula 8/10-1-2/7. Eaves relatively thick (0.4 mm on midline of valve viii in specimen 20 mm long), moderately spongy.

Girdle banded black and white, thick, muscular. Upper surface girdle elements (Figure 58) irregular in size and shape; most elements spinelet-like, up to 2000 μm long, 600 μm wide, relatively flattened in cross section; other elements scale-like, *i.e.*, much smaller in all dimensions, particularly in height, vaguely striated on outer face; in living or wet preserved specimens, girdle elements often separated by "nude" girdle, with occasional hyaline, needle-like elements, single or bunched, up to 120 \times 20 μm . Girdle bridges empty. Undersurface paved with transparent, subrectangular scales, about 40 \times 30 μm , becoming elongate to 70 \times 30 μm at periphery, with some

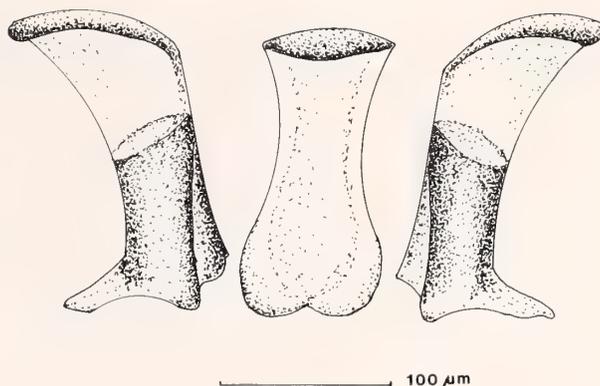


Figure 59

Acanthopleura lochooana (Broderip & Sowerby, 1829). Same specimen as in Figure 60. Radula median and first lateral teeth.

coarse striations, convex outer edge, concave inner edge. Marginal fringe of 1 or 2 rows of translucent spicules, up to 300 \times 50 μm , finely striate.

In specimen 29 mm long (CAS 009880: Taiwan), radula measures 12.8 mm in length (44% of specimen length), comprising 55 rows of mature teeth. Median tooth (Figure 59) 80 μm wide at anterior blade; first lateral teeth 110 μm wide at anterior blade; head of second lateral teeth discoid, 210 μm wide; outer marginal teeth 200 μm long, 150 μm wide (length/width, 1.4).

Distribution: The geographic range of *Acanthopleura lochooana* extends from Okinawa (26°31'N, 127°59'E) to Taiwan and Hong Kong (22°15'N, 114°10'E) (Figure 114-L). Listings of the species at Shizuoka, Japan (Is. TAKI, 1938, 1962) cannot be taken at face value.

Acanthopleura lochooana seems to be confined to the intertidal zone, on top of rocks in moderate surf areas.

Remarks: *Chiton lochooanus*, left unfigured, was considered by PILSBRY (1893c:244) as "absolutely unrecognizable . . . but . . . perhaps a member of the genus *Liolophura*." The original type material could not be found

Explanation of Figures 55 to 57, and 60 to 65

Figure 55. *Acanthopleura lochooana* (Broderip & Sowerby, 1829). Specimen from the neotype-lot (CAS 001627). Dorsal aspect of posterior valve.

Figure 56. *Acanthopleura lochooana* (Broderip & Sowerby, 1829). Same specimen as in Figure 55. Posterior aspect of posterior valve.

Figure 57. *Acanthopleura lochooana* (Broderip & Sowerby, 1829). Same specimen as in Figure 55. Ventral aspect of posterior valve.

Figure 60. *Acanthopleura lochooana* (Broderip & Sowerby, 1829); neotype (CAS 044306).

Figure 61. *Acanthopleura lochooana* (Broderip & Sowerby, 1829); neotype (CAS 044306). Close-up of girdle.

Figure 62. *Acanthopleura gaimardi* (Blainville, 1825). Magnetic Id., Qld., Australia (AJF 602); specimen 15 mm long.

Figure 63. *Acanthopleura gaimardi* (Blainville, 1825). Magnetic Id., Qld., Australia (AJF 602); specimen 30 mm long. Dorsal aspect of posterior valve.

Figure 64. *Acanthopleura gaimardi* (Blainville, 1825). Same specimen as in Figure 63. Posterior aspect of posterior valve.

Figure 65. *Acanthopleura gaimardi* (Blainville, 1825). Same specimen as in Figure 63. Ventral aspect of posterior valve.

(Solene Morris, BMNH, *in litt.*, 7 July 1983) and is presumed lost. The finding of specimens from the type locality (Okinawa) compatible with BRODERIP & SOWERBY's (1829) meager description of the species suggests the identification, albeit on subjective grounds. To obviate future uncertainties, a neotype (CAS 044306), 25 × 15 × 7 mm (including girdle) (Figures 60, 61), is here designated from neotype lot of 15 specimens preserved in alcohol (CAS 001627).

In the underdeveloped insertion teeth and pectinations of the posterior valve, *Acanthopleura loochooana* is similar to *A. brevispinosa*, *A. miles*, *A. araucariana*, *A. curtisiana*, and *A. arenosa*. The differences lie almost exclusively in the girdle elements: in *A. miles*, *A. araucariana*, and *A. curtisiana*, the girdle elements are clearly scales; in *A. brevispinosa*, they are thin and cylindrical spicules; and in *A. arenosa*, they are pointed spicules, almost conical, circular in cross section, and larger at base.

In its relatively limited range, *Acanthopleura loochooana* is sympatric with *A. japonica*, *A. miles*, and *A. gemmata*. Specimens of *A. loochooana* have been found exposed at low tide, up to 30 cm above water level, sharing habitat with specimens of *A. japonica* (A. J. Ferreira, field observations at Lantau Id. and Repulse Bay, Hong Kong, Sept. 1982).

Acanthopleura loochooana is present in a relatively narrow area in the zone of contact between *A. japonica* and *A. gemmata*. In this respect, *A. loochooana* seems to be related to *A. japonica* and *A. gemmata* in the vicinity of the Tropic of Cancer, as *A. arenosa* is to *A. gemmata* and *A. gaimardi* in the vicinity of the Tropic of Capricorn.

Acanthopleura gaimardi (Blainville, 1825)

Figures 62 to 67, and 114-D

Chiton gaimardi BLAINVILLE, 1825:546.

Liolophura gaimardi: PILSBRY, 1893c:240–241, pl. 53, figs. 30–35; NIERSTRASZ, 1905b:155 (in part: Sydney specimens only); HORST & SCHEPMAN, 1908:528 (in part: Sydney specimens only); ASHBY, 1918c:87, 1922c:581; HULL, 1923b:198, pl. 28, figs. 1–4; ASHBY, 1926b:384; IREDALE & HULL, 1926:262, pl. 37, figs. 13–16, 19, 31 (reprinted, 1927:125, pl. 15, figs. 13–16, 19, 31); BERGENHAYN, 1930a:32, pl. 8, figs. 76–77; ALLAN, 1959:238, fig. 6a; LELOUP, 1961b:42–44, text figs. 3, 5b, pl. 3, fig. 2; WU, 1969:109, figs. 5a, 5b, 47–58.

[Non: NIERSTRASZ, 1905a:108, 1905b:154–155, figs. 20–21; HORST & SCHEPMAN, 1908:528 (in part); LELOUP, 1939a:3–7, fig. 5A.]

Liolophura gaimardi queenslandica PILSBRY, 1894f:87–88; ASHBY, 1918c:87; DAVIS *et al.*, 1979:2, 18.

[Non: LELOUP, 1961b:67, fig. 5-B3].

Liolophura queenslandica: HULL, 1923b:199, pl. 28, figs. 5–8, 1925:115; IREDALE & HULL, 1926:263, pl. 37, figs. 23–25, 30, 32 (reprinted, 1927:126, pl. 15, figs. 23–25, 30, 32); ALLAN, 1959:239.

Chiton incanus GOULD, 1846:145 (reprinted, 1862:6), 1861 (Atlas):315, pl. 28, figs. 432, 432a.

Maugeria incana: GOULD, 1862:248.

Chiton (Acanthopleura) incanus: SMITH, 1884:81–82.

Acanthopleura incana: HADDON, 1886:25–30.

Liolophura incana: PILSBRY, 1893a:105.

“*Chiton piceus* Gmelin” ANGAS, 1867:223.

Type material and type locality:

Chiton gaimardi Blainville, 1825: Possible types at MNHN (*vide* ASHBY, 1922c:581), not examined; locality Port Jackson, New South Wales, Australia (33°50'S, 151°16'E).

Liolophura gaimardi queenslandica Pilsbry, 1894f: Lectotype (ANSP 64853) and paralectotype (ANSP 355874) herein designated; locality Bundaberg, Queensland, Australia (24°52'S, 152°21'E).

Chiton incanus Gould, 1846: Holotype (USNM 5823) and paratypes (MCZ 169189); locality “New South Wales,” Australia.

Material examined:

AUSTRALIA, Qld. Townsville, 11 specimens, largest 42 mm long (AJF 600); Radical Bay, Magnetic Id., 14 specimens, largest 30 mm long (AJF 602); Yeppoon, 33 specimens, largest 59 mm long (AJF 356; AMS C135480); Stradbroke Id., 9 specimens, largest 36 mm long (AMS C135478; AMS C13008); Port Curtis, Bagara Beach, 1 specimen (AMS C109294); Bundaberg, 13 specimens, largest 45 mm long (AJF coll., *leg.* Gail Chapman); Pt. Cartwright, 1 specimen, 28 mm long (NMV, *ex* Basset Hull coll.); Caloundra, 8 specimens, largest 61 mm long (NMV); Peel Is., Moreton Bay, 1 specimen, 38 mm long (AMS C109296). AUSTRALIA, N.S.W.: Holotype of *Chiton incanus* Gould, 1846 (USNM 5823); Flat Rock, north of Richmond River, 2 specimens, largest 50 mm long (AMS C50821); Byron Bay, 2 specimens, largest 50 mm long (CAS 012387); Sydney, 3 specimens, largest 32 mm long (WAM 1592-78; WAM 1590-78; CASG-SU 2868); Port Jackson, 11 specimens (WAM 1591-78; AMS C135482); Gunnamatta Bay, Port Hacking, 2 specimens, largest 35 mm long (AMS C135479).

Description: BLAINVILLE's (1825) description of *Chiton gaimardi* based on 3 specimens, “un pouce à quinze lignes” (27–34 mm) in length, collected by Quoy and Gaimard at Port Jackson, Australia, stresses the fact that insertion teeth are absent on the posterior valve but present and pectinate on the anterior valve. The species was further described and illustrated by PILSBRY (1893c), HULL (1923b), and IREDALE & HULL (1926), always with significance given to the callused, slitless and toothless posterior valve.

Among 112 specimens of *Acanthopleura gaimardi* here examined, largest 61 mm long (in alcohol) (NMV: Caloundra, Qld., Australia). Specimens (Figures 62–65) depressed, round-backed. Body width/length, mean 0.60. Intermediate valves beaked; posterior edge of valve ii forming 110–140° angle. Tegmentum grayish-green to grayish-brown often with wide black band at jugum. Lateral areas poorly defined, hardly raised, sculptured with inconspicuous, low-profile granules in vaguely defined radial rows, or coalesced into obsolete concentric ridges; anterior valve similarly sculptured. Central areas almost featureless except for transversely appressed lamellae, about 50 μm thick. Posterior valve rather flat, almost triangular

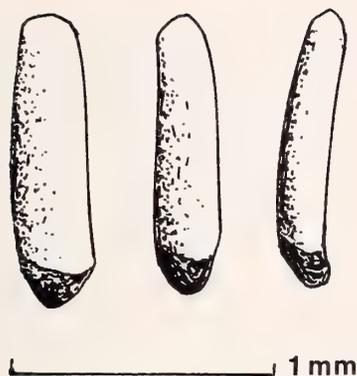


Figure 66

Acanthopleura gaimardi (Blainville, 1825). Yeppoon, Qld., Australia (AJF 356); specimen 45 mm long. Girdle spines.

in some specimens; mucro inconspicuous, decidedly posterior to terminal. Ocelli round to oval, 60–70 μm in diameter, randomly distributed throughout anterior valve, postmucro area of posterior valve, anterior $\frac{1}{2}$ to $\frac{2}{3}$ of lateral areas of intermediate valves, and (in about 50% of specimens examined) pleural areas. On valve i, tegmentum length/width, mean 0.5. On valve viii, tegmentum length/width, mean 0.4. Widths of tegmental surface of valves i/viii, mean 1.1. Gills with 35–50 plumes per side.

Articulamentum dark brown, often lighter on sutural laminae. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate mostly smooth. Insertion plates of anterior and intermediate valves, strongly pectinate on outside. On valve i, insertion teeth irregularly spaced, sometimes fused together; in midline, length of insertion plate/length of tegmentum, mean 0.14. Valve viii without insertion teeth; posterior aspect of transverse callus flat, crescentic, smooth, without slits or pectinations. Slit formula 8/12-1-0. Eaves thick, projecting conspicuously beyond articulamentum of posterior valve.

Girdle, thick, muscular, wide, often banded black-brown and white. Upper surface crowded with white to dark brown spinelets (Figure 66), often tipped with white, pointed to blunt, close together, straight to curved, somewhat conical, variable in size, from short and scale-like to 1.5 mm long, with vague to obsolete longitudinal striations; in fresh or wet-preserved material, spinelets often seen standing apart from each other, separated by "nude" girdle; amidst spinelets, in the "nude" girdle, needle-like elements may be found, single or clumped, pointed, hyaline, up to $120 \times 25 \mu\text{m}$. Girdle bridges empty. Under-surface paved with transparent, squarish to rectangular scales, about $60 \times 40 \mu\text{m}$, vaguely striate.

Radulae averaging 45% of specimen length, with 50 rows of mature teeth. In specimen 40 mm long (AJF 356: Yeppoon, Australia), median tooth (Figure 67) 50 μm wide at anterior blade; first lateral teeth 80 μm at anterior blade; head of second lateral teeth discoid, 230 μm wide;

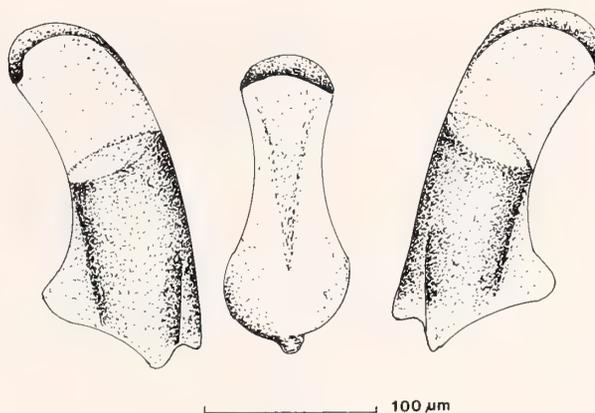


Figure 67

Acanthopleura gaimardi (Blainville, 1825). Same specimen as in Figure 66. Radula median and first lateral teeth.

outer marginal teeth, 220 μm long, 110 μm wide (length/width, 2.0).

Distribution: *Acanthopleura gaimardi* is confined to the eastern coast of Australia between Magnetic Id. (19°08'S) (AJF 602), the northernmost verified record, and Sydney (33°52'S) (IREDALE & HULL, 1926; Ferreira, herein), the southernmost verified record (Figure 114-D). The presence of the species southward to Port Hacking (34°05'S) (HULL, 1923b) is credible but requires corroboration. Reports of the species in the Moluccas Is. (NIERSTRASZ, 1905b; HORST & SCHEPMAN, 1908), Japan (LELOUP, 1939a), and Taiwan (WU, 1969) are in error.

Bathymetric range, confined to the intertidal zone, often exposed at low tide.

Remarks: *Acanthopleura quatrefagesi* ROCHEBRUNE, 1881a: 42 (misspelled as *quatrefagei* in ROCHEBRUNE, 1881b:117), from Table Bay, South Africa, was regarded by ASHBY (1931a) as a synonym of *A. brevispinosa* and by THIELE (1910), LELOUP (1961b), and KAAS & VAN BELLE (1980) as a synonym of *A. gaimardi*. LELOUP (1939a, fig. 5-B) figured a valve of a supposed "co-type." But type material has not been found at MNHN (A. Tillier, *in litt.* 15 April 1980) and may be presumed lost. Because ROCHEBRUNE's (1881a, b) accounts are totally inadequate, the species is here regarded as a *nomen dubium*.

Chiton incanus Gould, 1846, has been regarded as a synonym of *C. gaimardi* since PILSBRY (1893a). The holotype (USNM 5823) is accompanied by museum labels that read, in part, "... *Chiton incanus* Gould / New South Wales ...," and "... type ..."; a handwritten note states "2/8/18 ... compared to undoubted *Liolophura gaimardi* Blainville 1825 which it certainly is / E. Ashby." The single specimen, disarticulated with fragments of dry girdle, agrees with GOULD's (1846, 1852) description and illustration of the species. The report of the species at

Stewart Id., New Zealand (SMITH, 1884) has not been corroborated.

PILSBRY (1894b:87) established a subspecies, *Liolophura gaimardi queenslandica*, based solely on "the uniform black color of the girdle" and the "somewhat more slender [spinelets] than in *Gaimardi*." The type material consists of 2 specimens, dry, soft parts removed. The larger specimen, 42 mm long, 29 mm wide (including girdle), is a 7-valve specimen; the number "64853" is written on the articulamental surface of valve v (?); anterior valve missing; posterior valve, disarticulated showing white articulamentum and broad, flat, toothless callus; girdle spinelets all black and relatively slender. The smaller specimen, curled, estimated length 20 mm, soft parts removed, articulamentum dark brown, is here designated lectotype (ANSP 64853); the larger, partly disarticulated, 7-valve specimen, paralectotype (ANSP 355874). PILSBRY'S (1894b) designation of a subspecies, *queenslandica*, cannot be maintained, despite HULL (1923b) having raised it to species rank upon hardly spelled out differences in the tegmental sculpture of specimens collected between Port Hacking (34°05'S) and Broken Bay (33°34'S).

Acanthopleura gaimardi is remarkably similar to *A. japonica*. Yet, neither PILSBRY (1893c) nor subsequent workers devoted much space to contrasting them. Pilsbry stated only that *Liolophura gaimardi* differs from *L. japonica* "in the differently colored interior and sutural plates, in the details of girdle-structure, etc." (PILSBRY, 1893c:241), and that *L. japonica* differs "from *L. incana* [= *A. gaimardi*] by the uniform black color of the inner layer or articulamentum" (PILSBRY, 1893c:243). Diagnostic criteria (besides locality) have been increasingly obscured by subsequent authors. NIERSTRASZ (1905b:154-156, pl. 1, figs. 20-25) reported specimens of both *L. gaimardi* and *L. japonica* (as "var. *tesselata*") at the Moluccas Is., none of which agrees with the concept of *Liolophura* Pilsbry, 1893a. LELOUP (1939) identified Japanese specimens as *L. gaimardi*, and specimens from Indochina as *L. japonica*; and later LELOUP (1961:38) tabulated a single distinction between the two species, the girdle spinelets, said to be "of equal length" in *japonica*, "of different lengths" in *gaimardi*. WU (1969) identified specimens from Taiwan as *L. gaimardi*, with no reference to *L. japonica*.

In this study no reliable differences were found between putative specimens of *Acanthopleura gaimardi* from Australia and *A. japonica* from Japan in habitat, general shape, size, tegmental sculpture, articulamental features, slit formula, gills, girdle undersurface scales, or radula. However, the specimens were seen to differ in (1) the shape of the posterior valve (flat, somewhat triangular, mucro almost terminal in *A. gaimardi*; modestly elevated, somewhat oval, mucro posterior but not terminal in *A. japonica*), (2) the color of articulamentum (dark brown in *A. gaimardi*; almost black in *A. japonica*), (3) the callus of the posterior valve (with no vestiges of teeth or pectinations in *A. gaimardi*; often with some symmetrical pecti-

nations or vestigial teeth, particularly on outermost areas of the callus, in *A. japonica*), and (4) the spinelets of the girdle upper surface (pointed, irregular in size, rather conical in *A. gaimardi*; erect, blunt-ended, regular in size, often white-tipped, cylindrical or wide, and imbricating in *A. japonica*). Given the considerable variation observed in these characters and their relative unreliability, it remains difficult to decide whether there are two species, *A. japonica* and *A. gaimardi*, or disjunct populations of a single biological species of *Acanthopleura*. However, until and unless further studies (cytological, molecular, etc.) should produce evidence to the contrary, it is here recommended that the traditional view of two species, *A. japonica* and *A. gaimardi*, be maintained.

Morphologically, *Acanthopleura gaimardi* is also very close to *A. gemmata*, from which it differs only in (1) the shape of the posterior valve (oval, elevated, mucro almost central in *A. gemmata*; triangular, depressed, mucro almost terminal, in *A. gaimardi*), (2) insertion plate of posterior valve (with well developed teeth in *A. gemmata*; without teeth in *A. gaimardi*), (3) the tegmental sculpture of the central areas (an unreliable distinction, particularly considering the often extremely eroded condition of specimens of either species), (4) the presence of ocelli in the pleural areas in *A. gaimardi* (an inconstant feature), not in *A. gemmata*, (5) the smaller average size of *A. gaimardi*, and (6) the geographic distribution.

The differentiation between *Acanthopleura gaimardi* and *A. gemmata* is further complicated by the presence of a "transition" population between the two at their zone of contact, a population here regarded as of a different species, *A. arenosa*, but which further study may prove to be a *gaimardi-gemmata* hybrid (see Remarks on *A. arenosa*).

Liolophura gaimardi platispinosa LELOUP, 1939a:3-7, figs. 2, 5, reported from Japan and Gulf of Tonkin, is here regarded as a *nomen dubium*, because description and illustrations do not permit certain assignment to a known taxon; type material not examined.

Acanthopleura japonica (Lischke, 1873)

Figures 68 to 72, and 115-J

Chiton japonicus LISCHKE, 1873:22-23, 1874:71-72, pl. 5, figs. 8-11.

Chaetopleura japonica: DUNKER, 1882:158.

Acanthopleura japonica: THIELE, 1893:373, pl. 30, fig. 34.

Acanthopleura (Liolophura) japonica: THIELE, 1910a:115.

Liolophura japonica: PILSBRY, 1893c:242-244, pl. 53, figs. 41-44; NIERSTRASZ, 1905b:155, pl. 10, fig. 22; HORST & SCHEPMAN, 1908:528; THIELE, 1929:21; BERGENHAYN, 1933:39-40, pl. 1, fig. 12, pl. 3, figs. 60-67, text figs. 13a-c; IS. TAKI, 1938a:398-404, pl. 15, fig. 3, pl. 32, figs. 15-16, pl. 33, figs. 1-8, pl. 34, figs. 1-4, 1947:1269, fig. 3606, 1949:287, fig. 904; OKADA *et al.*, 1954:214, fig. 392; IS. TAKI, 1960:197, pl. 90, fig. 2; LELOUP, 1961:39-42, text figs. 1, 2, 5a, pl. 3, fig. 1; IS. TAKI, 1962:46; IW. TAKI, 1964b:412; VAN BELLE, 1982:473-474; INABA, 1982:32.

[*Non*: NIERSTRASZ, 1905b:155-156, pl. 10, figs. 23-25].

- Liolophura japonica tessellata* PILSBRY, 1893c:243–244, pl. 53, figs. 45–46.
[Non: HORST & SCHEPMAN, 1908:528].
- Liolophura japonica tenuispinosa* LELOUP, 1939a:1–3, figs. 1, 3, 4; 1952:59; VAN BELLE, 1980:33–35.
- Liolophura japonica unispinosa* IS. TAKI, 1962:46 (*nomen nudum*).
- Liolophura japonica planispinosa* IS. TAKI, 1962:46 (*nomen nudum*).
- "*Liolophura gaimardi* (Blainville)" WU, 1969:109, figs. 5a, 5b, 47–58.
- Chiton defilippii* TAPPARONE-CANEFRI, 1874:77; PILSBRY, 1893c:243–244 (as syn. of *Liolophura japonica*).
- Nuttallina allantophora* DALL, 1919:502; SMITH, 1961:82, 1977:253.
[Non: "*Nuttallina* sp. cf. *allantophora* Dall, 1919," STEINBECK & RICKETTS, 1941:555, pl. 26, fig. 6 (= *Nuttallina crossota* Berry, 1956).]

Type material and type locality:

- Chiton japonicus* Lischke, 1873: Types unascertained; locality Nagasaki, Japan (32°48'N, 129°55'E).
- Liolophura japonica tessellata* Pilsbry, 1893c: Lectotype (ANSP 35969) and 2 paralectotypes (ANSP 355873) herein designated; locality Enoshima, Japan (35°18'N, 139°29'E).
- Liolophura japonica tenuispinosa* Leloup, 1939a: Types unascertained; locality here restricted to Poulo Dama Is., Gulf of Thailand (9°40'N, 104°30'E).
- Chiton defilippii* Tapparone-Caneferri, 1874: Types unascertained; locality Japan.
- Nuttallina allantophora* Dall, 1919: Holotype (USNM 110360a); locality ? Japan (given in error as "Los Animas Bay," Baja California, Mexico).
- Liolophura gaimardi platispinosa* Leloup, 1939a: Types unascertained; locality Shikok Kamigari, Toso Pref., Japan.

Material examined:

HONSHU: Japan, Shiriya, Aomori Pref., 2 specimens, largest 48 mm long (LACM 17-82); Takojima, Ishikawa Pref., 1 specimen, 25 mm long (LACM 11-82); Sagami Bay, 21 specimens, largest 37 mm long (CAS 009871; CAS 015103; CAS 12390; CAS 12394; CAS 012395; CAS 012400; CAS 031641; NMV 1026); Awaji, 1 specimen (NMV); Toshijima, Mie Pref., 1 specimen, 48 mm long (UCM 28917); Cape Bansho-zaki, near Seto Marine Biological Station, Wakayama Pref., 20 specimens, largest 47 mm long (LACM 19-82); Wakayama Pref., 2 specimens (*ex* Iw. Taki coll.); Ise Wan, 4 specimens, largest 52 mm long (CAS, acc. no. 1658); Shiju-shima Id., Hiroshima Pref., 2 specimens, largest 62 mm long (*ex* K. Y. Arakawa coll.).

KYUSHU: North Kyushu, 8 specimens, largest 38 mm long (CAS 034180); Taujushima Id., near Amakusa Marine Biological Station, Kumamoto Pref., 4 specimens, largest 60 mm long (LACM 25-82); Amakusa Marine Biological Station, Tamioka Peninsula, 4 specimens, largest 51 mm long (LACM 26-82); Hana, 1 specimen, 18 mm long (CAS 030933); Moji, S of Kabura Shima, 28 specimens, largest 50 mm long (CAS 012370; CAS 012399); Nagasaki, 9 specimens, largest 30 mm long (CAS 012364; CAS 012362; CAS 12362).

SOUTH KOREA: Pusan, 48 specimens, largest 32 mm long (CAS 012396; CAS 034552; CAS 053347); Dadas Po Beach, 15 specimens, largest 35 mm long (CAS 053345); Tanang Mal, 4 specimens, largest 30 mm long (CAS 053346); Seogwipo, 18

specimens, largest 30 mm long (CAS 012391); Chesudo, 1 specimen, 20 mm long (CAS 000973).

HONG KONG: Cheung-Sha, Lantau Id., 1 specimen, 33 mm long (AJF 685); Repulse Bay, Hong Kong Id., 3 specimens, largest 37 mm long (AJF 686).

TAIWAN: Yehliu, Chilung Co., 1 specimen, 57 mm (UCM 27560); Chien-shaw, Pen-hu Co., 3 specimens, largest 23 mm long (UCM 28893).

THAILAND: Sattahip, Gulf of Thailand, 4 specimens, largest 80 mm long (CAS 012397; CAS 030931); Ko-I-lao, 3 specimens, 70 mm long (CAS 012389; CAS 012398); Ko-Phai, 3 specimens, largest 50 mm long (CAS 012358); Ko-Sichang, 14 specimens, largest 55 mm long (CAS 012393; CAS 012403; CAS 012404).

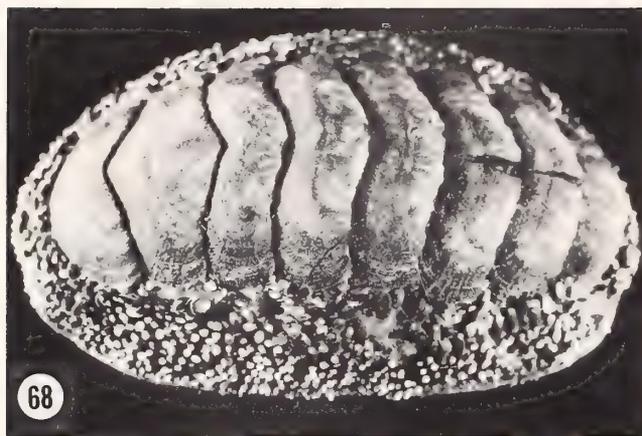
Description: LISCHKE (1873) described *Chiton japonicus* as "*Testa ovata, parum convexa, atro-fusca, griseo strigata, minutissime rugulosa, granulis parvis concentricis, ad latera interdum radiatim ordinatis sculpta; areae laterales indistinctae; valva postica perbrevis, planata, acutimarginata margo incertus; valvae anticae, incisurisque profundioribus 8 ad 10 irregulariter divisus, valvae posticae integer, valvarum reliquarum minute crenulatus et incisura unica bipartitus; ligamentum spinis calcareis erectis, obtusis, griseis, fuscis et fulvis densissime obtectum; pagina valvarum fusca, paene nigra.*—Long. 35, lat. 21 mill." (pp. 22–23), distinguishing it carefully from the similar *Chiton spiniger* Sowerby (= *A. gemmata*).

Among 175 specimens of *Acanthopleura japonica* here examined, largest 80 mm long (in alcohol) (CAS 030931: Sattahip, Gulf of Thailand). Body width/length, mean 0.64 (SD = 0.03; n = 10). Tegmentum dark brown. Lateral areas poorly defined, not elevated, sculptured with ill-defined, small granules. Central areas sculptureless except for subdued transverse growth lines. Posterior valve rather flat; mucro poorly defined, posterior to near terminal. Ocelli round to oval, 40–60 μ m in diameter, scattered through anterior valve, anterior $\frac{1}{3}$ of lateral areas, and postmucro area (Figure 68). Gills with 40–50 plumes per side.

Articulamentum dark brown. Sutural laminae well developed, triangular on valve ii, becoming subrectangular on valve viii. Sinus well defined. Insertion plates pectinate on outside. Posterior valve with no teeth but wide, transverse, flat-surfaced callus (Figure 69); occasionally (particularly in specimens from the Gulf of Thailand), a few, coarse pectinations or teeth seen at outer part of callus (one specimen shows large single tooth in middle of callus). Slit formula 8/11-1-0.

Girdle upper surface often banded brown-white, covered with erect spinelets, all about same size and appearance, usually cylindrical, blunt-ended, white-tipped, up to 700 μ m long (Figure 70); in some populations, specimens have variable girdle elements, from "typically" slim and cylindrical spinelets, to flattened, scale-like, imbricate elements (Figure 71). Girdle bridges empty. Undersurface paved with transparent, rectangular to squarish scales, 50 \times 40 μ m, arranged in rows, with convex outer edge articulating with concave inner edge of adjacent scale.

Radula averaging 35% of specimen length and 55 rows



Explanation of Figures 68, 69, and 73 to 76

Figure 68. *Acanthopleura japonica* (Lischke, 1873). Takojima, Ishikawa Pref., Japan Sea, Japan (LACM 82-11); specimen 18 mm long.

Figure 69. *Acanthopleura japonica* (Lischke, 1873). Shiriya, Aomori Pref., Japan (LACM 82-17); specimen 25 mm long. Ventral aspect of posterior valve.

Figure 73. *Acanthopleura hirtosa* (Blainville, 1825). Bremer Bay, W.A., Australia (WAM 47-74); specimen 25 mm long. Close-up of lateral areas of valves iii-iv and girdle.

Figure 74. *Acanthopleura hirtosa* (Blainville, 1825). Cockburn, W.A., Australia (WAM 201-74); specimen 40 mm long. Dorsal aspect of posterior valve.

Figure 75. *Acanthopleura hirtosa* (Blainville, 1825). Same specimen as in Figure 74. Posterior aspect of posterior valve.

Figure 76. *Acanthopleura hirtosa* (Blainville, 1825). Same specimen as in Figure 74. Ventral aspect of posterior valve.

of mature teeth. In a specimen 38 mm long (CAS 012399: Unose Hana, Kyushu, Japan), radula 22 mm in length, comprising 60 rows of mature teeth. Median tooth (Figure 72) 110 μm at anterior blade; first lateral teeth 170 μm wide at anterior blade; head of second lateral teeth

discoid, 300 μm in diameter; outer marginal teeth 250 μm long, 230 μm wide (length/width, 1.1).

Distribution: *Acanthopleura japonica* has been recorded at Hakodate, Hokkaido, Japan (41°45'N, 140°43'E) (Is.

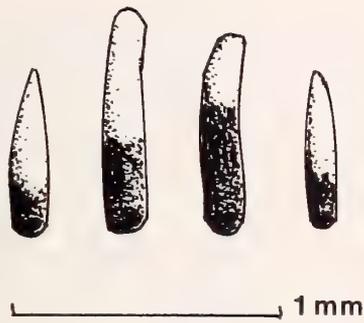


Figure 70

Acanthopleura japonica (Lischke, 1873). Thailand (CAS 018358); specimen 41 mm long. Girdle spines.

TAKI, 1938a; INABA, 1982), its northernmost record, along the coasts of Japan on the Sea of Japan, Inland Sea and Pacific Ocean, to Kyushu, the southern coast of Korea and Cheju-do (Is. TAKI, 1938a, 1962), Taiwan (WU, 1969, as "*Liolophura gaimardi*"), and Hong Kong (22°15'N, 114°10'E) (VAN BELLE, 1980, 1982; Ferreira, herein). A seemingly disjunct, perhaps relict population is present in the Gulf of Thailand (12°N, 102°E), with records at Poulo Dama Is., Poulo Condor (=Con Son Is.), Cap Saint-Jacques (=Vung-tau), Vietnam (LELOUP, 1939a, as *Liolophura japonica platispinosa*), and Sattahip, Thailand (Ferreira, herein) (Figure 115-J). The report of the species in the Moluccas (NIERSTRASZ, 1905b:155-156, pl. 10, figs. 23-25) is, from the illustrations, in error.

Bathymetric range confined to the intertidal zone, on top of rocks often exposed at low tide.

Remarks: PILSBRY (1893c), segregated *Liolophura japonica tessellata* from the "typical *japonica*" on account of its "much narrower [girdle] . . . conspicuously varied with alternate patches of white and scorched-brown or blackish . . . spinelets [which] are larger . . . [and] vary much in size, being small toward the outer edge of the girdle, large and flattened toward the inner edge . . ." (p. 243). Type material of *L. j. tessellata* (ANSP 35060) consists of 3 dry specimens, curled, soft parts removed, estimated lengths 35-38 mm, eroded; articulation black; insertion plate of posterior valves inaccessible for inspection; girdle spine-

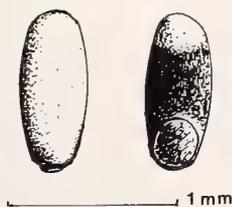


Figure 71

Acanthopleura japonica (Lischke, 1873). Same specimen as in Figure 69. Girdle scale-like spines.

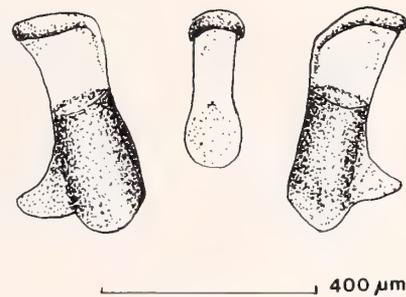


Figure 72

Acanthopleura japonica (Lischke, 1873). Same specimen as in Figure 69. Radula median and first lateral teeth.

lets as described and illustrated by PILSBRY (1893c). An old museum label on cardboard marked with a red dot to which the specimen had been glued, reads "Type of var. 35969 / *L. Japonica* Lischke. / var. *tessellata* Pils. / Fr. Stearns. Enoshima, Japan." The least eroded specimen is here designated lectotype (ANSP 35969); the other two as paralectotypes (ANSP 355873).

As observed by TAKI (1938a:402), *Liolophura japonica* exhibits such wide variations in size, color, and width of girdle spinelets as to render meaningless alleged subspecies based on such variations (yet, TAKI [1962] later introduced two such subspecies, *unispinosa* and *planispinosa*, left undescribed). Still, attention must be called to two other phenotypes. Specimens from the Gulf of Thailand differ from those of Japan not only by attaining conspicuously larger sizes, but in the girdle spinelets, which tend to be thinner, clearly cylindrical, closer together, equal-sized, and often white-tipped. Some specimens from Japan (LACM 7-82: Akasaki, Noto Peninsula [37°21.5'N, 137°15'E]; LACM 25-82: Tsujushima Id., Kumamoto [32°33'N, 130°07.7'E]) and from Korea have girdle elements that, being wide, flat, and clearly imbricate, are more properly called scales than spinelets (Figure 71), suggesting a distinct species (perhaps deserving a name such as "*planispinosa*," left *nudum* by TAKI [1938a]) were it not for the presence of spinelets with an intermediate form, and the fact that such specimens do not appear to differ from those of "typical" *Acanthopleura japonica* in any other respect. Further study of these populations is indicated.

Ornithochiton [sic] *caliginosus* Carpenter (in PILSBRY, 1893c:243-244, pl. 54, figs. 41-45), based upon specimens from the China Sea and Hong Kong, has been regarded by KAAS & VAN BELLE (1980) as a synonym of *Acanthopleura japonica*. However, as TAKI (1938a:402) pointed out, the specimen illustrated by PILSBRY (1893c) differs from *A. japonica* in the insertion plate of the posterior valve (specimen of *A. loochooana*?). The species-name, unquestionably referring to an *Acanthopleura*, is here suppressed as a *nomen dubium*.

The placement of *Chiton defilippii* in the synonymy of

Liolophura japonica proposed by PILSBRY (1893c) on subjective grounds is here accepted.

Nuttallina allantophora Dall, 1919, was shown to belong in the synonymy of *Liolophura japonica*, the type locality, "Los Animas Bay," Baja California, Mexico, being in error (SMITH, 1977). Examination of color slides of the holotype (CASIZ Color Slide Series Nos. 1992, 1993) substantiates Smith's conclusion.

LELOUP's (1939a) assignment of specimens from Japan and the Gulf of Tonkin to *Liolophura gaimardi platispinosa* and specimens from Indochina and the Gulf of Thailand to *L. japonica tenuispinosa* was left unjustified. The true nature of the former (see Remarks on *Acanthopleura gaimardi*) remains a matter of speculation.

In Hong Kong, *Acanthopleura japonica* is found sharing the intertidal habitat with *A. loochooana* on rocks exposed to mild surf (personal observations, Sept. 1982). In Taiwan, *A. japonica* is sympatric (or at least parapatric) with three other species of *Acanthopleura*, *A. spinosa*, *A. loochooana*, and *A. miles*.

Acanthopleura hirtosa (Blainville, 1825)

Figures 73 to 78, and 114-H

Chiton hirtosus BLAINVILLE, 1825:546; PILSBRY, 1894a:106; LAMY, 1923:263.

Acanthopleura (Liolophura) hirtosa: DUPUIS, 1917:533-534.

Liolophura hirtosa: DUPUIS, 1918:531; ASHBY, 1926:384; LELOUP, 1961:44-49, text figs. 4, 5c.

Liolophura (Chiton) hirtosus: ASHBY, 1922b:579-580.

Clavari zona hirtosa: HULL, 1923:199, pl. 28, figs. 9-12; IREDALE & HULL, 1926:261-262, pl. 37, figs. 9-12, 17, 21 (reprinted, 1927:124-125, pl. 15, figs. 9-12, 17, 21).

Liolophura (Clavari zona) hirtosa: THIELE, 1929:21; VAN BELLE, 1983:129-130.

Chiton georgianus QUOY & GAIMARD, 1835:379, pl. 75, figs. 25-30; IREDALE, 1910b:154.

Liolophura georgiana: PILSBRY, 1893c:241-242, pl. 53, figs. 36-40; TORR, 1911:100-101; ASHBY, 1921:45, 1922a:32.

Acanthopleura (Liolophura) georgiana: THIELE, 1911a:399-400, fig. 3; DUPUIS, 1918:533-534.

Plaxiphora pustulosa TORR, 1911:107, pl. 25, fig. 7.

Type material and type locality:

Chiton hirtosus Blainville, 1825: Type at MHNH (*vide* DUPUIS, 1917; ASHBY, 1922c; LAMY, 1923); locality "mers de l'île King" (in error) corrected to King George Sound, Western Australia (35°03'S, 117°57'E) (ASHBY, 1922c; IREDALE & HULL, 1926).

Chiton georgianus Quoy & Gaimard, 1835: Syntypes (4) at MNHN (*vide* ASHBY, 1922c); locality "port du Roi-Georges," Western Australia (35°03'S, 117°57'E).

Plaxiphora pustulosa Torr, 1911: Type "in coll. Torr" (*vide* IREDALE & HULL, 1926); locality Albany, Western Australia (35°02'S, 117°53'E).

Material examined:

AUSTRALIA, W.A.: Cape Cuvier, 1 specimen, 20 mm long (WAM 48-74); Point Quobba, 2 specimens, largest 35 mm long (WAM 43-74); Point Gregory, Peron Peninsula, Shark Bay, 3

specimens, largest 50 mm long (WAM N4726); Shark Bay, 1 specimen, 30 mm long (WAM 714-79); Dick Hartog Id., 1 specimen disarticulated (NMV, *ex* Ashby coll.); Kalbarri, 1 specimen, 35 mm long (WAM 1864-67, WAM-USNM Barrow Is. Exped., 18 August 1966); Abrolhos Is., 1 specimen, 40 mm long (AMS C31530); Geraldton, 1 specimen 30 mm long (WAM 7125); Dongara, 10 specimens, largest 30 mm long (WAM 6021); "W. Austr.," 2 specimens (NMV); Carnac Is., 3 specimens, largest 55 mm long (WAM 50-74; WAM 704-79); Leighton, 2 specimens, largest 40 mm long (WAM 13446/7); Cockburn Sound, 6 specimens, largest 60 mm long (WAM 200-74; WAM 201-74; WAM 476-74); Port Gregory, 1 specimen, 40 mm long (WAM 46-74); Fremantle District, 1 specimen, 20 mm long (AMS C31531); Fitzgerald Inlet, 2 specimens (WAM 42-74); Point Peron, 4 specimens, largest 60 mm long (WAM 45-74; WAM 278/9-1938); Bunbury, 1 specimen, 20 mm long (WAM 49-74); Lucky Bay, 1 specimen, 50 mm long (WAM 710-79); Geographe Bay, 3 specimens, largest 30 mm long (AMS C18012); Cottesloe, 1 specimen, 24 mm long (NMV); Bunker Bay, 1 specimen, 40 mm long (WAM 713-79); Rottneet Id., 1 specimen 35 mm long (AMS C32119); Foul Bay, 1 specimen (AMS C121194); Garden Id., 2 specimens, largest 45 mm long (WAM 706-79, with label "ident. as *Liolophura gaimardi* by E. Ashby"); Coweramup Bay, 1 specimen, 40 mm long (WAM 705-79); Augusta, 1 specimen, 50 mm long (WAM 708-79); Cape Leeuwin, 1 specimen disarticulated (NMV, *ex* Gatliff coll.); Nor-nalup, 2 specimens, largest 50 mm long (WAM 15568/69, *leg.* E. Ashby, August 1929); King George Sound, 8 specimens, largest 56 mm long (NMV, *ex* Basset Hull coll.); King George Sound, 5 specimens (NMV); Middleton Beach, King George Sound, 1 specimen, 42 mm long (AMS C69338); Albany, 4 specimens, largest 40 mm long (WAM N3272); Frenchman's Bay, 1 specimen, 25 mm long (WAM 707-79); Bremer Bay, 4 specimens, largest 40 mm long (WAM 47-74); Hopetown, 2 specimens, largest 17 mm long (WAM 495-74); Esperance, 1 specimen, 37 mm long (WAM 51-74); Seven Mile Beach, Esperance, 6 specimens, largest 40 mm long (NMV); Dempster Head, Esperance (NMV, *ex* Basset Hull coll.); Duke of Orleans Bay, 1 specimen, 40 mm long (WAM 709-79); Wilson Id., 1 specimen, 40 mm long (WAM); Mondrain Id., 5 specimens, largest 70 mm long (WAM 44-74; WAM 712-79).

Description: *Acanthopleura hirtosa* is adequately characterized in the descriptions of BLAINVILLE (1825), PILSBRY (1893c), and IREDALE & HULL (1926).

Among 96 specimens of *Acanthopleura hirtosa* here examined, largest 70 mm long (dry) (WAM 44-74: Mondrain Id.). Body width/length, mean 0.62. Tegmentum olive-green to brown, often with black patches and whitish band in jugal area. Anterior valve covered with round granules which tend to align in radial rows. Lateral areas of intermediate valves moderately elevated, with somewhat elongate granules in about 10-15 ill-defined radial rows (Figure 73). Central areas with transverse, juxtaposed lamellae on jugal area superimposed by round granules in parallel longitudinal rows, particularly well defined on pleural areas. Intermediate valves beaked; posterior edge of valve ii forming 100-110° angle. Mucro posterior to terminal; postmucro convex, sharply sloped. Ocelli round to oval, 20-50 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior ½ of lateral areas of intermediate valves. Widths of tegmental surfaces of valves i/viii, mean 1.17. On valve i,

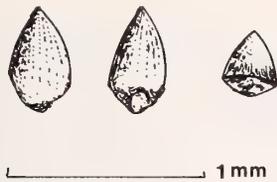


Figure 77

Acanthopleura hirtosa (Blainville, 1825). Bayonet Head, Albany, W.A., Australia (WAM N3272); specimen 32 mm long. Girdle scales.

tegumentum length/width, mean 0.51. Posterior valve somewhat triangular in outline (Figure 74); tegumentum length/width, mean ratio 0.38; articulamentum not wider than tegumentum. Eaves thick (0.5 mm in midline of valve viii of specimen 32 mm long), somewhat spongy. Gills with 25–35 plumes per side.

Articulamentum dark brown and white. Sutural laminae well developed, subtriangular on valve ii to subrectangular on valve viii. Insertion plates pectinate on outside. On valve i, insertion plate hardly extends beyond tegmental surface (measured in midline, length of insertion plate/length of tegmental surface, mean ratio, 0.10). On valve viii, insertion plate absent but with conspicuous, toothless, flat, wide callus (Figures 75, 76). Slit formula 8/11-1-0.

Girdle banded black-white in most specimens; at valve iv, girdle width up to 36% of width of valve in alcohol preserved specimens. Upper surface covered with calcareous, somewhat conical scales (Figure 77), irregular in size, averaging 400 μm in length, 500 μm in height, 200 μm in thickness, with 8–12 fine, converging striae; clusters of 3–8 relatively opaque spicules 100–200 μm long, 20–30 μm thick, may be seen amidst scales. Girdle bridges empty. Undersurface covered with transparent, subquadrate scales, 60 \times 50 μm , vaguely striate.

In specimen 40 mm long (WAM 201-74: Cockburn, SW Australia), radula measures 22 mm in length (55% of specimen length), comprising 68 rows of mature teeth. Median tooth (Figure 78) 100 μm wide at anterior blade; first lateral teeth 150 μm wide at anterior blade; head of second lateral teeth discoid, 260 μm in diameter; outer marginal teeth 270 μm long, 190 μm wide (length/width, 1.4).

Distribution: *Acanthopleura hirtosa* is confined to southwestern Australia (Figure 114-H) from Cape Cuvier (WAM 48-74) (24°14'S, 113°22'E), the northernmost verified record, to Mondrain Id., Recherche Arch. (WAM 44-74; WAM 712-19) (34°08'S, 122°15'E), the easternmost verified record on the south coast of Australia. HULL (1923) recorded the species from Point Cloates to Eyre.

Bathymetric range 0–2 m.

Remarks: *Acanthopleura hirtosa* is the only species of the genus in southwestern Australia. It is remarkably similar

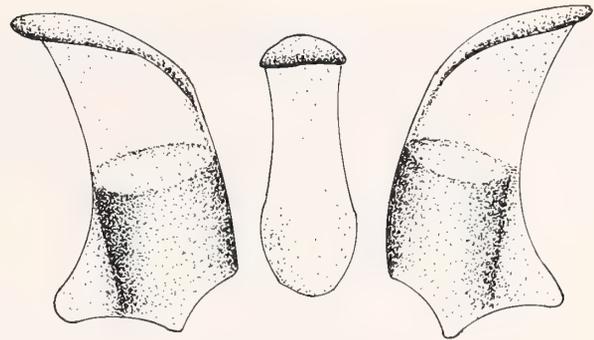


Figure 78

Acanthopleura hirtosa (Blainville, 1825). Same specimen as in Figure 77. Radula median and first lateral teeth.

to *A. gaimardi* from which it mainly differs in the girdle elements—conical scales in *A. hirtosa*, spinelets in *A. gaimardi*. HULL (1923) separated the two species at the generic level, erecting *Clavarizona* for *hirtosa*, but his action was refuted by ASHBY (1926) and LELOUP (1961). SMITH (1960:67) placed *Clavarizona* in the synonymy of *Liolophura*.

Acanthopleura arenosa Ferreira, spec. nov.

Figures 79 to 85, and 114-A

Diagnosis: Specimens quite similar to those of *Acanthopleura gaimardi* except for a moderately inflated (*i.e.*, not as flat) posterior valve, with a rounder posterior edge, and insertion teeth definitely present although underdeveloped to obsolete.

Type material:

Holotype (CAS 044305) and 11 paratypes (CAS 044304; BMNH 1985065; USNM 848001; ANSP A10648; LACM 2107; AJF coll.).

Type locality:

Pebbly Beach (about 25 km south of Port Douglas), Queensland, Australia (16°35'S, 145°22'E), 0.5 m below to 1 m above low tide water (AJF 604, *leg.* A. J. Ferreira & Sandy Motley, 14 Aug. 1981).

Other material:

AUSTRALIA, Qld.: Buchan's Point (30 km N of Cairns), 0 to 1 m above low tide water, 4 specimens, largest 25 mm long (AJF 605); Trinity Beach (some 15 km N of Cairns), 0 to 1 m above low tide water, 4 specimens, largest 28 mm long (AJF 606).

Description: Holotype (Figures 79, 80) preserved in alcohol, intact (except for disarticulated posterior valve), somewhat curled, 22 m long (if flattened), 14 mm wide (including girdle); dark brown on side, and well defined jugal band, whitish otherwise; valves somewhat beaked, round-backed. Tegumentum eroded at apex of valves; an-



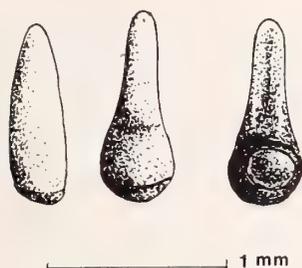


Figure 84

Acanthopleura arenosa Ferreira, spec. nov. Paratype (AJF coll.), 24 mm long. Girdle spinelets, outer and inner sides.

terior valve with roundish, poorly defined granules; lateral areas slightly elevated, with similar granules; central areas with weak, transversely appressed lamellae; posterior valve with tegmental surface semicircular, 7.5 mm wide, 3.6 mm long, with mucro (eroded) slightly post-central; gills holobranchial. Articulamentum of disarticulated posterior valve dark brown in middle, white at sutural laminae; sutural laminae subrectangular, about 2.8 mm wide, 1.5 mm long; sinus well defined, smooth, about 1.5 mm wide at anterior edge of tegmental surface; insertion plate reduced to transverse, roundish callus, pectinations clearly cut in outer $\frac{1}{3}$ but progressively ill-defined to absent in middle $\frac{1}{3}$, showing symmetrical slit on each side; eaves solid. Girdle banded black and white, crowded with pointed but short spinelets.

Paratypes (Figures 81–83) dark brown, most with brown jugal band flanked by white areas; largest 30 mm long (live). Body width/length, 0.65. Valves beaked, round-backed. Anterior valve with concentric rows of small, irregular, round to ovate granules 100–200 μm in diameter. Lateral areas poorly defined, hardly raised, similarly sculptured. Central areas (markedly eroded) featureless except for ill-defined, appressed, transverse lamellae. Posterior valve somewhat inflated (*i.e.*, not flat), with semicircular posterior edge; mucro not prominent, central to slightly posterior; postmucro convex, sloping. On valve i, tegmentum length/width, 0.5. On valve viii, tegmentum length/width, 0.4. Widths of tegmental surfaces of valves

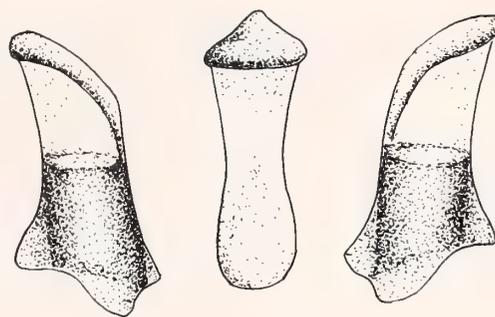


Figure 85

Acanthopleura arenosa Ferreira, spec. nov. Same paratype as in Figure 84. Radula median and first lateral teeth.

i/viii, 1.1. Ocelli round to oval, 50–60 μm in diameter. Gills with 30–35 plumes per side.

Articulamentum brown to bluish-white. Sutural laminae well developed, subtriangular to subrectangular; sinus well formed; sinusal plate smooth; relative width of sinus, 0.6. Insertion plates strongly pectinate on outside. On valve i, insertion teeth irregularly spaced; in midline, length of insertion teeth/length of tegmentum, 0.18. On valve viii, pectinations and insertion teeth extremely subdued, vestigial to absent in middle $\frac{1}{3}$; single, well cut, symmetrical slits on each outer $\frac{1}{3}$. Slit formula 9/10-1-2. Eaves thick (0.5 mm on midline of valve viii), somewhat spongy.

Girdle thick, muscular, banded blackish-brown and white. Upper surface with calcareous spinelets (Figure 84), somewhat pointed, straight to slightly curved, conical in outline, up to 1000 μm high, 300 μm thick at base. Undersurface with transparent scales, vaguely striate, squarish (40 \times 35 μm) to elongate (60 \times 30 μm) at periphery.

In paratype (AJF coll.) 24 mm long, radula 9 mm long (45% of specimen length), comprising 45 rows of mature teeth. Median tooth (Figure 85) 70 μm wide at anterior blade; first lateral teeth 120 μm wide at anterior blade;

Explanation of Figures 79 to 83 and 86 to 88

Figure 79. *Acanthopleura arenosa* Ferreira, spec. nov. Holotype (CAS 044305).

Figure 80. *Acanthopleura arenosa* Ferreira, spec. nov. Holotype (CAS 044305). Close-up of lateral areas of valves iii–v and girdle.

Figure 81. *Acanthopleura arenosa* Ferreira, spec. nov. Paratype (AJF coll.), 20 mm long. Dorsal aspect of posterior valve.

Figure 82. *Acanthopleura arenosa* Ferreira, spec. nov. Same paratype as in Figure 81. Posterior aspect of posterior valve.

Figure 83. *Acanthopleura arenosa* Ferreira, spec. nov. Same paratype as in Figure 81. Ventral aspect of posterior valve.

Figure 86. *Acanthopleura rehderi* Ferreira, spec. nov. Holotype (USNM 842113).

Figure 87. *Acanthopleura rehderi* Ferreira, spec. nov. Paratype (USNM 842114). Dorsal aspect of posterior valve.

Figure 88. *Acanthopleura rehderi* Ferreira, spec. nov. Same paratype as in Figure 87. Ventral aspect of posterior valve.

major lateral teeth with discoid head, 180 μm wide; outer marginal teeth 150 μm long, 140 μm wide (length/width, 1.1).

Other material essentially as type material.

Distribution: *Acanthopleura arenosa* is known only from the 80 km of coast between Peebly Beach and Trinity Beach, Queensland, Australia (Figure 114-A). Specimens are confined to the intertidal zone, exposed on rocks 0–1 m above low-tide water level.

Remarks: *Acanthopleura arenosa* is extremely similar to *A. gemmata* and *A. gaimardi*; in fact, only the posterior valve shows reliable distinctions in configuration and particularly in the characteristics of its insertion plate. The posterior valve of *A. arenosa* differs from that of *A. gaimardi* in being rounder (*i.e.*, not subtriangular), somewhat inflated (*i.e.*, not as flat), with central to moderately posterior (*i.e.*, not as terminal) mucro, and in the presence of insertion teeth and pectinations (completely absent in *A. gaimardi*) at the outer $\frac{1}{3}$ of the insertion plate; and it differs from that of *A. gemmata* in the underdevelopment (to obsolescence) of the insertion teeth. Otherwise, specimens of *A. arenosa* conform well with what *gemma-gaimardi* hybrids might be expected to be. Since, in addition, specimens of *arenosa* have been found exclusively in the zone of contact and overlap between *A. gemmata* and *A. gaimardi*, the possibility that they might be part of a hybrid population must be considered.

Hybridization in mollusks has been known in a few instances—in the prosobranch gastropods *Cypraea* (SCHILDER, 1962) and *Haliotis* (OWEN, 1961; OWEN *et al.*, 1971), the pulmonate gastropod *Cerion* (MAYR & ROSEN, 1956), and the pelecypods *Ostrea* (*Crassostrea*) (DAVIS, 1950; IMAI & SAKAI, 1961), *Pinctada* (MATSUI, 1958), *Mercenaria* (MENZEL, 1962; MENZEL & MENZEL, 1965), and *Tellina* (BOSS, 1964)—but not in chitons. Thus, unless further investigation should show otherwise, it seems appropriate to treat this population as a new species, which, judging from the abundance and relative uniformity of its specimens at the localities studied, is viable and self-reproductive.

The species is here named *arenosa* for the sandy beaches where it was found, and after Cecily "Sandy" Motley, Davis, California, who assisted in the collecting.

Acanthopleura rehderi Ferreira, spec. nov.

Figures 86 to 92, and 113-R

Diagnosis: Specimens small (to 2 cm) for the genus. Anterior valves with radial rows of round tubercles alternating with rows of ocelli. Lateral areas similarly sculptured. Central areas with well defined, parallel, longitudinal riblets. Posterior valve flat, subtriangular, mucro posterior to terminal. Slit formula 8/9-1-0. Girdle with spinelets. Radula with 4-cuspid major lateral teeth.

Type material:

Holotype (USNM 842113) and paratypes (USNM 842114; CAS 060405).

Type locality:

Palmerston Id., Cook Islands (18°04'S, 163°10'W).

Other material:

NIUE: Avatolo, 1 specimen, ca. 22 mm long, *leg.* R. Sixberry (USNM 685399); Alofi, 2 specimens, largest ca. 18 mm long, *leg.* R. Sixberry (USNM 685343).

Description: Holotype (Fig. 86), well preserved, dry, moderately curled, estimated 18 mm long (if flattened), 10 mm wide (including girdle), 4 mm high. Valves subcarinate, posterior edge beaked and angled at about 150°. Tegmentum (somewhat eroded) light tan with grayish-green suffusions towards margin and brown stripe along jugal area. Anterior valve with about 24 radial rows of ground granules. Lateral areas of intermediate valves raised, with 3 or 4 similar rows of round granules better defined at sutural edge, rendering it crenulate. Central areas with 18–20 longitudinal, parallel riblets, close together, as wide as interstices in between. Posterior valve rather flat, subtriangular; mucro posterior, almost terminal, somewhat pointed. Ocelli mostly oval, 50–60 μm maximum diameter, aligned in radial rows on anterior valve and most of lateral areas. Gills with 35–40 plumes per side.

Girdle upper surface covered with white, calcareous spinelets, close together, rather uniform in size, up to 700 μm long, 130 μm thick.

Paratypes quite similar to holotype. Disarticulated paratype (Figures 87, 88) ca. 20 mm long: Articulamentum white with brown discolorations at apex of valves; tegmentum reflected forward along posterior edge of valves; width of valve i/width of valve viii, 6.6 mm/6.2 mm = 1.1; sinus well defined, wide, deep, with pectinate sinusal plate; sutural laminae subrectangular; insertion plates pectinate on outside; slit formula 8-1-0; posterior valve with no teeth but well developed callus. Girdle upper surface with regular, straight, gently tapered, calcareous spinelets (Figure 89), mostly white, up to 900 μm long, 140 μm thick, with transverse "growth" striations and relatively abundant, glassy, sharply pointed spicules, up to 200 \times 15 μm , scattered in between. Undersurface covered with transparent, rectangular, coarsely striate scales (Figure 90), about 40 \times 30 μm , each with convex outer side that articulates into concave inner side of adjacent scale. Radula 5 mm long (25% of specimen length), comprising 45 rows of mature teeth; median teeth (Figure 91) elongate, 40 μm wide at anterior blade; first lateral teeth with elongate, bladed, anterolateral corner; second lateral teeth with basically discoid head, 140 μm wide, but with four short, rounded cusps (unique feature among *Acanthopleura*); spatulate teeth (Figure 92) with subrectangular spatula; outer marginal teeth elongate, 125 \times 80 μm .

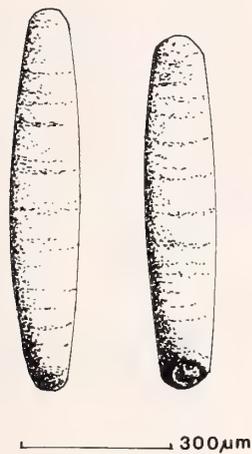


Figure 89

Acanthopleura rehderi Ferreira, spec. nov. Same paratype as in Figure 87. Girdle spinelets.

Specimens from Niue (USNM 685399; USNM 685343) agree in every respect with the types except for the slit formula, 9-1-0, of an 18 mm long specimen.

Distribution: The species is known only from Palmerston, Cook Islands ("outside reef nr. village," leg. R. Sixberry), type locality, and Niue (19°02'S, 169°52'W) (Figure 113-R), presumably in the intertidal zone.

Remarks: The specimens here referred to *Acanthopleura rehderi* are clearly distinct from those of *A. nigropunctata* Carpenter, 1865, described from the nearby Society Islands. Examination of the lectotype (USNM 19297) of the latter, here designated—an incomplete specimen missing valves vii and viii but conforming well to CARPENTER'S (1865) account of *nigropunctata*, which indicated the presence of slits in the posterior valve—corroborated its current generic assignment (since Carpenter in PILSBRY, 1893b:207) to *Tonicia*.

Acanthopleura rehderi, like *A. japonica*, *A. hirtosa*, *A. gaimardi*, and *A. nigra*, has no insertion teeth in the posterior valve, and, as such, it would fit in *Liolophura* Pilsbry, 1893a. However, despite articuamental similarities, *A. rehderi* clearly differs from the other four "*Liolophura*" in tegmental sculpture, girdle elements, and, above all, in its unique radula.

The radula of *Acanthopleura rehderi* with 4-cuspid major lateral teeth constitutes a departure from all congeners (and, to my knowledge, from all other chitonids), although the cusps seem to be based upon (or cut into) the discoid head characteristic of *Acanthopleura*. The possible evolutionary significance of such a radular modification is unknown, but it is tempting to speculate that it may represent an adaptive response to a new set of dietary conditions, perhaps presaging a new line of speciation. The question deserves further investigation.

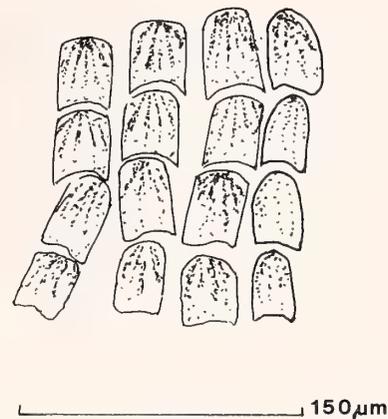


Figure 90

Acanthopleura rehderi Ferreira, spec. nov. Same paratype as in Figure 87. Girdle undersurface scales.

The species is here called *rehderi* after Dr. Harald A. Rehder, Professor Emeritus, National Museum of Natural History (Smithsonian Institution), Washington, D.C., who generously provided the specimens for study.

Acanthopleura granulata (Gmelin, 1791)

Figures 93 to 97, and 113-G

Chiton granulatus GMELIN, 1791:3205; WOOD, 1815:9; BLAINVILLE, 1825:545; ORBIGNY, 1853:200.

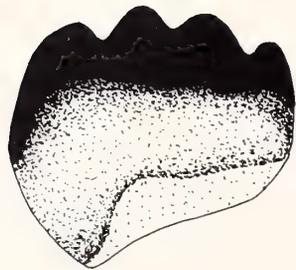
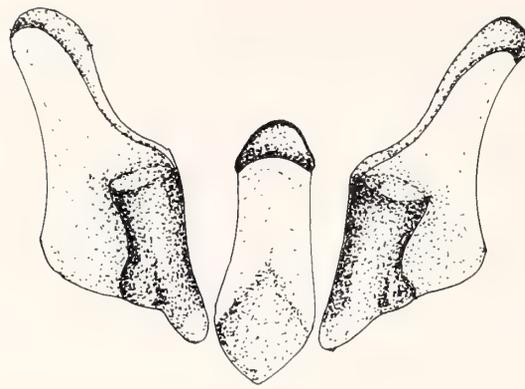
Acanthopleura granulata: HADDON, 1886:24-28; PILSBRY, 1893c:227-230, pl. 50, figs. 39-49 (in subgen. *Maugeria*; DAUTZENBERG, 1900:220-221; DALL & SIMPSON, 1901:454; HAMILTON, 1903:138; NIERSTRASZ, 1905a:102, 1905b:152 (in part); HORST & SCHEPMAN, 1908:527 (in part); THIELE, 1909:3, 1910b:112; REMINGTON, 1922:121; BERRY, 1925:173-175, pl. 12, figs. 1, 2; (?) PEILE, 1926:74; NIERSTRASZ, 1927:163; THIELE, 1929:21; HUMMELINCK, 1933:303, 306; JOHNSON, 1934:14; LELOUP, 1937a:146-150, figs. 13-15a (in part), 1941:44-45, pl. 1, fig. 1; SALISBURY, 1953:42; HIDALGO, 1956:4-8, pls. 3, 4; OLSSON & MCGINTY, 1958:23; LEWIS, 1960:398, 410, fig. 8; WARMKE & ABBOTT, 1961:220, fig. 33f; CONDE, 1966:287; ALTENA, 1969:37; GLYNN, 1970:1-21; KAAS, 1972:117-122, text figs. 239-244, pl. 9, figs. 1-3; GÖTTING, 1973:251, text fig. 2, pl. 11, fig. 14; ABBOTT, 1974:406, fig. 4755; BABOOLAL *et al.*, 1981:43, fig. 5; MOOK, 1983:101-105.
[Non: SUTER, 1905:70, 1913:44-45, 1915, pl. 2, fig. 21, pl. 5, fig. 2.]

Chiton piceus GMELIN, 1791:3205; BLAINVILLE, 1825:545; SOWERBY, 1840b:1, 10, sp. no. 10, fig. 147; SAUSSAYE, 1853:416; SHUTTLEWORTH, 1853:78-79 (in subgen. *Acanthopleura*); SCHIFF, 1858:12-47, pls. 1-2.
[Non: REEVE, 1847, pl. 13, sp. & fig. 70; ANGAS, 1867:223.]

Acanthopleura picea: MOSELEY, 1885:18, pl. 6, figs. 8, 9; DALL, 1889:174; THIELE, 1893:373, pl. 30, fig. 32.

Chiton salamander SPENGLER, 1797:80-81.

Acanthopleura salamander: THIELE, 1893:373, pl. 30, fig. 35.



100 μm

Figure 91

Acanthopleura rehderi Ferreira, spec. nov. Same paratype as in Figure 87. Radula median tooth, first lateral teeth, and head of major lateral tooth.

Chiton convexus BLAINVILLE, 1825:544.

Chiton occidentalis REEVE, 1847, pl. 14, sp. & figs. 76; SAUSSAYE, 1853:416.

Chiton (Acanthopleura) mucronulatus SHUTTLEWORTH, 1853:79.

Acanthopleura granulata mucronulata: DALL & SIMPSON, 1901:454.

Chiton (Acanthopleura) blaueri SHUTTLEWORTH, 1856:170-171.

Type material and type locality:

Chiton granulatus Gmelin, 1791: Based upon CHEMNITZ, (1785:fig. 806); locality "Oceano americano" (St. Thomas, West Indies, Caribbean Sea).

Chiton piceus Gmelin, 1791: Based upon CHEMNITZ (1785:figs. 807, 810); locality "mari americano & rubro" (St. Thomas, West Indies, Caribbean Sea).

Chiton salamander Spengler, 1797: Based upon CHEMNITZ (1785:fig. 806); locality St. Thomas, West Indies.

Chiton convexus Blainville, 1825: Types unascertained; locality "mers de l'archipel american."



100 μm

Figure 92

Acanthopleura rehderi Ferreira, spec. nov. Same paratype as in Figure 87. Radula spatulate tooth.

Chiton occidentalis Reeve, 1847: Types unascertained; locality "Savannah-le-mer, West Indies."

Chiton (Acanthopleura) mucronulatus Shuttleworth, 1853: Types unascertained; locality Puerto Rico, West Indies.

Chiton (Acanthopleura) blaueri Shuttleworth, 1856: Types unascertained; locality Puerto Rico, West Indies.

Material examined:

BAHAMAS: Grand Bahamas Id., 15 specimens (AJF coll., leg. A. J. Ferreira *et al.*, May 1971); Bimini Id., 15 specimens, largest 86 mm long (AJF 290; AJF 291); Long Island, 10 specimens (AJF 248); San Salvador Id., 15 specimens (AJF 439); New Providence Id., 24 specimens (CAS 010094); Nassau, 4 specimens, largest 40 mm long (CAS 034777); Chub Cay, 2 specimens, largest 8 mm long (IRCZM 61:066); Gun Cay, 3 specimens, largest 65 mm long (IRCZM 61:016).

FLORIDA KEYS: Bonefish Key, 18 specimens (AJF 426); Crawl Key, 2 specimens, largest 60 mm long (CAS 012259); between Windley and Plantation Keys, 4 specimens, largest 80 mm long (IRCZM 61:010).

BONAIRE: 50 specimens (AJF 210; AJF 208; AJF 264).

CURAÇAO: 20 specimens (AJF 260; AJF 263).

PANAMA: Galeta, 2 specimens (AJF coll., leg. H. Bertsch, Sept. 1974; IRCZM 61:013); Bocas del Toro, 10 specimens (AJF 216); Caledonia Bay, 5 specimens (LACM-AHF A 1-39).

HONDURAS: Roatan Id., 24 specimens, largest 74 mm long (AJF 309; CAS 012137; CAS 012138; CAS 012148; CAS 012149; CAS 021294).

NICARAGUA: Corn Id., 3 specimens (AJF coll., leg. B. Keagan, Sept. 1975).

JAMAICA: Montego Bay, 20 specimens (AJF 253; AJF 254); Negril, 10 specimens (AJF 256).

DOMINICAN REPUBLIC: Caracoles, 8 specimens (AJF coll., leg. B. Keagan, Jan.-Oct. 1976); Playas Bayabibe, 1 specimen (AJF coll., leg. B. Keagan, Sept. 1977).

BRITISH VIRGIN ISLANDS: Virgin Gorda Id., 1 specimen (AJF 297); Cooper Id., 4 specimens (AJF coll., leg. S. Motley, Feb. 1983); Peter Id., 3 specimens (AJF coll., leg. S. Motley, Feb. 1983).

ANTIGUA: 14 specimens (CAS 012135; CAS 012136; CAS 012150).

ST. LUCIA: Pigeon Id., 2 specimens (AJF coll., leg. B. Keagan, May 1977).

DOMINICA: Anse de Mai, 3 specimens (AJF coll., leg. B. Keagan, May 1977).

VENEZUELA: Puerto Mara, 2 specimens (AJF 347); Tortuga Id., 5 specimens, largest 102 mm long (LACM-AHF A20-39).

CAYMAN ISLANDS: Grand Cayman Id., 34 specimens, largest 65 mm long (AJF 420; AJF 421; IRCZM 61:030; IRCZM 61:031); Cayman Brac, 5 specimens (AJF 424).

TURK & CAICOS: Grand Turk Id., 20 specimens (AJF 443; AJF 444).

MEXICO: Cozumel Id., 35 specimens (AJF 511; AJF 512; AJF 514).

TOBAGO: Courland Point, 6 specimens (AJF 670); Bateau Bay, 2 specimens (AJF 672); Mt. Irvine Bay, 8 specimens (AJF 674); Store Bay, 12 specimens, largest 52 mm long (AJF 678).

BARBADOS: Paradise Beach, 6 specimens (AJF 679); River Bay, 5 specimens (AJF 680); St. Lawrence, 1 specimen, 50 mm long (AJF 684); Bathsbeba, 4 specimens, largest 39 mm long (CAS 012260).

TRINIDAD: Maracas Beach, 3 specimens, largest 39 mm long (AJF 668).

Description: Because there is only one *Acanthopleura* in the Caribbean, GMELIN's (1791) description of *Chiton granulatus* in "Oceano Americano," based upon a figure in CHEMNITZ (1758:fig. 806), has proved adequate to identify the species: "*Ch. piceus supra planus, punctis elevatis numerosis in series digestis, limbo lato coriaceo spinoso; areis nigris albisque alternis.*" The species has been repeatedly described by authors working with the Caribbean chiton fauna, and little remains to be added to such accounts (e.g., KAAS, 1972).

Among 472 specimens of *Acanthopleura granulata* examined, largest 102 mm long (in alcohol) (LACM-AHF A 20-39; Tortuga Id., Venezuela). Body width/length, mean 0.64. Specimens (Figure 93) depressed, round-backed, large, beaked; posterior edge of valve ii forming 100–120° angle. Tegmentum grayish-green to grayish-brown, often with dark longitudinal stripe in midline. Lateral areas poorly defined, hardly raised, sculptured with low, mostly round, coarse granules; anterior valve and postmucro area of posterior valve similarly sculptured. Central areas almost featureless except for smaller to obsolete granules in pleural areas, and thin, ill-defined, transverse lamellae appressed across jugal areas. Mucro central (in young specimens) to somewhat posterior (in older, larger ones); postmucro strongly convex, at 30–90° slope. Ocelli round to oval, 50–70 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and anterior $\frac{1}{3}$ to $\frac{2}{5}$ of lateral areas of intermediate valves. On valve i, length of tegmentum/width of tegmentum, mean 0.6. On valve viii, articulamentum not wider than tegmentum; length of tegmentum/width of tegmen-

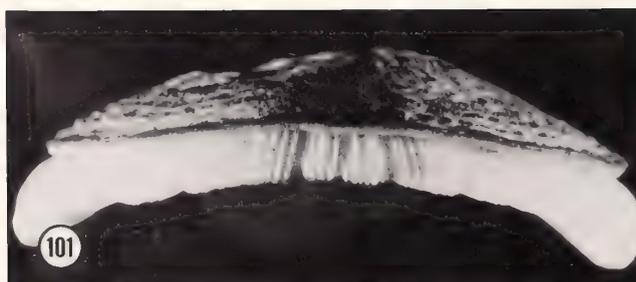
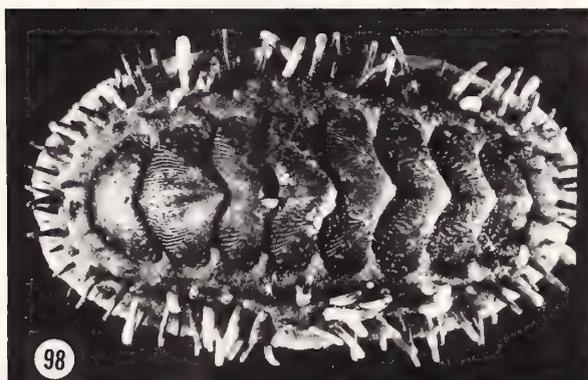
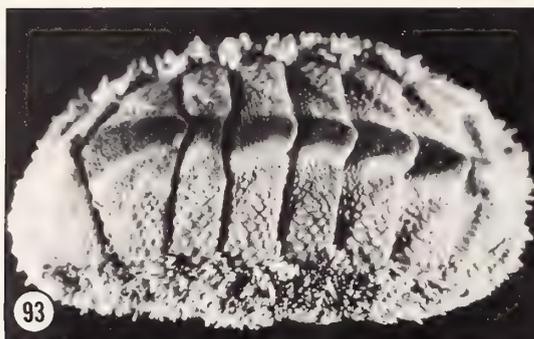
tum, mean 0.6. Widths of tegmental surfaces of valves i/viii, mean 1.2. Gills with 40–80 plumes per side.

Articulamentum blue to blue-green, often with purplish-brown spot at apex of valves. Sutural laminae well developed, relatively long, subtriangular on valve ii to subrectangular on valve viii. Sinus well formed; sinusal plate mostly smooth; relative width of sinus on valve viii, 0.7. Insertion teeth irregularly spaced, sometimes fused together; in midline, length of insertion plate/length of tegmentum, mean 0.2. On valve viii (Figures 94, 95), pectinations of insertion plate variable, often with incomplete slitting and poor definition of teeth (usually better defined than in *Acanthopleura gemmata*); teeth recurving forward, extending considerably beyond (more so than in *A. gemmata*) transverse callus. Slit formula 6/17-1-7/16. Eaves thick (0.5 mm wide on midline of valve viii of specimen 45 mm long), moderately spongy.

Girdle, often banded, thick, muscular, wide, shrinking appreciably with preservation; at level of valve iv, girdle may measure 60% of valve in live specimens, 40% in alcohol preserved specimens, 10% or less in dry specimens. Upper surface crowded with white or blackish, pointed to blunt, straight to curved, calcareous spinelets (Figure 96), up to 1.5 mm long in average specimens (up to 2.2 mm long in larger ones); occasional needle-like elements, pointed, crystalline, 200 \times 30 μm , interspersed amidst spinelets. Girdle bridges empty. Undersurface paved with imbricated, transparent, squarish scales, about 40 \times 40 μm , becoming elongate towards outer margin, showing some 8–10 coarse striations and riblets that seem to radiate from outer edge of scale.

Radulae averaging 43% of specimen length (range 38–55%, SD = 8.4%, n = 7) and 58 rows of mature teeth (range 40–70, SD = 9.3, n = 7). In specimen 43 mm long (AJF 248; Long Island, Bahamas), median tooth (Figure 97) 80 μm wide at anterior blade; first lateral teeth 220 μm wide at anterior blade; head of major lateral teeth discoid, 280 μm wide; outer marginal teeth 250 μm long, 180 μm wide (length/width, 1.6).

Distribution: *Acanthopleura granulata* is limited to the Caribbean Sea, having been recorded at practically every island or cay from the Florida Keys, Mexico, Central America coast to the Leeward Islands, from the Bahamas to the northern coast of South America (Figure 113-G). The northernmost verified record is Grand Bahama Id., Bahamas (26°40'N) (AJF coll., leg. A. J. Ferreira, May 1971); the report of *A. granulata* in Bermuda (PEILE, 1926) has not been corroborated in field work (A. J. Ferreira & W. E. Daily collecting trip to Bermuda, May 1977; Dr. John S. Pearse, personal communication upon field trip to Bermuda, July 1980) or museum material (Bermuda Aquarium, Natural History Museum, and Zoo, David D. Lonsdale, Curator: chiton collection on loan, Sept. 1979). The southernmost record is Trinidad (10°39'N) (BABOOLAL *et al.*, 1981; Ferreira, herein); the westernmost record, Cozumel Id., Mexico (86°55'W) (HIDALGO, 1956;



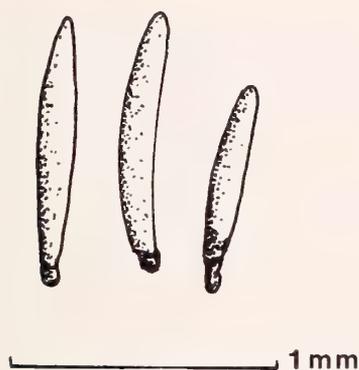


Figure 96

Acanthopleura granulata (Gmelin, 1791). Barbados (AJF 609); specimen 35 mm long. Girdle spinelets.

Ferreira, herein); the easternmost record, Barbados Id. (59°32'W) (THIELE, 1910b; LEWIS, 1960; CONDE, 1966; KAAS, 1972; Ferreira, herein). Reports of *A. granulata* in the Magellan Strait (NIERSTRASZ, 1905a, b) and at the Cape of Good Hope (NIERSTRASZ, 1905b) are obviously in error.

Acanthopleura granulata is confined to the intertidal zone, 0–1 m, often exposed, in crevices on coral limestone up to 1 m above low tide level.

Remarks: *Acanthopleura granulata* is the only species of the genus in the Atlantic Ocean. Likely, *A. granulata* and *A. gemmata* stem from the same ancestral species separated by the emergence of the Panama Isthmus. Still, *A. granulata*, a geographical isolate (MAYR, 1969), has not achieved sufficient phenotypic distance from *A. gemmata* to dispell the question of conspecificity. Although the question has not been previously addressed in the literature—and PILSBRY (1893c) went as far as allocating *A. granulata* and *A. gemmata* to different subgenera—the fact is that character-by-character comparison of Indo-Pacific specimens of *A. gemmata* with Caribbean specimens of *A. granulata* has failed to differentiate them in size, color, shape, tegmental sculpture, articulamental features, girdle elements, radula, and habitat.

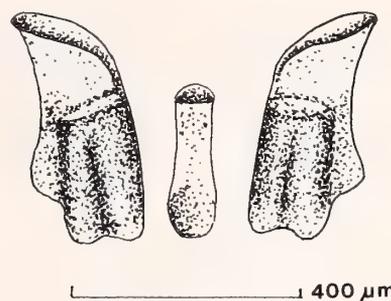


Figure 97

Acanthopleura granulata (Gmelin, 1791). Long Island, Bahamas (AJF 248); specimen 45 mm long. Radula median and first lateral teeth.

Admittedly, when compared with the Indo-Pacific *Acanthopleura gemmata*, a few, subtle, and variable characters do seem to earmark the Caribbean *A. granulata*: (1) the more regular and less often coalesced tegmental granules, (2) the somewhat reticular appearance of the pleural areas, (3) the less conspicuous lamellar sculpture of the central areas, (4) the brighter blue or bluish-green articulamentum, often with an apical dark brown spot, but never wholly brown, (5) the better defined teeth of the posterior valve, less recurved forward, extending farther beyond the callus, (6) the less well defined transverse callus of the posterior valve, and (7) the girdle spinelets not quite as long as sometimes seen in *A. gemmata*. But, considering the large intraspecific variation and wide geographic range of the respective populations, these equivocal distinctions can hardly be accepted as specific. Still, whether they are sibling species (*sensu* MAYR, 1969:183) or a single species cannot be decided on morphology alone and must await further and more sophisticated (electrophoretic, immunologic, genetic, *etc.*) studies. Thus, given their total geographic separation, it is here recommended that the traditional view be accepted, and the Caribbean and Indo-Pacific populations continue to be addressed as different species.

Chiton magellanicus GMELIN, 1791:3204, was based upon

Explanation of Figures 93 to 95 and 98 to 102

Figure 93. *Acanthopleura granulata* (Gmelin, 1791). Caracoles, Dominican Republic (AJF coll.); specimen 15 mm long.

Figure 94. *Acanthopleura granulata* (Gmelin, 1791). Villa del Mar Beach, Dominican Republic (AJF coll.); specimen 41 mm long. Posterior aspect of posterior valve.

Figure 95. *Acanthopleura granulata* (Gmelin, 1791). Villa del Mar Beach, Dominican Republic (AJF coll.); specimen 41 mm long. Ventral aspect of posterior valve.

Figure 98. *Acanthopleura echinata* (Barnes, 1824). Los Colorados, Chile (LACM 75-19); specimen 23 mm long.

Figure 99. *Acanthopleura echinata* (Barnes, 1824). Same specimen as in Figure 98. Close-up of anterior valves.

Figure 100. *Acanthopleura echinata* (Barnes, 1824). Tumbes, Chile (AJF coll.); specimen ca. 70 mm long. Dorsal aspect of posterior valve.

Figure 101. *Acanthopleura echinata* (Barnes, 1824). Same specimen as in Figure 100. Posterior aspect of posterior valve.

Figure 102. *Acanthopleura echinata* (Barnes, 1824). Same specimen as in Figure 100. Ventral aspect of posterior valve.

an illustration in CHEMNITZ (1785, 8:279, pl. 95, figs. 797, 798) with Magellan Strait as locality. PILSBRY (1983c), KAAS (1972), and KAAS & VAN BELLE (1980) assigned the figured specimen to the West Indies (*i.e.*, to *Acanthopleura granulata*); ROCHEBRUNE (1889) assigned it to Australia; NIERSTRASZ (1905b, 1906) to the Cape of Good Hope, South Africa. The name is here suppressed as a *nomen dubium*.

Chiton unguiculatus BLAINVILLE, 1825:544, is regarded here also as a *nomen dubium*, having no locality, no illustration, and lacking descriptive elements to differentiate it from other species of *Acanthopleura*.

Acanthopleura echinata (Barnes, 1824)

Figures 98 to 105, and 113-E

Chiton echinatus BARNES, 1824:71–72, pl. 3, figs. 4a, 4b; SOWERBY, 1840b:1, 9, sp. 1, fig. 47.

Corephium echinatus: GRAY, 1847a:68, 1847b:169, 1857:184; DALL, 1879:280, fig. 30 (radula).

Acanthopleura echinata: PILSBRY, 1893a:105, 1893c:217–219, pl. 47, figs. 6–17 (in subgen. *Mesotomura*); PLATE, 1898: 5–167, pls. 1–10, figs. 1–110; NIERSTRASZ, 1905a:102; SCHWEIKART, 1905:384–386, figs. 20, 26–28; HORST & SCHEPMAN, 1908:526; DALL, 1909:180, 248, pl. 23, fig. 6; AYRES, 1916:335; BERGENHAYN, 1930a:8, 31, 33; pl. 8, fig. 74; GIGOUX, 1934:281; BOUDET, 1945:130; LELOUP, 1956:55–58, figs. 28, 29; STUARDO, 1959:145–146, 1964:82; MARINOVICH, 1973:43, fig. 100; LELOUP, 1980a:1.

Rhopalopleura echinata: THIELE, 1893:374 (as syn. of "*Rhopalopleura aculeata* Linnaeus"), 1909:6.

Mesotomura echinata: THIELE, 1929:22.

Chiton tuberculiferus SOWERBY, 1825:29 (*nomen nudum*).

Chiton spiniferus FREMBLY, 1827:196–197, 1832 (plates):pl. 16, fig. 1; STEARNS, 1892:334 (in subgen. *Corephium*).

Acanthochiton spinifera: STEARNS, 1894b:449.

"*Chiton aculeatus* Linnaeus" REEVE, 1847:pl. 9, fig. 49 (with *C. spiniferus* and *C. tuberculiferus* as syn.).

[*Non*: Linnaeus, 1758 (*vide* DODGE, 1952:20–21).]

"*Rhopalopleura aculeata* Linnaeus" THIELE, 1893:373–374, pl. 30, fig. 37, 1909:6.

"*Corephium aculeatum* Linnaeus" MOSELEY, 1885:18–19, pl. 5, fig. 8, pl. 6, figs. 10–12 (aesthetes).

Type material and type locality:

Chiton echinatus Barnes, 1824: Types unascertained; locality "Coast of Peru," here restricted to Callao, Peru (12°02'S, 77°05'W).

Material examined:

PERU: Talara, 4 specimens (CAS 010147); Paita, 8 specimens, largest 100 mm long (CAS 010145; LACM 72-86); Lobos de Tierra Id., 1 specimen (LACM 74-10); Lobos de Afuera Id., 10 specimens, largest 75 mm long (LACM 74-5; LACM 74-6); Guanape Id., 2 specimens (LACM 74-2); Callao, 1 specimen (CAS 012793).

CHILE: Arica, 2 specimens (CASG-SU 33761); Iquique, 1 specimen, 110 mm long (CAS 010146); Cumbres Borascosas, Tarapaca Prov., 1 specimen, 45 mm long (LACM 75-14); Los Colorados, Antofagasta Bay, 4 specimens,

largest 42 mm long (LACM 75-19); Antofagasta, 7 specimens, largest 100 mm long (LACM 75-15); Los Molles, Aconcagua Prov., 1 specimen, 44 mm long (LACM 75-28); Isleta Concon, Valparaiso Prov., 1 specimen, 132 mm long (LACM 75-31); Valparaiso, 9 specimens, largest 112 mm long (CAS 030914; CAS 030942); Punta Tumbes, Bahía de Concepcion, 7 specimens, largest 105 mm long (AJF coll., *leg.* E. Bay-Schmith).

Description: Owing to the accompanying illustration, BARNES' (1824) brief description of *Chiton echinatus*, based upon two specimens from Peru, is quite sufficient to identify the species.

Among 59 specimens of *Acanthopleura echinata* here examined, largest 132 mm long (in alcohol) (LACM 75-31; Isleta Concon, Valparaiso Prov., Chile) (largest specimen reported, 200 mm long [PLATE, 1898: Pajaros Id., off Coquimbo, Peru]). Specimens (Figures 98–102) depressed, subcarinate. Body width/length, mean 0.57 (SD = 0.06; n = 17), specimens becoming relatively wider with growth (width/length ratio *vs.* specimen length, $r = 0.58$, $P < 0.02$, n = 17) (Figure 103). Tegmentum smooth to shiny (but often eroded), dark reddish-brown, with occasional small blue spots. Lateral areas hardly raised, smooth except for two radial rows, one of 5–9 round granules along diagonal line, another of 5–9 elongate granules indenting sutural edge. Anterior valve with some 10 radial rows of round granules; space between rows smooth. Central areas with raised, well defined, smooth jugal band bordered by shallow, longitudinal grooves with short, wavy, longitudinally oriented riblets on pleural areas. Mucro elevated, prominent, central to posterior; postmucro sharply sloped. Ocelli round to oval, 40–50 μm in diameter, throughout anterior valve, postmucro area of posterior valve, and lateral areas of intermediate valves. Eaves somewhat spongy. Gills with 50–70 plumes per side.

Articulamentum white, often with red discolorations at apex of valves. Central part of all valves show conspicuous, transverse, strongly engraved lines. Sutural laminae subrectangular; sinus well defined, pectinate; on valve viii, relative width of sinus, 0.44. Insertion plates strongly pectinate on outside; sinus minutely pectinate. Posterior valve with pectinate insertion plate with 1–3 slits (none in small specimens), irregularly and variably arranged, often with one particularly better defined on or near midline. Slit formula 8-1-0/3. Width of valves i/viii, 0.87. Valve viii tegmental surface length/width, 0.61.

Girdle upper surface with erect, strong, spikelike spines (Figure 104), round in cross section, up to 8 mm long in large specimens (longer if not broken), often encrusted; in addition, abundant spinelet-like elements averaging 300 \times 80 μm , separated by about 100–200 μm or more of "nude" girdle. Girdle bridges empty. Undersurface with transparent scales, about 35 \times 35 μm , with convex outer edge, concave inner edge, vaguely striate.

In specimen 70 mm long (AJF coll.: Tumbes, Chile), radula 31 mm long (44% of specimen length), comprising 65 rows of mature teeth. Median tooth (Figure 105) 130

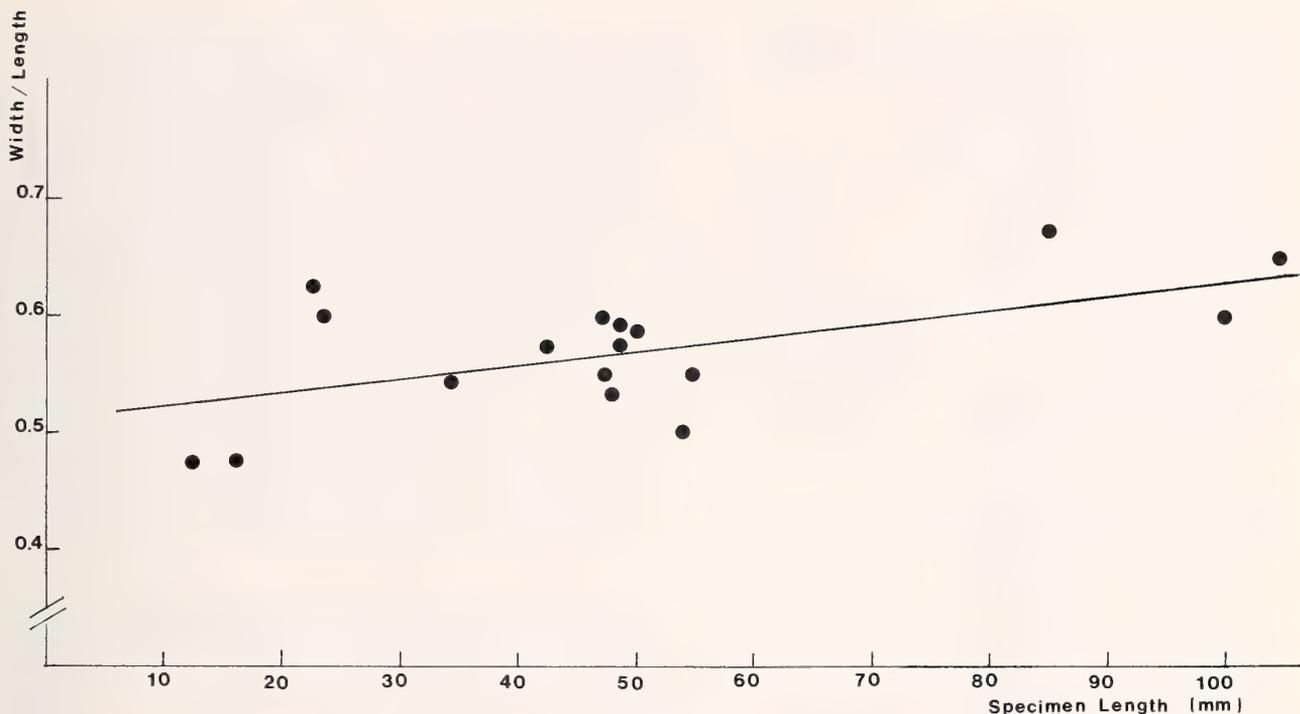


Figure 103

Acanthopleura echinata (Barnes, 1824). "Wideness" of specimen (body width/length ratio) as a function of specimen length (mm): Large specimens are relatively wider than smaller ones ($r = 0.58$; $n = 17$; $P < 0.02$).

μm wide at anterior blade; first lateral teeth $200 \mu\text{m}$ wide at anterior blade; head of second lateral teeth discoid, $550 \mu\text{m}$ wide; outer marginal teeth $350 \mu\text{m}$ long, $350 \mu\text{m}$ wide (length/width, 1.0).

Distribution: *Acanthopleura echinata* is confined to the western coast of South America (Figure 113-G), from Talara, Peru ($4^{\circ}35'S$), the northernmost verified record (CAS 010147), to Punta Tumbes, Bahía de Concepcion, Chile ($36^{\circ}37'S$), the southernmost verified record (AJF coll., leg. E. Bay-Schmith, Feb.–Sept. 1977). Reports of the species at the Galápagos Islands, Ecuador (PILSBRY, 1893c; STEARNS, 1894; NIERSTRASZ, 1905a; DALL, 1909), have not been confirmed (see SMITH & FERREIRA, 1977).

Acanthopleura echinata is limited to the intertidal zone and shallow subtidal, 0–4 m, on rocks often exposed to heavy surf.

Remarks: Among early authors, *Chiton echinatus* Barnes, 1824, occasioned some taxonomic confusions. SOWERBY (1825:29) named the species *Chiton tuberculiferus* as a replacement for "*Aculeatus*, Barnes" (!), apparently confusing the name *echinatus* with *aculeatus*, for nowhere did BARNES (1824) use the latter name. FREMBLY (1827) described and illustrated "*tuberculiferus*," which SOWERBY (1825) had left as a *nomen nudum*, and renamed it *spiniferus* "because the name *aculeatus* given to it by Barnes [!] was long since previously occupied; that of *tuberculifer-*

us [Sowerby, 1825] was given from an old specimen, in which the spines were reduced in length by being broken, so that it is not applicable [!]; we have therefore now called it *spiniferus*" (p. 197). REEVE (1847b) compounded the confusion by stating that "the *C. spiniferus* of Fremby . . . is the old Linnaean *C. aculeatus* in fine condition . . . [and figured] in Chemnitz, Conch. Cab. v. 10. pl. 173. f. 1692." It must only be added that the cited figure 1692 in CHEMNITZ (1788) does not conform at all, in morphology or locality (Nicobar Is.), to *echinatus* Barnes, 1824!

Chiton echinatus was first allocated to *Acanthopleura* by PILSBRY (1893a) in the monotypic subgenus *Mesotomura* Pilsbry, 1893a (= *Corephium* Gray, 1847a [not Browne, 1827]). The material here examined shows that PILSBRY's (1893c) "single median-posterior slit," characterizing *Mesotomura*, is not a constant feature of *A. echinata*, which may have 1 to 3 slits (none, in small specimens) on the posterior valve, and not necessarily in the midline.

In the uniqueness of its tegmental sculpture, articulation, and girdle *A. echinata* differs sharply from all other species of *Acanthopleura*. It is a curious fact, then, that workers since PILSBRY (1893c) have easily accepted *echinata* as a member of the genus *Acanthopleura* while relegating species much closer to its type (*A. spinosa*), such as *A. gaimardi*, *A. japonica*, *A. miles*, or *A. curtisiana*, to other genera.

Throughout its range, *Acanthopleura echinata* is sym-

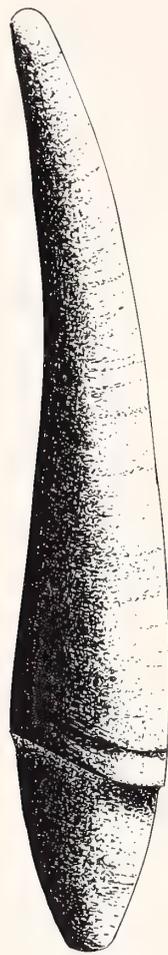


Figure 104

Acanthopleura echinata (Barnes, 1824). Same specimen as in Figure 100. Girdle spikelike spine.

patric with *A. nigra* from which it clearly differs in tegmental sculpture and girdle elements.

Acanthopleura nigra (Barnes, 1824)

Figures 106 to 111, and 113-N

Chiton niger BARNES, 1824:71, pl. 3, fig. 3; GRAY, 1828:6 (with *C. coquimbensis* Frembly as syn.).

Enoplochiton niger: GRAY, 1847a:69, 1847b:169, 1857:181; MOSELEY, 1885:19, pl. 4, figs. 6-9; THIELE, 1893:375, pl. 30, fig. 40; PILSBRY, 1893c:252-253, pl. 52, figs. 22-29; PLATE, 1898:208-215, pl. 9, figs. 86-88, pl. 12, figs. 135-140; NIERSTRASZ, 1905a:106; HORST & SCHEP-MAN, 1908:528; DALL, 1909:181, 248, pl. 23, fig. 8; THIELE, 1929:21; BERGENHAYN, 1930a:32-34, pl. 8, figs. 78-79, pl. 9, figs. 81-82; GIGOUX, 1934:281; LELOUP,

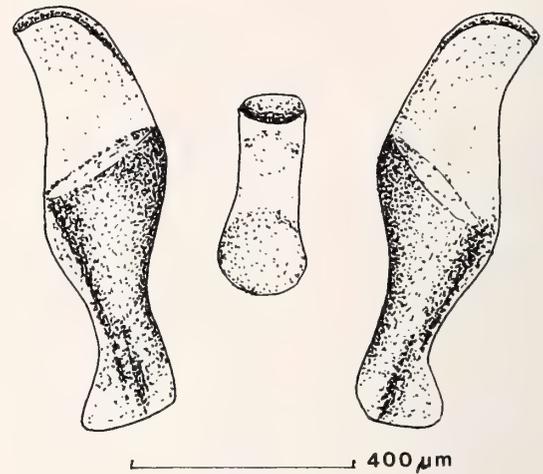


Figure 105

Acanthopleura echinata (Barnes, 1824). Same specimen as in Figure 100. Radula median and first lateral teeth.

1939b:6-9, figs. 5, 6, 1956:54-55; STUARDO, 1959:144, 146, 1964:82; MARINCOVICH, 1973:43, fig. 99.

Chiton coquimbensis FREMBLY, 1827:197-198, 1832 (plates): pl. 16, fig. 2; REEVE, 1847, pl. 4, sp. & fig. 22.

Type material and locality:

Chiton niger Barnes, 1824: Types unascertained; locality "Coast of Peru," here restricted to Iquique, Chile (20°13'S, 70°10'W).

Chiton coquimbensis Frembly, 1827: Types unascertained; locality Coquimbo Bay, Peru (29°58'S, 71°21'W).

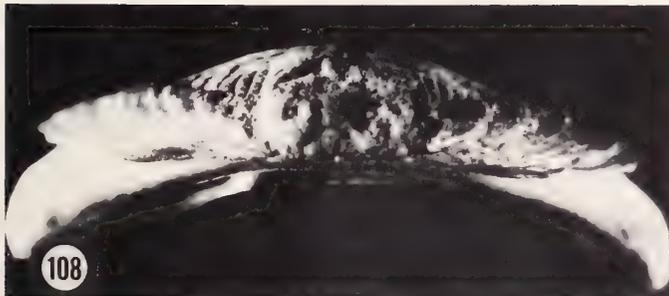
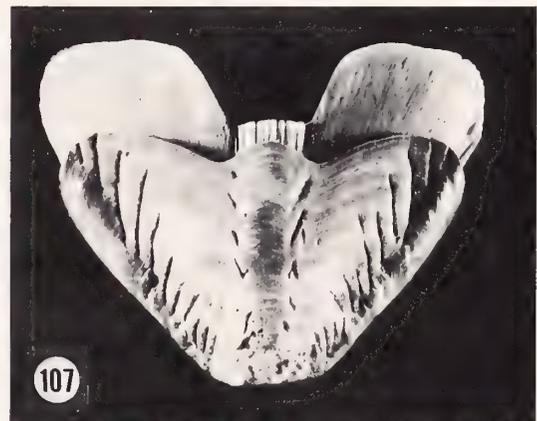
Material examined:

PERU: Talara, 2 specimens, largest 59 mm long (CAS 010148); Pisco, 3 specimens (CASG-SU 35328); Callao, 17 specimens (CAS 012791).

CHILE: Independencia Bay, 2 specimens (LACM-AHF 380-35); Arica, 3 specimens, largest 90 mm long (CASG-SU 33760); Iquique, 5 specimens, largest 131 mm long (LACM 64-16; LACM 75-12; CAS 010144); Cumbres Barascosas, Antofagasta Prov., 1 specimen, 93 mm long (LACM 75-14); Antofagasta, 7 specimens, largest 61 mm long (LACM 75-15); Coquimbo Bay, 1 specimen (CASG-SU 32955).

Description: BARNES' (1824) brief description but good illustration of *Chiton niger* is sufficient to identify the species.

Among 41 specimens of *Acanthopleura nigra* here examined, largest 131 mm long (in alcohol) (LACM 64-16; Iquique, Chile). Body width/length, mean 0.48 (n = 9). Specimens (Figures 106-109) round-backed, depressed. Tegmentum dark chocolate-brown, shiny, but easily eroded. Valves beaked; posterior edge of valve ii forming 110-120° angle. Anterior valve with 4-6 concentric, zig-zagged furrows. Lateral areas elevated, well defined by strong round rib at diagonal line, with zig-zagged furrows as on anterior valve. Central areas well defined, smooth jugum



Explanation of Figures 106 to 109

Figure 106. *Acanthopleura nigra* (Barnes, 1824). Iquique, Chile (LACM 75-12); specimen 32 mm long.

Figure 107. *Acanthopleura nigra* (Barnes, 1824). Same specimen as in Figure 106. Dorsal aspect of posterior valve.

Figure 108. *Acanthopleura nigra* (Barnes, 1824). Same specimen as in Figure 106. Posterior aspect of posterior valve.

Figure 109. *Acanthopleura nigra* (Barnes, 1824). Same specimen as in Figure 106. Ventral aspect of posterior valve.

bordered by narrow, depressed area with irregular, short, oblique furrows; para-jugal area smooth; pleural area with longitudinal, parallel furrows, not usually reaching anterior border of valve. Mucro posterior, almost terminal. Ocelli round to oval, 20–30 μm in diameter, throughout anterior valve and anterior half of lateral areas of intermediate valves. Gills with 70–80 plumes per side.

Articulamentum dark chocolate-brown, with transverse, strongly engraved lines at middle of valves (also seen in *A. echinata* but not in any other *Acanthopleura* species). Sutural laminae somewhat elongate; sinus well defined, sinusal laminae pectinate. Insertion teeth strongly pectinate on outside. Posterior valve without insertion teeth but with well developed transverse callus. Slit formula 8/9-1-0.

Girdle thick, muscular. Upper surface dark brown, conspicuously dotted with light brown scales (Figure 110); scales irregular in size (larger in middle $\frac{1}{3}$ of girdle), up

to 1.5–2 mm long in specimens 50 mm long (larger in larger specimens), vaguely striate, usually eroded at upper edge, clearly separated from each other by area as wide as scale (in alcohol preserved specimens); on outer $\frac{1}{5}$ of girdle, scales much smaller, shorter, dark brown, erect, spine-like; girdle surface completely covered otherwise with minute, dark brown, lanceolate spicules, up to 100 μm long, 25 μm thick. Girdle bridges, empty in middle third, but crowded with small, dark brown spiculoid elements (akin to those on girdle proper) in outer thirds. Under-surface covered with transparent squarish scales, about 40 \times 40 μm , in columnar arrangement, with coarse, irregular striations.

In specimen 49 mm long, radula measures 15 mm in length (30% of specimen length) and comprises 60 rows of mature teeth. Median tooth (Figure 111) 100 μm wide at anterior blade; first lateral teeth about 500 μm long, 150 μm wide at anterior blade; head of major lateral teeth



Figure 110

Acanthopleura nigra (Barnes, 1824). Same specimen as in Figure 106. Girdle scales, outer and inner sides.

discoïd, 300 μm in width; outer marginal teeth 300 μm long, 250 μm wide (length/width, 1.2).

Distribution: *Acanthopleura nigra* is confined to the western temperate coast of South America, the Peru-Chilean zoogeographic province (BRIGGS, 1974) (Figure 113-N), from Talara, Peru (4°34'S) (CAS 010148), the northernmost verified record, to Coquimbo Bay, Chile (29°58'S) (CASG-SU 32955), the southernmost verified record.

Bathymetric range limited to the intertidal zone.

Remarks: *Chiton niger* has been generically segregated from *Acanthopleura* by authors since GRAY (1847a) and PILSBRY (1893c) on account of three taxonomic characters: (1) the girdle elements, (2) the articulamentum of the posterior valve, and (3) the ocelli.

The girdle elements of *Chiton niger* have made for easy identification of the species; the light-colored, "rude" scales, clearly separated from each other by the fleshy girdle, do confer on *C. niger* a unique appearance. However, close observation of the scales shows that, although in shape, size, and placement (*i.e.*, apart from each other) they have no similarity, they show no major departure from the girdle elements in other species of *Acanthopleura*. In addition, their implantation in the girdle through a rough, irregular, and variously shaped facet (Figure 110) conforms well to that of scales and spinelets in other species of *Acanthopleura*. The conspicuous separation of the scales by the girdle is a feature also seen, though less conspicuously, in other species of *Acanthopleura* (*e.g.*, *A. miles*, *A. curtisiana*, *A. araucariana*).

The absence of teeth in the posterior valve of *Chiton niger* led PILSBRY (1983c) to group the species with *Liolophura* and *Onithochiton* Gray, 1847a. Yet, toothless posterior valves are seen not only in other members of *Acanthopleura*—*A. gaimardi*, *A. japonica* (the "*Liolophura*"), *A. hirtosa*, and *A. rehderi*)—and in *Onithochiton*, but also in other genera and other families, such as in the acanthochitonid *Cryptoplax* Blainville, 1818, the schizochitonids *Aulacochiton* Shuttleworth, 1853 (= *Lorica* Adams & Adams, 1852, preoccupied by *Lorica* Bronn, 1848, a crustacean) and *Componochiton* Milne, 1963, and the mopalid *Plaxiphora* Gray, 1847a, indicating that similar modifications of the posterior valve have occurred more than once in the evolution of chitons.

The ocelli in *Chiton niger* were said to be, in contrast

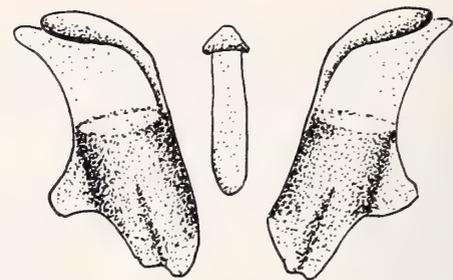


Figure 111

Acanthopleura nigra (Barnes, 1824). Same specimen as in Figure 106. Radula median and first lateral teeth.

to those of *Acanthopleura* species, "excessively minute" (MOSELEY, 1885:19) and "extremely minute and oval instead of round" (PILSBRY, 1893c:252). These statements are here in part refuted. Careful evaluation of ocelli in *Acanthopleura* shows that in *A. nigra* the ocelli are smaller (average diameter: 25 μm in *A. nigra*, 45 μm in other species of *Acanthopleura*) but not more "oval instead of round" than in other species of *Acanthopleura*.

Thus, except for the fact that the girdle scales of *Acanthopleura nigra* are distinct enough to immediately diagnose the species, there seems to be no compelling reason to segregate the species in the monotypic *Enoplochiton* Pilsbry, 1893c, and so obscure its relationship with other members of *Acanthopleura*.

Acanthopleura nigra is sympatric with *A. echinata* along the Peru-Chile coast.

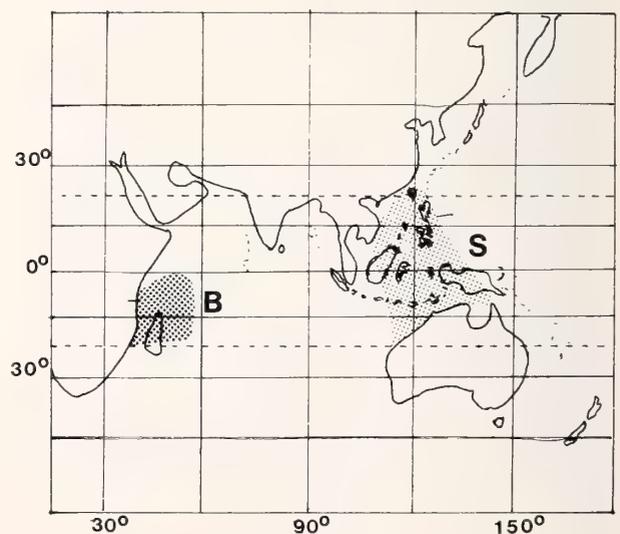


Figure 112

Geographic distribution of: S = *Acanthopleura spinosa* (Bruguère, 1792); B = *Acanthopleura brevispinosa* (Sowerby, 1840).

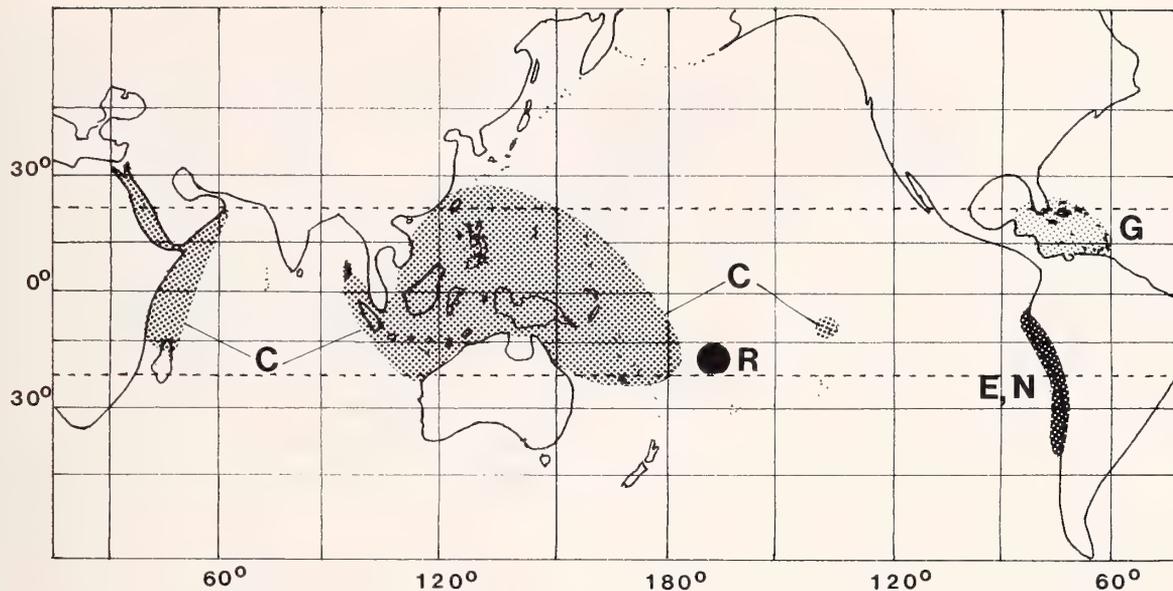


Figure 113

Geographic distribution of: C = *Acanthopleura gemmata* (Blainville, 1825); R = *Acanthopleura rehderi* Ferreira, spec. nov.; E = *Acanthopleura echinata* (Barnes, 1824); N = *Acanthopleura nigra* (Barnes, 1824); G = *Acanthopleura granulata* (Gmelin, 1791).

DISCUSSION

As here understood, the genus *Acanthopleura* corresponds to the subfamily Acanthopleurinae (*sensu* VAN BELLE, 1983:126–130), with the genera *Liolophura*, *Enoplochiton*, and *Squamopleura* suppressed as synonyms. Although the particular reasons for such an action were given previously in the account of the respective species, they bear restating here since they may not be immediately apparent to chiton taxonomists.

Liolophura Pilsbry, 1893a, erected to accommodate *Chiton incanus* (= *C. gaimardi*) and *C. japonicus*, was distinguished from *Acanthopleura* by the presence of a “smooth crescentic callus in place of the insertion-teeth” (PILSBRY, 1893a:105) in the posterior valve. Despite obvious affinity with *Acanthopleura*, PILSBRY (1893a) placed the taxon “in the immediate vicinity of *Onithochiton*,” and grouped it, instead, with *Enoplochiton* and *Onithochiton* in the subfamily Liolophurinae Pilsbry, 1893c. Although Liolophurinae was rejected by some chiton workers (NIERSTRASZ, 1905a; THIELE, 1909, 1929; BERGENHAYN, 1930a, 1933), *Liolophura*, as a generic taxon, has remained in general usage.

On introducing *Liolophura*, PILSBRY (1893a, c) assumed that in species of this genus the insertion teeth of the posterior valve had been replaced by a callus. But the interpretation was faulty. Close examination of specimens of *Liolophura* species suggests that the callus in the posterior valve appears not “in place of insertion-teeth” as PILSBRY (1893a:105) asserted, but as a result of their disappearance. In fact, a transverse callus is present in the

posterior valve of most other species of *Acanthopleura*, only less developed and “hidden” by the pectinations and teeth on its posterior aspect. In this respect, it may be noted that in specimens of *A. japonica* (previously segregated in *Liolophura*) vestigial insertion teeth are often seen as coarse pectinations or rugosities on the sides (occasionally, even in the middle) of an otherwise smooth, flat-surfaced, crescentic callus, indicating by the irregularity of their presence, position, shape, and size, their vanishing, relict nature. The taxonomic significance of the absence of teeth in “*Liolophura*” is further diminished by the observation that they are absent also in other genera and families (see Remarks on *A. nigra*), and that in several other species of *Acanthopleura* (*A. brevispinosa*, *A. loochooana*, etc.) the posterior valves show “in between” forms of insertion plates where insertion teeth are present but underdeveloped. Because members of *Liolophura* and *Acanthopleura* (*sensu* Pilsbry) do not seem to differ in any other major character, the two genera are here regarded as synonymous.

Enoplochiton Gray, 1847a, erected to accommodate *Chiton niger*, has been accepted by chiton workers without dissent. Apparently, the unique appearance of *C. niger*, with its conspicuously large, light-colored (*i.e.*, eroded) scales distinctly separated by the “velvety” girdle, has been regarded as demonstration of sufficient evolutionary distance to justify assignment to a distinct genus. However, in the course of this study it became apparent that overall similarities between *C. niger* and members of *Acanthopleura* are greater than generally assumed. The girdle scales of *C. niger*, peculiar looking as they are, cannot be re-

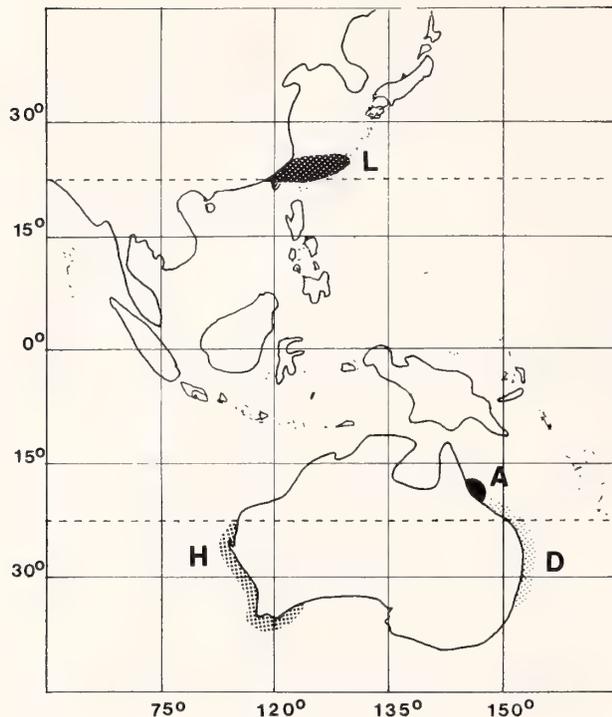


Figure 114

Geographic distribution of: H = *Acanthopleura hirtosa* (Blainville, 1825); L = *Acanthopleura loochooana* (Broderip & Sowerby, 1829); A = *Acanthopleura arenosa* Ferreira spec. nov.; D = *Acanthopleura gaimardi* (Blainville, 1825).

garded as a “major modification of the girdle armature” (ASHBY, 1929:160) of *Acanthopleura*; in fact, they do not seem to be more evolutionarily “distant” from the spines of *A. spinosa* (type species of *Acanthopleura*) than, say, the spinelets of *A. gemmata*, or the spikes of *A. echinata*. And since the modification in girdle elements is not accompanied by changes in “some more stable character” (ASHBY, loc. cit.)—in their large size, oval body shape, heavy and beaked valves, shape and distribution of ocelli (though smaller in diameter), pectinate insertion teeth, radula with discoid major lateral teeth, and intertidal habitat, specimens of *C. niger* do conform well with other *Acanthopleura* species—it seems that segregation of *C. niger* in the monotypic *Enoplochiton* is unjustified.

Acanthozostera Iredale & Hull, 1926, and *Planispina* Taki, 1962, have been long regarded as synonyms of *Acanthopleura* (SMITH, 1960; VAN BELLE, 1983).

Clavarizona Hull, 1923, was erected to accommodate a single species, *Chiton hirtosus*, distinguished from *Liolophura* for “the girdle covering which consists of . . . scales” (HULL, 1923:199). But, as already pointed out by LELOUP (1961:47), the girdle elements in *C. hirtosus* do not differ from those of other *Liolophura* “except in dimensions . . . [they appear] not as scales . . . but as spines . . . [and] their arrangement on the girdle is not regular like that of the

scales of the Chitoninae and the Ischnochitoninae; their implantation is that of the spines . . .” Thus *Clavarizona* has been synonymized to *Liolophura* (ASHBY, 1926; SMITH, 1960; LELOUP, 1961), although accepted by THIELE (1929) and VAN BELLE (1983) as a subgenus of *Liolophura*.

Squamopleura Nierstrasz, 1905a (= *Sclerochiton* Carpenter in Pilsbry, 1893b [not Kraatz, 1859]), was introduced also on account of the girdle scales: spinelets (“*kalkigen Stacheln und Dornen*”) in *Acanthopleura*, scales (“*Kalkschuppen*”) in *Squamopleura*. THIELE (1929), and presently VAN BELLE (1983), regarded the finding of needle-like spicules amidst the girdle scales of *Squamopleura* species as of generic significance. Again, close study of the girdle elements of species hitherto allocated to *Squamopleura* (*Chiton miles* and *C. curtisianus*) revealed that they are essentially the same as those of *C. hirtosus* (i.e., variable in shape and size, and implanted like a spine, in a manner already observed by LELOUP [1961b] for *C. hirtosus*), and, further, that the needle-like spicules amidst larger girdle elements are no different from those to be found in virtually all species of *Acanthopleura*. SMITH (1960), probably overlooking the presence of ocelli in *Squamopleura* species, regarded it as a subgenus of *Chiton* Linnaeus, 1758.

Acanthopleura attains greatest species diversity in the Central Indo-Pacific, in the “fertile triangle” (BRIGGS, 1974:14) of the Indo-Malayan region (EKMAN, 1953), with a “center of origin” at Taiwan where five species (*A. spinosa*, *A. gemmata*, *A. japonica*, *A. miles*, and *A. loochooana*) have been recognized.

In the central Indo-Pacific, the north-south distribution of *Acanthopleura* maps out in a curiously symmetrical manner: *Acanthopleura gemmata*, the most common species, is present virtually everywhere in the tropics. To the north of the Tropic of Cancer (approximately), in Korea, Taiwan, and Japan, *A. gemmata* is replaced in the intertidal zone by *A. japonica*; and to the south of the Tropic of Capricorn (approximately), *A. gemmata* is similarly replaced by *A. gaimardi* on the east and *A. hirtosa* on the west coasts of Australia. What is intriguing is the realization that the three species “replacing” *A. gemmata* in temperate waters, i.e., *A. japonica*, *A. gaimardi*, and *A. hirtosa*, all differ from *A. gemmata* in a single major feature, the absence of insertion teeth in the posterior valve. It is curious, too, that, in the northern hemisphere, *A. loochooana* (with posterior valve insertion teeth present but considerably underdeveloped) is confined to the zone of contact between *A. gemmata* and *A. japonica*; and, similarly, in the southern hemisphere, *A. arenosa* (with underdeveloped insertion teeth in the posterior valve) is limited to the zone of contact between *A. gemmata* and *A. gaimardi*. This correlation between the reduction or loss of insertion teeth and high latitude (both north and south) is impressive. It is tempting to speculate that the implied difference in water temperature may be a factor influencing the articulation changes, although the possible adaptive value of such changes is obscure.

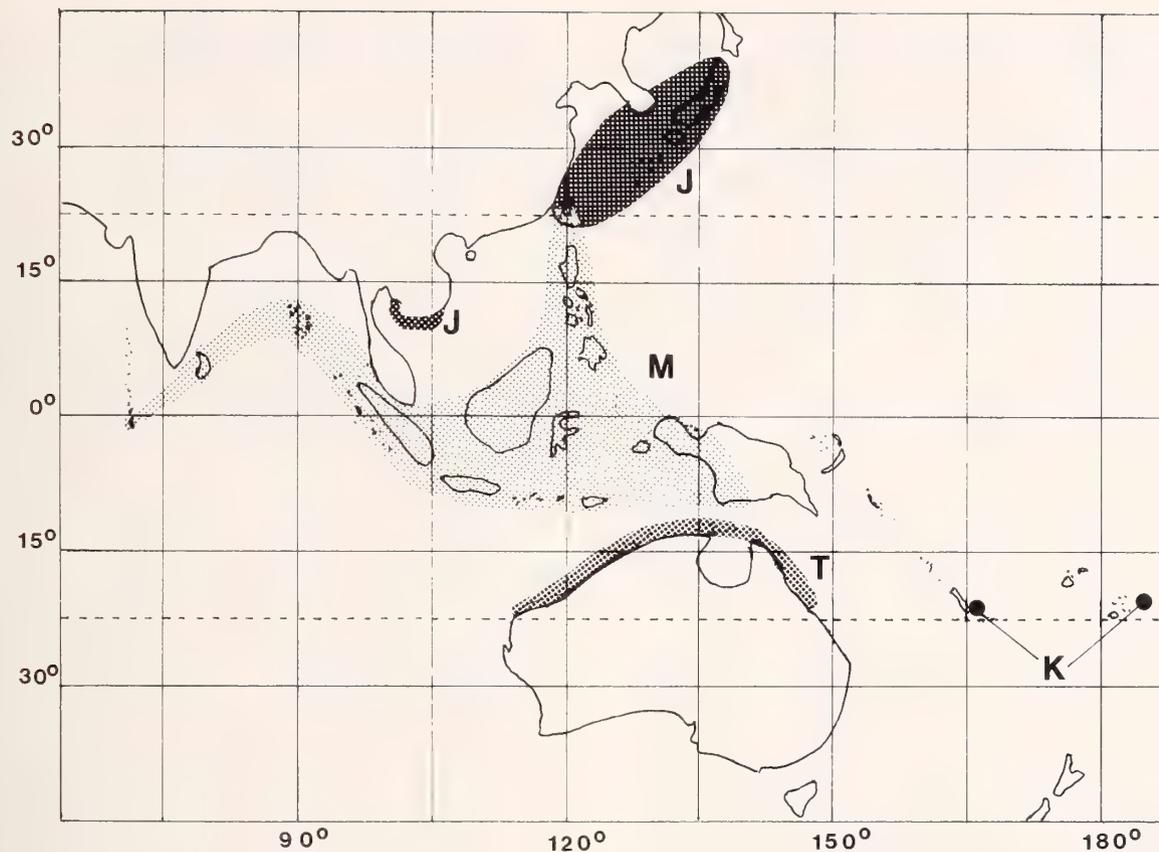


Figure 115

Geographic distribution of: T = *Acanthopleura curtisiana* (Smith, 1884); J = *Acanthopleura japonica* (Lischke, 1873); M = *Acanthopleura miles* (Carpenter in Pilsbry, 1893); K = *Acanthopleura araucariana* (Hedley, 1898).

The differential diagnosis of *Acanthopleura* species may be quite difficult at times, particularly when one is faced with dry, and eroded specimens. The fifteen species of *Acanthopleura* here recognized are remarkably similar to each other, bespeaking their congeneracy, and explaining the difficulties encountered in unraveling the group. The following summary of comparative points and comments regarding the morphology of *Acanthopleura* species may be of value:

(1) The relatively large size of the specimens, drab and eroded tegmentum, and intertidal habitat (on top of rocks, beaten by surf, emergent at low tide, often exposed to sun) are common to all *Acanthopleura* species.

(2) The valves, heavy and beaked, are usually (easily?) eroded; but even among pristine, young specimens, interspecific distinctions in the tegmental sculpture are minor and hard to draw out (except in *A. spinosa*, *A. echinata*, and *A. nigra*), making for difficulties in the differential diagnosis of the species. In all species, the tegmentum recurves forward at the ventroposterior portion of the valve, forming an underfold or hypotyche (see HOARE *et al.*, 1983).

(3) The ocelli are essentially identical in distribution, shape, and size in all species, although somewhat smaller in *A. nigra*. They are assumed to be light-sensitive organs (BOYLE, 1969, 1972). In this respect, it is curious to observe that in *Tonicia*, *Onithochiton*, or *Schizochiton*, whose specimens are hardly ever eroded, the ocelli are likely to remain functional throughout life; but in *Acanthopleura* their usefulness appears short-lived, because they are soon destroyed by erosion (though a few are usually seen at the periphery of the growing shell). The possible sensory function of the hypotyche (HOARE *et al.*, 1983:996), well developed in *Acanthopleura*, may conceivably compensate for the loss of sensory input resulting from erosion of the ocelli. No ocelli have been found in the hypotyche of *Acanthopleura* species.

(4) The significant differential features in the articulation of *Acanthopleura* species are limited to the posterior valve, where the insertion teeth may be well developed (*A. spinosa*, *A. gemmata*, and *A. granulata*), absent (*A. gaimardi*, *A. japonica*, *A. hirtosa*, *A. rehderi*, and *A. nigra*), or poorly and irregularly developed (in the other species). In *A. echinata* and *A. nigra*, sympatric species

along the Peru–Chile coast, the articulamental surface shows an area of strongly engraved transverse lines in the middle of the valves; curiously, this feature is not present in any other species of *Acanthopleura*, but is seen in species of the genus *Mopalia* Gray, 1847a.

(5) The girdle upper surface main elements may be spikelike (*A. echinata*), spines (*A. spinosa*), spinelets (*A. gemmata*, *A. granulata*, *A. brevispinosa*, *A. arenosa*, *A. loochooana*, *A. gaimardi*, *A. japonica*, and *A. rehderi*), or scales (*A. miles*, *A. araucariana*, *A. curtisiana*, *A. hirtosa*, and *A. nigra*). The undersurface shows no significant distinctions among species.

(6) With the exception of *A. brevispinosa* and *A. rehderi*, the radula is remarkably constant in *Acanthopleura*, revealing no species-specific features.

Acanthopleura has no fossil record, a rather intriguing fact for a group so widely distributed, and containing specimens that, in most of the fifteen species known, are relatively large and abundant in the intertidal zone. However, the presence of *Acanthopleura* in the Caribbean, as *A. granulata*, indicates that the genus antedates the closure of the Pacific-Atlantic seaway which, as it may be inferred from GEISTER's (1977) work on corals, did not take place until the late Pleistocene.

A diagnostic key to the species of *Acanthopleura* is here suggested. In the case of very similar species where the question of conspecificity is still at issue (*A. gaimardi* vs. *A. japonica*, and *A. granulata* vs. *A. gemmata*) it was thought preferable to use couplets based upon broad geographic localities rather than give artificial importance to some minor and/or inconstant character. In this manner it is hoped the diagnostic key will better fulfill its main purpose: to provide a practical tool for the nonspecialist.

Diagnostic Key of *Acanthopleura* Species

- 1. Posterior valve with no insertion teeth 2
 Posterior valve with insertion teeth 6
- 2. Girdle with scales 3
 Girdle with spinelets 4
- 3. Girdle scales large (1–2 mm long in large specimens), separated from each other by girdle (Peru–Chile coast) *A. nigra*
 Girdle with moderate size scales (less than 0.5 mm long even in large specimens) relatively close together (southwest Australia) ... *A. hirtosa*
- 4. Radula major lateral teeth with tetracuspid head *A. rehderi*
 Radula major lateral teeth with discoid head .. 5
- 5. Specimens from north of Tropic of Cancer (or Gulf of Thailand) *A. japonica*
 Specimens from south of Tropic of Capricorn *A. gaimardi*
- 6. Posterior valve with well developed insertion teeth 7
 Posterior valve with poorly developed insertion teeth 8

- 7. Specimens from the Caribbean Sea ... *A. granulata*
 Specimens from the Indo-Pacific *A. gemmata*
- 8. Girdle with spikelike elements (Peru–Chile) coast *A. echinata*
 Girdle with scales, spines or spinelets but not spikelike elements 9
- 9. Girdle with long, blackish, thin spines; tegmentum reddish; intermediate valves often two-slitted *A. spinosa*
 Girdle with scales or spinelets; tegmentum gray to dark brown; intermediate valves uni-slitted 10
- 10. Tegmentum purple-brown to black with coarsely round granules throughout; girdle with equal-sized cylindrical, black (often white-tipped) spinelets; specimens length often attaining 50 mm (Indian Ocean) *A. brevispinosa*
 Tegmentum gray to light brown; girdle elements not usually cylindrical; specimens length rarely attaining 50 mm (Indo-Pacific) 11
- 11. Girdle with regular, equal-sized elements 12
 Girdle with irregular, unequal-sized elements .. 14
- 12. Girdle with spinelets *A. arenosa*
 Girdle with scales 13
- 13. Girdle scales small (up to 400 μ m long); pleural areas with granules *A. curtisiana*
 Girdle scales large (up to 800 μ m long); pleural areas almost featureless *A. miles*
- 14. Lateral areas hardly raised; girdle elements variable in size and shape but mostly spinelet-like *A. loochooana*
 Lateral areas markedly raised; girdle elements also variable in shape but mostly scale-like *A. araucariana*

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LITERATURE CITED

- ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold Co.: New York. 663 pp., 4000+ figs., 24 color pls.
- ADAMS, A. 1855. Descriptions of two genera and several new species of Mollusca, from the collection of Hugh Cuming, Esq. Proc. Zool. Soc. Lond. 23(1855):119-124.
- ADAMS, H. & A. ADAMS. 1852. On a new genus of Chitonidae. Ann. Mag. Natur. Hist. 2(9):355.
- ADAMS, H. & A. A. ADAMS. 1853-1858. The genera of Recent Mollusca arranged according to their organization. 3 vols. John van Voorst: London. 1(1854):467-484.
- ALLAN, J. 1959. Australian shells. Griffin Press: Melbourne. 487 pp., 112 figs., 44 pls.
- ALTENA, C. O. VAN R. 1969. The marine Mollusca of Suriname (Dutch Guiana) Holocene and Recent. Zool. Verhand., No. 101:1-49, pls. 1-4.
- ANG, E. Z. 1967. Loricates of the Philippines. Natur. Appl. Sci. Bull. Univ. Philippines 20:383-464, 11 pls.
- ANGAS, G. F. 1867. A list of species of marine Mollusca found in Port Jackson Harbour, New South Wales, and on the adjacent coasts, with notes on their habits, etc. Proc. Zool. Soc. Lond. (for 1867):185-233.
- ARNOLD, A. F. 1901. The sea-beach at ebb-tide. A guide to the study of seaweeds and the lower animal life found between tide-marks. 490 pp., 600+ figs. [republished unabridged, 1968, Dover Publications Inc., New York].
- ASHBY, E. 1918. Notes on South Australia Polyplacophora with additions to the fauna; together with a list of Australian Polyplacophora showing their distribution in the Australian States. Trans. Roy. Soc. South Australia 42:79-87.
- ASHBY, E. 1920. Further notes on Australian Polyplacophora, with additions and corrections of the 1918 distribution list. Trans. Roy. Soc. South Australia 44:283-292.
- ASHBY, E. 1921. Notes on some Western Australian chitons (Polyplacophora) with additions to the fauna, and the description of a new species of *Rhyssoplax*. Trans. Roy. Soc. South Australia 45:40-49, pl. 3.
- ASHBY, E. 1922a. Notes on the Australian representatives of the genus *Acanthopleura*, Guilding, together with a description of Polyplacophora in the Western Australian Museum. J. Proc. Roy. Soc. West. Australia 8:29-34.
- ASHBY, E. 1922b. Types of species of Australasian Polyplacophora described by De Blainville, Lamarck, De Rochebrune, and others, now in the Muséum d'Histoire Naturelle, in Paris. Trans. Roy. Soc. South Australia 46:572-582.
- ASHBY, E. 1923a. A review of *Ischnochiton (Haploplax) smaragdinus* Angas, 1867, and its congeners, together with the description of two new chitons from Papua. Trans. Roy. Soc. South Australia 47:224-229, pls. 16-19.
- ASHBY, E. 1923b. Notes on a collection of Polyplacophora from Carnarvon, Western Australia, with definitions of a new genus and two new species. Trans. Roy. Soc. South Australia 47:230-236, pls. 16-19.
- ASHBY, E. 1926. The regional distribution of Australian chitons (Polyplacophora). Rep. Seventh Meeting of Australasian Assoc. Adv. Sci. Adelaide, August 1924, Proc. of Section D, 17:366-393.
- ASHBY, E. 1928. Notes on a collection of chitons (Polyplacophora) from the Capricorn Group, Queensland. Trans. Proc. Roy. Soc. South Australia 52:167-173, pl. 12.
- ASHBY, E. 1929. Taxonomic value of characters in the order Polyplacophora. Proc. Malacol. Soc. Lond. 18(4):159-164.
- ASHBY, E. 1931. Monograph of the South African Polyplacophora (chitons). Ann. South Africa Mus. 30(1):1-59, 2 text figs., 7 pls.
- AYRES, B. 1916. Catálogo das conchas exóticas existentes no Museu Zoológico da Universidade de Coimbra. Vol. 1, 386 pp., Coimbra.
- BABOOLAL, S., S. JOHNATTY & Z. ALI. 1981. Studies on the Trinidad chitons. "Living World," J. Trinidad Field Naturalists Club 1981:39-45, figs. 1-9.
- BARNARD, K. H. 1963. Contributions to the knowledge of South African marine Mollusca. Polyplacophora. Ann. S. African Mus. 47(2):327-344.
- BARNES, D. H. 1824. Description of five species of *Chiton*. Amer. J. Sci. 7(1):69-72, pl. 3, figs. 1-4.
- BASTOW, R. A. & J. H. GATLIFF. 1907. New species of Australian chiton from Queensland, *Enoplochiton torri*. Proc. Roy. Soc. Victoria 20(N.S.):27-30, pls. 3, 4.
- BERGENHAYN, J. R. M. 1930a. Kurze Bemerkungen zur Kenntnis der Schalenstruktur und Systematik der Loricaten. Kungl. Svenska Vetensk. Akad. Handl. (3)9(3):3-54, 5 text figs., 10 pls.
- BERGENHAYN, J. R. M. 1930b. Die Loricaten von Prof. Dr. Sixten Bocks Pazifik-Expedition 1917-1918 mit spezieller Berücksichtigung der Perinotumbildungen und der Schalenstruktur. Kungl. Vetenskaps- och Vitterhets-Samhälles Handl., ser. B., 1(12):1-52, pls. 1-3.
- BERGENHAYN, J. R. M. 1933. Die Loricaten von Prof. Dr. Sixten Bocks Expedition nach Japan und den Bonin-Inseln 1914. Kungl. Svenska Vetensk. Handl., Stockholm 12(4):3-58, 3 pls., 17 text figs.

- BERGENHAYN, J. R. M. 1955. Die fossilen schweidschen Loricaten nebst einer vorläufigen Revision des Systems der ganzen Klasse Loricata. Lunds Univ. Årsskrift. (Avd. 2, N.S.) 51(8):1-43, 2 pls. [Kungl. Fysiogr. Sällsk. Handl. N.F. 66(8):3-42, 2 tpls.].
- BERRY, S. S. 1925. On an abnormal specimen of the chiton *Acanthopleura granulata*. Ann. Mag. Natur. Hist. (9)16:173-175, pl. 12.
- BERRY, S. S. 1956. Diagnoses of few eastern Pacific chitons. Leaflets in Malacol. 1(13):71-74.
- BLAINVILLE, H. D. DE. 1818. *Cryptoplax*, 12:124. In: F. Cuvier (ed.), Dictionnaire des Sciences Naturelles . . . Paris & Strasbourg, 60 vols.
- BLAINVILLE, H. D. DE. 1825. Oscabrion, *Chiton*, 36:519-55. In: F. Cuvier (ed.), Dictionnaire des Sciences Naturelles . . . Paris & Strasbourg, 60 vols.
- BOSCH, D. & E. BOSCH. 1962. Seashells of Oman. Longman Group: New York. 206 pp.
- BOSS, K. J. 1964. Notes on a hybrid *Tellina* (Tellinidae). Nautilus 78(1):18-21 [not seen].
- BOYLE, P. R. 1969. Fine structure of the eyes of *Onithochiton neglectus*. Zeitschr. Zellforsch. Mikroskop. Anat. 102:313-332.
- BOYLE, P. R. 1972. The aesthetes of chitons. 1. Role in the light response of the whole animals. Mar. Behav. Physiol. 1:171-184.
- BOUDET, I. 1945. Los Quitones Chilenos. Rev. Chilena Hist. Natur. 48:122-140.
- BRIGGS, J. C. 1974. Marine zoogeography. McGraw-Hill: New York. 475 pp., 65 figs.
- BRODERIP, W. J. & G. B. SOWERBY (1ST). 1832-1833. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. Proc. Zool. Soc. Lond. (for 1832):25-33 (April 21, 1832); 50-61 (June 5, 1832); 104-108 (July 31, 1832); 124-126 (August 14, 1832); 173-179 (January 14, 1833); 194-202 (March 13, 1833).
- BRONN, H. G. 1848. Index Palaeontologicus oder Übersicht der bis jetzt bekannten fossilen Organismen. Stuttgart. lxxxiv + 1381 pp.
- BROWNE, P. 1789. The civil and natural history of Jamaica. 2nd ed. B. White & Son: London. viii + 503 pp., 49 pls., 1 map.
- BRUGUIÈRE, J. G. 1792. De deux coquilles des genres de l'Oscabrion et de la Pourpre. J. Hist. Natur. (Paris) 1:20-32, pl. 2, figs. 1, 2.
- BUCKNILL, C. E. R. 1930. Further microscopical details of New Zealand Loricata. Trans. Proc. New Zealand Inst. 60(4):521-531.
- BURROW, E. I. 1815. Elements of conchology according to the Linnaean system. xix + 245 pp., 28 pls.
- CARPENTER, P. P. 1865. Diagnoses specierum et varietatum novarum moluscorum, prope Sinum Pugetianum a Kennerlio Doctore, nuper decesso, collectorum. Proc. Acad. Natur. Sci. Phila. 17(2):54-64.
- CHELAZZI, G., S. FOCARDI & J. L. DENEUBOURG. 1983. A comparative study on the movement patterns of two sympatric tropical chitons (Mollusca: Polyplacophora). Mar. Biol. 74:115-125.
- CHEMNITZ, J. H. 1785. In: Martini & Chemnitz, Neues systematisches Conchylien-Cabinet. Nurnberg. 8:252-293, pls. 94-96, figs. 788-810.
- CHEMNITZ, J. H. 1788. In: Martini & Chemnitz, Neues systematisches Conchylien-Cabinet. Nurnberg. 10:370-376, pl. 173, figs. 1688-1692.
- CHENU, J. C. 1859. Manuel de conchyliologie et de paléontologie conchyliologique. Paris. 499 pp., 3707 text figs.
- CONDE, V. 1966. Studies on the ecology and distribution of the marine shelled Mollusca of Barbados. Master's Thesis, McGill Univ., Montreal, P.Q., Canada. 378 pp.
- COSSMAN, A. E. M. 1888. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. Ann. Roy. Malacol. Belgique 23:3-339, pls. 1-12.
- DALL, W. H. 1879. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. Proc. U.S. Natl. Mus. (1878) 1:281-344, 5 pls.
- DALL, W. H. 1881. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877-79, by the United States Coast Survey Steamer "Blake," Lieutenant-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XV. Preliminary report on the Mollusca. Bull. Mus. Compar. Zool., Harvard 9(2):33-144.
- DALL, W. H. 1882. On the genera of chitons. Proc. U.S. Natl. Mus. (for 1881) 4:279-291.
- DALL, W. H. 1889. Preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. Bull. U.S. Natl. Mus. 37:3-221, 74 pls.
- DALL, W. H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological Province. Proc. U.S. Natl. Mus. 37(1704): 147-294, pls. 20-28.
- DALL, W. H. 1919. Descriptions of new species of chitons from the Pacific Coast of America. Proc. U.S. Natl. Mus. 55(2283):499-516.
- DALL, W. H. & C. T. SIMPSON. 1901. The Mollusca of Porto Rico. Bull. U.S. Fish Commission 20(1):351-524, pls. 53-58.
- DAUTZENBERG, P. 1900. Croisières du yacht Chazalie dans l'Atlantique. Mém. Soc. Zool. France 13:145-265, pls. 9-10.
- DAUTZENBERG, P. 1923. Liste préliminaire des Mollusques marins de Madagascar et description de deux espèces nouvelles. J. Conchyl. 68:21-74.
- DAUTZENBERG, P. 1929. Mollusques testacés marins de Madagascar. In: G. Petit, Faune des colonies Françaises. Paris. 3:321-636.
- DAVIS, G. M., R. ROBERTSON & M. MILLER. 1979. Catalog of the chiton types of the Academy of Natural Sciences of Philadelphia. Tryonia, Misc. Publ. Dept. Malacol. Acad. Natur. Sci. Phila. 1:1-60.
- DAVIS, H. C. 1950. On interspecific hybridization in *Ostrea* (*Crassostrea*). Science 111(2889):522 [not seen].
- DESHAYES, G. P. 1827. Oscabrion. In: Bory de Saint-Vincent et al., Dictionnaire classique d'Histoire Naturelle. Paris. 12: 446-457.
- DESHAYES, G. P. 1863. Catalogue des mollusques de l'Île de la Réunion (Bourbon). In: L. Maillard, Notes sur l'Île de la Réunion. Paris. 144 pp., color pls. 28-40.
- DODGE, H. 1952. A historical review of the mollusks of Linnaeus. Part 1. The classes Loricata and Pelecypoda. Bull. Amer. Mus. Natur. Hist. 100:1-263.
- DUNKER, G. 1882. Index molluscorum Maris Japonici. 301 pp., 16 pls.
- DUPUIS, P. 1917. Notes prises au cours de l'examen de la collection de Polyplacophores du Muséum de Paris. Bull. Mus. Natl. Hist. Natur. Paris 23(6):533-538.
- DUPUIS, P. 1918. Notes concernant les Polyplacophores. Bull. Mus. Natl. Hist. Natur. 24(7):525-533.
- EKMANN, S. 1953. Zoogeography of the sea. Sidgwick & Jackson: London [1967 edition]. 417 pp.

- FERREIRA, A. J. 1983a. The genus *Chaetopleura* Shuttleworth, 1853 (Mollusca: Polyplacophora) in the warm-temperate and tropical eastern Pacific, Southern California to Peru, with the description of two new species. *Veliger* 25(3):203–224, 4 pls., 15 text figs.
- FERREIRA, A. J. 1983b. Researches on the coast of Somalia. The chiton fauna (Mollusca: Polyplacophora). *Monit. Zool. Italiano* 18(Suppl.):249–297.
- FISCHER, P. 1880–1887. *Manuel de conchyliologie et de paléontologie conchyliologique*. Paris. 1369 pp., 23 pls. [chitons—9:870–884, 31 Aug. 1885].
- FISCHER, P.-H. 1939. Résistance à l'exondation chez quelques Mollusques marins. *J. Conchyl.* 83(1):35–38.
- FISCHER, P.-H. 1978. L'habitat littoral parmi les mollusques polyplacophores. *J. Conchyl.* 115(1–2):30–35.
- FREMBLY, J. 1827. A description of several new species of chitones, found on the coast of Chili, in 1825; with a few remarks on the method of taking and preserving them. *Zool. J.* 3(10):193–205.
- FREMBLY, J. 1832. Supplementary plates to the *Zoological Journal*, Part IV, color pls. 16, 17.
- GEISTER, J. 1977. Occurrence of *Pocillopora* in late Pleistocene Caribbean coral reefs. Pp. 378–388 *In*: Second Symposium international sur les coraux et récifs coralliens fossils. Paris, Sept. 1975, B.R.G.M. (Paris), Mém. 89 [not seen—cited by J. W. Durham, 1980:68. A new fossil *Pocillopora* (coral) from Guadalupe Island, Mexico. *In*: D. M. Power (ed.), *The California Islands: Proceedings of a multidisciplinary symposium*, Santa Barbara, California, pp. 63–70, pls. 1, 2].
- GIGOUX, E. E. 1934. Los moluscos marinos de Atacama. *Rev. Chilena Hist. Natur.* 38:274–286.
- GLYNN, P. W. 1970. On the ecology of the Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linné: density, mortality, feeding, reproduction, and growth. *Smithsonian Contrib. Zool.* No. 66:21 pp., 10 figs.
- GMELIN, J. F. 1791. *Vermes Testacea*. *In*: Caroli A. Linné, *Systema naturae per regna tria naturae* Editio decima tertia, aucta, reformata. Lipsiae, Rudolphipoli, Litteris Bergmannianis. 1(6):3021–3910.
- GÖTTING, K. J. 1973. Die Polyplacophora der karibischen Küste Columbiens. *Arch. Moll.* 103(4/6):243–261, pls. 8–11, 6 text figs.
- GOULD, A. A. 1846. On the shells collected by the United States Exploring Expedition. *Proc. Boston Soc. Natur. Hist.* 2(14):141–145 [reprinted, 1862, *Otia Conchologica*].
- GOULD, A. A. 1852, 1856, 1861. Mollusca and shells. *In*: United States Exploring Expedition during the years 1839–1842 under the command of Charles Wilkes, U.S.N. Boston, Mass. 12:xv + 510 pp. [1852]. Addenda and Corrigenda, Philadelphia, pp. 499–509 [1856]. *Atlas*, Philadelphia, 16 pp., 52 pls. [1861].
- GOULD, A. A. 1862. *Otia Conchologica: descriptions of shells and mollusks, from 1839 to 1862*. Gould and Lincoln Publishers: Boston. 256 pp.
- GRAY, J. E. 1821. A natural arrangement of Mollusca, according to their internal structure. *London Med. Rep.* 15: 229–239.
- GRAY, J. E. 1828. *Spicilegia Zoologica; or original figures and short systematic descriptions of new and unfigured animals*. Part I, 8 pp., 6 pls. British Museum: London.
- GRAY, J. E. 1847a. On the genera of the family Chitonidae. *Proc. Zool. Soc. Lond.* 15:63–70 [June, 1847].
- GRAY, J. E. 1847b. A list of the genera of recent Mollusca, their synonyma and types. *Proc. Zool. Soc. Lond.* 15(178): 129–219 [Nov. 1847].
- GRAY, J. E. 1857. Guide to the systematic distribution of Mollusca in the British Museum. Part 1. Printed by Order of the Trustees: London. xii + 230 pp.
- GREENFIELD, M. L. 1972. Feeding and gut physiology in *Acanthopleura spinigera* (Mollusca). *J. Zool. (Lond.)* 166: 37–47.
- GUILDING, L. 1829. Observations on the Chitonidae. *Zool. J.* 5(17):25–35.
- HADDON, A. C. 1886. Report on the Polyplacophora collected by H.M.S. Challenger during the years 1873–1876. *Challenger Reports* 15(43):1–50, pls. 1–3.
- HAMILTON, S. H. 1903. Habits of *Acanthopleura granulata*. *Nautilus* 16:138.
- HANLEY, S. 1855. *Ipsa Linnaei Conchylia*. London. 556 pp., 5 pls.
- HEDLEY, C. 1898. Descriptions of new Mollusca, chiefly from New Caledonia. *Proc. Linn. Soc. New So. Wales* 23:97–105.
- HEDLEY, C. 1910. The marine fauna of Queensland. Report of the Twelfth Meeting of the Australasian Association for the Advancement of Science (1909):329–371.
- HEDLEY, C. & A. F. B. HULL. 1909. Descriptions of new and notes on other Australian Polyplacophora. *Rec. Austral. Mus.* 7(4):260–266, pls. 73–74.
- HIDALGO, E. 1956. Algunos moluscos de la Isla de Cozumel, Quintana Roo, Mexico. *Acta Zool. Mexicana* 1(10):1–24, 4 pls.
- HIDALGO, J. G. 1905. Noticia sobre las faunas malacológicas del Archipiélago de Joló e Islas Mariana. I—Moluscos marinos. *Rev. Real Acad. Cienc. Exactas, Físicas y Naturales de Madrid* 2(4):3–16.
- HOARE, R. D., R. H. MAPES & D. E. ATWATER. 1983. Pennsylvanian Polyplacophora (Mollusca) from Oklahoma and Texas. *J. Paleontol.* 57(5):992–1000, 5 figs.
- HORST, R. & M. M. SCHEPMAN. 1894–1908. *Catalogue systématique des Mollusques (Gastropodes, Prosobranches et Polyplacophora)*. *Mus. Hist. Natur. Pays-Bas [Polyplacophora]*, 1908, 13:514–528].
- HULL, A. F. B. 1923. New Australian Loricata and notes on the distribution of certain species. 1. II. *Australian Zool.* 3: 195–201, pls. 27–28.
- HULL, A. F. B. 1925. New Queensland loricates. *Proc. Roy. Soc. Queensland* 36(7):109–116, pl. 21.
- HUMMELINCK, P. W. 1933. *Zoologische Ergebnisse einer Reise nach Bonaire, Curacao und Aruba im Jahre 1930*. No. 1. *Reisebericht. Zool. Jahrb. (Systematik)* 64(3/5):289–326.
- IMAI, T. & S. SAKAI. 1961. Study of breeding of Japanese Oyster, *Crassostrea gigas*. *Tohoku J. Agricult. Res.* 12(2): 125–163 [not seen].
- INABA, A. 1982. Molluscan fauna of the Seto Inland Sea, Japan. *Hiroshima Shell Club* (ed. by K. Y. Arakawa & T. Hoshino). 181 pp., 4 pls.
- IREDALE, T. 1910a. Notes on Polyplacophora, chiefly Australasian (Part I). *Proc. Malacol. Soc. Lond.* 9(2):90–105.
- IREDALE, T. 1910b. Notes on Polyplacophora, chiefly Australasian (Part II). *Proc. Malacol. Soc. Lond.* 9(3):153–162.
- IREDALE, T. 1914a. Some more notes on Polyplacophora. Part 1. *Proc. Malacol. Soc. Lond.* 9(2):123–131.
- IREDALE, T. 1914b. Report on Mollusca collected at the Monte Bello Islands. *Proc. Zool. Soc. Lond.* (for 1914):665–675.
- IREDALE, T. & A. F. B. HULL. 1926. A monograph of the Australian loricates (Phylum Mollusca—Order Loricata). VII. *Australian Zool.* 4(4):256–276, pls. 37–39 [reprinted: *Roy. Zool. Soc. New South Wales* 1927:119–138].
- JAY, J. C. 1850. A catalogue of the shells, arranged according to the Lamarckian system, with their authorities, synonymys,

- and references to works where figured or described, contained in the collection of John C. Jay, M.D. 4th ed., New York. 459 pp.
- JOHNSON, C. W. 1934. List of marine Mollusca of the Atlantic coast from Labrador to Texas. Proc. Boston Soc. Natur. Hist. 40(1):1-204.
- KAAS, P. 1972. Polyplacophora of the Caribbean region. Studies on the fauna of Curacao and other Caribbean islands. 41(137):162 pp., 247 text figs., 9 pls. Martinus Nijhoff: The Hague.
- KAAS, P. 1979. The chitons (Mollusca: Polyplacophora) of Mozambique. Ann. Natal Mus. 23(3):855-879.
- KAAS, P. & R. A. VAN BELLE. 1980. Catalogue of living chitons. Dr. Backhuys Publish.: Rotterdam. 144 pp.
- KRAATZ, G. 1859. Arch. Naturgesch. Berlin. 25:133 [not seen].
- KURODA, T. 1941. A catalogue of Molluscan shells from Taiwan (Formosa), with descriptions of new species. Mem. Fac. Sci. & Agric., Taihoku Imp. Univ. 22(4):65-216, 7 pls.
- LAMARCK, J. B. P. A. DE M. 1819. Histoire naturelle des animaux sans vertèbres. 7 vols., Paris. [Chitons: 6(1):318-321.]
- LAMY, E. 1923. Notes sur les chitons rapportés au Muséum National de Paris par Péron et Lesueur (1803). Bull. Mus. Natl. Hist. Natur., Paris 3:260-265.
- LAMY, E. 1936. Liste des Mollusques recueillis par la Mission Franco-Belge à l'Île de Paques (1934). Bull. Mus. Hist. Natur., Paris (2)8(3):267-268.
- LAMY, E. 1938. Mollusca Testacea. Mission Robert Ph. Dollfus en Égypte. Mém. Inst. Égypte 37:1-90, 1 pl.
- LELOUP, E. 1933a. Amphineures. Mem. Mus. Roy. Hist. Natur., Bruxelles, (h.s.) 2(3):15-33, 2 pls.
- LELOUP, E. 1933b. Chitons des Philippines et Célèbes. Bull. Mem. Roy. Hist. Natur. Belgique 9(17):1-6.
- LELOUP, E. 1937a. Polyplacophora. In: Résultats scientifiques des croisières du navire-école belge "Mercator." Vol. I. Mém. Mus. Roy. Hist. Natur. Belgique (2)9:129-151, 15 figs.
- LELOUP, E. 1937b. Diagnoses de six nouvelles espèces d'Amphineures Polyplacophores de la région Indo-Pacifique. Bull. Mus. Roy. Hist. Natur. Belgique 13(38):1-3.
- LELOUP, E. 1939a. À propos des amphineures *Liolophura japonica* (Lischke, 1873) et *L. gaimardi* (Blainville, 1825): deux nouvelles formes. Bull. Mus. Roy. Hist. Natur. Belgique 15(1):1-7.
- LELOUP, E. 1939b. À propos de deux amphineures, *Squamopleura miles* (Pilsbry, 1892) et *Enoplochiton niger* (Barnes, 1824). Bull. Mus. Roy. Hist. Natur. Belgique 15(28):1-9.
- LELOUP, E. 1939c. Caractères anatomiques de certains amphineures du genre *Squamopleura*. Bull. Mus. Roy. Hist. Natur. Belgique 15(33):1-12.
- LELOUP, E. 1940. À propos des espèces du genre *Squamopleura* Nierstrasz, 1905 (Amphineures). Bull. Mus. Roy. Hist. Natur. Belgique 16(9):1-7.
- LELOUP, E. 1941. Résultats scientifiques des croisières du navire-école belge "Mercator." Vol. III. II. Polyplacophora. Mem. Mus. Roy. Hist. Natur. Belgique (2)21:35-45.
- LELOUP, E. 1952. Polyplacophores de l'Océan Indien et des côtes de l'Indochine Française. Mém. Inst. Roy. Sci. Natur. Belgique (2)47:3-69, 6 pls.
- LELOUP, E. 1956. Polyplacophora. Reports of the Lund University Chile Expedition 1948-49, no. 27. Lunds Univ. Årsskrift., N.F., Avd. 2, 52(15). Kungl. Fysiogr. Sällskap. Handl., N.F. 67(15):94 pp., 53 text figs.
- LELOUP, E. 1960. Amphineures du golfe d'Aquaba et de la Péninsule Sinai (Contributions to the knowledge of the Red Sea, no. 20). Bull. Sea Fish. Res. Stn. Israel 29:29-55, 14 text figs., 2 pls.
- LELOUP, E. 1961. Species of the genus *Liolophura* Pilsbry, 1893 (Mollusca: Polyplacophora). J. Malacol. Soc. Australia 5:38-49.
- LELOUP, E. 1980a. Polyplacophores Chiliens et Brésiliens. Bull. Inst. Roy. Soc. Natur. Belgique 52(16):1-12, 3 pls., 6 figs.
- LELOUP, E. 1980b. Chitons de la Mer Rouge, du Golfe de Suez et de la Méditerranée. Bull. Inst. Roy. Sci. Natur. Belgique 52(5):1-14, 2 pls.
- LELOUP, E. 1980c. À propos d'*Acanthopleura*. Bull. Inst. Roy. Sci. Natur. Belgique 52(15):1-12, 1 map.
- LELOUP, E. 1981. Chitons de Tuléar, Réunion, Maurice et Tahiti. Bull. Inst. Roy. Sci. Natur. Belgique 53(3):1-46, 22 text figs., 4 pls.
- LEWIS, J. B. 1960. The fauna of rocky shores of Barbados, West Indies. Canadian J. Zool. 38(2):391-435.
- LINNAEUS, C. 1758. Systema naturae per regna tria naturae. Editio decima, reformata. Stockholm, vol. 1, Regnum animale, 824 pp.
- LISCHKE, C. E. 1873. Diagnosen neue Meeres-Conchylien aus Japan. Malakozool. Blätter (for 1873) 21:19-25.
- LISCHKE, C. E. 1874. Japanische Meeres-Conchylien. Cassel. 123 pp., 9 pls.
- MACKAY, J. S. 1930. Notes on loricates (chitons) collected on the coast of Queensland in 1928 and 1930. Australian Zool. 6(3):287-300.
- MARINCOVICH, JR., L. 1973. Intertidal mollusks of Iquique, Chile. Natur. Hist. Mus. Los Angeles Co., Sci. Bull. 16:49 pp., 102 figs.
- MARTENS, E. VON. 1880. Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen bearbeitet von K. Möbius, F. Richters und E. von Martens nach Sammlungen, angelegt auf einer Reise nach Mauritius von K. Möbius. Mollusken. Pp. 179-352, 4 pls.
- MARTENS, E. VON. 1887. List of the shells of Mergui and its Archipelago, collected for the Trustees of the India Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. J. Linn. Soc. Lond. (Zool.) 21:155-219, pls. 14-16.
- MATSUI, Y. 1958. Aspects of the environment of pearl-culture grounds and the problems of hybridization in the genus *Pinctada*. Pp. 519-531. In: Buzzati-Traverso (ed.), Perspectives in marine biology. Univ. Calif. Press: Berkeley & Los Angeles [not seen].
- MAWE, J. 1823. The Linnean system of conchology. London. 207 pp.
- MAYR, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co.: New York. 428 pp.
- MAYR, E. & C. B. ROSEN. 1956. Geographic variation and hybridization in populations of Bahama snails (*Cerion*). Amer. Mus. Novitates 1806:48 pp. [not seen].
- MELVILL, J. C. 1909. Report on the marine Mollusca obtained by Mr. J. Stanley Gardiner, F.R.S., among the islands of the Indian Ocean in 1905. Trans. Linn. Soc. Lond., 2, Zool. 13(1):65-138, 5 pls.
- MELVILL, J. C. & R. STANDEN. 1899. Report on the marine Mollusca obtained during the First Expedition of Prof. A. C. Haddon to the Torres Straits, in 1888-89. J. Linn. Soc. Lond. (Zool.) 27:150-206, pls. 10-11.
- MENZEL, R. W. 1962. Seasonal growth of northern and southern quahogs *Mercenaria mercenaria* and *M. campechiensis*, and their hybrids in Florida. Proc. Natl. Shell Fisheries Assoc. 53:111-119 [not seen].
- MENZEL, R. W. & M. Y. MENZEL. 1965. Chromosomes of

- two species of quahog clams and their hybrids. *Biol. Bull.* 129(1):181-188 [not seen].
- MOOK, D. 1983. Homing in the West Indian chiton *Acanthopleura granulata* Gmelin, 1791. *Veliger* 26(2):101-105.
- MOSELEY, H. N. 1884. On the presence of eyes and other sense organs in the shells of the Chitonidae. *Ann. Mag. Natur. Hist.* (5)14:141-147.
- MOSELEY, H. N. 1885. On the presence of eyes in the shells of certain Chitonidae, and on the structure of these organs. *Quart. J. Microsc. Sci.* (for 1885):2-26, pls. 4-6.
- NIERSTRASZ, H. F. 1905a. Die Chitoniden der Siboga-Expedition. *Siboga-Expedition* 48:112 pp. + addendum, 8 pls.
- NIERSTRASZ, H. F. 1905b. Bemerkungen ueber die Chitoniden-Sammlung im Zoologischen Museum zu Leiden. *Notes Leyden Mus.* 25(10):141-159, pls. 9, 10.
- NIERSTRASZ, H. F. 1906. Beiträge zur Kenntnis der Fauna von Süd-Afrika. VI. Chitoniden aus der Kapkolonie und Natal. *Zool. Jahrb. (System.)* 23:487-520, pls. 26-27.
- NIERSTRASZ, H. F. 1908. Remarks on the Chitonidae. *Tijdschrift Nederlandsche dierkundige Vereeniging* 10:141-172, pl. 3.
- NIERSTRASZ, H. F. 1927. Chitonida. Bijdrage tot de kennis der fauna van Curaçao. *Bijdr. Dierk. Amsterdam* 25:162-163.
- ODHNER, N. H. 1919. Contribution à la faune malacologique de Madagascar. *Arkiv. Zool.* 12(6):1-52, 4 pls.
- OKADA, Y. K., IS. TAKI, T. SAKAI & T. ABE. 1954. Illustrated pocket book of the Japanese fauna in colour. The Hokuryukan Co.: Tokyo [in Japanese].
- OLSSON, A. A. & T. L. MCGINTY. 1958. Recent marine mollusks from the Caribbean coast of Panama with the description of some new genera and species. *Bull. Amer. Paleontol.* 39(177):1-58, pls. 1-5.
- ORBIGNY, A. C. V. D. D^r. 1853. Mollusques. *In: Ramón de la Sagra, Histoire physique, politique et naturelle de l'île de Cuba.* Vols. 6-7.
- OWEN, B., J. H. MCLEAN & R. J. MEYER. 1971. Hybridization in the eastern Pacific abalones (*Haliotis*). *Bull. Los Angeles Co. Mus. Natur. Hist., Sci.* no. 9:37 pp.
- OWEN, R. S. 1961. Hybridization in western American haliotids (Abstract). *Amer. Malacol. Union Ann. Rep.* for 1961, 28:34 [not seen].
- PAETEL, F. 1869. *Molluscorum systema et catalogus.* Dresden. xiv + 119 pp.
- PAETEL, F. 1873. *Catalogue der Conchylien-Sammlung.* Berlin. 172 pp.
- PALLARY, P. 1926. Explication des planches de J. C. Savigny. *Mém. Inst. Égypte* 11:1-139, pls. 1-18.
- PEARSE, J. S. 1978. Reproductivity periodicities of Indo-Pacific invertebrates in the Gulf of Suez. IV. The chitons *Acanthopleura haddoni* Winckworth and *Onithochiton lyelli* (Sowerby), and the abalone *Haliotis pustulata* Reeve. *Bull. Mar. Sci.* 28(1):92-101.
- PEARSE, J. S. 1979. Polyplacophora. *In: A. C. Giese & J. S. Pearse (eds.)*. Reproduction of marine invertebrates. Molluscs. Pelecypods and lesser classes. 5:27-85. Academic Press: New York.
- PEILE, A. J. 1926. The Mollusca of Bermuda. *Proc. Malacol. Soc. Lond.* 17:71-98.
- PELSENER, P. 1899. Recherches morphologiques et phylogénétiques sur les mollusques archaïques. *Mém. Acad. Roy. Sci. Lettres et Beaux-Arts Belgique* 57:112 pp., 24 pls.
- PILSBRY, H. A. 1892. Polyplacophora. *In: G. M. Tryon (ed.)*, *Manual of Conchology* 14:65-128, pls. 16-30.
- PILSBRY, H. A. 1893a. On *Acanthopleura* and its subgenera. *Nautilus* 6(9):104-105.
- PILSBRY, H. A. 1893b. Polyplacophora. *In: G. M. Tryon (ed.)*, *Manual of Conchology* 14:129-208, pls. 31-40.
- PILSBRY, H. A. 1893c. Polyplacophora. *In: G. M. Tryon (ed.)*, *Manual of Conchology* 14:209-350, i-xxxix, pls. 41-68.
- PILSBRY, H. A. 1894a. Polyplacophora. *In: G. M. Tryon (ed.)*, *Manual of Conchology* 15:65-132, pls. 11-17 (March 19).
- PILSBRY, H. A. 1894b. List of Port Jackson chitons collected by Dr. J. C. Cox, with a revision of Australian Acanthochitonidae. *Proc. Acad. Natur. Sci. Phila.* 46:62-88.
- PLATE, L. H. 1898-1901. Die Anatomie und Phylogenie der Chitoniden. *In: Fauna Chilensis. Zool. Jahrb., Suppl.* 4:1-243, pls. 1-12 [1898]; 5(11):5-216, pls. 2-11 [1899]; 5(2):281-600, pls. 12-16 [1901].
- QUOY, J. R. C. & J. P. GAIMARD. 1835. Voyage de découvertes de l'Atalante, exécuté par ordre du Roi, pendant les années 1826-1827-1828-1829, sous le commandement de M. J. Dumont D'Urville. *Zoologie.* Vol. 3. J. Tastu, Editeur-Imprimeur: Paris. 644 pp.
- RAFINESQUE, C. S. 1815. *Analyse de la nature, ou tableau de l'univers et des corps organisés.* Palerme [reprinted in: Wm. G. Binney & George W. Tryon, Jr. (eds.), *The complete writings of Constantine Smltz Rafinesque on Recent & Fossil conchology.* New York. 1864].
- REES, W. & A. STUCKEY. 1952. The "Manihine" expedition to the Gulf of Aqaba 1948-1949. VI. Mollusca. *Bull. British Mus. (Natur. Hist.)* 1(8):183-203, pls. 28-29.
- REEVE, L. 1842. *Conchologia systematica, or complete system of conchology.* London. 2:7-13, pls. 131-135.
- REEVE, L. A. 1847. Monograph of the genus *Chiton*. 28 pls., 194 figs. *In: Conchologia iconica, or illustrations of the shells of molluscos animals.* Vol. 4. Reeve, Benham, & Reeve: London. 20 vols.
- REMINGTON, P. S. 1922. Rambles of a midshipman. I. *Nautilus* 35(4):118-121.
- ROCHEBRUNE, A. T. DE. 1881a. Diagnoses speciorum novarum familiarum Chitonidarum. I. Species Africanæ. *J. Conchyl.* 29:42-46.
- ROCHEBRUNE, A. T. DE. 1881b. Diagnoses d'espèces nouvelles de la famille des Chitonidae. *Bull. Soc. Philomath. Paris* (7) 5:115-121.
- ROCHEBRUNE, A. T. DE. 1882. Diagnoses d'espèces nouvelles de la famille des Chitonidae (Premier supplément). *Bull. Soc. Philomath. Paris* (7)6:190-197.
- ROCHEBRUNE, A. T. DE. 1889. Polyplacophores. *In: Mission scientifique du Cap Horn, 1882-1883.* 6(2) (Zoologie: Mollusques):131-143, pls. 9.
- SALISBURY, A. E. 1953. Mollusca of the University of Oxford expedition to the Cayman Islands in 1938. *Proc. Malacol. Soc. Lond.* 30:39-54, pl. 7.
- SAUSSAYE, PETIT DE LA. 1853. Supplément au catalogue des coquilles trouvés à l'île de la Guadeloupe par M. Beau. *J. Conchyl.* 4:413-419.
- SCHIFF, M. 1858. Beiträge zur Anatomie von *Chiton piceus*. *Zeitschr. Wissenschaft. Zool.* 9:12-47, pls. 1, 2.
- SCHILDER, F. A. 1962. Hybrids between *Cypraea tigris* Linnaeus, 1758, and *Cypraea patherina* Solander, 1786. *Veliger* 5(2):83-87.
- SCHWEIKART, A. 1905. Beiträge zur Morphologie und Genese der Eihüllen der Cephalopoden und Chitoniden. *Zool. Jahrb., Suppl.* 6 (Fauna Chilensis):351-406, pls. 23-26.
- SHUTTLEWORTH, R. J. 1853. Diagnosen neuer Mollusken. No. 4. Ueber den Bau der Chitoniden, mit Aufzählung der die

- Antillen und die Canarischen Inseln bewohnenden Arten. Bern Mittheil. Pp. 45-83.
- SHUTTLEWORTH, R. 1856. Description de nouvelles espèces. Première décade: espèces nouvelles pour la faune des Antilles. J. Conchyl. 5:168-175.
- SIMROTH, H. 1892-1895. Mollusca. Polyplacophora, [1893] 3:234-240, [1894] 3:241-336, pls. 11-14. In: H. G. Brown, Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. Leipzig.
- SMITH, A. G. 1960. Amphineura. Pp. 41-76, figs. 31-45. In: R. C. Moore (ed.), Treatise on invertebrate paleontology. Part I, Mollusca 1. Univ. Kansas Press: Lawrence, Kansas. xxiii + 351 pp.
- SMITH, A. G. 1961. Four species of chitons from the Panamic Province (Mollusca: Polyplacophora). Proc. Calif. Acad. Sci. (4)30(4):81-90, pls. 8-9.
- SMITH, A. G. 1977. Rectification of west coast chiton nomenclature (Mollusca: Polyplacophora). Veliger 19(3):215-258.
- SMITH, A. G. & A. J. FERREIRA. 1977. Chiton fauna of the Galápagos Islands. Veliger 20(2):82-97, 4 pls.
- SMITH, E. A. 1884. Mollusca. Pp. 34-116, pls. 4-7. In: Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert," 1881-2. London. xxv + 684 pp., 54 pls.
- SMITH, E. A. 1891. On a collection of marine shells from Aden, with some remarks upon the relationship of the molluscan fauna of the Red Sea and the Mediterranean. Proc. Zool. Soc. Lond. for 1891:390-430, pl. 33.
- SMITH, E. A. 1903. Marine Mollusca. In: J. S. Gardiner (ed.), The fauna and geography of the Maldive and Laccadive Archipelagos 2(2):589-630, pls. 35-36.
- SMITH, E. A. 1910. On South Africa marine Mollusca, with description of new species. Ann. Natal Mus. 2(2):175-220, pls. 7, 8.
- SOLEM, M. 1953. Marine and fresh-water mollusks of the Solomon Islands. Fieldiana-Zool. 34(22):213-227.
- SOWERBY, G. B. (1ST). 1825. A catalogue of the shells contained in the collection of the late Earl of Tankerville, arranged according to the Lamarckian Conchological System; together with an appendix containing descriptions of many new species. London. Pp. i-vii, 1-92; app. i-xxxiv, 9 pls.
- SOWERBY, G. B. (1ST). 1840a. Descriptions of some new chitons. Magaz. Natur. Hist. (2)4:287-294, pl. 16.
- SOWERBY, G. B. (1ST AND 2ND). 1840b. A catalogue of the Recent species of Chitones, pp. 1-8; Corrected list of figures, pp. 9, 10. In: The conchological illustrations. London, 1833-1841 [plates of chitons, 1833].
- SOWERBY, G. B. (1ST). 1841. Descriptions of several new species of Chitones, brought by H. Cuming, Esq., from the Philippine Islands. Proc. Zool. Soc. Lond., pp. 61-62.
- SPENGLER, L. 1797. Udførlig Beskrivelse over det mængs-kallede Konkylieslaegt af Linnaeus kaldet Chiton met endeel nye Arter og Varieter. Skrivt. Nat. Selsk. Kjöbenhavn 4(1):62-103, pl. 6.
- STEARNS, R. E. C. 1892. List of shells collected on the west coast of South America, principally between latitudes 7°30'S and 8°49'N by Dr. W. H. Jones, surgeon, U.S. Navy. Proc. U.S. Natl. Mus. (for 1891) 14:307-335.
- STEARNS, R. E. C. 1894. Scientific results of exploration by the U.S. Fish Commission steamer "Albatross." XXV. Report on the mollusk fauna of the Galapagos Islands with descriptions of new species. Proc. U.S. Natl. Mus. (for 1893) 16:353-450, pls. 51, 52 (map).
- STEINBECK, J. & E. F. RICKETTS. 1941. Sea of Cortez. P. P. Appel: New York (reprinted). x + 598 pp., 40 pls., 2 charts.
- STUARDO, J. 1959. Ensayo de una clave para familias y generos chilenos de Polyplacophora, con generalidades del grupo e inclusion de algunas especies comunes. Invest. Zool. Chilenas 5:139-148.
- STUARDO, J. 1964. Distribucion de los moluscos marinos litorales en Latinoamerica. Bol. Inst. Biol. Marina, No. 7: 79-91. Mar del Plata, Argentina.
- STURANY, R. 1904. Gastropoden des Rothen Meeres. Denkschr. Akad. Wiss. Wien, Mathem.-Naturw. Cl. 74:209-283, pls. 1-7.
- SUTER, H. 1905. Supplement to the revision of the New Zealand Polyplacophora with descriptions of new species. J. Malacol. 12(4):65-71, pl. 9.
- SUTER, H. 1913. Manual of the New Zealand Mollusca. Wellington. 1120 pp.
- SUTER, H. 1915. Manual of the New Zealand Mollusca. Atlas of plates. Wellington. 72 pls.
- SWAINSON, W. 1840. A treatise on malacology, or shells and shell-fish. London. 419 pp.
- SYKES, E. R. 1907. Report on the marine biology of the Sudanese Red Sea. V. On the Polyplacophora, or chitons. J. Linn. Soc. Lond. (Zool.) 31:31-34.
- TAKI, IS. 1938. Report of the biological survey of Mutsu Bay. 31. Studies of chitons of Mutsu Bay with general discussion on chitons of Japan. Sci. Rep. Tohoku Imp. Univ. Sendai, Japan (4)12(8):323-423, pls. 14-34, 5 text figs.
- TAKI, IS. 1947. General accounts on Amphineura: figures and descriptions of chitons of Japan. Pp. 1263-1269, figs. 3594-3608. In: Illustrated encyclopedia of the fauna of Japan (exclusive of insects). Revised ed. Hokuryukan: Tokyo [in Japanese].
- TAKI, IS. 1949. *Liolophura japonica*. P. 287, fig. 904. In: Y. Okada *et al.* (eds.), Students encyclopedia fauna of Japan. Nanjo-Shoten: Tokyo [in Japanese].
- TAKI, IS. 1954. *Liolophura japonica*. P. 214, text fig. 392. In: Y. Okada *et al.* (eds.), Illustrated pocket book of the Japanese fauna in colour: II (Students' edition). Hokuryukan: Tokyo [in Japanese].
- TAKI, IS. 1960. Polyplacophora. 3:197-200, pls. 90-91. In: Y. Okada *et al.* (eds.), Encyclopedia zoologica illustrated in colours. Hokuryukan: Tokyo [in Japanese].
- TAKI, IS. 1962. A list of the Polyplacophora from Japanese Islands and vicinity. Venus 22(1):29-53.
- TAKI, IW. 1964. Classification of the Class Polyplacophora, with a list of Japanese chitons. Venus 22(4):401-414.
- TAPPARONE-CANEFRI, C. 1874. Malacologia. In: Zoologia del viaggio intorno al Globo della regia fregata Magenta durante gli anni 1865-68. 162 pp., 4 pls.
- THIELE, J. 1893. Das Gebiss der Schnecken zur Begründung einer natürlichen Classification. Polyplacophora. 2:351-401, pls. 30-32. Berlin.
- THIELE, J. 1909-1910a. Revision des systems der chitonen. 1: 1-70, pls. 1-6, 5 text figs. (1909); 2:71-132, pls. 7-10 (1910a). Stuttgart.
- THIELE, J. 1910b. Molluskenfauna Westindiens. Zool. Jahrb. (System.), Suppl. 11:109-132, pl. 9.
- THIELE, J. 1911. Polyplacophora. In: W. Michaelsen & R. Hartmeyer (eds.), Die Fauna sudwest Australiens. 3:405, pl. 6, figs. 18-26.
- THIELE, J. 1929. Handbuch der systematischen Weichtierkunde. Loricata 1(1):1-22, figs. 1-22. Jena.
- TILLIER, L. & A. BAVAY. 1905. Les Mollusques testacés du Canal de Suez. Bull. Soc. Zool. France 30:170-181.

- TOMLIN, J. R. LE B. 1927. The Mollusca of the "St. George" expedition. (1) The Pacific coast of S. America. *J. Conchol.* 18(6):153-170.
- TORR, W. G. 1911. Western Australian Polyplacophora. *Trans. Proc. Rep. Roy. Soc. So. Australia* 35:94-107, pls. 24-25.
- TRYON, G. W., JR. 1883. Structural and systematic conchology: an introduction to the study of the Mollusca. 2:430 pp. Philadelphia.
- VAN BELLE, R. A. 1980. On a small collection of chitons from Hong Kong (Mollusca: Polyplacophora). Pp. 33-35. *In*: B. S. Morton (ed.), *Proceedings of the First International Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong Univ. Press.
- VAN BELLE, R. A. 1982. Supplementary notes on Hong Kong chitons (Mollusca: Polyplacophora). Pp. 469-483. *In*: B. S. Morton & C. K. Tseng (eds.), *The marine flora and fauna of Hong Kong and southern China*. Hong Kong Univ. Press.
- VAN BELLE, R. A. 1983. The systematic classification of the chitons (Mollusca: Polyplacophora). *Inform. Soc. Belge Malacol.* 11(1-3):1-178, 13 pls.
- VIADER, R. 1937. Revised catalogue of the testaceous Mollusca of Mauritius and its dependencies. *Mauritius Instit. Bull.* 1(2):1-111.
- WARMKE, G. L. & R. T. ABBOTT. 1961. Caribbean seashells. A guide to the marine Mollusca of Puerto Rico and other West Indian Islands, Bermuda and the lower Florida Keys. Livingston Co.: Narberth, Pennsylvania. 348 pp., 44 pls., 34 figs., 19 maps.
- WAY, K. & R. D. PURCHON. 1981. The marine shelled Mollusca of west Malaysia and Singapore. Part 2. Polyplacophora and Gastropoda. *J. Moll. Stud.* 47:313-321.
- WELLS, F. E. 1977. Type specimens in the Department of Molluscs, Western Australia Museum. *Rec. West. Australia Mus.* 6(1):33-61.
- WELLS, F. E. 1981. Molluscan fauna of the Admiralty Gulf, Cape Voltaire, and the Institut Islands, Kimberley, Western Australia. Chitons, Meso- and Neogastropods. *Biological Survey of Mitchell Plateau and Admiralty Gulf, Kimberley, Western Australia*. Western Australia Museum: Perth. Pp. 249-263.
- WINCKWORTH, R. 1927. New species of chitons from Aden and South India. *Proc. Malacol. Soc. Lond.* 17(5-6):206-208, pls. 28-29.
- WOOD, W. 1815. General conchology, or a description of shells arranged according to the Linnean system and illustrated with plates, drawn and coloured from nature. Vol. 1. London. lxi + 246 pp., 60 pls.
- WOOD, W. 1825. *Index Testaceologicus; or a catalogue of shells, British and foreign, arranged according to the Linnaean system; with the Latin and English names, references to authors, and places where found*. London. xxxii + 190 pp., 38 pls.
- WU, S.-K. 1969. Some chitons from Taiwan (Formosa). *Malacol. Rev.* 2:103-111.
- WU, S.-K. 1975. The chitons of Lanshu, Taiwan. *Bull. Chin. Malacol. Soc.* 2:69-75.

Cerithidea reidi, spec. nov., from Western Australia

by

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Abstract. *Cerithidea (Cerithidea) reidi*, spec. nov. closely resembles *C. obtusa* (Lamarck) and, to a lesser degree, *C. anticipata* Iredale. Its distinctive radula has a very tiny, narrow rachidian tooth. The shell is the largest in the genus. The new species is endemic to Western Australia and lives above the water on the trunks of mangrove trees.

INTRODUCTION

DURING A REVIEW OF the Indo-Pacific species comprising the genus *Cerithidea* Swainson, 1840, it became apparent that there existed a large undescribed species, endemic to Western Australia, that is very similar in size and shape to *Cerithidea obtusa* (Lamarck, 1822) and similar in sculpture to the smaller *C. anticipata* Iredale, 1929. Some museum collections had referred the new species to *C. obtusa* because no modern taxonomic review of the Indo-Pacific *Cerithidea* species exists and the limits of intraspecific variation in *C. obtusa* were unknown. The purpose of the present paper is to analyze these taxa morphometrically and anatomically. This will provide a range of characters and a sufficient data base to recognize the new species as distinct from *C. obtusa* and to formulate a description of the new taxon that includes radula and some soft-part anatomy.

MATERIALS AND METHODS

Specimens were examined from the Western Australian Museum, Perth (WAM), The Australian Museum, Syd-

ney (AMS), and from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Preserved snails were dissected using Methylene Blue solution under a Wild M-5 dissecting scope. Scanning electron micrographs of radulae were made on Cambridge Stereoscan 100 and Cambridge 250 Mark II Stereoscan scopes. For morphometric studies of shells, principal components and discriminant analyses were made using raw data from measurements of *Cerithidea reidi* (n = 14) and *C. obtusa* (n = 14). Variables included total shell length, width, aperture length, aperture width, number of whorls, number of nodes on penultimate whorl, and aperture length-shell length ratio.

The following abbreviations have been used in this paper: AMS = Australian Museum, Sydney; USNM = United States National Museum; WAM = Western Australian Museum.

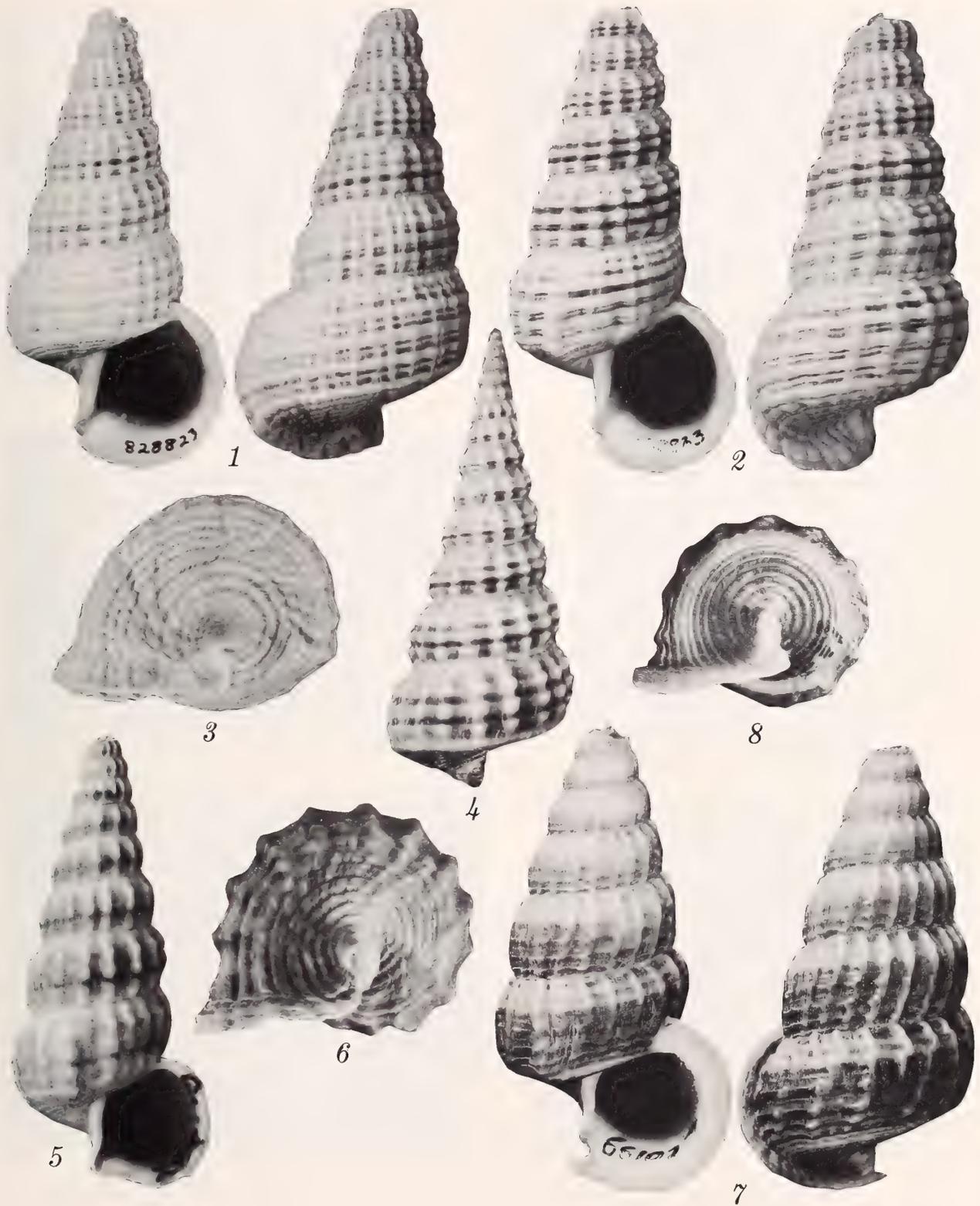
Material examined: Port Warrender, Admiralty Gulf (WAM 553-77, 72-83); near Yarrada, May River, W Kimberly (WAM 56-83); Buccaneer Archipelago (AMS c42225); Derby jetty, Derby (WAM 53-83, 64-83); Der-

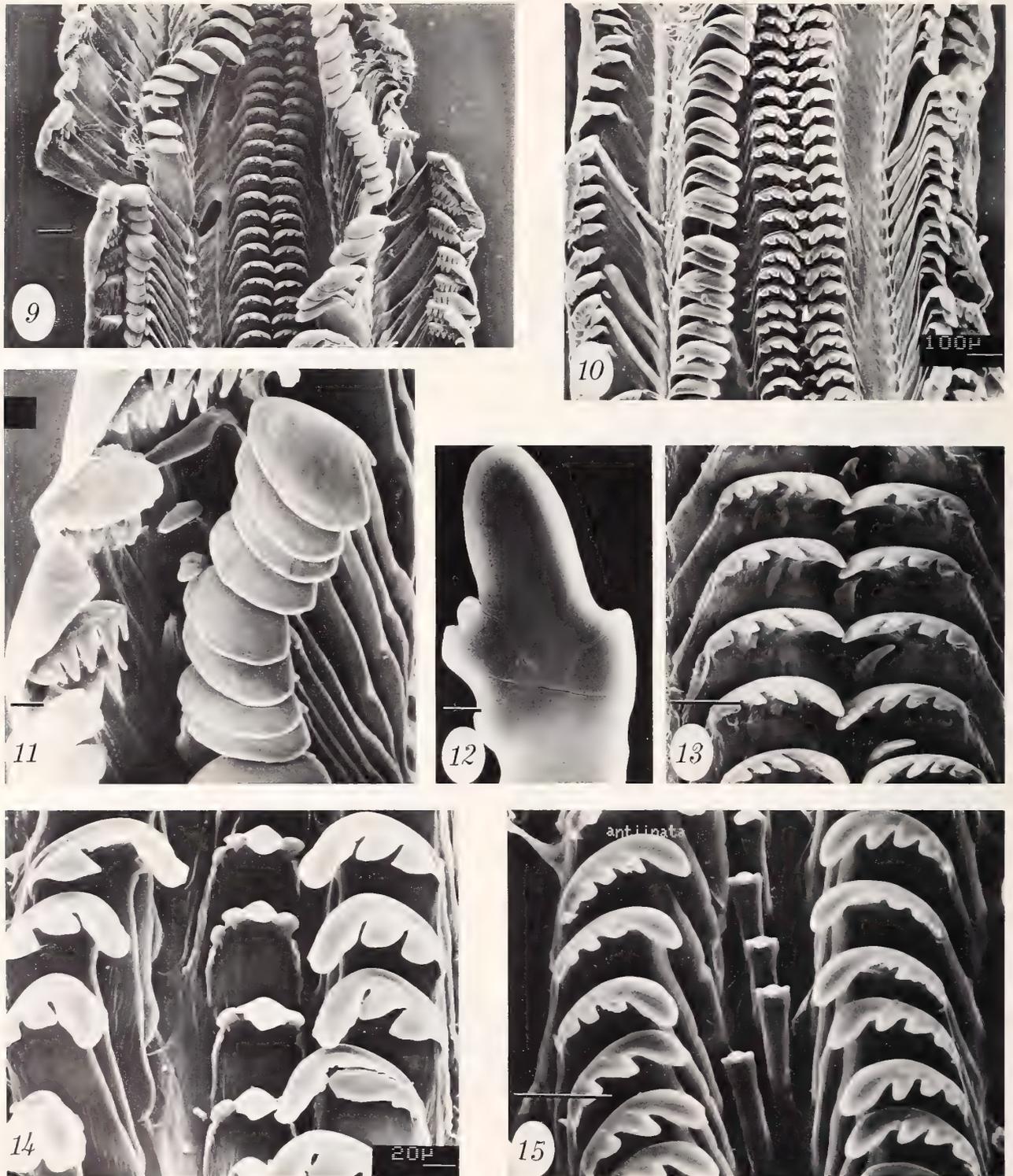
Explanation of Figures 1 to 8

Figures 1-4. *Cerithidea reidi*, spec. nov. All specimens from *Cerriops* trunks on salt pan near Willies Creek, N of Broome, Western Australia. Figures 1, 3, 4. Paratypes (USNM 828823), 54.1 mm, 53.5 mm, 24.8 mm. Figure 2. Holotype (WAM 3380-84) 53.6 mm. (Figure 4 is an immature, non-decollate specimen.)

Figures 5-6. *Cerithidea anticipata* Iredale, showing apertural view (31.9 mm) and enlarged anterior view, 12.3 mm; Prince Regent River Reserve, Western Australia (WAM 254-75).

Figures 7-8. *Cerithidea obtusa* (Lamarck) showing apertural (42.6 mm), dorsal (42.6 mm), and anterior (20.4 mm) views; NE corner of Palau Lumut, Port Swettenham, Malaysia (USNM 661023). Compare with *C. reidi* (Figures 1-4) for sculptural differences.





Explanation of Figures 9 to 15

Figures 9, 11–13. Radula of *Cerithidea reidi*, spec. nov., from Bay of Rest, Exmouth Gulf, Western Australia (WAM 2432-84). Figure 9. General view of radula of *C. reidi* with marginal

teeth spread back to reveal tiny rachidian teeth (bar = 100 μm). Figure 11. *Cerithidea reidi*, detail of marginal teeth. Note large lateral flange on outer marginal teeth (bar = 20 μm). Figure 12.

by (AMS c69288); Beagle Bay (AMS c108460); Cape Lambert (WAM 78-83); back of Dampier Creek on trunks and branches of mangroves, Broome (USNM 828818); near creek on salt pan on *Cerriops* trunks, Willies Creek, N of Broome (USNM 828823); Willies Creek, Broome (WAM 2431-84); Broome (AMS c68507, c69267, c78156, c51059, c108441, c108442, c106273, WAM 2435-84, 48-83); Finucane Id. Causeway, Port Hedland (AMS); Port Hedland (WAM 52-83, 271-33); NE of Dampier (WAM 2435-33, 62-83, 60-83); Dampier Salt, Dampier (WAM 2433-84); Barrow Id. (USNM 694228); Bay of Rest, Exmouth Gulf (WAM 2432-84); Gales Bay, Exmouth Gulf (WAM 2434-84).

DESCRIPTION

Family POTAMIDIDAE H. & A. Adams, 1854

Genus *Cerithidea* Swainson, 1840

Subgenus *Cerithidea* Swainson, 1840

Cerithidea reidi Houbrick, spec. nov.

(Figures 1-4, 9, 11-13)

Shell (Figures 1-4; Table 1): Shell large, of light structure, ranging in length from 51 to 61 mm and from 31 to 41 mm in width. Shell turreted and comprising about 6-7 decollate, inflated whorls. Early missing portion of shell comprising about 15 elongate tapering whorls. Whorls sculptured with 16-25 slightly curved axial ribs crossed by 5 spiral cords, the first 3 subsutural cords bearing nodules or beads at intersections creating cancellate pattern. Spiral cords separated by broad, brown, spiral grooves. The first subsutural spiral cord narrow and finely beaded. Early whorls inflated, angulate with thickened axial ribs and 2 spiral cords. Mid-whorls with 3 spiral cords. Suture distinct. Body whorl large, having on its base 6 or 7 major spiral cords and about 8 smaller spirals, the latter crossed by axial incised lines. Major varix opposite outer lip of aperture on base of body whorl. Aperture large, circular, over one-third the shell length, and with slightly flaring lip somewhat thickened along edge and extending into a flange at its base that slightly extends over the short anterior siphonal canal. Columella straight with thin columellar wash on parietal area of aperture. Anal canal a slight groove at posterior of aperture. Shell color flesh to tan with broad subsutural white band and 3 or 4 thin, brown, spiral bands per whorl. Spiral cords and beads white or very light tan. Aperture interior purple, outer lip and columella white.

Table 1

Shell statistics for *Cerithidea reidi*, spec. nov. (n = 14).

Character	Range	\bar{X}	SD	CV
Total length	51-61.3	54.80	3.04	5.55
Length of last two whorls	31.2-41.4	35.61	2.71	7.62
Shell width	22.6-27.8	24.81	1.40	5.66
Aperture length	18.1-22.4	20.77	1.43	6.89
Aperture width	14.8-19	17.18	1.33	7.76
Number of ribs	16-25	21.14	2.83	13.36
Aperture length/length	0.54-0.62	0.59	0.03	4.43

Operculum completely fills shell aperture and is thin, corneous, circular, and multispiral with central nucleus.

Radula (Figures 9, 11-13): Taenioglossate, one-seventh the shell length. Rachidian tooth very narrow, long, and tapering, becoming triangular and asymmetric at tip. Tip of rachidian tooth with one large central cusp having 2 tiny denticles on one side and 1 on the other. Lateral tooth with broad basal plate and broad cutting edge having long sharp inner cusp and 3 or 4 smaller outer denticles. Inner marginal tooth with spatulate tip and 2 tiny inner denticles. Outer marginal tooth with 5 or 6 smaller sharp denticles and large lateral flange extending the length of its outer side and partly covering outer marginal tooth on next row.

Animal: Preserved specimens tan to whitish. Foot large and with numerous longitudinal grooves on sole. Propodial mucus gland present. Head and snout broad; highly extensible, large snout divided by a median groove. Tentacles long and tapering with eye at outer peduncular base. Mantle edge smooth. Pallial eye present on under-surface of that portion of mantle edge forming inhalant siphon. Pallial eye larger than cephalic eyes, spherical with large lens and embedded in pitlike eye-cup lined interiorly with white pigment and surrounded on exterior surface by reddish and black pigment. Thin, straight ridge-like osphradium adjacent to ctenidium, becoming vermiform near inhalant siphon. Wide, shallow, rudimentary ctenidium extending length of mantle cavity. Each ctenidial filament thick and papillate at its origin but becoming very thin, tapering as it extends over the mantle roof. Pallial gonoducts open. Esophageal gland present.

Type locality: Willies Creek, N of Broome, near creek on salt pan on trunks of *Cerriops* mangroves.

←

Detail of cusp formation on rachidian tooth of *C. reidi* (bar = 4 μ m). Figure 13. Detail of rachidian and lateral teeth of *C. reidi* (bar = 50 μ m).

Figure 10. General view of radula of *Cerithidea obtusa* (Lamarck) from Rayong, Thailand (USNM 777233).

Figure 14. Detail of rachidian and lateral teeth of *Cerithidea obtusa* (Lamarck), same locality as Figure 13.

Figure 15. Detail of rachidian and lateral teeth of *Cerithidea anticipata* Iredale, from Warrender, Admiralty Gulf, Western Australia (WAM) (bar = 50 μ m).

Table 2

Comparison of shell and radula characters among *Cerithidea obtusa*, *C. reidi*, spec. nov., and *C. anticipata*.

Character	<i>C. obtusa</i>	<i>C. reidi</i>	<i>C. anticipata</i>
Shell size	large (to 52 mm)	very large (to 61 mm)	small (to 44 mm)
Shell weight	thick, heavy	thin, light	thin, light
Shell color	dark brown	flesh color, tan	gray, brown
Aperture interior	light brown	purple	brown, tan
Outer lip	shelflike, thick	flaring, moderately thin	flaring, thin
Shell base	spiral sculpture only	spiral and axial sculpture	spiral and axial
Sculpture	no subsutural beads	spiral row of subsutural beads	subsutural beads usually absent
	axial ribs markedly sinuous	spiral cords weak or absent	prominent spiral cords
	axial ribs dominant	axial ribs less sinuous	axial ribs rarely sinuous
		axial ribs crossed by spiral cords and incised lines	axial ribs dominant
Radula	wide rachidian, cusps symmetrical	narrow rachidian, cusps asymmetrical	narrow rachidian, cusps symmetrical
	narrow lateral, 3 or 4 cusps	broad lateral, 4 or 5 cusps	broad lateral, 3 or 4 cusps
	outer marginal with closely fused cusps	outer marginal with well separated cusps	well separated cusps
	rachidian wide	rachidian very narrow	rachidian narrow

Holotype (Figure 2): WAM 3380-84, length 53.6 mm, width 24.7 mm; 1 **paratype** AMS c144144; 10 **paratypes**, USNM 828823.

Etymology: Named for Dr. David Reid who first called my attention to this species.

DISCUSSION

Cerithidea reidi is undoubtedly the largest of all *Cerithidea* (*sensu lato*) species and is easily recognized by its thin shell, cancellate sculpture, purple aperture, and light color pattern. Other prominent distinguishing characters are the broad, spiral grooves that cross the axial ribs, the spiral row of subsutural beads, and the axial grooves on the shell base. Poor preservation of soft parts did not allow determination of the arrangement of the pallial gonoducts. The new species is allocated to the genus *Cerithidea* Swainson, 1840, subgenus *Cerithidea* as defined by HOUBRICK (1984: 16).

Although a common species in northwestern Australia, it has been previously cited in the literature as *Cerithidea obtusa*. Among Recent *Cerithidea* species, *C. obtusa* and *C. reidi* are the largest in shell size and look somewhat alike; consequently, they are the two species most likely to be confused. *Cerithidea reidi* differs from *C. obtusa* (Figures 7, 8), its closest morphological relative, by its larger, lighter, more tapering shell, a purple aperture, and in lacking the thick, shelflike edge of the outer apertural lip. *Cerithidea obtusa* has a brown colored shell with more highly inflated whorls that lack or have weak spiral cords. It possesses fewer axial ribs, and these are more sinuous and curved more strongly to the left than in *C. reidi*. In addition, *C. obtusa* lacks the subsutural row of beads and the

axial grooves on the base of the shell. The new species has a shorter radular ribbon and a much narrower rachidian tooth than does *C. obtusa*. The latter has a broad rachidian with a wide central cusp flanked by two denticles on each side; moreover, the lateral tooth is narrower than that of *C. reidi* and has a cutting edge of only three cusps that are spatulate rather than pointed (Figures 13, 14). The cusps on the outer marginal tooth are more closely fused in *C. obtusa* than in *C. reidi*. A summary and comparison of these characters is presented in Table 2.

To test the hypothesis that the shells differ between the two species, a discriminant analysis, using the shell data of *Cerithidea reidi* summarized in Table 1, was made. The discriminant variables are total length (TL), length of the last two whorls (L), aperture width (AW), and number of ribs on the penultimate whorl (R); total length is the most important variable and was the first step used in the analysis. Results show significant differences between *C. reidi* and *C. obtusa* (F-test: df = 4,23; F = 22.96; P = 0.01). The discriminant equation is: $0.423(TL) + 0.277(L) - 1.15(WA) + 0.096(R) - 13.324$. Comparison of the two species resulted in 100% of the specimens being correctly classified. *Cerithidea obtusa* does not appear to be sympatric with *C. reidi* in Western Australia. Indeed, the former species does not appear to be common in Australia, although there are some reliable records from Queensland. What has usually been called *C. obtusa* in Australia is probably either *C. anticipata* or *C. reidi*.

The only other species that may be confused with *Cerithidea reidi* is *C. anticipata* Iredale, 1929 (Figures 5, 6), formerly known as *C. kieneri* (Hombron & Jacquinet, 1852). *Cerithidea anticipata* (Figures 5, 6) is a much smaller narrower species, adult shells ranging from 28 to 44

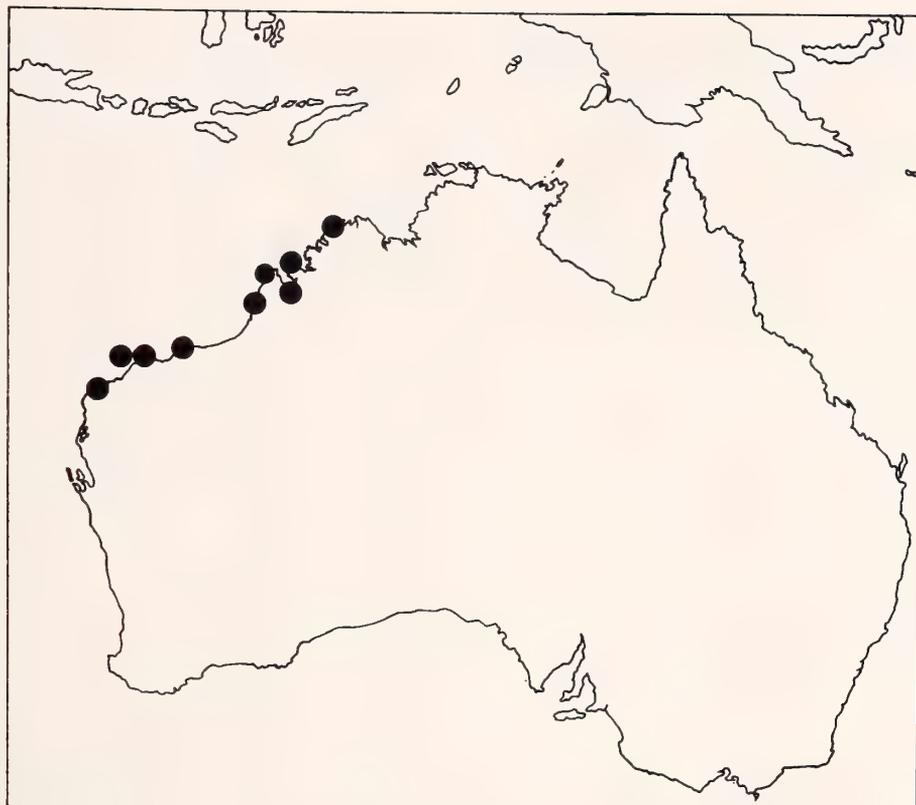


Figure 16

Geographic distribution of *Cerithidea reidi*, spec. nov.

mm in length, about one-half the size of *C. reidi*. The former has sculpture similar to *C. reidi* but the suture is more deeply impressed and the whorls more inflated. The aperture is never purple. In contrast to *C. reidi*, it either lacks or has weak spiral cords, incised lines, and subsutural beads. As the axial ribs are not as deeply crossed by the spiral sculptural elements, it is not as cancellate as *C. reidi*. The early whorls of *C. reidi* are more angulate anteriorly than in *C. anticipata*. Although adults are readily distinguished, juveniles and sub-adults of the two species are more difficult to separate. Young snails of *C. reidi* are normally more cancellate in sculpture and have a wider whorl angle. The radula of *C. anticipata* (Figure 15) has a narrow rachidian tooth with a cutting edge of one large central cusp flanked by a tiny denticle on each side. This differs from the rachidian tooth of *C. reidi*, which is narrower, has more irregular denticles, and is asymmetrical in cusp distribution (see Table 2 for comparisons).

Cerithidea anticipata occurs in mangrove forests in Queensland and extends north and across northern Australia to the Admiralty Gulf, where it overlaps slightly with *C. reidi*. Few specimens of *C. anticipata* have been seen from this region, but those examined are larger than specimens from northern Australia and Queensland and

are more similar to *C. reidi* in shell sculpture. These larger *C. anticipata*, while resembling *C. reidi*, never have a purple aperture and do not attain the large size of *C. reidi*. These two species are probably very closely related, as their radulae and shell sculptures are morphologically similar even though there is great size disparity.

The origins and distribution of *Cerithidea reidi* may be explained by vicarism due to the isolation of western Australia from the northern and eastern marine faunas by the Tertiary landbridge joining Australia and New Guinea (DOUTCH, 1972:1). Although I herein accord the new taxon specific recognition, future detailed studies using more extensive comparative material from the Northern Territory may reveal a subspecific relationship between *C. anticipata* and *C. reidi*.

Cerithidea reidi lives on the trunks of mangroves such as *Rhizophora*, *Ceriops*, and *Aegialitis*, and appears to be endemic to mangrove forests in Western Australia (Figure 16). It may also occur in Northern Territory but I have seen no records from this region. In the Admiralty Gulf, WELLS & SLACK-SMITH (1981:268) found this species (although cited as *C. obtusa*, their voucher lots show a mixture of *C. anticipata* and *C. reidi*) to be the most abundant mollusk in the upper two mangrove zones (*Ceriops* and

Aegialitis) where it lives on tree trunks from the mud level to 2 m above the mud surface and occurs in densities up to 1.65/m². *Cerithidea obtusa* occurs in similar habitats in northern Queensland, New Guinea, Indonesia and continental southeast Asia. It has also been found on wet mud banks and has been observed living around small pools dug by *Periophthalmus*, the mud skipper (BENTHEM JUTTING, 1956:434). PFLUGFELDER (1930) recorded *C. obtusa* on *Acanthus ilicifolius* at the edge of the mangrove zone and it has also been reported living on branches of *Rhizophora* and *Avicennia* about 1 m above the ground (BENTHEM JUTTING, 1956:434-435).

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LITERATURE CITED

- ADAMS, H. & A. ADAMS. 1813-1878. The genera of Recent Mollusca. 3 volumes. London. 389 pp., 138 pls.
- BENTHEM JUTTING, VAN W. S. S. 1956. Systematic studies on the non-marine Mollusca of the Indo-Australian archipelago. V. Critical revision of the Javanese freshwater gastropods. *Treubia* 23(2):259-477.
- DOUTCH, H. F. 1972. The paleogeography of northern Australia and New Guinea and its relevance to the Torres Strait area. In: D. Walker (ed.), *Bridge and barrier: the natural and cultural history of Torres Strait*. Research School of Pacific Studies, Department of Biogeography and Geomorphology (Canberra) Publication BC/3:1-10.
- HOUBRICK, R. S. 1984. Revision of higher taxa in genus *Cerithidea* (Mesogastropoda: Potamididae) based on comparative morphology and biological data. *Amer. Malacol. Bull.* 2(1984):1-20.
- IREDALE, T. 1929. Queensland molluscan notes, no. 1. *Memoirs of the Queensland Museum* 9(3):261-297.
- LAMARCK, M. DE. 1822. *Histoire naturelle des animaux sans vertèbres*. Paris. Vol. 7:1-711.
- PFLUGFELDER, O. 1930. Das Mantelauge von *Potamides obtusus* Lam. *Zoologischer Anzeiger* 89:276-283.
- SWAINSON, W. 1840. *A treatise on malacology or shells and shell-fish*. London. viii + 419 pp.
- WELLS, F. E. & S. M. SLACK-SMITH. 1981. Zonation of mollusks in a mangrove swamp in the Kimberly, Western Australia. Pp. 265-274. In: *Biological survey of Mitchell Plateau and Admiralty Gulf, Kimberly, Western Australia*. Western Australian Museum: Perth.

Two New Bulimulid Land Snail Species from Isla Santa Cruz, Galápagos Islands

by

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Abstract. Two new species, *Naesiotus steadmani* and *Naesiotus kublerensis* (Bulimulidae), are described from Isla Santa Cruz, Galápagos Islands, Ecuador. These snails are known only from limited shell material collected from surface samples and excavations of fossil deposits in lava tubes.

INTRODUCTION

RECENT STUDIES OF terrestrial fossils are providing new insights into the evolution and historical distributions of the vertebrate fauna of the Galápagos Islands, Ecuador (STEADMAN, 1981, 1982, in press a, in press b; STEADMAN & RAY, 1982). During their field investigations, Steadman and his colleagues also collected land snail shells from cave excavations and surface samples on Floreana and Santa Cruz islands. These Holocene land snail faunas, which are associated with the fossil vertebrate faunas, are described in detail in another paper (CHAMBERS & STEADMAN, in press). That analysis has revealed two taxa that are distinct at the species level. These two species are described in the present paper.

Recognition of the new species is based on study of the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the California Academy of Sciences, San Francisco (CAS), the reviews of DALL (1896) and DALL & OCHSNER (1928), all published descriptions of the Galápagos bulimulid species, and the analysis of *Naesiotus* characters by BREURE & COPPOIS (1978). Whorl numbers in the data tables were counted to the nearest ¼ whorl.

The present descriptions are based only on shell material; neither living specimens nor preserved soft parts are known to the author. There is evidence of recent declines and likely extinction in Galápagos land snails (CHAMBERS & STEADMAN, in press), so it is possible that both newly described species are already extinct.

TAXONOMY

Family BULIMULIDAE Tryon, 1867

Genus *Naesiotus* Albers, 1850

Naesiotus steadmani Chambers, spec. nov.

Figure 1

Description: Shell conical, consisting of up to 7 whorls, narrowly umbilicate to rimate, reaching 11.8–13.3 mm in height and 6.3–7 mm in width, with proportion of width to height ranging from 0.5 to 0.54 and sides convex in outline. Protoconch consisting of 1.75–2 whorls, with sculpture of fine undulating and anastomosing axial riblets and extremely fine spiral threads. Postembryonic whorls convex and with fine, slightly sigmoid or undulating axial ribs and very fine spiral threads on the first 1.75–2.5 postembryonic whorls, forming small beads at intersections with axial ribs. Sutures weakly impressed. Axial sculpture becoming increasingly more pronounced on body whorl, forming coarse, irregular folds within ¼ turn of the aperture. Base of body whorl flattened, making the shell outline somewhat fusiform. Aperture ovate-lunate, somewhat narrowed by flattened parietal wall. When viewed from side, peristome straight, its plane forming an angle of about 30° with axis of shell. Columellar margin reflected and continuous with a thick parietal callus, basal and palatal margins simple or slightly thickened. Parietal lamella 1–2 mm in length and directed toward midpoint of the outer lip and recessed about 3 mm from outermost

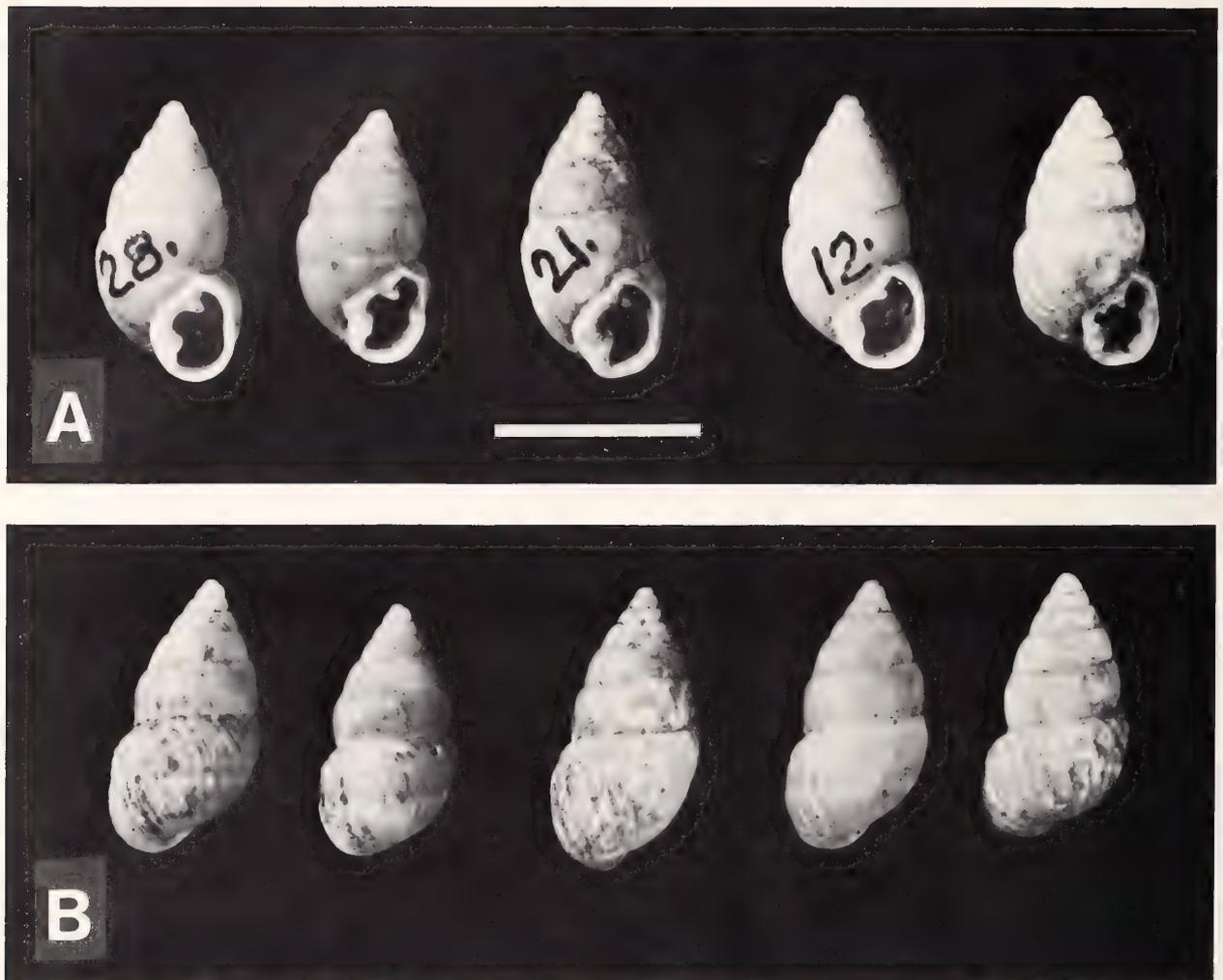


Figure 1

Two views (A and B) of *Naesiotus steadmani* material. Far left, the holotype. Next, three paratypes. Far right, USNM 842297 from Cueva de Kubler. Scale bar is 10 mm.

extent of peristome. Columellar lamella thicker and not as high as parietal lamella and usually extending to the peristome. Palatal thickening extending to edge of peristome. Shell light brown, sometimes with pale spiral band down middle of body whorl, with peristome white.

Diagnosis: A *Naesiotus* with a finely sculptured, somewhat fusiform shell, and with parietal and columellar lamellae and a palatal thickening within the aperture.

Differential diagnosis: This species resembles in overall form the shell of *Naesiotus sculpturatus* (Pfeiffer, 1846) figured by SMITH (1972), but the latter species lacks apertural lamellae (as does *Naesiotus tanneri* [DALL, 1895]) and is roughly sculptured. *Naesiotus akamatus* (Dall, 1917), *Naesiotus adelphus* (Dall, 1917), *Naesiotus lycodus* (Dall,

1917), and *Naesiotus wolfi* (Reibisch, 1892) have similar apertural features and are about the same height as *N. steadmani*, but all of the former are substantially broader.

Etymology: This species is named in honor of Dr. David W. Steadman, pioneer in the study of Galápagos terrestrial fossil faunas.

Type material: Holotype (CAS 059358) and 67 paratypes (CAS 038052). The type material was collected on 24 February 1964, by Allyn G. Smith from under lava rocks at a lava cliff west of the DeRoy's house and near the Devine house, Academy Bay, Isla Santa Cruz, Galápagos Islands (according to museum labels and description of Station G-113 in Allyn G. Smith's Station List for the Galápagos International Scientific Project, on file in the

Table 1
Measurements of some *Naesiotus steadmani*.

	Height (mm)	Width (mm)	Height/width	No. whorls			No. post- protoconchal whorls with spiral cords
				Protoconch	Other	Total	
Holotype (CAS 059358)	12.9	7.0	0.54	1.75	4.75	6.5	1.75
Paratypes (CAS 038052)	13.3	6.9	0.52	1.75	4.75	6.5	2.75
	12.7	6.7	0.53	2	5	7	3
	12.4	6.5	0.52	1.75	5	6.75	3
	11.8	6.3	0.53	1.75	4.75	6.5	3
	12.4	6.5	0.52	2	4.75	6.75	2
	12.7	6.3	0.50	1.75	5	6.75	2.5
USNM 842297	12.6	6.7	0.53	—	—	6.25*	—
Mean	12.6	6.6	0.52	1.8	4.9	6.63	2.6
Standard deviation	0.43	0.26	0.01	0.1	0.1	0.23	0.5

* Total number of whorls only is given for this shell, which is weathered so that the protoconch is indistinguishable from later whorls.

Department of Invertebrate Zoology of the California Academy of Sciences). There is no indication on the labels or station list that any individuals were collected alive, and many shells are entirely white owing to weathering. Measurements of some of this material are presented in Table 1.

Additional material: A single fossil specimen from a depth of 20 to 30 cm in Excavation IIE in Cueva de Kubler (Figure 2), a large lava tube 1.5 km north of Puerto Ayora, Isla Santa Cruz (USNM 842297), collected by D. W. Steadman, E. N. Steadman, and J. R. Hill on 6 November 1980. Excavation IIE is in a deposit of unstratified, unindurated, richly fossiliferous sediments. Alongside the much more abundant and mineralized remains of native vertebrates, Excavation IIE contains specimens of rodents (*Mus*, *Rattus*), which were introduced to Santa Cruz in the early 20th century. The age of this deposit is late Holocene, ranging from at least 1750 years BP up until just decades ago. This locality is described in STEADMAN (1981) and CHAMBERS & STEADMAN (in press). USNM 842297 was the only specimen of this species known to the author until the previously collected but unidentified material was found in the collections of the Department of Invertebrate Zoology at CAS.

Naesiotus kublerensis Chambers, spec. nov.

Figure 3

Description: Shell conical, consisting of up to 7.75 whorls, fairly thin, narrowly umbilicate, reaching 10–12 mm in height and 4.8–5.7 mm in width, with proportion of width/height ranging from 0.4 to 0.51 and sides nearly straight in outline. Suture impressed. Protoconch of 1.5 to 1.75 whorls, sculptured with fine straight axial riblets. Postem-

bryonic whorls convex, very slightly shouldered at periphery, sculptured with fine axial wrinkles that become larger, rougher, and more irregular on later whorls, making last half of body whorl heavily wrinkled or rugose. Spiral sculpture of numerous closely spaced and very fine threads forming fine beads (visible under 10× magnification) as they pass over all but largest axial wrinkles. Peristome elongate-ovate and simple, except columellar margin reflected and continuous with a thin callus on parietal surface; when viewed from side, peristome straight and forming angle of about 25° with shell axis. Small parietal swelling within aperture sometimes present. Color brown or tan to cream, sometimes with pale band just below periphery.

Diagnosis: A *Naesiotus* with a slightly elongate bulimoid shell that is sculptured with irregular axial wrinkles that become rugose on the last half of the body whorl. The shell aperture lacks lamellae, although a parietal swelling is sometimes present.

Differential diagnosis: This species' overall form is much like that of *Naesiotus hirsutus* Vagvolgyi, 1977, and *Naesiotus jacobi* (Sowerby, 1883), but it has definite axial sculpture, becoming rugose on the body whorl, that is absent in those species. It resembles *Naesiotus rabidensis* (Dall, 1917), but its whorls are not definitely shouldered as in that species. It is stouter but, in other respects, similar to *Naesiotus nesioticus* (Dall, 1896). Shells of *N. kublerensis*, *N. nesioticus*, and *Naesiotus reibischi* (Dall, 1895) have been found together without apparent intergradation in Cueva de Kubler. Fossil records and quantitative morphological analysis of these three species will be presented elsewhere (CHAMBERS & STEADMAN, in press).



Figure 2

Cueva de Kubler, type locality for *Naesiotus kublerensis*, and where a single specimen of *N. steadmani* was collected. Photograph by D. W. Steadman.

Etymology: Named for Cueva de Kubler, the type locality.

Type material: Holotype (USNM 842298) and 7 paratypes (USNM 842299) were collected by Steadman in December 1980 from surface rubble at the entrance of Cueva de Kubler (Figure 3), about 8 m southwest of Ex-

cavation IIA, Isla Santa Cruz (see comments on this locality under *Naesiotus steadmani*). One additional paratype (USNM 842300) was collected by Steadman, E. N. Steadman, and J. R. Hill from a depth of 0–20 cm in Excavation IIA on 18 November 1980. Additional paratypes were collected from the surface just outside the entrance to Cueva de Kubler to represent a “modern” snail

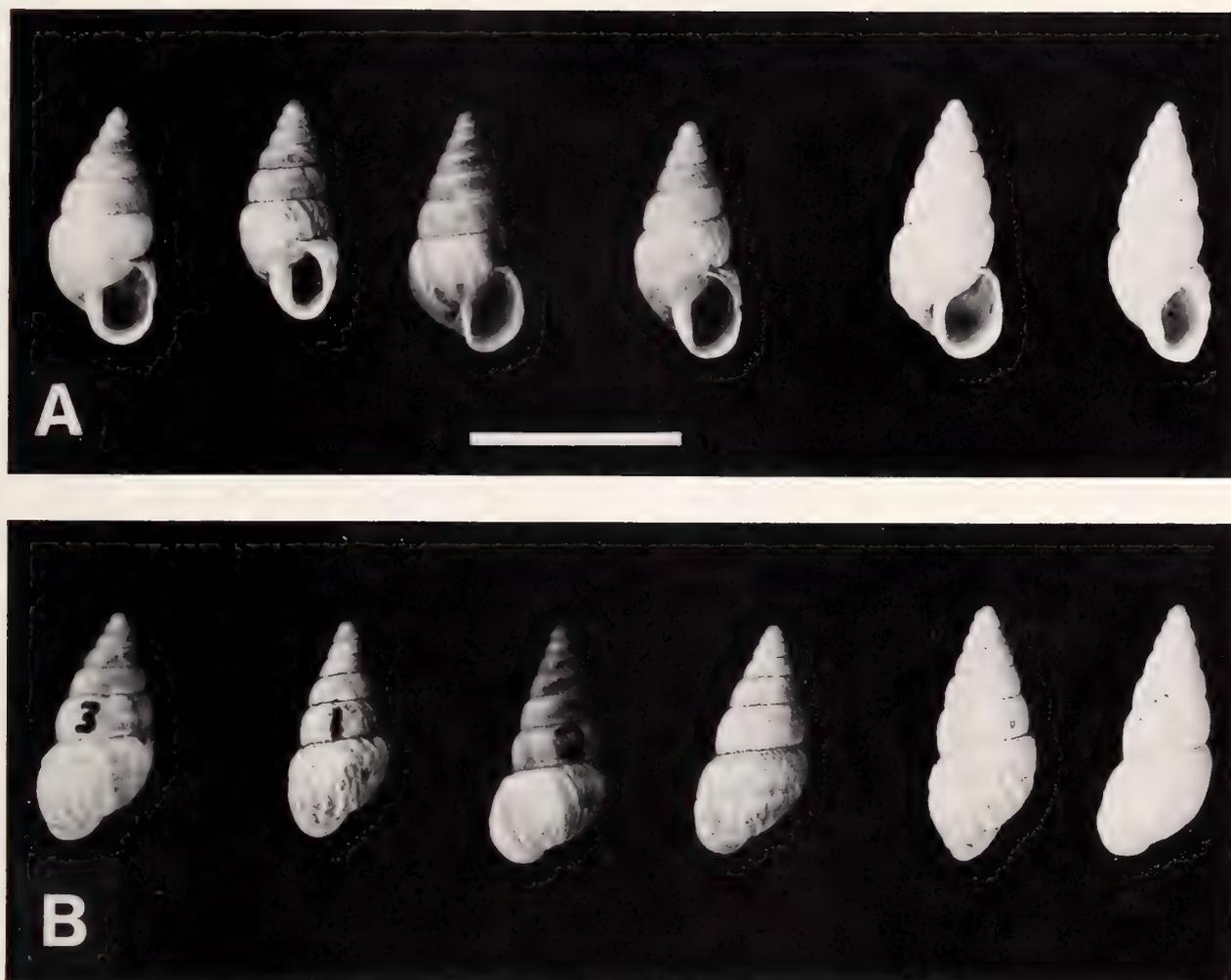


Figure 3

Two views (A and B) of some type material of *Naesiotus kublerensis*. Far left, holotype. Next, two paratypes (USNM 842299) from rubble at the entrance of Cueva de Kubler. Right, three paratypes (USNM 842301) from just outside the entrance of Cueva de Kubler. Scale bar is 10 mm.

sample: 7 in USNM 842301, collected by D. W. Steadman on 25 December 1980, 7 m SSW of the entrance; 5 in USNM 842302, collected by Steadman, P. S. Martín, and M. K. O'Rourke on 19 December 1980, from 8 m SE of the entrance; and 25 in USNM 842303, collected by Steadman on 25 December 1980, from 8 m SW of the entrance. Measurements of some type and other material are presented in Table 2. The specimen from Excavation IIA: 0–20 cm may be anywhere from approximately 1750 years old up to modern. All other type material of *N. kublerensis* was taken from the interstices between boulders. Some shells were rather exposed, while others were fairly sheltered beneath the boulders. All are modern in appearance, although some appear worn and/or bleached, and none were taken as live animals.

Additional material: One shell (USNM 842304) collected from the surface near the trail to Tortuga Bay, Santa Cruz, 1 km from the main road on 12 July 1979, by D. W. Steadman and M. Pozo. Four additional lots of this species, collected during the Galápagos International Scientific Project in 1964, were located at CAS. Three of these (CAS 037883, CAS 037963, and CAS 038061) were collected by Allyn G. Smith (Stations G-6, G-77, and G-4 respectively). The fourth lot (CAS 038041) was collected by A. and J. DeRoy. All of the recorded localities are on the "old trail" (described by SMITH, 1972) that connects Bahia Academy with upland areas of Santa Cruz. Smith's labels with CAS 037883, CAS 038041, and CAS 038061 indicate that he considered this a new species. There is no indication that any of this material was taken alive.

Table 2
Summary of measurements of some shells of *Naesiotus kublerensis*.

	N	Height (mm)	Width (mm)	Height/ width	No. whorls	
					Protoconch	Other
Cueva de Kubler:						
Entrance:						
Holotype (USNM 842298)	1	10.9	5.1	0.47	1.75	4.25
Paratypes (USNM 842299)	2					
Mean		10.7	5.1	0.48	1.75	5.50
Range		10.2-11.2	4.9-5.3	0.47-0.48	1.75	5.25-5.75
Excavation IIA:						
Paratype (USNM 842300)	1	11.3	4.5	0.40	1.75	6
Surface:						
Paratypes:						
USNM 842301	7					
Mean		11.3	5.1	0.45	1.7	5.4
Range		10.4-12.1	4.8-5.4	0.42-0.48	1-1.75	5.25-5.75
Standard deviation		0.7	0.2	0.02	0.1	0.2
USNM 842302	2					
Mean		10.5	5.0	0.48	1.75	5
Range		10.2-10.8	4.8-5.2	0.47-0.48	1.75	5
USNM 842303	7					
Mean		11.4	5.4	0.47	1.6	5.4
Range		10.7-12.0	5.0-5.7	0.44-0.52	1.5-1.75	4.75-6
Standard deviation		0.49	0.29	0.03	0.1	0.4
CAS 037883	2					
Mean		11.6	5.3	0.46	1.75	5.38
Range		11.5-11.7	5.0-5.6	0.43-0.49	1.75	5-5.25
CAS 037963	1	10.0	5.1	0.51	1.75	5
CAS 038061	3					
Mean		10.9	5.0	0.46	1.6	5.2
Range		10.6-11.3	4.9-5.1	0.45-0.46	1.5-1.75	5-5.5
Standard deviation		0.36	0.10	0.01	0.1	0.3

ACKNOWLEDGMENTS

I am extremely grateful to D. W. Steadman for introducing me to his Galápagos gastropod material and encouraging me to undertake its study. T. M. Gosliner and B. Roth of CAS allowed access to and loans of specimens. I also thank the staff of the Division of Mollusks of the National Museum of Natural History, Smithsonian Institution, for access to collections and continuing patience and courtesy. The manuscript was improved by comments from Steadman, who also provided Figure 2, and from C. C. Christensen and B. Roth. Figures 1 and 3 were photographed by V. Krantz. This is Contribution Number 382 of the Charles Darwin Foundation for Galápagos. This paper is dedicated to the memory of Dr. Joseph Rosewater.

LITERATURE CITED

- BREURE, A. S. H. & G. COPPOIS. 1978. Notes on *Naesiotus* Albers, 1850 (Mollusca, Gastropoda, Bulimulidae). Netherlands J. Zool. 28:161-192.
- CHAMBERS, S. M. & D. W. STEADMAN. In press. Holocene terrestrial gastropod faunas from islas Santa Cruz and Floreana, Galápagos. Trans. San Diego Soc. Natur. Hist.
- DALL, W. H. 1896. Insular landshell faunas, especially as illustrated by the data obtained by Dr. G. Baur in the Galápagos Islands. Proc. Acad. Natur. Sci. Phila. 1896:395-460.
- DALL, W. H. & W. H. OCHSNER. 1928. Landshells of the Galápagos Islands. Proc. Calif. Acad. Sci., 4th series, 17: 141-185.
- SMITH, A. G. 1966. Land snails of the Galápagos. Pp. 240-251. In: R. I. Bowman (ed.), The Galápagos; proceedings of the Symposia of the Galápagos International Scientific Project. University of California Press: Berkeley and Los Angeles.
- SMITH, A. G. 1972. Three new land snails from Isla Santa Cruz (Indefatigable Island), Galápagos. Proc. Calif. Acad. Sci., 4th series, 39:7-24.
- STEADMAN, D. W. 1981. Vertebrate fossils in lava tubes in the Galápagos Islands. Proc. 8th Int. Cong. Speleology 2:549-550.
- STEADMAN, D. W. 1982. The origin of Darwin's finches (Fringillidae, Passeriformes). Trans. San Diego Soc. Natur. Hist. 19:279-296.

- STEADMAN, D. W. In press a. Vertebrate paleontology of the Galápagos Islands. Natl. Geographic Res. Rep.
- STEADMAN, D. W. In press b. Holocene vertebrate fossils from Isla Floreana, Galápagos. Smithsonian Contrib. Zool., No. 413.
- STEADMAN, D. W. & C. E. RAY. 1982. The relationships of *Megaoryzomys curioi*, a large cricetine rodent (Muroidea, Muridae) from the Galápagos Islands, Ecuador. Smithsonian Contrib. Paleobiol., No. 51.

Nassarius (Gastropoda: Neogastropoda) from the Galápagos Islands¹

by

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Abstract. Nine species of *Nassarius* have been reported from the Galápagos Islands, but the occurrence of only six species is substantiated. *Nassarius nodicinctus* (A. Adams) and *N. versicolor* (C. B. Adams) are the two commonly recorded shallow-water species. However, *N. nodicinctus* is the senior synonym of the mainland species *N. angulicostis* (Pilsbry & Lowe), and the name is erroneously applied to the Galápagan species. The distinct species from the Galápagos Islands is described and named *N. caelolineatus*, spec. nov. The first occurrence of one more shallow-water species (*N. shaskyi*) is reported; four deep-water species (*N. townsendi*, *N. exarcus*, *N. goniopleura*, *N. catallus*) are reviewed; and spurious records are discussed.

INTRODUCTION

NINE SPECIES OF *Nassarius* have been reported from Pleistocene and Recent faunas in the Galápagos Islands, Ecuador. Results of a paleontological expedition to the Galápagos Islands in 1982 (LIPPS & HICKMAN, 1982; PITT & JAMES, 1984) included revised age assignments of fossiliferous deposits and new molluscan species, including one *Nassarius* species. With this material at hand, we re-considered the current records of *Nassarius* from the Islands. The most notable feature is that only one shallow-water species (*N. caelolineatus*, spec. nov.) and two of the substantiated deep-water species (*N. townsendi*, *N. exarcus*) are endemic. The others are also distributed along the tropical eastern Pacific coast. Most nassariids, including the deep-water species, have planktotrophic larvae, and, therefore, the potential for wide dispersal. But far fewer *Nassarius* species are on the Islands than on the mainland. Biogeographic affinities of Galápagan nassa-

riids are consistent with the proposal by JAMES (1984) that there is a slower rate of evolution for marine biota than terrestrial biota on the Galápagos Islands.

Acronyms used in the text are as follows: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum of Natural History; CAS, CASIZ, and CASG, California Academy of Sciences; CDRS, Charles Darwin Research Station, Galápagos Islands; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; UCMP, Museum of Paleontology, University of California, Berkeley; USNM, United States National Museum.

All CAS numbers quoted are station numbers.

TAXONOMY

Family NASSARIIDAE

Genus *Nassarius* Dumeril, 1806

Nassarius caelolineatus Nesbitt & Pitt, spec. nov.

(Figures 1, 2, 17a)

Nassarius nodicinctus A. ADAMS, 1852:110; TOMLIN, 1927:160; HERTLEIN & STRONG, 1939:373; DEMOND, 1952:

¹ Contribution No. 369 of the Charles Darwin Foundation.

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315; HERTLEIN, 1972:29. [Not *Nassa nodicincta* A. Adams, 1852.]

Alectrion versicolor var. *nodicincta* C. B. Adams: DALL & OCHSNER, 1928:96. [Not *Nassa versicolor* C. B. Adams, 1852; not *Nassa nodicincta* A. Adams, 1852.]

Description of holotype: Protoconch consisting of 4 smooth, bulbous whorls, boundary between protoconch and teleoconch indistinct over $\frac{1}{4}$ whorl; teleoconch consisting of 5 whorls sculptured by axial ribs and spiral lines, whorl profile straight sided, shoulders smooth and angled, noded at posterior end (top) of ribs; sutures wavy; first two teleoconch whorls with numerous axial ribs, third teleoconch whorl with 10 rounded axial ribs, 2 narrow, incised spiral lines crossing axials; penultimate whorl with 10 rounded axial ribs, 4 narrow, incised spiral lines below shoulder nodes, one above shoulder nodes crossing axial ribs; body whorl straight sided with 9 strongly noded axial ridges over entire width of whorl, 9 narrow, incised spiral lines, regularly spaced, one distinct spiral line immediately above node, two spiral traces between that spiral line and suture; fossa filled; anterior canal short, open, notched; aperture ovate, outer lip slightly thickened, non-varicose, weakly lirate within; inner lip bordered by a narrow callus that broadens posteriorly, clearly delimited from parietal surface of body whorl, forming small posterior notch.

Height 11.7 mm, width of body whorl 6.7 mm, aperture height 5.4 mm; protoconch width 0.83 mm.

Type material: Holotype: CASIZ 058038; **paratypes:** CASIZ 058039. In addition 6 paratypes have been sent to each of the following: AMNH, ANSP, BMNH, CDRS, LACM, MCZ, USNM, UCMP.

Type locality: north side of Academy Bay, Isla Santa Cruz, Galápagos Islands (90°18'5"W, 0°44'40"S); coral sand and mud, 5–10 fathoms. Collected by A. G. Smith and J. De Roy, February 1964; CAS 38914.

Etymology: from the Latin *caelo*, meaning "to engrave in bas relief" and *lineatus*, "of a line."

Discussion: *Nassarius caelolineatus*, spec. nov. is a small, slender, turreted *Nassarius*, differing from other Panamic *nassariids* by having regularly spaced, incised spiral lines and a shallow in-filled fossa.

We examined about 1200 specimens of *Nassarius caelolineatus*, both recent and fossil, from the Galápagos Islands, and several hundred specimens of *N. nodicinctus* from the continental coast; the latter were obtained from CAS, LACM and BMNH collections, as well as material borrowed from the private collections of T. Bratcher and D. Shasky. We also examined the type specimens of *N. nodicinctus*, *N. angulicostis*, and *N. versicolor* (C. B. Adams).

The syntypes of *Nassarius nodicinctus* (BMNH 1973154; Figures 3, 4) closely match the holotype of *N. angulicostis* (Pilsbry & Lowe, 1932) (ANSP 155331; Figures 5, 6). A. ADAMS (1852) described *N. nodicinctus* from the Cum- ing collection (BMNH Accession no. 1829) and there is evidence that the original locality information of "Galá-

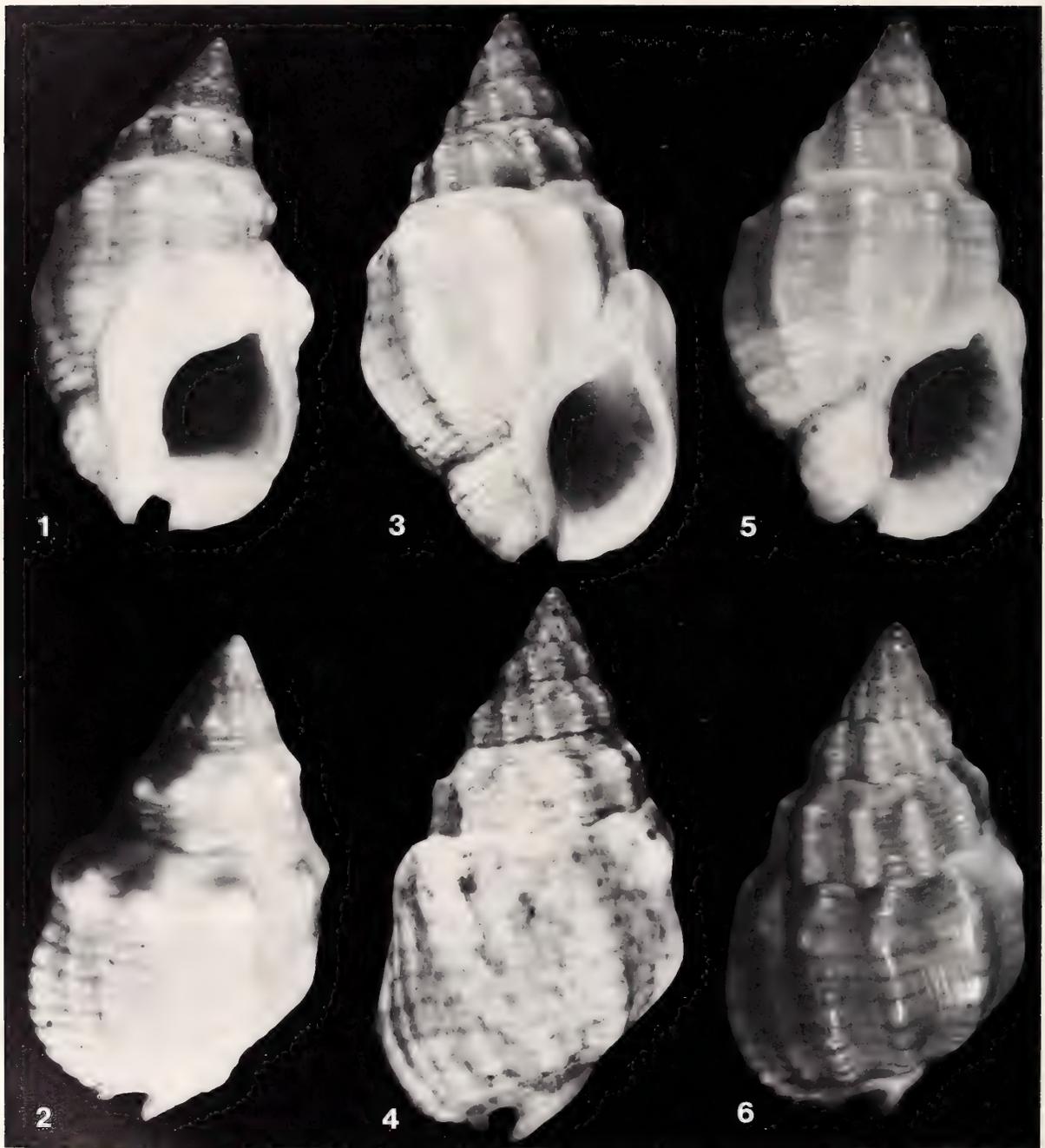
pagos Islands" is incorrect. MARINCOVICH (1977) placed *Polinices galapagosus* (Recluz) in synonymy with *P. otis* (Broderip & Sowerby). He stated (p. 257) that "because *P. (P.) otis* is not known to occur in the Galápagos, the locality data with the syntypes are probably in error." The syntypes of *N. nodicinctus* came from the same Cum- ing collections as the syntypes of *P. galapagosus* (BMNH Acc. no. 1829), and most probably did not come from the Galápagos Islands. KEEN (1958) described, but did not illustrate, *N. nodicinctus*. KEEN (1971) illustrated types of *N. angulicostis* and *N. nodicinctus* (figs. 1291, 1307), and thus did not include a figured specimen of *N. caelolineatus*.

There is little intraspecific variation in either *Nassarius caelolineatus* or *N. nodicinctus* compared to other eastern Pacific *Nassarius* species (Nesbitt, in prep.). Size ranges of adult specimens (minimum of 8 whorls) are height 10.8 to 16.1 mm, width of body whorl 5.8 to 15.9 mm, and aperture height 4.9 to 6.2 mm. The protoconch diameter divided by the number of protoconch volutions is an indicator of larval mode of life in gastropods (SHUTO, 1974). For *N. caelolineatus* this index is 0.2, which falls within the range of planktotrophic larval types. The color pattern is pale yellow to mottled red-brown. The distinct periostracum forms a reticulate pattern of thickening along the spiral grooves and between the axial ribs.

This species occurs throughout the Galápagos Islands to a depth of 70 m. Fossils occur in late Pliocene/early Pleistocene deposits on Isla Baltra (CASG 61388), Pleis- tocene deposits on Isla Santa Cruz (CASG 61225, 61234, 61236) and Isla Isabela (CASG 61229), and Quaternary indurated beach sands on Isla Isabela (CASG 61399) (DALL & OCHSNER, 1928; HERTLEIN & STRONG, 1939; HERTLEIN, 1972; PITT *et al.*, in press).

Radulae were prepared for light microscopy, and one isolated central and lateral tooth from a paratype are il- lustrated (Figure 17b). The radula is similar to the com- mon radula pattern of most eastern Pacific *nassariids*, and is adapted basically for an unspecialized scavenging habit (Nesbitt, in prep.). The lateral tooth has 3 to 5 subcusps medially, variation frequently occurring on the same rad- ula ribbon. There are 14 cusps on the central tooth.

Compared to *Nassarius caelolineatus*, the syntypes of *N. nodicinctus* and the holotype of *N. angulicostis* are more robust, with narrow, brown, spiral lines that are not in- cised, less tabulate shoulders, with poorly developed nodes, a broader posterior region of the callus, and a deep fossa. Only *N. caelolineatus* and *N. versicolor* (C. B. Adams) are recorded from the Galápagos Islands. *Nassarius ver- sicolor* differs from *N. caelolineatus* by having closely spaced, fine spiral ridges on the early whorls, a variable number of irregularly spaced incised spiral lines on the body whorl, less pronounced nodes, a shallower fossa, and a narrower callus. Based on shell and radular features, *N. caelolineatus* is the sister group of *N. versicolor* and not *N. nodicinctus*. It has been found only in the Galápagos Islands and apparently originated there.



Explanation of Figures 1 to 6

Figures 1 and 2. Holotype of *Nassarius caelolineatus*, spec. nov., CASIZ 058038 (height 11.7 mm).

Figures 3 and 4. Lectotype of *Nassarius nodicinctus* (A. Adams), BMNH 1973154/1 (height 16.1 mm).

Figures 5 and 6. Holotype of *Nassarius angulicostis* (Pilsbry & Lowe), ANSP 155331 (height 12.9 mm).

Nassarius nodicinctus (A. Adams, 1852)

(Figures 3–6, 17b)

Nassa nodicincta A. ADAMS, 1852:110.*Nassarius nodicinctus*: KEEN, 1958:410, 1971:607, fig. 1307; CERNOHORSKY, 1975:128–129, figs. 20–24.*Alectrion nodicinctus*: DALL, 1917:576 (in part).*Nassa angulicostis*: PILSBRY & LOWE, 1932:69, pl. 6, fig. 2.*Nassarius angulicostis*: KEEN, 1958:408, fig. 568, 1971:604, fig. 1291.

Based on a study of type specimens, CERNOHORSKY (1975) synonymized *Nassarius angulicostis* with *N. nodicinctus*. This species ranges from Gulf of California to Ecuador (SHASKY, 1984), and is not known to occur in the Galápagos Islands. The species from the Galápagos Islands that was erroneously called *N. nodicinctus* is herein named *N. caelolineatus*. *Nassarius nodicinctus* is characterized by numerous thin, brown, spiral lines on the body whorl, a deep fossa, and well developed axial ribs extending the entire length of the body whorl. We have selected a lectotype, BMNH 1973154/1 (Figures 3, 4), and paralectotype, BMNH 1973154/2, from A. Adams' syntypes.

The radula of *Nassarius nodicinctus* (Figure 17b; CASIZ 058031) is notably different from those of other Panamic species of *Nassarius* (Nesbitt, in prep.). The subcusps on the central tooth are partially fused, and there is an indication of extra thickening of the radula ribbon around the medial edge of each lateral tooth, which is in the position of the accessory plate in some western Pacific species, e.g., *N. conoidalis* (Deshayes & Belanger) from Kao Hsuing, Taiwan (CASIZ 058032) (Nesbitt, in prep.).

This species shows little variation of shell shape and ornamentation, compared with other eastern Pacific species of *Nassarius* (Nesbitt, in prep.). The protoconch, of 3 smooth bulbous whorls, has a diameter/volution ratio of 0.25, which is within the range inferring a planktotrophic larval type (SHUTO, 1974). The species ranges from the intertidal zone to a depth of 40 m, and has not been found in the fossil record.

Nassarius versicolor (C. B. Adams, 1852)

(Figures 7, 8, 17c)

Nassa versicolor C. B. ADAMS, 1852:290–291; TURNER, 1956: 97–98, pl. 6, fig. 8 (figured lectotype).*Nassa (Hima) versicolor*: TRYON, 1882:50, 51, pl. 15, figs. 270–272, 275.*Nassarius versicolor*: TOMLIN, 1927:161, 1932:43, 95; GRANT & GALE, 1931:677; HERTLEIN & STRONG, 1939:370; DEMOND, 1952:310, 312, pl. 1, fig. 5; KEEN, 1958:412, fig. 587, 1971:609, fig. 1314.*Alectrion versicolor*: DALL, 1917:576.*Nassa versicolor* var. *striatula* C. B. ADAMS, 1852:290; TURNER, 1956:98.*Nassa glauca* C. B. ADAMS, 1852:285–286.*Nassa proxima* C. B. ADAMS, 1852:288–289.*Nassa striata* C. B. ADAMS, 1852:289–290.*Nassa crebristriata* CARPENTER, 1857:499; KEEN, 1968:426, pl. 58, fig. 60.*Alectrion crebristriata*: DALL, 1917:577.*Nassa rufocincta* A. ADAMS, 1852:106.*Nassa albipunctata* REEVE, 1855:pl. 21, no. 144.

The numerous synonyms indicate variability in shell morphology of this widespread and common species. TRYON (1882) synonymized C. B. Adams' species, *Nassarius glauca*, *N. proxima* and *N. striata* with *N. versicolor*. TURNER (1956) illustrated C. B. Adams' type specimens and these show the range of shell shapes and ornamentation. Most of Adams' types are from single specimens or small lots, and all were collected around the island of Taboga, Panama Bay, Panama. The original description of *N. versicolor*, quoted below, requires some addition.

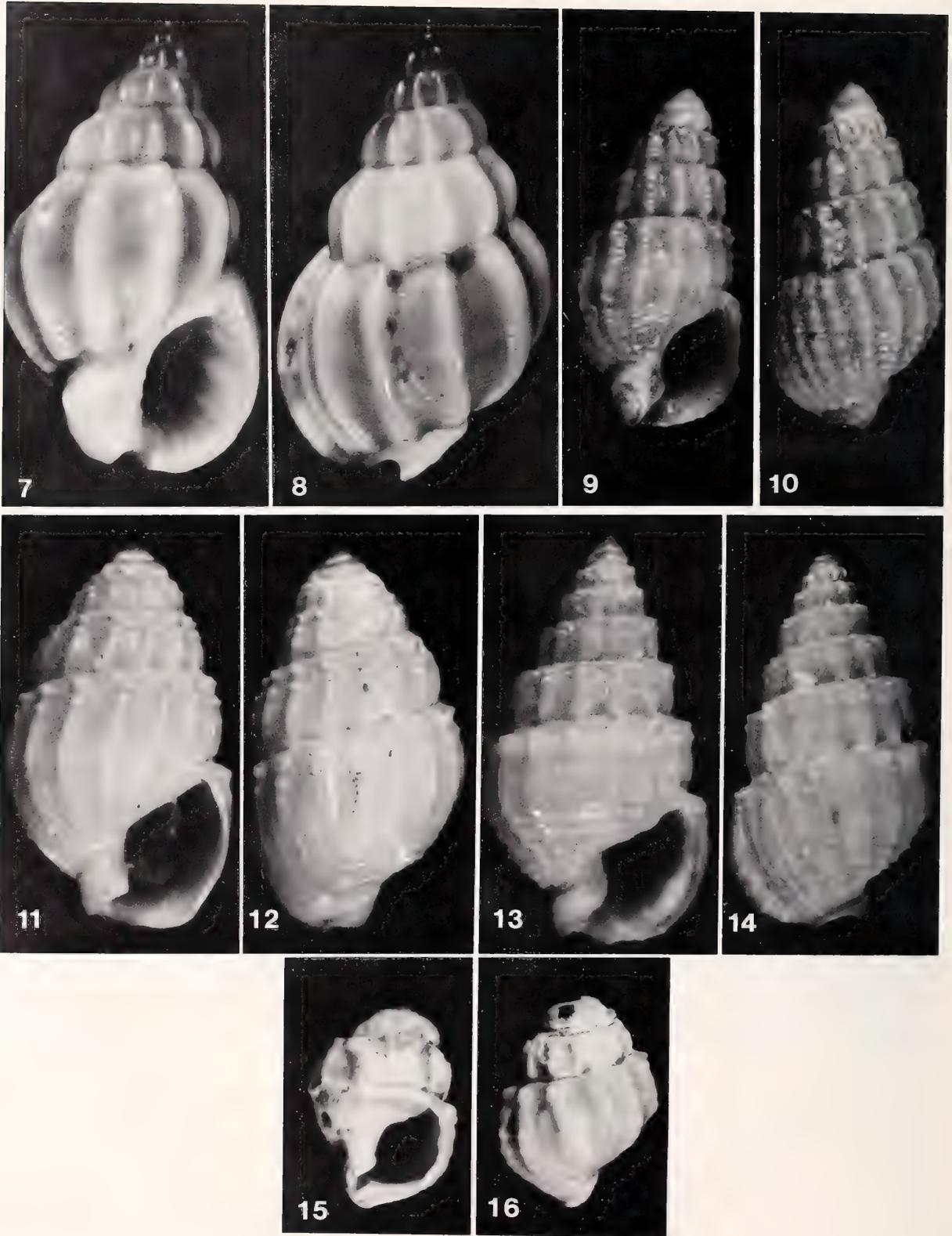
“Shell long ovate conic: pale yellowish brown, or nearly white, with a darker sutural line, or blackish brown: sometimes the ends of summits of the ribs are whiter than the interspaces; sometimes the sutural fascia covers the anterior part of the last whorl: with, on each whorl, nine or ten narrow very prominent ribs; with very minute spiral striae, which are nearly obsolete on the middle of the whorls; spire with the outlines nearly or quite rectilinear: apex acute; whorls eight, slightly convex, with a well impressed suture; last whorl spirally canaliculate anteriorly: aperture subelliptical: labrum subacute, thickened with a stout varix: labrium thickened, not appressed, finely wrinkled: notch deep. Var. *striatula* is covered with very distinct striae.

Mean divergence about 45°; length .6 inch; breadth .33 inch; length of spire .35 inch” (C. B. ADAMS, 1852).

Additional description: (1) 8–11 axial ribs, across entire length of body whorl, ranging from poorly developed to subnodal on shoulders. (2) Numerous, closely packed, minute, spiral striae on early postnuclear whorls, with little intraspecific variation; from third post-nuclear whorl a wide range of spiral ornamentation, varying from whorls being completely covered in minute incised striae (the “*striatula*” and “*proxima*” forms) to very few, poorly developed striae on body whorl (“*glauca*” form). The majority of specimens studied have unevenly developed and unevenly spaced incised spiral lines on the penultimate and body whorls. (3) Profile varies from globose to slender and high spired (“*proxima*” form).

Nassa rufocincta A. Adams and *Nassa albipunctata* Reeve are based on single specimens, synonymized with *Nassarius versicolor* by TOMLIN (1932), and figured by CERNOHORSKY (1975). *Nassa crebristriata* Carpenter was first synonymized with *Nassarius versicolor* by KEEN (1968). We studied the type specimens of all these species and concur.

The radula of *Nassarius versicolor* (Figure 17c; CASIZ 058033) is typical of most nassariids, and has a variable number of subcusps medially on the lateral tooth, with 9 or 10 cusps on the central tooth.



Distribution: Living from Magdalena Bay, Baja California, and the Gulf of California, Mexico, to south of Paita, Peru. Pleistocene fossils from Isla San Salvador, Galápagos Islands (CAS 27255; HERTLEIN & STRONG, 1939), and a single specimen from Quaternary indurated beach sands, Isla Isabella (CASG 61399).

Lectotype: MCZ 177145.

Nassarius exsarcus (Dall, 1908)

(Figures 9, 10)

Alectrion (Tritia) exsarcus DALL, 1908:308, fig. 12.

Nassarius exsarcus: KEEN, 1971:606, fig. 1297; CERNOHORSKY, 1975:146, fig. 52.

Nassarius exsarcus was described from a specimen dredged from the *Albatross* off the Galápagos Islands, at a depth of 300 fathoms (549 m) (CERNOHORSKY, 1975), not 200 fathoms as recorded by Dall. Specimens have also been dredged by A. & J. De Roy off Isla Pinzon (Duncan Island) from 366 m (LACM 105307).

This species is high spired and turreted with prominent axial ribs and a narrow, well defined callus. The most distinguishing feature is a large globose, porcelaneous protoconch, consisting of 5 smooth whorls. The first three whorls have a flattened conical profile, whereas the most anterior two are more globose. There is a distinct spiral keel on the anterior half of each whorl. The whorl diameter/volution index is 0.37, suggesting that the larvae are most probably planktotrophic.

Holotype: USNM 110565.

Nassarius townsendi (Dall, 1890)

(Figures 11, 12)

Nassa townsendi DALL, 1890:326, pl. 12, fig. 9.

Nassarius townsendi: KEEN, 1971:608, fig. 1313a; CERNOHORSKY, 1975:146-147, fig. 54.

The only record of this species is the holotype, which was dredged off the *Albatross* from 1486 m. CERNOHORSKY (1975) mentioned the similarity of this species and *Nassarius babylonica* (Watson, 1882) (Figures 13, 14), a somewhat more common deep-water species from the western Pacific and Indian Oceans (SALISBURY, 1984; CER-

NOHORSKY, 1978). However, *N. babylonica* is distinguished by distinctly tabulate shoulders and a straight-sided whorl profile. The two species may be closely related, but with so few specimens it is not possible to come to any reliable conclusions.

Nassarius townsendi is characterized by a small ovoid shell with comparatively rounded whorl profile, 15 axial ridges on the upper half of the body whorl, and a narrow, well delimited callus. The protoconch, consisting of 4 smooth bulbous whorls, is large and low spired, and the diameter/volution index is 0.3, within the range for a planktotrophic larval mode (SHUTO, 1974).

Holotype: USNM 96473.

Nassarius goniopleura (Dall, 1908)

(Figures 15, 16)

Alectrion (Tritia) goniopleura DALL, 1908:308-309.

Nassarius goniopleura: KEEN, 1971:606, fig. 1301.

This species was described from a single, damaged specimen, dredged by the *Albatross* at 1194 m, off the Galápagos Islands. The sculpturing on the body whorl, the only part preserved, is distinct and unlike any other known *Nassarius* species from the Pacific. However, no other specimen has been recorded, and it cannot be substantiated as a Galápaguan species.

Holotype: USNM 110630.

Nassarius catallus (Dall, 1908)

Nassa hanleyana MARRAT, 1880:75, 83; TOMLIN, 1940:36

(not *Buccinum hanleyanum* Dunker, 1847 = *Nassarius*).

Alectrion (Hima) catallus DALL, 1908:307, pl. 11, fig. 11.

Alectrion catallus: DALL, 1917:576.

Alectrion polistes DALL, 1917:577.

Nassarius catallus: STRONG, 1945:4; DEMOND, 1952:312, fig. 8; KEEN, 1958:408, fig. 569; ADDICOTT, 1965:B11; KEEN, 1971:606, fig. 1292; CERNOHORSKY, 1975:126, figs. 12-19.

CERNOHORSKY (1975) figured the holotype of *Nassarius catallus*, and the types of *N. polistes* and *N. hanleyana* (a secondary homonym of *Buccinum hanleyanum* Dunker, *vide* CERNOHORSKY [1975]). *Nassarius catallus* is characterized by a strong, smoothly reticulate ornamentation and nar-

Explanation of Figures 7 to 16

Figures 7 and 8. Lectotype of *Nassarius versicolor* (C. B. Adams), MCZ 177145 (height 14.4 mm).

Figures 9 and 10. Holotype of *Nassarius exsarcus* (Dall), USNM 110565 (height 9.0 mm).

Figures 11 and 12. Holotype of *Nassarius townsendi* (Dall), USNM 96473 (height 10.5 mm).

Figures 13 and 14. A syntype of *Nassarius babylonica* (Watson), BMNH 1887.2.9.6-8 (height 11.0 mm).

Figures 15 and 16. Holotype of *Nassarius goniopleura* (Dall), USNM 110630 (height 5.5 mm).

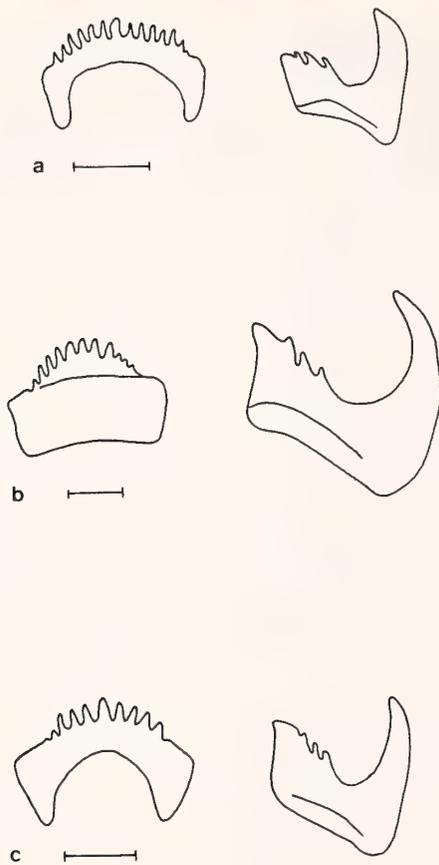


Figure 17

One lateral and one central tooth from the radula of: a, *Nassarius caelolineatus*, spec. nov., paratype, CASIZ 058039, Galápagos Islands; b, *N. nodicinctus* (A. Adams), CASIZ 058031, Guaymas, Mexico; and c, *N. versicolor* (C. B. Adams), CASIZ 058033, Sonora, Mexico. Scale = 0.1 mm.

row, well developed parietal callus. It is a rare, deep-water inhabitant, reported from Baja California to Peru, with one confirmed lot dredged from 180–280 m off Isla Wolf, Galápagos Islands (LACM AHF143-35).

Holotype: USNM 123013.

Nassarius shaskyi McLean, 1970

Nassarius shaskyi McLEAN, 1970:128–129, fig. 41; KEEN, 1971:606, fig. 1312.

Nassarius shaskyi is characterized by obsolete spiral sculpture, and, on the body whorl, pronounced apical nodes on concave axial ridges, and a well defined callus. It is a rare, shallow-water species with a widespread distribution from the outer coast of Baja California, and from the Gulf of California to Colombia. In addition, McLean (personal communication, 1984) collected one adult specimen from 23 to 30 m off Isla Wolf, Galápagos Islands in May 1984.

Holotype: LACM 1405.

Spurious Records of *Nassarius* Species from the Galápagos Islands

Nassarius anguliferus and *N. pagodus*: *Nassarius anguliferus* (A. Adams, 1852) was described from the Cuming collection. The locality was stated to be the Galápagos Islands, and this was repeated by REEVE (1853:34), CARPENTER (1857:361), STEARNS (1853:406), and PILSBRY & VANATTA (1902:554). The erroneous locality record probably has the same source as that for the type specimens of *N. nodicinctus* and *Polinices galapagosus*. We cannot locate the specimens reported by PILSBRY & VANATTA (1902) to be in the Stanford University collection, but other specimens labeled *N. anguliferus* from early CAS and Stanford collections are *N. nodicinctus* (as described herein).

TRYON (1882:45) stated that *Nassarius anguliferus* is a juvenile specimen of the common and variable Panamic species *N. pagodus* (Reeve). Comparisons with the type specimens, and with a large size range of *N. pagodus* specimens from the Gulf of California to Ecuador, confirm this. Thus, the spurious account of *N. pagodus* from the Galápagos is the result of Tryon's synonymy. TOMLIN'S (1932) synonymy of *N. anguliferus* with the Mediterranean species *N. migra* (Bruguère) and KEEN'S (1971) with *N. dentifer* (Powys) from the Peruvian Province are therefore incorrect.

Nassarius nodifera: POWYS (1835) described *Nassa nodifera* from the Cuming collection, with the locality records "Galápagos Islands and beaches of Panama." This locality information was copied by REEVE (1853:23), CARPENTER (1857:361), STEARNS (1893:406), and KEEN (1958:410). TRYON (1882:28) synonymized the species with *N. hirtus* (Kiener), and stated that the "localities of 'Panama and Galápagos' are almost certainly incorrect." This species is common in the western Pacific and the Indian Ocean, and has not been recorded subsequently from the Galápagos Islands.

Nassarius tegula: SMITH (1940) stated that *N. tegula* (Reeve) occurs along the western tropical mainland and the Galápagos Islands. This species is a southern geographic subspecies of *N. tiarula* (Kiener) which has only been recorded from California to Panama.

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LITERATURE CITED

- ADAMS, A. 1852-53. Catalogue of species of *Nassa*, a genus of gastropodous Mollusca belonging to the family Buccinidae, in the collection of Hugh Cuming Esq., with the description of some new species. Proc. Zool. Soc. Lond. 19:94-114.
- ADAMS, C. B. 1852. Catalogue of shells collected at Panama, with notes on synonymy, station and geographical distribution. Ann. Lyceum Natur. Hist. New York 5:229-549.
- ADDICOTT, W. O. 1965. Some western American Cenozoic gastropods of the genus *Nassarius*. U.S. Geol. Surv. Prof. Pap. 503B:1-24.
- CARPENTER, P. P. 1857. Catalogue of the collection of Mazatlan shells in the British Museum: collected by Frederick Reigen . . . London (British Museum). Reprinted, Paleoc. Res. Inst. Ithaca, N.Y. 1967. i-iv + ix-xvi + 552 pp.
- CERNOHORSKY, W. O. 1975. The taxonomy of some west American and Atlantic Nassariidae based on their type specimens. Rec. Auckland Inst. Mus. 12:121-173.
- CERNOHORSKY, W. O. 1978. Tropical Pacific marine shells. Pacific Publications: Sydney. 352 pp.
- DALL, W. H. 1890. Scientific results for exploration by the U.S. Fish Commission Steamer Albatross. VII. Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887-'88. Proc. U.S. Natl. Mus. 12:219-362.
- DALL, W. H. 1908. Reports on the dredging . . . XIV. The Mollusca and Brachiopoda. Bull. Mus. Comp. Zool. Harvard 43:205-487.
- DALL, W. H. 1917. Summary of the mollusks of the family Aletrionidae of the west coast of America. Proc. U.S. Natl. Mus. 53:575-579.
- DALL, W. H. & W. H. OCHSNER. 1928. Tertiary and Pleistocene Mollusca from the Galápagos Islands. Proc. Calif. Acad. Sci., ser. 4, 17:89-137.
- DE FOLIN, L. 1867. Les Meleagrinoles: especes nouvelles. Harvre Imprimerie Lepelletier. 74 pp.
- DEMOND, J. 1952. The Nassariidae of the west coast of North America between Cape San Lucas, Lower California, and Cape Flattery, Washington. Pacific Sci. 4:300-317.
- GRANT, U. S., IV & H. R. GALE. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Mem. San Diego Soc. Natur. Hist. 1:1-1036.
- HERTLEIN, L. G. 1972. Pliocene fossils from Baltra (South Seymour) Island, Galápagos Islands. Proc. Calif. Acad. Sci., ser. 4, 39:25-46.
- HERTLEIN L. G. & A. M. STRONG. 1939. Marine Pleistocene mollusks from the Galápagos Islands. Proc. Calif. Acad. Sci., ser. 4, 23:367-380.
- JAMES, M. J. 1984. A new look at evolution in the Galápagos: evidence from the late Cenozoic marine molluscan fauna. Biol. J. Linn. Soc. 21:77-95.
- KEEN, A. M. 1958. Seashells of tropical west America. Stanford Univ. Press: Stanford, Calif. 624 pp.
- KEEN, A. M. 1968. West American mollusk types at the British Museum (Natural History) IV. Carpenter's Mazatlán collection. Veliger 10:389-439.
- KEEN, A. M. 1971. Seashells of tropical west America. 2nd ed. Stanford Univ. Press: Stanford, Calif. 1064 pp.
- LIPPS, J. H. & C. S. HICKMAN. 1982. Paleontology and geologic history of the Galápagos Islands. Geol. Soc. Amer. Abstracts with Programs 14(7):548.
- MCLEAN, J. H. 1970. New species of tropical eastern Pacific Mollusca. Malacol. Rev. 2:115-130.
- MARINCOVICH, L., JR. 1977. Cenozoic Naticidae (Mollusca: Gastropoda) of the northeastern Pacific. Bull. Amer. Paleontol. 70(294):1-453.
- MARRAT, F. P. 1880. On the varieties of the shells belonging to the genus *Nassa* Lam. 104 pp.
- PILSBRY, H. A. & H. N. LOWE. 1932. West Mexican and Central American mollusks collected by H. N. Lowe, 1929-31. Proc. Acad. Natur. Sci. Phila. 84:35-144.
- PILSBRY, H. A. & E. G. VANATTA. 1902. Papers from the Hopkins Stanford Galápagos expedition, 1898-99, no. 13, marine Mollusca. Proc. Wash. Acad. Sci. 4:549-560.
- PITT, W. D. & M. J. JAMES. 1984. Late Cenozoic marine invertebrate paleontology of the Galápagos Islands. West. Soc. Malacol. Ann. Rep. 15:14-15.
- POWYS, W. L. 1835. Undescribed shells contained in Mr. Cumings collection . . . accompanied by characters by Mr. G. B. Sowerby and Mr. W. Lytellton Powys. Proc. Zool. Soc. Lond. Pp. 93-96.
- REEVE L. 1853-55. Conchologia Iconica: or illustrations of the shells of molluscous animals. VIII. *Nassa*. London.
- SALISBURY, R. 1984. Guam's *Nassarius* community. Hawaiian Shell News 32, new series, 290:1,8-9.
- SHASKY, D. R. 1984. A preliminary checklist of marine mollusks from Manabi Province, Ecuador. Ann. Rep. West. Soc. Malacol. 16:25-32.
- SHUTO, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. Lethaia 7:239-256.
- SMITH, M. 1940. World-wide sea shells. Tropical Photo. Lab.: Lantana, Florida. 139 pp.
- STEARNS, R. E. C. 1893. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. XXV. Report . . . Proc. U.S. Natl. Mus. 16:353-450.
- STRONG, A. M. 1945. Distributional list of west American marine mollusks from San Diego to the Polar Sea. In: J. G. Burch (ed.), Proc. Conch. So. Club Calif. 51:3-5.
- TOMLIN, J. R. 1927. The Mollusca of the "St. George" expedition. J. Conch. 18:153-170.
- TOMLIN, J. R. 1932. Notes from the British Museum. II. Arthur Adams' types of *Nassa*. Proc. Malacol. Soc. Lond. 20:41-44.
- TOMLIN, J. R. 1940. Marrat's species of *Nassa*. Proc. Malacol. Soc. Lond. 24:34-40.
- TRYON, G. W. 1882. Manual of conchology: structural and systematic. 4:276 pp. Philadelphia.
- TURNER, R. D. 1956. The eastern Pacific marine mollusks described by C. B. Adams. Occas. Pap. Mollusks, Mus. Comp. Zool. Harvard 2:21-135.
- WATSON, R. B. 1882. Mollusca of the H.M.S. "Challenger" expedition—XIII. J. Linn. Soc. Lond. 16:358-392.

On Pleurobranchomorpha from Italian Seas (Mollusca: Opisthobranchia)

by

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Abstract. Ten species of pleurobranchomorph opisthobranchs are reported from Italian waters, with special reference to the diets of the animals and the structure of the radular teeth and jaw platelets.

INTRODUCTION

IN THE MEDITERRANEAN SEA the order Pleurobranchomorpha is represented by a small number of species, some widely distributed and well known, others uncommon and plagued by problems of taxonomy. Recent reports have come from widely separated localities within the Mediterranean: Villefranche-sur-mer (HAEFELFINGER, 1960), Marseille (VICENTE, 1967), Tuscany (SORDI, 1969), Costa Brava (ROS, 1975), Israel (BARASH & DANIN, 1971, 1977), and Gulf of Taranto (PERRONE, 1983). Although some mention of the order was made in a preliminary communication by SCHMEKEL (1968), they were omitted from consideration in the recent compendium *Opisthobranchia des Mittelmeeres* (SCHMEKEL & PORTMANN, 1982).

While studying opisthobranch samples from Italian seas, 10 species of Pleurobranchomorpha were collected, mostly by diving on hard substrata to a depth of 50 m. Particular attention was paid to the radulae, jaws, and diets of the species collected.

PLEUROBRANCHOMORPHA

Pleurobranchaea meckeli Leue, 1813

Material collected: Ligurian Sea: Gulf of Genoa (August 1978, at 50 m depth); Gulf of Marconi (August-September 1982, on sandy and muddy bottoms from 40 to 90 m).

Description: This large (maximally 15 cm in length) and common species (Figure 3) has a broad oral veil, blunt rhinophores, and a large gill. The back is covered by a mottled brown and yellow pattern. A shell is lacking. The radular formula is 50-60 × 65(55).1.(55)65. The rachidian tooth is not always visible and can fall out of the preparation as reported for *Pleurobranchaea maculata* by WILAN (1983). The other teeth are long and bicuspidate as

shown by PRUVOT-FOL (1954). The jaw platelets are changeable in length and breadth: they cannot be utilized for separation of species (MARCUS & GOSLINER, 1984). The large gill bears 28-30 pinnae.

Diet: The diet is variable and consists of vegetable debris, polychaetes (*Eteone* [*Mysta*] *picta*, *Phyllodoce* sp.), amphipods (mainly *Pseudoprotella phasma* and some *Photis longicaudata*), nudibranchs (Facelinidae), colonial ascidians, turbellarians, nemertines, and nematodes. In one specimen, an ectoparasitic isopod (*Meinertia oestroides*) was found near the genital apertures.

Discussion: Recently MARCUS & GOSLINER (1984) described two new Mediterranean species (*Pleurobranchaea notmec* and *Pleurobranchaea vayssierei*) and found, along the Israelian coast, an Atlantic species (*Pleurobranchaea inconspicua*). These three species are distinguished from *P. meckeli* by vaginal and penial characters: in my collection all specimens appear similar to the description of *P. meckeli*, with a long, looped cuticular penis and a long vagina.

This species has been recently recorded from France (HAEFELFINGER, 1960; VICENTE, 1967), Turkey (SWENNEN, 1961), Israel (BARASH & DANIN, 1971), Spain (ROS, 1975) and Italy (PERRONE, 1983).

Pleurobranchus (Oscanius) membranaceus
(Montagu, 1803)

Material collected: Ligurian Sea: Gulf of Genoa, in the collection of the Zoological Institute of the University of Genoa, one specimen labeled "*Pleurobranchus* sp. ? 1886 Genoa." Tyrrhenian Sea: Gulf of Naples, Pozzuoli (June 1963, one specimen at 40 m depth, collected by L. Capocaccia).

Description: The mantle, pale brown with dark brown patches, bears many tubercles. Lengths of the two pre-

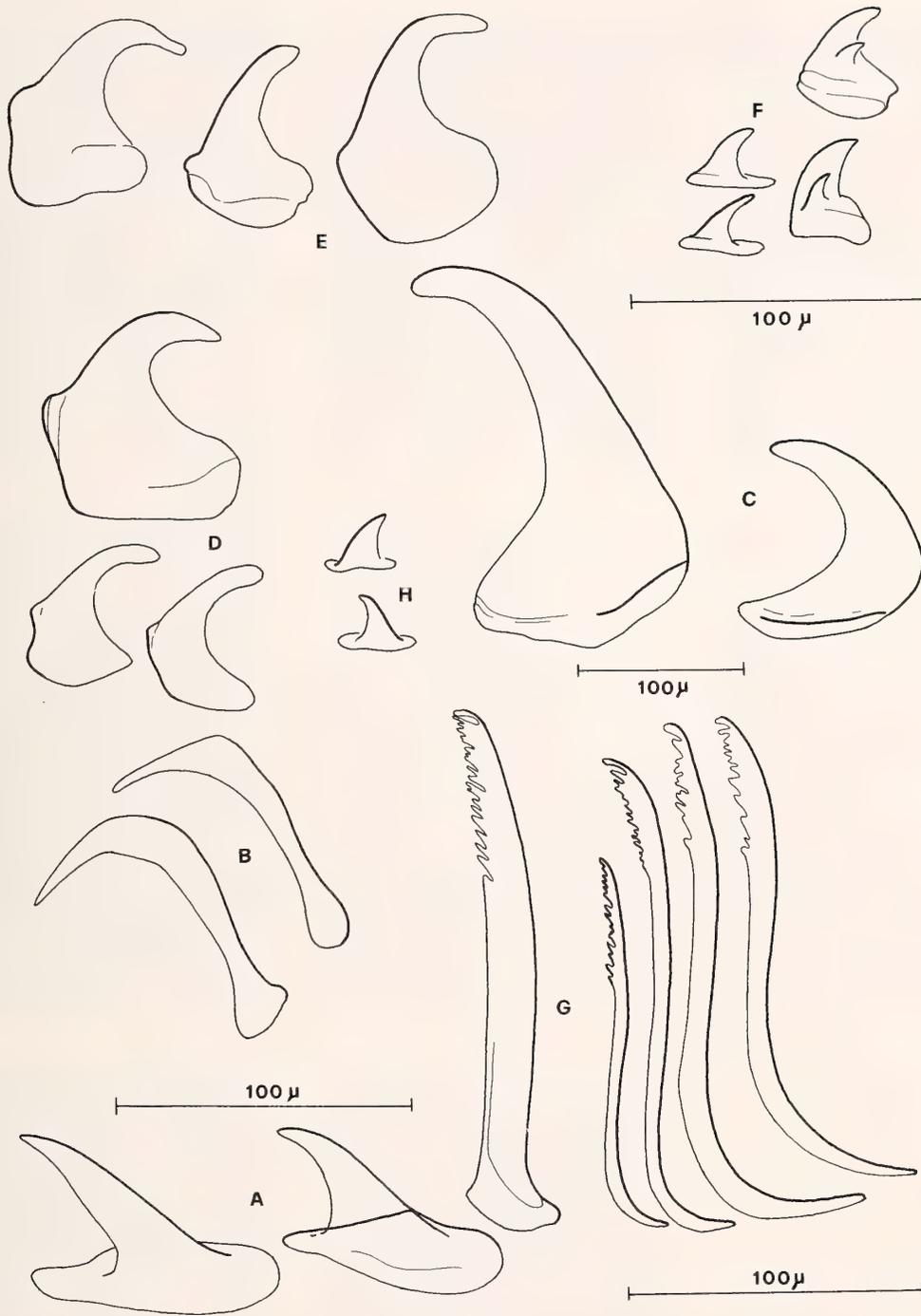


Figure 1

Teeth of Mediterranean Pleurobranchomorpha. A, *Pleurobranchus membranaceus* (inner lateral teeth); B, *Pleurobranchus membranaceus* (outer lateral teeth); C, *Pleurobranchus testudinarius*; D, *Berthella ocellata*; E, *Berthella* sp. 1; F, *Berthella* sp. 2; G, *Berthellina citrina*; H, *Berthella aurantiaca*.

served specimens are 30 mm (Genoa) and 35 mm (Pozzuoli). In the 30 mm long specimen, the dimensions of the shell are 25×17 mm. The radular formula is $36-45 \times 60(100).0.(100)60$. The teeth nearest the rachis (Figure 1A) do not bear a subterminal spine, contrary to assertions by VAYSSIÈRE (1885), BERGH (1899), and THOMPSON (1976). The lateral teeth are longer and thinner (Figure 1B). The mandibular platelets (80–130 μm long) bear 3 large denticles (Figure 2A). The gill rachis is tuberculate and bears from 24 to 26 pinnae. A pedal gland is present. There is a flap of flesh around the genital apertures, which are contiguous.

Diet: Nothing was found in the alimentary canals of the specimens studied.

Discussion: This species has been recently recorded from France (HAEFELFINGER, 1960; VICENTE, 1967) and Spain (ROS, 1975). It seems to be uncommon in Italian Seas; however, PERRONE (1983) collected several specimens in the Gulf of Taranto.

Pleurobranchus (Susania) testudinarius
(Cantraine, 1840)

Material collected: Tuscany Archipelago: Isle of Elba (October 1982, one specimen from 45 m); Montecristo Isle (June 1983, two specimens from 40 m).

Description: This species (Figure 4) has a red ground color. The mantle is formed by large tubercles, which around their polygonal bases have a thin purple line. On top of the mantle there are two rows of larger tubercles. The Elba specimen was 15 cm in length, those from Montecristo smaller (12 cm). In these three specimens a shell was not found. The radular formula is $220-250 \times 220(250).0.(250)220$. The hooked teeth are simple and uniform (Figure 1C). The jaws of the largest specimen are 15 mm long, and their platelets, 370 μm in length, have 2 or 3 lateral denticles (Figure 2B). The large tuberculate gill (45 mm long in the Elba specimen) bears 18–20 pinnae. A pedal gland is present.

Diet: Colonial ascidians (Didemnidae) were found in the stomachs, together with bivalves (*Musculus marmoratus*) and plant debris.

Discussion: This species lives on sandy to muddy bottoms, but recently ROS & GILI (1984) found it in an underwater cave at Majorca (Balearic Isles). Recent records come also from France (HAEFELFINGER, 1960), Italy (SCHMEKEL, 1968), Israel (BARASH & DANIN, 1971), and Spain (ROS, 1975).

Berthella plumula (Montagu, 1803)

Material collected: Ligurian Sea: Isle of Gallinara (August 1976, one specimen under a stone at 0.5 m depth).

Description: This specimen measured 5 mm in length and was light yellow in color. The mantle has reticulate markings as reported by THOMPSON (1976). The oval, white internal shell covers all the contracted body. The radular formula is $40 \times 55.0.55$. The teeth are simple hooks, while the mandibular platelets exhibit 2 or 3 lateral denticles on either side of the cusp (Figure 2E). The gill has 16 pinnae on either side of the smooth rachis.

Diet: No sponge spicules were found in the alimentary canal. This agrees with a diet of slime-sponges (*e.g.*, *Oscarella lobularis*) as reported by DELALOI & TARDY (1976) or colonial tunicates.

Discussion: This species has been recorded in recent times from France (HAEFELFINGER, 1960), Italy (SCHMEKEL, 1968; PERRONE, 1983), and Israel (BARASH & DANIN, 1971).

Berthella aurantiaca (Risso, 1818)

Material collected: Tyrrhenian Sea: Gulf of Procchio, Isle of Elba (June 1978, one specimen in a meadow of *Posidonia oceanica* at 14 m depth).

Description: The specimen was 6 mm long and yellow in color. Through the skin of the smooth mantle calcareous deposits could be discerned. A large oral veil is present, and the white internal shell covers the entire contracted body. The radular formula is $50 \times 60.0.60$. In the preserved state, this species can be distinguished from *B. plumula* by its larger mandibular elements (Figure 2D), but the radular teeth do not differ significantly (Figure 1H). The gill has 18 pinnae on either side of the smooth rachis.

Diet: No sponge spicules were found in the alimentary canal.

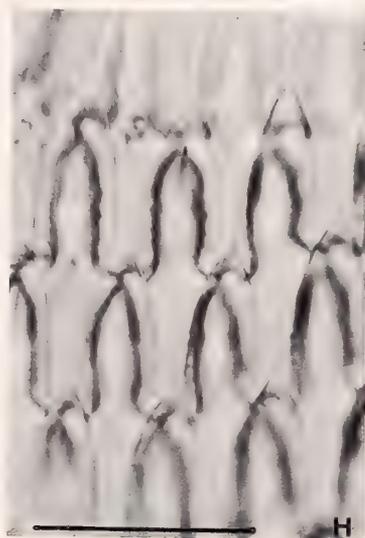
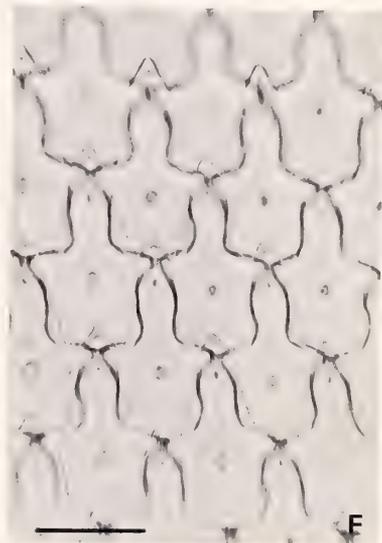
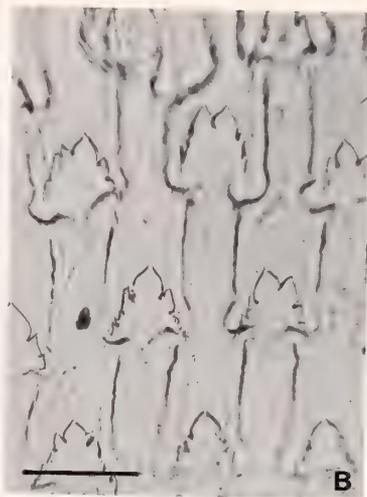
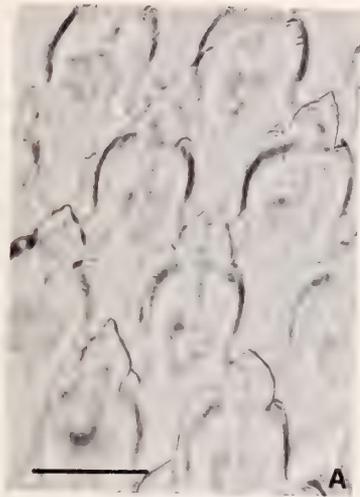
Discussion: Recent records have come from France (HAEFELFINGER, 1960), Italy (SCHMEKEL, 1968; SORDI, 1969; PERRONE, 1983), Yugoslavia (STARMÜHLNER, 1969), Israel (BARASH & DANIN, 1971), and Spain (ROS, 1975; ALTIMIRA *et al.*, 1981; ROS & GILI, 1984).

Berthella ocellata (Delle Chiaje, 1828)

Material collected: Tyrrhenian Sea: Gulf of Naples (May 1979, in the Mitigliano Cave on the Sorrentine Peninsula at 12 m depth).

Figure 2

Mandibular platelets of Mediterranean Pleurobranchomorpha (bar = 50 μm). A, *Pleurobranchus membranaceus*; B, *Pleurobranchus testudinarius*; C, *Berthella* sp. 2; D, *Berthella aurantiaca*; E, *Berthella plumula*; F, *Berthella* sp. 1; G, *Berthella ocellata*; H, *Berthellina citrina*.



Description: The ground color of this species is tan, and the mantle has many whitish spots (*ocelli*) surrounded by opaque white oval rings (MAZZARELLI, 1891). The specimen measured 18 mm in length and had a white oval internal shell, 4.5 mm long. The radular formula is $60 \times 65.0.65$. The teeth are squat and hook-shaped (Figure 1D). The mandibular elements are smooth (Figure 2G), which is unusual in this genus but has been reported also for *B. monterosati* (VAYSSIÈRE, 1885), a synonym. The gill has 15 pinnæ on either side of the smooth rachis.

Diet: In the Mitigliano Cave, *Berthella ocellata* feeds upon sponges, e.g., *Plakina trilopha* and *Plakinastrella copiosa*.

Discussion: Recent records have come from Marseille (VICENTE, 1967), Tuscany (SORDI, 1969), and Costa Brava, Spain (ROS, 1975).

Berthella sp. 1

Material collected: Ligurian Sea: Paraggi, Portofino Promontory (June 1978, one specimen from 13 m depth, hard bottom).

Description: This specimen resembles *B. ocellata*, but the coloration is different: the brown mantle has only sparse white patches, which are not organized into *ocelli*. The body length is 20 mm, and the white, subtriangular shell is 7 mm long. The radular formula is $85 \times 80.0.80$; the teeth are simple hooks, like those of other species of *Berthella* (Figure 1E). The mandibular elements are smooth (Figure 2F). The smooth rachis of the gill bears 18 pinnæ.

Diet: Spicules of the sponge *Corticium candelabrum* were found in the alimentary canal.

Berthella sp. 2

Material collected: Ligurian Sea: off Alassio (May 1975, one specimen from 185 m, coll. G. Albertelli).

Description: The shape of this specimen, which was 9 mm long and had a smooth, yellow mantle, resembles that of *Berthellina citrina*. A large oval veil is present, and the internal shell is approximately $\frac{1}{4}$ the body length. The radular formula is $40 \times 35.0.35$. Teeth from the central part of the radula bear an additional subterminal spine, as in *Berthella tupala* Marcus, 1957, and many species of *Pleurobranchus* (Figure 1F). The mandibular platelets generally have one or two very distinct denticles on either side of the cusp and are more like the elements of *Pleurobranchus membranaceus* than those of the other *Berthella* species (Figure 2C). The gill, lacking tubercles, has 20 pinnæ on either side. An external penial sheath is present. The salivary glands are long and ribbon-shaped.

Diet: There were no sponge spicules in the alimentary canal of the specimen.

Berthellina citrina (Rüppell & Leuckart, 1828)

Material collected: Ligurian Sea: Paraggi, Portofino Promontory (July 1979, one specimen from 25 m depth, under a stone). Tyrrhenian Sea: Gulf of Naples (June 1979, June 1980, June 1981, many specimens in submarine caves along the sorrentine Peninsula).

Description: The color of this species is yellow-orange and it may be confused with *Berthella aurantiaca* on external features alone. However, the tooth-shape is unmistakable (Figure 1G). The oval shell is small and white; one specimen from Mitigliano Cave had no shell. The radular formula is $45-80 \times 160(200).0.(200)160$. The elongate teeth bear serrations on their posterior edge. (Figure 1G). The platelets are smooth (Figure 2H). The number of gill pinnæ varies from 16 to 20 in specimens 6-11 mm in body length. A pedal gland is lacking.

Diet: Observations on the diet of *Berthellina citrina* have been published by CATTANEO (1982). In the present collection, the specimen from Paraggi contained spicules of the sponges *Hemimycale* sp. and *Batzella* sp.

Discussion: WILLAN (1983) discussed whether or not *Berthellina citrina* and *Berthellina engeli* Gardiner, 1936, are the same species. Here, they are considered synonyms, as did THOMPSON (1976). According to BURN (1962) these two species differ mainly in the shape of the jaw platelets, which are smooth in *B. engeli* and bear 1-3 indistinct lateral denticles in *B. citrina*. In the same paper, however, Burn reports the presence of smooth platelets in *B. citrina* from Australian waters: this is in agreement with THOMPSON's (1976) description of *B. citrina* from European waters.

Recent records of *Berthellina citrina* include localities in France (HAEFELFINGER, 1960), Italy (SCHMEKEL, 1968), and Israel (EALES, 1970; BARASH & DANIN, 1977).

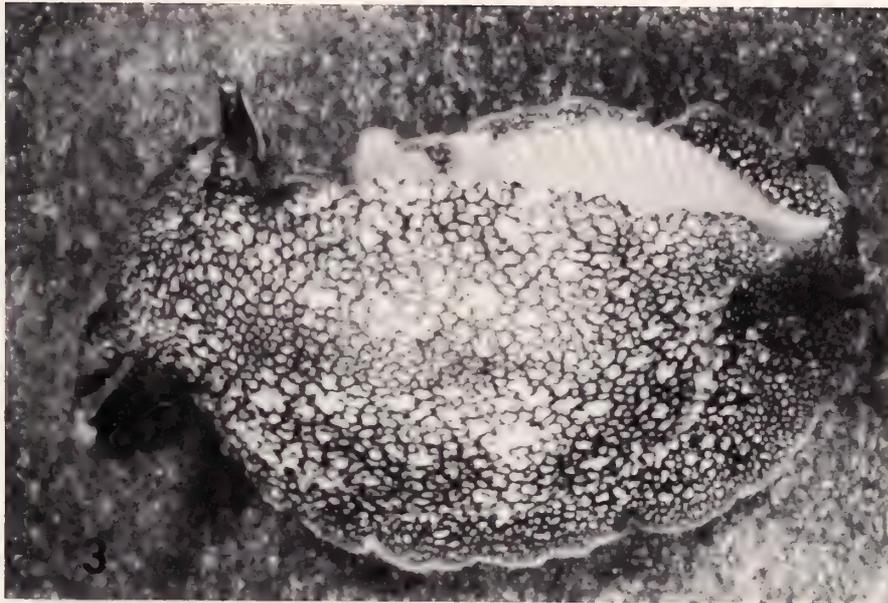
Umbraculum mediterraneum (Lamarck, 1812)

Material collected: Tyrrhenian Sea: Isle of Montecristo (July 1980; July 1982 in a submarine cave at 30 m depth). Sicily Channel: Isle of Linosa (August 1978 in a small cave at 4 m).

Description: This species, unmistakable with a flat external shell, is well described by MOQUIN-TANDON (1870) and PRUVOT-FOL (1954). The radular formula is up to $150 \times 1000.0.1000$. The teeth, numerous and all alike, are hook-shaped. In smaller specimens (length 30 mm) from the Isle of Montecristo, the gills are not present around the front of the body as in the larger individuals (length 85 mm).

Diet: The diet consists of several sponges: *Tethya citrina*, *Diplastrella unistellata*, *Jaspis johnstoni*, *Alectona millaris*, *Agelas* sp., *Aaptos aaptos*, and *Spirastrella cunctatrix*.

Discussion: This species is quite common in caves and in shaded habitats. Recent records of *Umbraculum* have come



Explanation of Figures 3 and 4

Figure 3. *Pleurobranchaea meckeli*, 10 cm length. Ligurian Sea, Genoa, on muddy bottom at 50 m depth.

Figure 4. *Pleurobranchus testudinarius*, 15 cm length. Tyrrhenian

Sea, Isle of Elba, on sandy bottom at 45 m depth. The rhinophores are on the left side. Photo by R. Pronzato.

from France (HAEFELFINGER, 1960; VICENTE, 1967), Turkey (SWENNEN, 1961), Italy (SCHMEKEL, 1968), Israel (BARASH & DANIN, 1971), and Spain (ROS, 1975).

CONCLUSIONS

If we exclude several species imperfectly described by FORBES (1844), PHILIPPI (1844), and VÉRANY (1846) and all considered *incertae sedis* by PRUVOT-FOL (1954), the

Pleurobranchomorpha present in the Mediterranean Sea are as follows:

Superfamily Pleurobranchacea

Family Pleurobranchaeidae

Pleurobranchaea meckeli Leue, 1813

Pleurobranchaea inconspicua Bergh, 1897

Pleurobranchaea vayssierei Marcus & Gosliner, 1984

Pleurobranchaea notmec Marcus & Gosliner, 1984

Family Pleurobranchidae

- Pleurobranchus (Oscanius) membranaceus* (Montagu, 1803)
Pleurobranchus (Susania) testudinarius Cantraine, 1840
Pleurobranchus forskali (Rüppell & Leuckart, 1828)
Berthella plumula (Montagu, 1803)
Berthella aurantiaca (Risso, 1818)
Berthella ocellata (Delle Chiaje, 1828)
Berthella stellata (Risso, 1826)
Berthella perforata (Philippi, 1844)
Berthella elongata (Cantraine, 1835)
Berthellina citrina (Rüppell & Leuckart, 1828)

Superfamily Umbraculacea

Family Umbraculidae

- Umbraculum mediterraneum* (Lamarck, 1812)

Family Tyloidinidae

- Tyloдина perversa* (Gmelin, in L., 1791)
Tyloidinella trinchesei Mazzarelli, 1897

The list is probably incomplete because of the past nomenclatural confusion. Some of the taxonomic problems are, at present, insoluble, but progress continues to be made. *Berthella stellata*, for example, was recently validated by detailed re-description of Adriatic specimens by THOMPSON (1981), while MARCUS & GOSLINER (1984) provided an exhaustive review of the Pleurobranchaeidae. Unfortunately, many other problems persist. *Berthella elongata* was recorded by VICENTE (1967) from the Gulf of Marseille and by PERRONE (1983) from the Salentin coast of the Gulf of Taranto, but the specific validity seems to be uncertain because of the poorness of the descriptions. The status of *Berthella perforata* remains enigmatic also, and there is confusion between past records of *Berthella plumula*, *B. aurantiaca*, and *Berthellina citrina*. It is necessary to inspect the radula and jaws in order to differentiate between species of *Berthella* and *Berthellina*, and distinguishing between *B. aurantiaca* and *B. plumula* remains difficult, especially when the specimens have been preserved (TERRENI & CAMPANI, 1980). When alive, *B. plumula* can be seen to have conspicuous reticulate markings on the dorsal mantle. The description of *Gymnotoplax barashi* Marcus, 1977, was undoubtedly based in error upon a distorted specimen of *Pleurobranchus membranaceus*, as pointed out by WILLAN (1978). Although *Tyloidinella trinchesei* is listed here, PRUVOT-FOL & FISCHER-PIETTE (1934) and BERTSCH (1980) have raised justifiable doubts about its validity.

Two further notes on the records of pleurobranchomorphs warrant mention. First, *Tyloдина perversa* is a rare species, recently recorded from the Gulf of Naples (SCHMEKEL, 1968) and the Gulf of Taranto (PERRONE, 1983). In the Ligurian Sea it was photographed at 15 m depth off Portofino in October 1962 by Dr. G. Pulitzer-Finali. Second, *Pleurobranchus forskali* has been recorded in the eastern Mediterranean Sea (BARASH & DANIN, 1977) and it is an example of Lessepsian migration.

The observations reported here confirm that the Pleurobranchomorpha are carnivorous. Furthermore, those species that live on hard substrata show a more highly specific diet (usually species of sponge) than the more catholic species that live on soft bottoms.

ACKNOWLEDGMENTS

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LITERATURE CITED

- ALTIMIRA, C., M. F. HUELIN & J. ROS. 1981. Molluscs benthonic of les Iles Medes (Girona). Bull. Inst. Cat. Hist. Natur. 47(sec. Zool., 4):69-75.
 BARASH, A. & Z. DANIN. 1971. Opisthobranchia (Mollusca) from the Mediterranean waters of Israel. Isr. J. Zool. 20: 151-200.
 BARASH, A. & Z. DANIN. 1977. Additions to the knowledge of Indopacific Mollusca in the Mediterranean. Conchiglie (Milano) 13(5-6):85-116.
 BERGH, L. S. R. 1899. Nudibranches et *Marsenia* provenant des campagnes de la Princesse Alice (1891-1897). Res. Camp. Sci. Monaco 14:1-45.
 BERTSCH, H. 1980. A new species of Tyloidinidae (Mollusca: Opisthobranchia) from the northeastern Pacific. Sarsia 65: 233-237.
 BURN, R. 1962. On the new pleurobranch subfamily Berthellinae (Moll.: Gastropoda); a revision and new classification of the species of the New South Wales and Victoria. Mem. Nat. Mus. Victoria 25:129-148.
 CATTANEO, R. 1982. Opisthobranch molluscs of the Sorrentine Peninsula caves. Boll. Mus. Ist. Biol. Univ. Genova, 50(suppl.):376-377.
 DELALOI, B. & J. TARDY. 1976. Régime alimentaire et éthologie prédatrice de *Berthella plumula* (Montagu, 1803), Mollusque Opisthobranchie. Haliotis 6:273-280.
 EALES, N. B. 1970. On the migration of tectibranch molluscs from the Red Sea to the eastern Mediterranean. Proc. Malacol. Soc. Lond. 39:217-220.
 FORBES, E. 1844. Report on the Mollusca and Radiata of the Aegean Sea and on their distribution, considered as bearing on geology. Rep. British Assoc. Adv. Sci. 13:130-193.
 HAEFELFINGER, H. R. 1960. Catalogue des Opisthobranches de la Rade de Villefranche-sur-mer et ses environs (Alpes Maritimes). Rev. Suisse Zool. 67(27):323-351.
 MARCUS, EV. & T. GOSLINER. 1984. Review of the family Pleurobranchaeidae (Mollusca, Opisthobranchia). Ann. So. Afr. Mus. 93(1):1-52.
 MAZZARELLI, G. 1891. Intorno alle specie di *Pleurobranchus* del Golfo di Napoli. Boll. Soc. Natur. Napoli 5(1):69-76.
 MOQUIN-TANDON, G. 1870. Recherches anatomiques sur l'Ombrelle de la Méditerranée. Theses pr. Fac. Sc. Paris, n° 326:1-303.
 PERRONE, A. 1983. Opisthobranchi (Aplysiomorpha, Pleurobranchomorpha, Sacoglossa, Nudibranchia) del litorale salentino (Mar Jonio) (Elenco-contributo primo). Thalassia Salentina Taranto 13:118-144.
 PHILIPPI, R. A. 1844. Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit. II. Halis Saxonum 1-4:1-303.

- PRUVOT-FOL, A. 1954. Mollusques Opisthobranches. Faune de France 58:1-460.
- PRUVOT-FOL, A. & E. FISCHER-PIETTE. 1934. Sur la *Tylodina citrina* et sur la famille de Tylodinidae. Bull. Soc. Zool. France 59:144-151.
- ROS, J. 1975. Opisthobranquios (Gastropoda: Euthyneura) del litoral iberico. Inv. Pesq. 39(2):269-372.
- ROS, J. & J. M. GILL. 1984. Opisthobranches des grottes sous-marines de l'île de Majorca (Balears). C.I.E.S.M., XXIX^e Congrès-Assemblée plénière, Lucerne, 11-19 Octobre 1984. Session commune Benthos-Pénétration de l'Homme sous la mer: Le peuplement des grottes: 1-4.
- SCHMEKEL, L. 1968. Ascoglossa, Notaspidea und Nudibranchia im litoral des Golfes von Neapel. Rev. Suisse Zool. 75(6):103-155.
- SCHMEKEL, L. & A. PORTMANN. 1982. Opisthobranchia des Mittelmeeres: Nudibranchia und Saccoglossa. Springer-Verlag. 410 pp.
- SORDI, M. 1969. Biologia delle secche della Meloria. II. Gastropodi Opistobranchi. Boll. Pesca Pisc. Idrobiol. 24(2): 105-114.
- STARMÜHLNER, F. 1969. Zur Molluskenfauna des felslitorals bei Rovinj (Istrien). Malacologia 9(1):217-242.
- SWENNEN, C. 1961. On a collection of Opisthobranchia from Turkey. Zool. Meded. Leiden 38(3):41-75.
- TERRENI, G. & E. CAMPANI. 1980. Sul ritrovamento di due Opistobranchi della subfamiglia: Pleurobranchinae e la loro problematica identificazione. Quad. Mus. St. Nat. Livorno 1:33-40.
- THOMPSON, T. E. 1976. Biology of opisthobranch molluscs. Ray Society, no. 151:1-207.
- THOMPSON, T. E. 1981. Taxonomy of three misunderstood opisthobranchs from the northern Adriatic Sea. J. Moll. Stud. 47(1):73-79.
- VAYSSIÈRE, A. 1885. Recherches zoologiques et anatomiques sur les mollusques opisthobranches du Golfe de Marseille. I. Tectibranches. Ann. Mus. Hist. Natur. Marseille 2(3): 1-181.
- VÉRANY, G. B. 1846. Descrizione di Genova e del Genovesato. Regno animale: Molluschi. Comune di Genova 1(2):90-110.
- VICENTE, N. 1967. Contribution a l'étude des gastéropodes opisthobranches du Golfe de Marseille. Rec. Trav. St. Mar. Endoume 42(58):133-179.
- WILLAN, R. C. 1978. An evaluation of the Notaspidean genera *Pleurobranchopsis* Verrill and *Gymnotoplax* Pilsbry (Opisthobranchia: Pleurobranchinae). J. Conchol. 29:337-344.
- WILLAN, R. C. 1983. New Zealand side-gilled sea slugs (Opisthobranchia, Notaspidea, Pleurobranchidae). Malacologia 23(2):221-270.

Swimming Tracks of *Aplysia brasiliana*, with Discussion of the Roles of Swimming in Sea Hares

by

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Abstract. Surface-swimming *Aplysia brasiliana* were tracked at two locations in southwest Florida in order to document the magnitude of movement that can be achieved by this method of locomotion. Twenty sea hares released near a shoreline swam for a median duration of 9.9 min and traveled a median distance of 52 m. One animal swam continuously for 114 min in a weak to slack current, and traveled 953 m. Sea hares released in a lagoon influenced by tidal currents showed a tendency to swim for shorter periods in stronger currents. The swimming tracks of some sea hares were influenced by physical features in their environment.

INTRODUCTION

ALTHOUGH MOST GASTROPOD mollusks are exclusively benthic and locomote only by crawling, some normally benthic species occasionally swim (FARMER, 1970). Twelve of the *Aplysia* species recognized by EALES (1960) have been observed swimming. Sea hares swim using two large flaps (the parapodia) which project dorsolaterally from the foot. The biomechanics of swimming and its neuro-motor control are described by VON DER PORTEN *et al.* (1982) and previous workers.

Other research has examined the orientation of swimming and the modulation of water speed in *Aplysia brasiliana* (HAMILTON & AMBROSE, 1975; HAMILTON & RUSSELL, 1982a, b; HAMILTON, 1984). Because these studies involved analyses of only short periods (60 or 90 sec) of swimming, and because the popular neurophysiological model, *A. californica*, apparently does not swim at all, some biologists may assume that aplysiid swimming is an ecologically insignificant behavior. The literature contains few details on the duration of uninterrupted swims, and no information on tracks of uninterrupted swims or on the effect of current conditions on swimming. In order to document the role of swimming as a means of achieving significant horizontal movement in sea hares, I present here some simple descriptive data for the uninterrupted swimming tracks of 40 animals released at two locations exposed to different current conditions. Tracks were recorded for released animals, instead of for animals found swimming naturally, so that the time and location where swimming began could be known accurately.

MATERIALS AND METHODS

Sea hares, *Aplysia brasiliana* Rang, were studied in Charlotte County, Florida (for map see HAMILTON & RUSSELL, 1982a:fig. 1). Adult animals (200-970 g) were collected from shallow-water grassbeds or, within 3 h after sunrise, from beaches where they had become stranded by overnight high tides. They were maintained in floating cages up to 4 d before release, and were fed *Hypnea* and other red algae, their natural food (KRAKAUER, 1971).

The first set of releases was conducted at Mote Beach, on the northeast shore of Placida Harbor. Currents at Mote Beach are primarily influenced by wind-driven waves rather than tidal changes (HAMILTON & RUSSELL, 1982a). Tall trees grow supratidally, and a band (10-25 m wide) of sand bottom slopes gradually ($<3^\circ$) from the high tide line to lower intertidal and subtidal grassbeds. During the releases water depth varied from 20 to 60 cm at the single release point within the band of sand bottom, and current speeds were slack to weak. Each animal was held on the bottom, facing offshore, for 10 sec before release.

The second set of releases was conducted in B3 Lagoon, which comprises one of several connections between Gasparilla Pass (which opens to the Gulf of Mexico) and Gasparilla Sound. The Lagoon is well protected from wind and waves, but strong tidal currents occur there. Each sea hare was removed from a floating cage anchored near the shore and transported quickly by boat to a release site. Animals were released at several sites near the center of the rectangular-shaped lagoon, depending on current con-

Table 1

Characteristics of uninterrupted swims by 20 sea hares released at Mote Beach during slack to weak current conditions.

Variable	Minimum	Maximum	Median
Swim duration (min)	4.5	114.0	9.9
Swim distance (m)	24	953	52
Ground speed (m/min)	2.5	9.2	5.3

ditions, but all sites were in water deeper than 5 m. Each sea hare was hand-placed into the water and gently agitated until it began to flap the parapodia and swim freely. Current speed beneath a bridge at one end of the Lagoon was classified as strong, moderate, weak, or slack for each release.

At both Mote Beach and B3 Lagoon, swimming sea hares were tracked by rowing 2–4 m behind them in a small boat. An animal had to swim for at least 3 min after release to be tracked, for reasons described in the Results. Directions were measured to the nearest 1° with an aimable prismatic compass. Directions to two or (usually) three landmarks were recorded from the point of release, along the swimming track at 3-min intervals thereafter, and from the point where an animal stopped swimming or was lost from sight. A map of each release area was made using a USGS map for Placida, Florida (N2645-W8215/7.5) and on-site measurements of distances and directions between landmarks. Data on directions to landmarks were used to plot positions along swimming tracks. Track lengths were measured using a curvimeter. For the Mote Beach tracks, a directness (or straightness) value was computed for each track as described in HAMILTON (1977). Median values and ranges are used to summarize durations and distances of swims because the frequency distributions of both variables were positively skewed.

RESULTS

About 60 sea hares were released at Mote Beach during slack to weak current conditions. A frequency distribution of the swim durations for these 60 animals would show two distinct groups or modes. About 40 sea hares swam for less than 1.5 min. Grassbeds located 5 to 6 m offshore from the release point were reached by all sea hares in about 1 min, and about 40 animals immediately dove to the bottom upon reaching these grassbeds. Twenty sea hares did not dive to the bottom upon reaching the grassbeds, and swam longer than 3 min; their mode was in the 9–10 min range.

The swimming tracks for the latter group of 20 sea hares are summarized in Table 1. These sea hares trav-

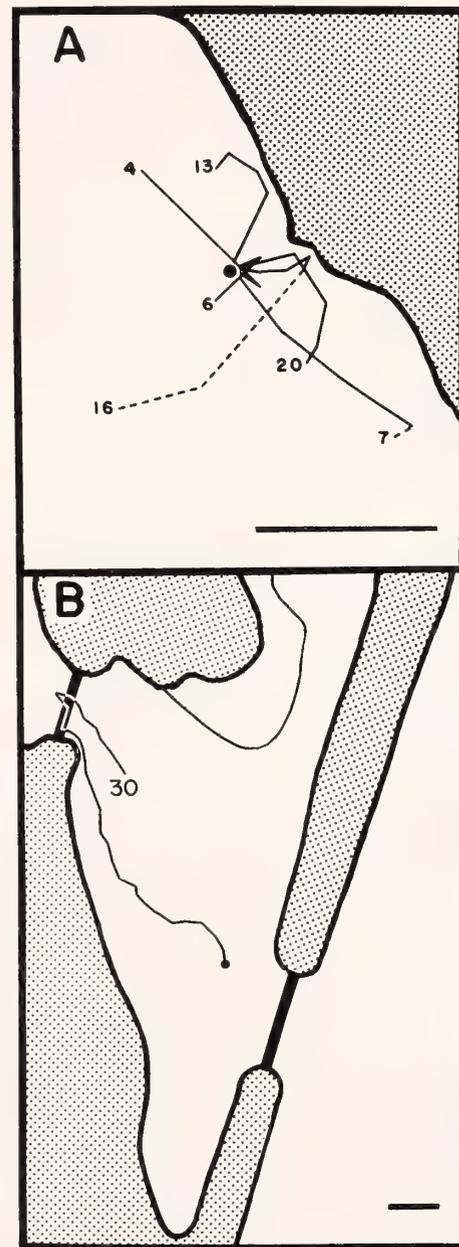


Figure 1

Sea hare swimming tracks may be influenced by physical features in their environment. A. Swimming tracks of the six sea hares that were released at Mote Beach and began swimming in the onshore direction. All six eventually reversed their heading, thus avoiding becoming stranded. Dashed lines for animals #7 and #16 indicate swimming tracks subsequent to brief stops on the bottom. B. Swimming track of one animal (#30), released in B3 Lagoon, that reversed its heading after passing beneath the bridge and swam back into the Lagoon against a weak outgoing tide. This type of response has been observed in other sea hares. Scale bars are 50 m.

Table 2

Characteristics of uninterrupted swims by 20 sea hares released at B3 Lagoon during two current conditions.

Variable	Minimum	Maximum	Median
Current moderate to strong (n = 9)			
Swim duration (min)	3.0	33.5	7.8
Swim distance (m)	88	673	237
Ground speed (m/min)	15.6	43.5	30.3
Current slack to weak (n = 11)			
Swim duration (min)	6.0	87.0	21.0
Swim distance (m)	24	469	120
Ground speed (m/min)	2.9	10.1	6.7

eled at a median ground speed of 5.3 m/min for a median duration of 9.9 min, and covered a median distance of 52 m. One animal swam for 114 min and traveled 953 m from the release point. The track directness (straightness) values for 14 of the 20 sea hares were greater than 0.9, thus revealing considerable ability to maintain a relatively straight track over time. Five of the six sea hares with values less than 0.9 started swimming in the onshore direction, and subsequently reversed their headings (see below and Figure 1A).

About 80 sea hares were released in B3 Lagoon. As for Mote Beach, a frequency distribution of the swim durations for these 80 animals would show two distinct modes. About 60 sea hares dove to the bottom and were lost from sight within about 10 sec after release. Twenty animals did not dive immediately, and swam longer than 3 min; their mode was in the 7–8 min range.

The range of current conditions occurring in B3 Lagoon permitted examination of the effect of current on swimming tracks at a single location. The 20 tracked sea hares were divided into two groups according to the current conditions during their release. Their swimming tracks are summarized in Table 2. Because swimming *Aplysia* cannot achieve water speeds greater than about 14 m/min (HAMILTON, 1984), the median ground speed of 30.1 m/min for sea hares released in moderate to strong currents clearly reflects the contribution of tidal current to horizontal displacement. Although it is not surprising that sea hares traveled at lower ground speeds and moved shorter distances when released in slack or weak currents, it is surprising that such sea hares swam for longer periods than those released in stronger currents. The swim durations for the moderate–strong group (median = 7.8 min) and slack–weak group (median = 21.0) are significantly different (Mann-Whitney $U = 77.5$; $P < 0.05$).

The tracks of two groups of sea hares seemed to be influenced by physical features in their environment. At Mote Beach, six of the 20 tracked sea hares began swimming in the onshore direction (Figure 1A), but all eventually reversed their heading and began swimming off-

shore. Animals #6, #13, #16, and #20 all entered water shallower than about 12 cm, but did not touch bottom, before reversing their headings. Animal #6 reversed its heading at about $T = 2$ min, and so it had already moved back offshore when its $T = 3$ min position was recorded. Animal #16 stopped swimming soon after heading offshore.

At B3 Lagoon, undisturbed sea hares swimming on an outgoing tide have often been observed passing beneath the bridge at one end of the Lagoon. Although such animals do not appear to have similar headings when they are still some distance from the bridge, many swing around and adopt an up-current heading as they get about 10–15 m from the bridge. Despite their swimming efforts, a strong tidal current carries them backward, beneath the bridge and out into Gasparilla Pass. Five of the 20 sea hares tracked in B3 Lagoon passed beneath bridges, and adoption of an up-current heading was observed in two of the five. The heading change was quite striking for animal #30, which was released on a weak outgoing tide, and which eventually swam back into the Lagoon from beneath the bridge (Figure 1B).

Thirty-eight of the 40 sea hares tracked at Mote Beach and B3 Lagoon dove to the bottom or were lost from sight in water 1–5 m deep. Most of these animals began making short “excursion” dives down to as much as 50–100 cm beneath the surface, a few minutes before their final dive or loss from sight. Although the rate of parapodial flapping was not recorded for any animal, sea hares seemed to swim normally during both the descending and ascending phases of excursion dives.

DISCUSSION

Sea hares released at both study sites formed two distinct and natural groups according to swimming time: those which swam only until they reached a nearby grassbed (less than 90 sec) or which immediately dove to the bottom, and those which swam longer than 3 min. The purpose of this study was to document how far and how long *Aplysia brasiliensis* are capable of swimming. Consequently, this study focused on the behavior of the second group.

The data presented here should be considered minimum estimates of the swimming capabilities of the tracked sea hares. Wave height, sky conditions, water turbidity, and swimming depth all influenced how long an animal could be kept in view. All distances traveled by the tracked sea hares are underestimated because positions were recorded only once every 3 min, and the actual paths during these 3-min intervals were never perfectly straight.

The influence of current speed in B3 Lagoon on ground speed and swimming distance was expected, and is probably due to passive displacement effects of current on swimming animals. However, the significant influence of current speed on swimming duration must involve an active response by animals, and this suggests an ability to detect current speed. It would be interesting to learn how current speed is detected. Sea hares were released from a

drifting boat, so they were essentially up-to-speed with the water mass from the time they commenced swimming. The Thrust Modulation Response (TMR) of *Aplysia brasiliana* involves detection of current direction, and it is influenced by current speed (HAMILTON, 1984).

The heading reversals of those sea hares that almost stranded on the shore at Mote Beach (Figure 1A), and the up-current headings adopted by some sea hares as they pass beneath bridges in B3 Lagoon (Figure 1B), may both depend on visual detection of objects above the water's surface (e.g., bridge, treeline). HAMILTON & RUSSELL (1982b) demonstrated that, under field experimental conditions, an unblocked view of the sky is required for sea hares to maintain a consistent swimming direction. *Littorina irrorata*, a gastropod possessing eyes of a similar design yet half the size of those possessed by *Aplysia*, can detect bar-shaped targets filling as little as 1° of visual arc (HAMILTON & WINTER, 1982; HAMILTON *et al.*, 1983). Regardless of the mechanisms involved in the heading reversals of sea hares at Mote Beach, this response suggests that those few animals that oriented onshore during previous studies (HAMILTON & AMBROSE, 1975; HAMILTON & RUSSELL, 1982a) eventually would have turned around had they been allowed to swim for longer than 60 or 90 sec.

The adaptive function of swimming in *Aplysia* has not been studied systematically, but several hypotheses exist. In at least some other opisthobranchs (e.g., EDMUNDS, 1968), swimming seems to serve as an escape response from benthic predators. However, the sea hare's swimming capabilities seem far too sophisticated for just this function, and no evidence supports this hypothesis exclusively. It is clear that sea hares that are stranded on gradually sloping beaches or sand bars can use swimming to move into deeper water, if they are resubmerged by a subsequent high tide before succumbing to desiccation and insolation stresses. Swimming probably enables sea hares to move within or between grassbeds on a daily basis. The adaptive value for such movements could involve searches for prospective mates, concentrations of algal food, or more suitable physicochemical conditions.

Finally, swimming may facilitate seasonal migration in *Aplysia brasiliana*. An incursion of sea hares into shallow water occurs in south Florida during the early spring (HAMILTON *et al.*, 1982), the period of peak algal abundance. By late summer, sea hares are not found in shallow water, where water temperatures approach or exceed the lethal limit (27–31°C). A similar seasonal pattern of *A. brasiliana* abundance in shallow water was reported for the southern hemisphere by SAWAYA & LEAHY (1971), who also suggested a migration hypothesis. Seasonal movements between deep and shallow water could be as-

sisted by directionally advantageous tidal currents. Direct evidence of migration, in the form of movement records of tagged individuals, is lacking for all opisthobranchs and most other mollusks suggested to migrate (HAMILTON, 1985).

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LITERATURE CITED

- EALLES, N. B. 1960. Revision of the world species of *Aplysia* (Gastropoda: Opisthobranchia). Bull. Brit. Mus. Natur. Hist. Zool. 5:268–404.
- EDMUNDS, M. 1968. On the swimming and defensive response of *Hexabranchnus marginatus* (Mollusca, Nudibranchia). J. Linn. Soc. Lond. Zool. 47:425–429.
- FARMER, W. M. 1970. Swimming gastropods (Opisthobranchia and Prosobranchia). Veliger 13(1):73–89.
- HAMILTON, P. V. 1977. The use of mucous trails in gastropod orientation studies. Malacol. Rev. 10:73–76.
- HAMILTON, P. V. 1984. Factors influencing the water speed of swimming sea hares, *Aplysia brasiliana*. Anim. Behav. 32: 367–373.
- HAMILTON, P. V. 1985. Migratory molluscs, with emphasis on swimming and orientation in the sea hare, *Aplysia*. Pp. 212–216. In: M. A. Rankin (ed.), Migration: mechanisms and adaptive significance, Suppl. to Contrib. Mar. Sci., Vol. 27.
- HAMILTON, P. V. & H. W. AMBROSE. 1975. Swimming and orientation in *Aplysia brasiliana* (Mollusca: Gastropoda). Mar. Behav. Physiol. 3:131–144.
- HAMILTON, P. V., S. C. ARDIZZONI & J. S. PENN. 1983. Eye structure and optics in the intertidal snail, *Littorina irrorata*. J. Comp. Physiol. 152A:435–445.
- HAMILTON, P. V. & B. J. RUSSELL. 1982a. Field experiments on the sense organs and directional cues involved in off-shore-oriented swimming by *Aplysia brasiliana* Rang (Mollusca: Gastropoda). J. Exp. Mar. Biol. Ecol. 56:123–143.
- HAMILTON, P. V. & B. J. RUSSELL. 1982b. Celestial orientation by surface-swimming *Aplysia brasiliana* Rang (Mollusca: Gastropoda). J. Exp. Mar. Biol. Ecol. 56:145–152.
- HAMILTON, P. V., B. J. RUSSELL & H. W. AMBROSE. 1982. Some characteristics of a spring incursion of *Aplysia brasiliana* into shallow water. Malacol. Rev. 15:15–19.
- HAMILTON, P. V. & M. A. WINTER. 1982. Behavioural responses to visual stimuli by the snail *Littorina irrorata*. Anim. Behav. 30:752–760.
- KRAKAUER, J. M. 1971. The feeding habits of aplysiid opisthobranchs in Florida. Nautilus 85:37–38.
- SAWAYA, P. & W. M. LEAHY. 1971. Fisiocologia e etologia de *Aplysia* L. (Mollusca—Opisthobranchia). Boletim de Zool. e Biol. Marinha, N.S. 28:1–17.
- VON DER PORTEN, K., D. W. PARSONS, B. S. ROTHMAN & H. PINSKER. 1982. Swimming in *Aplysia brasiliana*: analysis of behavior and neuronal pathways. Behav. Neural Biol. 36:1–23.

A Short-term Study of Growth and Death in a Population of the Gastropod *Strombus gibberulus* in Guam

by

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Abstract. A month-long study of tagged *Strombus gibberulus gibbosus* Röding, 1798, in Pago Bay, Guam, during the spring of 1981 revealed very high mortality (at least 11%), most of which (93%) was due to shell breakage. No differences in shell size, lip thickness, or age were detectable among snails that died, sustained sublethal injury, and survived unscathed. It is concluded that the thickened adult lip was ineffective in conferring resistance to shell-breaking agents (chiefly xanthid crabs) in this population of *S. gibberulus*.

Juvenile growth rates were very high (mean 0.16 mm/day). Snails cease to grow in length once the lip assumes the flared adult form.

INTRODUCTION

SMALL STROMBID GASTROPODS pose a curious enigma in that they sustain heavy mortality due to breakage despite the strongly thickened and flared outer lip that characterizes the adult shell. Inspection of "dead" shells (including fragments) suggests that breakage accounts for 50 to 100% of the mortality in most populations of *Strombus gibberulus* Linnaeus, 1758, in the tropical western Pacific (VERMEIJ, 1979, 1982). Although the thick lip proved to be an obstacle to the predaceous crab *Calappa hepatica* (L.) in the laboratory, it appeared to be ineffective against other crabs such as *Carpilius maculatus* (Linnaeus) and *Daldorfia horrida* (Linnaeus) (ZIPSER & VERMEIJ, 1978; VERMEIJ, 1982). If such powerful agents of breakage are commonly encountered by *S. gibberulus*, how is the thick lip maintained by selection, and how can populations persist in the face of heavy mortality? These are the questions that prompted the present short-term study.

MATERIALS AND METHODS

We studied a sample of 230 individuals of *Strombus (Gibberulus) gibberulus gibbosus* Röding, 1798, from the inshore part of the reef flat in a cove near the center of Pago Bay, Guam, Mariana Islands. The study area is covered by at least 3 cm of water at all times and is floored by a thin layer of white sand. There are several intertidal raised limestone ledges with undercut margins. *Strombus gibberulus* is found in and on the sand. The dorsum of the adult shell is always exposed above the sand, and is frequently fouled and pitted by small algae.

All individuals observed during the week of 21-28 May 1981 were collected and marked, and were subsequently censused periodically until final recovery from 21-25 June. We measured shell length (distance from apex to tip of siphonal canal) and lip thickness (at a point midway between the eye-notch and the posterior end of the lip). Each shell was inspected for the presence of repaired injuries (scars) on the body whorl. These scars appear as irregular traces that depart from the normal course of the growth lines. They result from damage to the outer lip, which is repaired by the mantle edge before growth recommences.

In order to mark the snails, two methods were used. First, the anterior dorsal shell surface was filed clean, and a numbered beetag (Fabrik für Bienenzuchtgeräte, 7056 Weinstadt-Endersbach, West Germany) was affixed with underwater epoxy. The dorsal and ventral surfaces of the spire were also filed and labeled with a permanent marker. Secondly, a spot of nail polish was painted on the ventral surface of the penultimate whorl, so that individuals that had lost their tags could still be recognized as belonging to the marked sample. If their measurements matched those of a labeled individual that had not hitherto been recovered, the tagless snails were retagged with that number. After the epoxy had dried sufficiently in air, the animals were returned to the field site for release. The 3-h period of exposure to air that was required for labeling apparently had no adverse effect, for snails began to kick actively as soon as they were placed in buckets of seawater for transport back to the field.

The incidence of scars was assessed in two ways. The proportion of repaired individuals was calculated as the

Table 1

Characteristics of the *Strombus gibberulus* population at the time of marking.

Characteristic	Juveniles	Adults
Number tagged	21	209
Proportion of repaired snails	38%	17%
Frequency of repair	0.52	0.18
Lip thickness	0.2–0.8 mm	1.3–2.5 mm

number of snails with scars on the body whorl divided by the total number of snails in the sample. The frequency of repair is the number of scars divided by the number of individuals in the sample. The latter figure is by definition higher than is the former if some members of the scarred population have multiple scars.

If large size and a thick lip conferred resistance to shell-breaking agents in the field, individuals surviving unscathed or in damaged condition would be expected to be larger and to have thicker lips than would individuals that had died as a result of shell breakage. This hypothesis was tested against the null hypothesis of no difference by comparing survivors with individuals recovered as broken shells with respect to the shell length and lip thickness of these individuals at the time of labeling. Because lip thickness in adults was independent of shell length, *t*-tests were used throughout.

RESULTS

Characteristics of the Population

Most of the population of *Strombus gibberulus* is composed of thick-lipped adults (Table 1). Shell repair on the body whorl was much more frequent in juveniles than in adults (Table 1). Two factors may contribute to this difference. In the first place, adult lips are less susceptible to sublethal damage than are thin delicate lips of juveniles. Secondly, the scars on the body whorl of a juvenile come to lie on the penultimate whorl or even in the spire whorls of adults, and would thus not be counted in the adult shell. The overall frequency of repair in the population (0.21) is similar to that in several other Guamanian populations of *S. gibberulus*, but it is higher than are the frequencies of repair in populations of this species from other parts of the tropical western Pacific (VERMEIJ, 1982). Given the high incidence of scars in the Pago Bay population, the potential for selection in favor of breakage-resistant traits is high.

Mortality and Its Causes

We recovered 89 tagged living snails one month after the 230 original animals had been released. Another 7 snails with apical marks but without their numbered tags were also recovered, so that a total of 96 individuals (42%

Table 2

Comparison of dead and surviving members of the *Strombus gibberulus* population one month after initial marking. Means are given with standard deviations.

Characteristic	Dead individuals	Survivors
Shell length at time of marking (mm)	36.21 ± 3.41	36.89 ± 3.32
Lip thickness at time of marking (mm)	1.71 ± 0.38	1.85 ± 0.33
Percentage of juveniles	6.3%	7.3%
Frequency of repair	0.24	0.22

of the original sample) was found again after one month. The percentage of recapture of juveniles (33%) was not significantly lower than that of adults (43%). Two survivors (one juvenile and one adult) sustained sublethal shell injury during the period of observation.

Of the 134 individuals not recovered alive after one month, 26 were found dead during our study. The minimum mortality for the period of observation was, therefore, 11%. Most (93%) of the dead, recovered individuals had been crushed. The 17 broken shells that we were able to identify by tag did not differ from individuals that were recovered alive after one month in shell length, lip thickness, proportion of juveniles, or frequency of repair (Table 2). The ratio of juveniles to adults in the sample of broken shells was $1/16 = 0.063$, as compared to $7/96 = 0.073$ among survivors.

The xanthid crabs *Carpilius maculatus* and *Eriphia sebana* (Shaw & Nodder) live under ledges and large boulders in the study area, and appear to have been largely responsible for the breakage-related deaths of *Strombus gibberulus*. Nearly all broken shells had the ventral or dorsal portion of the body whorl broken away, or had severed spires, and the lip was frequently either missing or cut in half. These types of damage are typical of the prey of large xanthids with molarlike dentition in the crusher claw (ZIPSER & VERMEIJ, 1978). The spiral peeling characteristic of the prey of *Calappa hepatica*, which also occurs in the study area, was observed in only one dead individual. The porcupinefish *Diodon hystrix* (Linnaeus) hunts over the Pago Bay reef flat at night, and we have recovered fragments of *S. gibberulus* from its gut contents. The broken shells that we recovered in the field, however, were too large to have been passed through the digestive system and defecated by the porcupinefish, so that the contribution of that predator to the mortality of *S. gibberulus* could not be established.

Another agent of mortality whose impact we were unable to assess is man. QUOY & GAIMARD (1834:67) already observed that *Strombus gibberulus* was a favorite item of food for the people of Guam. Toward the end of our study, we encountered a girl, about ten years old, clutching six labeled snails and many unlabeled individ-

Table 3

Growth rates of *Strombus gibberulus* juveniles and adults over a period of 30 days. Means are given with standard deviations; numbers of individuals are given in parentheses.

Characteristic	Juveniles	Adults
Growth in shell length (mm)	3.33 ± 1.14 (9)	-0.035 ± 0.3 (81)
Growth in lip thickness (mm)	0.81 ± 0.53 (9)	0.063 ± 0.21 (81)
Daily growth in length (mm)	0.16 ± 0.072 (7)	

uals. We persuaded her to release the marked individuals, but the possibility that many of our labeled snails died in the soup-pot or on the grill cannot be eliminated.

Growth

Measurements of labeled individuals revealed that juvenile growth rates in *Strombus gibberulus* were extremely high, whereas growth ceases once the adult lip has assumed the adult configuration (Table 3). In two juveniles whose lip edge was marked, growth rate in the spiral direction was calculated to be 0.6 and 0.7 mm/day. At these rates, hatchlings could be expected to reach a length of 30 mm (minimum adult length in the Pago Bay population) in about six months. Because small juveniles probably grow even faster than did the rather large juveniles we monitored, all of which exceeded 27 mm in initial length (Table 1), the time required to reach minimum adult size may well be substantially shorter.

DISCUSSION

Although the high incidence of scars in the Pago Bay population of *Strombus gibberulus* suggests a high potential for selection in favor of breakage-resistant traits such as a thick lip, we were unable to detect differences in shell length or lip thickness between snails that survived after one month and those that we recovered as dead broken shells. If selection in favor of resistance to breakage took place, it involved characters we did not examine.

The thick lip may function as a deterrent to predation in other populations of *Strombus gibberulus*. The species is common in grassbeds and on sand flats where boulders under which large shell-crushing crabs find shelter are absent. We suspect that the lip is chiefly effective against calappid crabs, which live in sand, and that the boulder-strewn sand patches of the Pago Bay reef flat are very different in terms of the types of predators encountered by *S. gibberulus* from inshore environments where rocky bottoms are absent. The Pago Bay population may well persist not by virtue of morphological adaptation, but by

exceptionally high juvenile growth rates and presumably by high rates of larval settlement, although the latter point requires confirmation.

It is also possible that the thick lip is not adaptive in resisting predators in any population of *Strombus gibberulus*, and that it is instead retained as a legacy of a well-established pattern of determinate growth that was fixed very early in the history of the Strombidae. The combination of determinate growth, modified adult outer lip, and short post-larval life-span is found not only in *S. gibberulus*, but in many other small Indo-west-Pacific strombids and tropical cerithiids as well (HOUBRICK, 1974). Like the larger and longer-lived members of these and other gastropod families, these small species have high growth rates in the juvenile phase. Both adult size and juvenile growth rate may vary by a factor of two to three among individuals from the same site (RANDALL, 1964; FRANK, 1969; SPIGHT *et al.*, 1974; YAMAGUCHI, 1977; VERMEIJ, 1980). If, as seems likely from studies of other gastropods, growth and size are partially determined by genetic factors, these tropical species should display substantial genetic variation on which selection could act.

We realize that the present study concerns only one population during one month in a possibly atypical habitat. It will be interesting to repeat our study in environments in which calappid crabs are the chief predators, and to monitor populations over the course of an entire year or more.

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LITERATURE CITED

- FRANK, P. W. 1969. Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. *Oecologia* 2:232-250.
- HOUBRICK, R. S. 1974. Growth studies on the genus *Cerithium* (Gastropoda: Prosobranchia) with notes on ecology and microhabitat. *Nautilus* 88:14-27.
- QUOY, J. R. C. & J. P. GAIMARD. 1834. Voyage de découvertes de l'*Astrolabe*. Zoologie, 3ème tome. J. Tastu: Paris.
- RANDALL, J. E. 1964. Contribution to the biology of the queen conch, *Strombus gigas*. *Bull. Mar. Sci. Gulf Caribbean* 14: 246-295.
- SPIGHT, T. M., C. BIRKELAND & A. LYONS. 1974. Life histories of large and small murexes (Prosobranchia: Muricidae). *Mar. Biol.* 24:229-242.
- VERMEIJ, G. J. 1979. Shell architecture and causes of death in Micronesian reef snails. *Evolution* 33:686-696.
- VERMEIJ, G. J. 1980. Gastropod growth rate, allometry, and adult size: environmental implications. Pp. 379-394. *In*: D. C. Rhoads & R. A. Lutz (eds.), *Skeletal growth of aquatic*

- organisms: biological records of environmental change. Plenum: New York.
- VERMEIJ, G. J. 1982. Gastropod shell form, repair, and breakage in relation to predation by the crab *Calappa*. *Malacologia* 23:1-12.
- YAMAGUCHI, M. 1977. Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Mariana Islands. *Mar. Biol.* 44:249-263.
- ZIPSER, E. & G. J. VERMEIJ. 1978. Crushing behavior of tropical and temperate crabs. *J. Exp. Mar. Biol. Ecol.* 31: 155-172.

Aspects of the Reproduction of Rocky Intertidal Mollusks from the Jordan Gulf of Aqaba (Red Sea)

by

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Abstract. Reproductive and spawning periodicity, type of spawn, and spawning behavior of an intertidal chiton, 11 prosobranch gastropods, and one pulmonate gastropod, and two pelecypods from the Jordan Gulf of Aqaba are given. Reproduction was continuous in seven species, restricted to the warmer period and lowered sea level in seven, and in one species occurred during the colder and higher sea level period. No direct relationship between temporal reproduction and tide level or vertical position in the intertidal zone was seen.

INTRODUCTION

THE LITTLE INFORMATION available on the fauna of the rocky intertidal of the Red Sea, including the Gulf of Aqaba, is concerned primarily with zonation (SAFRIEL & LIPKIN, 1964; FISHELSON, 1971; AYAL & SAFRIEL, 1980; SAFRIEL *et al.*, 1980). SAFRIEL (1969) reported on various aspects of the ecology of *Nerita* spp. and JORNÉ & SAFRIEL (1979) on the behavior of *Nerita polita* Linnaeus. Data on the reproduction of Red Sea intertidal mollusks are lacking except for very limited data given by SAFRIEL (1969) on *Nerita polita* and FAO (1972) on *Ostrea forskali* Chemnitz.

Various aspects of the reproduction of 15 intertidal mollusks from the Jordan coast of the Gulf of Aqaba have been investigated. The aspects include reproductive and spawning periodicity, type of spawn, and spawning behavior. The relationships of these to external environmental factors including position in the intertidal zone, temperature, changes in sea level, and primary production are discussed.

MATERIALS AND METHODS

A minimum of 10 specimens of each species was collected around the middle of each month for at least 12 months. The species were usually collected from the same locality each month, in some cases from two different localities. Collections were spatially random but biased toward larger sizes to ensure obtaining sexually mature individuals. An investigation of the minimum size of sexual maturity of most species was conducted.

In the laboratory, specimen length was measured to the

nearest 0.1 mm using vernier calipers; microscopic measurements to the nearest 0.01 mm were made with an ocular micrometer.

The shells of the gastropods were cracked using a hammer, those of the bivalves opened, the foot of the chiton removed, and the whole animal of limpets removed to examine the gonads under a dissecting microscope. Either teasing or microdissection of the gonads and/or associated structures was employed to determine the presence or absence of gametes. When necessary, fresh preparations were examined under a compound microscope.

Additional investigations including ones on the deposition of eggs and hatching were conducted in the laboratory for some of the species. Specimens were kept in individual aerated seawater aquaria.

The terminology used for the zones in the rocky intertidal is that of STEPHENSON & STEPHENSON (1949) and SAFRIEL & LIPKIN (1964). The littorinid zone of Safriel & Lipkin is within the supralittoral fringe of Stephenson & Stephenson; the chthamalid and *Tetraclita* zones of Safriel & Lipkin are within the midlittoral zone of the Stephensons. FISHELSON (1971) included the entire rocky intertidal of the Red Sea in the infralittoral and referred to it as the *Tectarius armatus-Tetraclita squamosa rufotincta* community.

Adult specimens of all 15 species studied as well as egg capsules, masses, and ribbons are deposited in the reference collection of the Marine Science Station, Aqaba, Jordan, and are available for examination upon request. In addition, voucher specimens of all species have been deposited in the Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

DESCRIPTION OF THE ROCKY INTERTIDAL ZONE

The region of the Jordan Gulf of Aqaba is within the very warm portion of the Saharan bioclimatic zone. The terrestrial component exerts greater influences on the intertidal and shallow marine zones than vice versa. The greater influences are due to the limited areal extent of the Gulf with respect to the surrounding terrestrial area, a narrow and clear-cut interface between the terrestrial and marine environments, land-to-Gulf hot and dry winds reducing transport of moisture in the opposite direction, and low rainfall.

The prevailing winds are N-NNE, with Beauforts 2 through 4 occurring 84% of the time (HULINGS, 1979). Mean air temperatures range from about 16°C in January to 32°C in August (Jordan Meteorological Department) and surface water temperatures from 20°C in February to 27°C in August–September (MORCOS, 1970). In the absence of river runoff and in combination with low rainfall (35 mm/yr, Jordan Meteorological Department) and dry and hot winds, the evaporation rate is high (up to 4 m/yr, ANATI, 1976) resulting in high, constant salinity of 40.5 to 41.0 ppt (PALDOR & ANATI, 1979). There is a major period of primary productivity during December–January and a minor period during May–June (HULINGS & ABU HILAL, 1983). LEVANON-SPANIER *et al.* (1979) consider the northern Gulf of Aqaba to be oligotrophic from April through November.

According to MORCOS (1970) the tides of the Gulf of Aqaba are influenced by those of the Red Sea proper and the direct effects of the moon and sun are comparatively small. In addition, the tides are usually out of phase with the moon (Hulings, unpublished data). The tide in the Jordan Gulf is mixed, with diurnal inequality of the highs averaging 4.2 cm and that of the lows 4.7 cm (Hulings, unpublished data). The spring tide range averages about 1.0 m, the range of the neaps about 50 cm (FISHELSON, 1973; Hulings, unpublished data). Fluctuation of sea level, up to 1 m, occurs annually, being higher during the period December through May and lower from July through October (FISHELSON, 1973; Hulings, unpublished data). Although the vertical ranges and variations in tides are small, the net effect of the level and duration of submergence and emergence on the generally low profile beaches is considerable.

The substratum of the rocky intertidal includes boulders (ranging from granitic to huge masses of conglomerate or fossil reef), mostly medium to large-sized granitic and dike multi-colored pebbles underlain by sand, and platform or slab. The latter is extremely variable and includes sandstone, conglomerate (calcium carbonate cemented sand, gravel, and pebble mixtures) and beach rock (usually gravel sized and continuously forming). Eroded fossil coral reefs, composed mostly of a variety of coral heads surrounded by solidified calcium carbonate detritus

(FRIEDMAN, 1965), are also included as part of the slab substrata or platform beaches. It is common to find mixtures of two or more of the slab substrata at any particular locality. The horizontal profile of the slab beaches is generally very gentle, whereas that of the pebble beaches is somewhat steeper. In addition, wave action is minimal on the usually protected slab beaches and moderate on the more exposed pebble beaches.

ASPECTS OF REPRODUCTION

Class Polyplacophora

Family CHITONIDAE

Acanthopleura haddoni Winkworth, 1927

Habitat: Most common in the *Tetraclita* (midlittoral) zone.

Specimens examined: 375 averaging 50 mm long from June 1982 through May 1984 for state of reproduction; 39 specimens 16–42 mm long for minimum length at which gonads appear.

Sex ratio: 1.0 male:0.8 female.

Reproduction: The testes are dark red when immature, pinkish when mature; immature ovaries are tan, mature ovaries dark to black brown. Gametes were present in both sexes from June through December. Among the females, all were ovigerous from September through November; during other months, ovigerous and nonovigerous individuals occurred. Ova with a chorion (KUMÉ & KATSUMA, 1957) were found from August through November. The majority of the males had enlarged testes with sperm from June through October. The major period of reproduction (the time that most specimens of both sexes had gametes) is from June through October.

The smallest female with ovaries was 24 mm long, the smallest male with testes 27 mm long.

Class Gastropoda, subclass Prosobranchia

Family PATELIDAE

Cellana radiata (Born, 1778)

Nomenclature: According to Dr. J. Rosewater (personal communication), *Cellana radiata* is synonymous with and has priority over *C. rota* (Gmelin, 1791) reported by SAFRIEL & LIPKIN (1964), FISHELSON (1971), MERGNER & SCHUHMACHER (1974), and MASTALLER (1979).

Habitat: Characteristic of the *Tetraclita* (midlittoral) zone.

Specimens examined: 597 averaging 33.0 mm long (range, 16.7–48.0) from March 1982 through May 1984 for state of reproduction; 129 specimens 3.6–23.5 mm long for minimum length with gonads.

Sex ratio: 1.0 male:1.0 female.

Reproduction: Gametes were present in most individuals of both sexes each month. The smallest male was 9.5 mm long, the smallest female 12.0 mm; the smallest male with sperm was 10.2 mm long, the smallest female with ova 12.0 mm long.

Comments: RAO (1973) reported a sex ratio of 1.0 male: 0.8 female in *Cellana radiata* from tropical southeast India. Developing or spawning gonads were present each month during a 12-month period with spawning occurring from June to February or March. Sexual maturity occurred at a length of 9 mm, and sex distinction could be made in individuals 10 mm long. RAO (1976) later reported continuous breeding in *C. radiata* and sexual maturity at a shell length of 10–15 mm.

Family TROCHIDAE

Monodonta dama (Philippi, 1848)

Habitat: A mobile midlittoral species ranging from above the chthamalid zone to the *Tetraclita* (midlittoral) zone.

Specimens examined: 296 from April 1982 through May 1983 for state of reproduction; 62 specimens 5.7–12.3 mm high for minimum size with gonads.

Sex ratio: 1.0 male: 1.1 female.

Reproduction: Dark green ovaries with ova and cream-colored testes with sperm occurred each month. The smallest male with testes was 8.1 mm long, the smallest female with ovaries 9.0 mm long and was ovigerous.

Spawn: Spawning was observed on several occasions in a seawater table with continuously circulating seawater. Most spawning individuals were paired or in clusters, and masses of gametes were released in spurts by both sexes. The ova, averaging 0.13 mm in diameter, were surrounded by a membrane averaging 0.15 mm in diameter. Spawning occurred irrespective of lunar or tidal cycles.

Early development: Veligers averaging 0.19 mm long and lacking eyes and an operculum appeared within 24 h after spawning.

Family NERITIDAE

Nerita forskalii Recluz, 1844

Nomenclature: This species has been reported from the Jordan Gulf of Aqaba as *Nerita sanguinolenta* Menke, 1820, by MERGNER & SCHUHMACHER (1974) and *N. albicilla* Linnaeus, 1758, by MASTALLER (1979). SAFRIEL (1969) noted that the species is *N. forskalii* based on shell morphology.

Habitat: Has a wide vertical distribution on a variety of solid substrata and in varied microhabitats, including tide pools, on pebble beaches, and slab, within the *Tetraclita* (midlittoral) zone. Occurs lower than the other of the sympatric pair, *Nerita polita* Linnaeus.

Specimens examined: 350 averaging 18.4 mm long (range, 7.7–24.8) from April 1982 through May 1983 for reproductive state; 41 specimens 5.9–11.6 mm long for presence of gonads.

Sex ratio: 1.0 male: 1.1 female.

Reproduction: Ova and spermatophores, the latter averaging 6.3/female (range, 0–16), and sperm were present in the seminal vesicle (BERRY *et al.*, 1973) each month. The smallest male with testes was 7.7 mm long, the smallest female with ovaries 8.7 mm long.

Copulation was observed in the field every month except August and September and occurred only during submergence. The copulating behavior and the action of the cephalic penis were essentially the same as that described by IRIKI *et al.* (1963). Spermatophores were occasionally found in aquaria indicating unsuccessful copulation.

Spawn: The egg capsules have the basic structure described by ANDREWS (1935). They are reddish brown in color and the presence of the irregular shaped, dark red spherulites give the capsules a faceted appearance. The capsules are more elliptical than round, averaging 2.2 mm wide × 2.8 mm long.

Egg capsule deposition was noted during July, October, and January through May; there were no observations during the other months. The capsules were found on a wide variety of exposed surfaces including glass, metal, shells of other gastropods (living and dead), and the girdle of chitons, as well as on rocky surfaces from small pebbles to slab. The deposition of capsules on a wide variety of surfaces coincides with its wide-ranging distribution and the fact that it usually does not go into hiding during emergence.

Early development: Various stages of embryonic development from uncleaved ova, averaging 0.15 mm in diameter, to veligers with eyes, averaging 0.20 mm long, were found enclosed within the membrane that lined the capsule. The average number of ova-veligers per capsule was 117 (range, 60–211).

Hatched veligers with eyes and operculum averaged 0.21 mm long. Exit of the veligers from the capsule appeared to be through the top.

Nerita polita Linnaeus, 1758

Habitat: Occurs above *Nerita forskalii* in the midlittoral, approximately equivalent to the chthamalid zone and is restricted to areas of pebbles underlain by sand.

Specimens examined: 347 averaging 17.7 mm long (range, 9.0–22.8) from April 1982 through May 1983 for state of reproduction; 24 specimens 5.7–11.0 mm long for minimum size with gonads.

Sex ratio: 1.0 male: 1.4 female.

Reproduction: Ova and spermatophores (the latter averaged 5.8/female, range, 0–20) and sperm in the seminal

vesicle (BERRY *et al.*, 1973) were present each month. The smallest male with testes was 8.0 mm long, the smallest female with ovaries 9.6 mm long.

Copulation was observed in the field from May through July and September through March and was essentially like that described by IRIKI *et al.* (1963) in terms of the behavior and action of the cephalic penis. Copulation occurred only among emergent pairs and during day and night. SAFRIEL (1969) and HUGHES (1971) reported copulation in *Nerita polita* from May through the beginning of August during investigations from April through the beginning of August.

Spawn: The egg capsules, having the basic structure described by ANDREWS (1935), are white due primarily to the irregular and small spherulites, and have a finely granulated appearance. They are circular, averaging 1.7 mm in diameter. The average number of ova-veligers per capsule was 35 (range, 22–55).

Capsule deposition was noted from May through July and during December; deposition is, however, probably more frequent. The capsules are deposited in groups on the sides of large pebbles that are well-anchored in the sand. Deposition is always beneath the surface of the sand and on relatively smooth surfaces. The site of deposition is in keeping with the snail's behavior of burrowing into sand and attaching, by means of the foot, to the sides of pebbles during maximum ebb and maximum flood tides. Emergence occurs during flooding and ebbing tides during day and night. Variable patterns of behavior in *Nerita polita*, ranging from primarily nocturnal (SAFRIEL, 1969; HUGHES, 1971) to no nocturnal activity (ZANN, 1973), have been reported.

Early development: Uncleaved ova, averaging 0.19 mm in diameter, through veligers, averaging 0.25 mm long, with eyes and an operculum were observed enclosed in the membranous lining of the capsule. Veligers apparently leave the capsule near the base. Hatched veligers averaged 0.25 mm long and were kept alive for 14 d, during which no significant morphological changes occurred.

Family LITTORINIDAE

Littorina scabra scabra (Linnaeus, 1758)

Nomenclature: According to Dr. J. Rosewater (personal communication) the species and subspecies names are provisional, pending the publication of a revision by Dr. D. Reid.

Habitat: Found at only one locality, on boulders in the main port of Aqaba. It occurred in the transitional littorinid-chthamaliid (supralittoral fringe–midlittoral) zones from May 1982 through January 1983.

Specimens examined: 61 averaging 12.6 mm long (range, 7.2–18.1).

Sex ratio: 1.0 male:1.3 female.

Reproduction: The ovoviviparous females were ovigerous and the males contained sperm in the vas deferens each month.

Early development: The ctenidial brood pouch (ROSEWATER, 1970) contained various stages of development during each month except September and January. The stages ranged from early cleavage to free, eyeless veligers averaging 0.11 mm long.

Nodilittorina millegrana (Philippi, 1848)

Nomenclature: ROSEWATER (1970) states that *Littorina novaezelandiae* Reeve, 1857, reported by SAFRIEL & LIPKIN (1964) and *Littorina urieli* described by BIGGS (1966) from Eilat, Israel, are synonyms of *Nodilittorina millegrana*.

Habitat: Characteristic of the littorinid (supralittoral fringe) zone and most common on near vertical surfaces of boulders. It is the second highest mollusk in vertical distribution in the rocky intertidal zone.

Specimens examined: 371 averaging 9.0 mm long (range, 3.2–14.3) from April 1982 through May 1983 for reproductive state; 270 specimens 1.0–6.5 mm long for minimum size of sexual maturity.

Sex ratio: 1.0 male:1.7 female.

Reproduction: Males with sperm in the vas deferens and females with ova in the oviduct were found each month. The smallest male possessing a rudimentary penis was 2.5 mm long and the smallest with a fully developed penis and sperm in the vas deferens was 3.3 mm. The smallest ovigerous female was 4.1 mm long.

Spawn: *Nodilittorina millegrana* produces pelagic egg capsules. Each capsule contains a single egg, is transparent and dome-shaped, being flattened on one side and elevated on the opposite in three tiers (two rings) (TOKIOKA & HABE, 1953; ROSEWATER, 1970). The capsules averaged 0.19 mm in diameter and 0.08 mm in height. The area containing the egg averaged 0.08 mm in diameter.

Early development: Based on observations of capsules isolated in culture dishes, the development from zygote (average, 0.07 mm in diameter) into the veliger stage occurred within about 24 h. During the next 24 h, veligers having an operculum but lacking eyes left the capsule via a torn area on the flattened side. Veligers remained alive for 5 d following hatching and averaged 0.13 mm long. Neither eyes nor any other major morphological feature developed during this period.

Nodilittorina subnodosa (Philippi, 1847)

Nomenclature: What SAFRIEL & LIPKIN (1964) reported as *Tectarius armatus* Issel from the littorinid zone at Eilat, Israel, and FISHELSON (1971) reported is *Nodilittorina subnodosa*. According to Dr. J. Rosewater (personal com-

munication), *T. armatus* appears to be a fossil and is probably a trochid.

Habitat: The highest occurring mollusk in the rocky intertidal zone and characteristic of the upper littorinid (supralittoral fringe) zone. It is most common on nearly horizontal slab substrata.

Specimens examined: 339 averaging 9.0 mm long (range, 4.3–13.2) from May 1982 through May 1983 for state of reproduction; 112 specimens 2.2–5.0 mm long for minimum size of sexual maturity.

Sex ratio: 1.0 male:2.1 female.

Reproduction: All females contained ova in the oviduct and all males had sperm in the vas deferens from June through September. Females with and without ova and males with and without sperm were found in May and October. The major period of reproduction is considered to be June through September. From October through April there was no noticeable degeneration in the size of the penis, as PALANT & FISHELSON (1968) saw during the non-reproductive period of *Littorina neritoides* (Linnaeus, 1758).

The smallest male having a recognizable, rudimentary penis was 2.4 mm long and the smallest male with a fully developed penis and sperm in the vas deferens was 3.4 mm. The smallest ovigerous female was 4.1 mm long.

Spawn: Each pelagic egg capsule contains a single egg. The capsules are similar in shape and transparency to those of *Nodilittorina millegrana*. They differ, however, in having four tiers (three rings) and being larger, averaging 0.25 mm in diameter and 0.15 mm in height. The area containing the zygote averaged 0.11 mm in diameter.

Early development: In culture dishes, veligers hatched within about 24 h after isolation of uncleaved ova (averaging 0.07 mm in diameter). The newly hatched veligers averaged 0.11 mm long and had an operculum but lacked eyes. The veligers remained alive for 5 d, at which time they still lacked eyes, but the shell length had increased to 0.13 mm.

Family PLANAXIDAE

Planaxis sulcatus (Born, 1780)

Habitat: A wide-ranging component of the chthamaliid-*Tetraclita* (midlittoral) zones on pebble and slab substrata.

Specimens examined: 409 averaging 15.8 mm long (range, 8.7–21.6) from May 1982 through November 1983 for state of reproduction; 139 specimens 7.5–13.9 mm long for minimum size of sexual maturity.

Sex ratio: 1.0 male:1.2 female.

Reproduction and early development: This species is ovoviparous with a brood chamber at the termination of

the pallial oviduct in the dorsal head-foot (RISBEC, 1935; THORSON, 1940). During December and through March, neither the males nor females had gametes. The gonads were reduced in size but retained the coloration of dark-orange to rust-colored testes and cream ovaries characteristic of the reproductive period.

Beginning in April, males with sperm in the vas deferens and some females with ova (0.12 mm in diameter) in the oviduct appeared, and gametes were present in some individuals of both sexes through November. From May through October, the brood chamber was filled with stages of development from uncleaved zygotes (average diameter, 0.12 mm) within a membrane to free (*i.e.*, not enclosed in a membrane) veligers lacking eyes but having an operculum and averaging 0.13 mm long. In most cases, the contents of the brood chamber were uniform in that only one developmental stage, or closely sequential stages, were present. In a few cases, the brood chamber contained uncleaved ova and a few free veligers, indicating that the brood chamber is filled following the release of veligers. When the brood chamber was filled, the oviduct usually contained ova. The major period of reproduction, based on the occurrence of a majority of mature individuals and brooding females, is from June through September.

The smallest male, based on gonad coloration, was 8.7 mm long, and sperm were present in the vas deferens. The smallest female with a cream-colored ovary was 9.6 mm long, the smallest with ova in the oviduct 10.0 mm long, and the smallest with the brood chamber occupied was 10.3 mm long.

Comments: RISBEC (1935) described the reproduction of *Planaxis sulcatus* from New Caledonia and THORSON (1940) did so from Bushire, Iran, Persian Gulf. The entire process described by Risbec and Thorson (through the free veliger stage, including the lack of eyes in hatched veligers) and the process found in specimens from the Jordan Gulf of Aqaba are essentially the same. However, the suppression of the pelagic larval stage and the development of the veligers into small snails in the brood chamber found by Thorson in the Persian Gulf was not found in the Gulf of Aqaba.

Both RISBEC (1935) and THORSON (1940) reported a low number of males compared to females. Based on this finding, and coupled with not having seen *Planaxis sulcatus* copulating, Thorson proposed parthenogenetic development. *Planaxis sulcatus* lacks a penis; actual sperm transfer was not observed in this study, nor is the mechanism known. Clustering, however, is a common pattern of behavior during submergence and emergence. The cluster may include a large number of individuals; in one case a total of 867 specimens were counted in one cluster. In another case a 1:1 male to female ratio was found within a cluster (compare with the above 1.0:1.2 ratio). MAGNUS & HAACKER (1968) attributed the clustering behavior of *P. sulcatus* to physical factors, including prevention of

drying during exposure and protection against wave action. It is proposed herein that another aspect of clustering is the transfer of sperm, probably during submergence.

Based on the above, parthenogenetic development, as proposed by THORSON (1940), is considered unlikely. The high female to male sex ratio found by RISBEC (1935) and THORSON is considered a sampling problem. My experience is that a skewed sample with respect to sex in this and other species with an approximate 1:1 ratio is not uncommon. This is especially the case in small-sized samples.

Family CERITHIIDAE

Cerithium caeruleum Sowerby, 1855

Habitat: This is the largest of the cerithiids occurring in the intertidal zone. It usually occurs between the two cerithiids described below, from above to below the *Tetraclita* (midlittoral) zone on smooth fossil reef bottoms and other slab having a sand cover.

Specimens examined: 416 averaging 27.3 mm long (range, 14.0–34.2) from August 1982 through May 1984 for reproductive state; 101 specimens 10.0 to 23.0 mm long for minimum size of sexual maturity.

Sex ratio: Distinction between male and female can only be made when gametes are present. For 161 with gametes, the sex ratio was 1.0 male:0.6 female.

Reproduction: Males with sperm in the vas deferens were found from January through September but most commonly from February through August. Females with ova in the oviduct were present from April through September but most commonly from April through August. The latter period is considered to be the major period of reproduction. The smallest male, based on the presence of sperm, was 17.3 mm long, and the smallest female having ova was 20.2 mm long.

The actual process of sperm transfer was not observed. Pairing was observed frequently in the field and laboratory and was similar to that of *Cerithium muscarum* Say, 1832, described by HOUBRICK (1973).

Spawn: Specimens kept in aquaria from mid-April through early June deposited egg masses on the aquarium sides as well as on pebbles and clumps of algae during the day and night on 27 of 54 days. The deposition was not related to a particular lunar or tidal cycle. The masses were typically pale yellow in color and arranged in a continuous linear series of tight folds or loops up to 4 mm high and 50 mm long. The arm of the folds was 0.4 to 0.5 mm thick. The individual capsules suspended in a gelatinous matrix averaged 0.15 mm in diameter, and the contained zygote was 0.09 mm in diameter.

Early development: Within 5 to 6 d following deposition of egg masses, veligers, averaging 0.14 mm long, hatched.

The veligers were kept alive for 4 d after hatching and did not develop eyes.

Clypeomorus bifasciata (Sowerby, 1855)

Nomenclature: According to Dr. R. S. Houbrick (personal communication), this species is probably the same as *Clypeomorus morus* (Bruguière, 1792) reported by MASTALLER (1979).

Habitat: Characteristic of the chthamaliid (midlittoral) zone and is the highest occurring of the three intertidal cerithiids.

Specimens examined: 332 averaging 15.9 mm long (range, 9.8–20.5) from June 1982 through May 1984, except August 1982, for state of reproduction; 51 specimens 9.0–13.0 mm long for minimum size of sexual maturity.

Sex ratio: The sexes could be determined only when gametes were present; for 179 specimens, the ratio was 1.0 male:1.4 female.

Reproduction: Some males with sperm in the vas deferens were found each month except December 1982 and 1983 and February 1983. Oviparous females were absent or least abundant from September through February–March and most common from April through August. The latter period is considered as the major period of reproduction. Both the smallest male with sperm in the vas deferens and the smallest female with ova in the oviduct were 9.2 mm long.

Spawn: In an aquarium, *Clypeomorus bifasciata* deposited white egg masses on the underside of clumps of the alga *Enteromorpha*. The masses were usually 2–3 mm wide, variable in length, and the mass had an irregular shape. The individual capsules within the gelatinous mass were aligned in rows perpendicular to the width. The capsules averaged 0.13 mm in diameter, and the contained zygote was 0.08 mm in diameter.

Early development: Hatching of eyed veligers occurred 3–4 d after egg mass deposition and were 0.13–0.14 mm long. They were kept alive for 10 d following hatching and no significant morphological changes occurred.

Clypeomorus petrosa gennesi (Fisher & Vignal, 1901)

Nomenclature: According to Dr. R. S. Houbrick (personal communication), this taxon is synonymous with *Clypeomorus tuberculatus* (Linnaeus, 1758) reported by MASTALLER (1979).

Habitat: Occurs below the *Tetraclita* (midlittoral) zone, most commonly in depressions with sand occurring in the fossil reef substratum.

Specimens examined: 287 averaging 20.2 mm long (range, 14.2–24.5) from June 1982 through March 1984 for state of reproduction; 105 specimens 7.8–19.1 mm long for minimum size with gametes.

Sex ratio: 1.0 male:0.5 female based on 201 specimens with gametes.

Reproduction: Males with sperm in the vas deferens were found during each month except December 1982 and January 1983. Females with ova in the oviduct were most common from May through September; some ovigerous females with few ova were found in April and from October through January. The major period of reproduction is considered to be from May through September. The smallest male with sperm in the vas deferens was 14.4 mm long, the smallest ovigerous female 15.8 mm long.

Pairing was observed on numerous occasions in the field and laboratory but actual sperm transfer was not; pairing was essentially the same as noted above for *Cerithium caeruleum*.

Spawn: In an aquarium, deposition of yellowish egg masses occurred on the underside of *Enteromorpha* clumps or, in the absence of algae, on the sides of the aquarium. The sand and detritus covered masses were a continuous string 2–3 mm wide and with individual capsules suspended in a gelatinous matrix. The capsules averaged 0.13 mm in diameter, the zygotes 0.09 mm in diameter.

Early development: Veligers with eyes hatched 5 d after deposition and averaged 0.13 mm long. The veligers remained alive for 1 wk and no significant morphological changes occurred.

Class Gastropoda, subclass Pulmonata

Family SIPHONARIDAE

Siphonaria laciniosa Linnaeus, 1758

Nomenclature: According to BARASH & DANIN (1972), *Siphonaria laciniosa* and *S. kurracheensis* Reeve, 1856, are synonymous.

Habitat: Most common in the chthamalid zone and between the *Tetraclita* and chthamalid (midlittoral) zones. In the absence of a recognizable chthamalid zone, it occurs most commonly above the *Tetraclita* zone.

Specimens examined: 245 from March 1983 through May 1984 averaging 14.0 mm long (range, 9.1–22.2).

Reproduction: The presence of gametes was determined by teasing apart the gonad (ovotestis) and the hermaphroditic duct. Sperm were present every month except July, August, and September, whereas the presence of ova was restricted to December through May, being most abundant from January through March. The latter period is considered the major period of reproduction.

During the major period of reproduction, the gonad

was bright yellow and reached a maximum size of 3.2 mm wide × 5.2 mm long. By contrast, when ova were absent, the gonad was burnt orange and greatly reduced in size, the minimum being 0.8 mm wide × 1.6 mm long.

Actual copulation was not observed but behavior similar to that reported for *Siphonaria japonica* (Donovan, 1824) by HIRANO & INABA (1980) was observed.

Spawn: *Siphonaria laciniosa* deposits benthic egg ribbons. The ribbons were typically dome-shaped, yellowish, and coated externally with sand. The shape of the ribbon varied from a "C" to a loose coil and ranged in size from 1.2 mm wide × 10 mm long to 1.8 × 54 mm. Larger ribbons were seen in the field but not measured. Capsules containing the zygote were suspended within the ribbon, were ovate in shape, and averaged 0.17 mm wide × 0.23 mm long.

The deposition of ribbons in the field and laboratory lasted from early January to late April. In the field, the ribbons were deposited on exposed surfaces, coated with sand, and exposed to the air during spring ebb tides. Deposition was not related to a particular lunar or tidal cycle but occurred only at night. The latter is consistent with other behaviors of *Siphonaria laciniosa*, which is a homing species active only after sunset and when submerged (HULINGS, 1985).

Early development: Hatching of operculate but eyeless veligers occurred about 10 d after deposition. Eyes appeared within 2 to 3 days. The hatched veligers averaged 0.18 mm long (range, 0.17–0.19) and remained alive for 2 wk, during which no obvious morphological changes occurred.

Comments: THORSON (1940) reported two siphonarians from the Persian Gulf, *Siphonaria kurracheensis* (= *S. laciniosa*) and *S. siphonaria* Sowerby. The descriptions of the shape, size, and color of the egg ribbon, the size and shape of the egg capsule, and the embryological development and hatching reported for *S. siphonaria* by Thorson are almost identical to those of *S. laciniosa* from the Jordan Gulf of Aqaba. In addition, Thorson reported direct development in *S. kurracheensis* (= *S. laciniosa*), i.e., the veliger stage was completed in the capsule and at hatching, crawling juveniles emerged. This is in contrast to the hatching of veligers in *S. laciniosa* in the northern Gulf of Aqaba.

Class Bivalvia

Family MYTILIDAE

Brachidontes variabilis (Krauss, 1848)

Habitat: Most characteristic between the chthamalid and *Tetraclita* (midlittoral) zones or in the middle midlittoral (SAFRIEL *et al.*, 1980). This species typically occurs as dense beds in depressed areas of beach rock or fossil reef.

Specimens examined: 247 from October 1982 through May 1984 averaging 19.5 mm long (range, 12.8–27.3).

Sex ratio: 1.0 male:0.8 female.

Reproduction: The gonads penetrate into the mantle. The coloration of the mantle lobe containing the ovaries is typically reddish, although variable in shade, and that containing the testes is cream colored. Gametes were present in at least some if not all of the specimens of both sexes each month. In addition, at least some individuals of both sexes had enlarged gonads each month.

Comments: WILSON & HODGKIN (1967) found spawning of *B. variabilis* in Western Australia to be restricted to March–April although they noted that spawning probably continued throughout the summer. They found in *B. variabilis*, compared to other mytilids, significant differences in the time of year and the length of spawning, as well as the beginning of gametogenesis and the presence of a “reproductively neutral phase.”

Family OSTREIDAE

Ostrea forskali Chemnitz, 1785

Nomenclature: According to MASTALLER (1979), *Ostrea cucullata* Born, 1780, is synonymous with *O. forskali*. The former species has been variously placed in *Saccostrea* (BRALEY, 1982), *Crassostrea* (FAO, 1972), or *Lopha* (MASTALLER, 1978).

Habitat: Characteristic of the *Tetraclita* (midlittoral) zone.

Specimens examined: 144 averaging 39 mm long (range, 19–62) from April 1982 through June 1983.

Sex ratio: 1.0 male:2.6 female based on 43 specimens with gametes.

Reproduction: Ovigerous females occurred from June through November and in January. The greatest abundance occurred from July through October–November. Males with sperm were found from June through October. The major period of reproduction is considered to be from July through October–November. The possibility of hermaphroditism in *Ostrea forskali* was not investigated.

Comments: FAO (1972) found the greatest density of spat occurred during December–January, although *Ostrea forskali* spat were often absent or in the minority compared to those of other oysters. BRALEY (1982) reported low level and continuous reproduction in *O. forskali* with, however, peaks in November–December, March–April, and late June. He also found no correlation between reproduction and temperature, and a planktonic larval life of 3–4 wk.

DISCUSSION

Various aspects of the reproduction of 15 dominant species of mollusks from the rocky intertidal zone along the Jordanian coast of the Gulf of Aqaba have been investigated. The species range in vertical distribution from the supralittoral fringe to the lower midlittoral.

The fauna can be divided into continuous reproducers (*i.e.*, those that reproduce the year round) and restricted reproducers, with periods of reproduction being indicated by the majority of specimens having ova in the oviduct and sperm in the vas deferens or similar structures at the same time. The continuous reproducers include *Cellana radiata*, *Monodonta dama*, *Nerita forskalii*, *Nerita polita*, *Littorina scabra scabra* (probable), *Nodilittorina millegrana*, and *Brachidontes variabilis*. The restricted reproducers include *Acanthopleura haddoni*, *Nodilittorina subnodosa*, *Planaxis sulcatus*, *Cerithium caeruleum*, *Clypeomorus bifasciata*, *Clypeomorus petrosa gennesi*, *Siphonaria laciniosa*, and *Ostrea forskali*. Cycles within the continuous reproducers may exist; in addition, there may be longer or shorter periods of reproduction within the restricted reproducers. For example, among the latter group, there were often specimens with or without gametes in the ducts at the beginning and end of the major period of reproduction. There were also species in which sperm were present before and after the presence of ova (*P. sulcatus*, *C. caeruleum*, *C. bifasciata*, *C. petrosa gennesi*, and *S. laciniosa*). An investigation of gametogenesis (in progress) may provide additional information on the above and other aspects of reproductive periodicity.

The temporal patterns of reproduction noted above are not related to tide level or a species' vertical position in the intertidal zone. For example, the highest species in the supralittoral fringe, *Nodilittorina subnodosa*, had a restricted period of reproduction, while the next highest, *N. millegrana*, reproduced the year round. The supralittoral fringe–upper midlittoral *Littorina scabra scabra* is assumed to reproduce continuously. Within the midlittoral, both continuous and restricted reproducers were found.

Water temperature in the northern Gulf of Aqaba has a narrow annual range, 20 to 27°C, whereas average annual air temperature has a much wider range, 16 to 32°C. Among the species investigated there was no direct relationship between temperature and reproduction or spawning in the continuous reproducers. They reproduced and spawned throughout the annual range in air and water temperature. Among the restricted reproducers, 7 out of 8 of the species reproduced when annual water and air temperatures were warmer (generally May through October). In two species (*Cerithium caeruleum* and *Clypeomorus bifasciata*), however, reproduction in April coincided with a 4°C increase in annual air temperature but little increase in water temperature. The other restricted reproducer, *Siphonaria laciniosa*, reproduced during the coldest period of annual air and water temperatures. Thus, the pattern of the relationship between reproduction or spawning and temperature is highly variable. If there is a relationship, as seems to be the case for some species, air temperature, having a wide range, may be more significant than water temperature, having a narrow range. And as noted previously, the terrestrial environment exerts greater influence on the intertidal zone of Jordan than the marine environment.

Vertical migration of most of the mobile species occurs with the change in sea level, from high during December–May to low during July–October (Hulings, unpublished data). The continuous reproducers, including the sessile *Brachidontes variabilis*, reproduced irrespective of changes in sea level. Among the restricted reproducers, including the sessile *Ostrea forskali*, all reproduced during lowered sea level except *Siphonaria laciniosa*. The latter, a permanent homer and non-migrant (HULINGS, 1985), reproduced during the period of higher sea level, a period during which the egg ribbons were submerged more often than exposed.

There was no consistent pattern between tide level or vertical position and type of spawning except in species of the supralittoral fringe. Both *Nodilittorina millegrana* and *N. subnodosa* deposited pelagic egg capsules. *Littorina scabra scabra*, transitional between the supralittoral fringe and the upper midlittoral, brooded and hatched veligers. Within the midlittoral, a wide variety of spawning patterns occurred.

The absence of a relationship between reproduction (or spawning) and tidal levels and lunar cycles may result from the tidal levels and lunar cycles being out of phase. In addition, the annual changes in sea level modify the tide levels. HULINGS (1985) found that activity patterns in *Cellana radiata* and *Siphonaria laciniosa* were not related to tidal level (except that these animals are active only when submerged) or lunar cycles.

The hatching of veligers occurred before, during, and after the relatively short periods of primary productivity, as well as during the extended period of oligotrophic conditions. Hatching occurred up to 7 d following deposition of the spawn, and the resulting veligers were small, less than 0.20 mm in length. It appears that the length of veliger life is short, based on their small size and the generally low primary productivity in the area.

Indirect development is characteristic of all the species, based on direct observation or literature sources. Development through, and hatching of, veligers was observed in all species except *Acanthopleura haddoni*, *Cellana radiata*, *Brachidontes variabilis*, and *Ostrea forskali*. Among the veligers were those with, without, or developing eyes prior to or after hatching. Veligers with eyes prior to hatching included those of *Nerita forskalii*, *N. polita*, *Clypeomorus bifasciata*, and *C. petrosa gennesi*. Those lacking eyes prior to and up to 1 wk following hatching included *Monodonta dama*, *Littorina scabra scabra*, *Nodilittorina millegrana*, *N. subnodosa*, *Planaxis sulcatus*, and *Cerithium caeruleum*. The veligers of *Siphonaria laciniosa* developed eyes 2 to 3 d after hatching. The significance of the presence or absence of eyes in the veligers at hatching is not known.

ACKNOWLEDGMENTS

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helpful comments on the manuscript. Thanks are also expressed to Dr. Elias Salameh, Department of Geology, University of Jordan, for rock-type determinations. Financial support provided by the Office of the Dean of Research, Yarmouk University, is gratefully acknowledged.

LITERATURE CITED

- ANATI, D. A. 1976. Balances and transports in the Red Sea and the Gulf of Elat (Aqaba). *Israel J. Earth Sci.* 25:104–110.
- ANDREWS, E. A. 1935. The egg capsules of certain Neritidae. *J. Morphol.* 57:31–59.
- AYAL, Y. & U. N. SAFRIEL. 1980. Intertidal zonation and key-species associations of the flat rocky shores of Sinai, used for scaling environmental variables affecting cerithiid gastropods. *Israel J. Zool.* 29:110–124.
- BARASH, A. L. & Z. DANIN. 1972. The Indo-Pacific species of Mollusca in the Mediterranean and notes on a collection from the Suez Canal. *Israel J. Zool.* 21:301–376.
- BERRY, A. J., R. LIM & A. S. KUMAR. 1973. Reproductive systems and breeding conditions in *Nerita birmanica* (Archeogastropoda: Neritacea) from Malayan mangrove swamps. *J. Zool.* 170:189–200.
- BIGGS, H. E. J. 1966. A new species of *Littorina* from Eilat, Israel, and notes on its affinities with *Littorina novaezelandiae* Reeve. *J. Conchol.* 26:137–139.
- BRALEY, R. D. 1982. Reproductive periodicity in the indigenous oyster *Saccostrea cucullata* in Sasa Bay, Apra Harbor, Guam. *Mar. Biol.* 69:165–173.
- FAO. 1972. Report to the Government of Israel on the potential for oyster culture at Elat on the Gulf of Aqaba. Based on the work of P. R. Walne, FAO/TA Consultant Rep. FAO/UNDP(TA), 3076. 13 pp.
- FISHELSON, L. 1971. Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. *Mar. Biol.* 10: 113–133.
- FISHELSON, L. 1973. Ecological and biological phenomena influencing coral-species composition on the reef tables at Eilat (Gulf of Aqaba, Red Sea). *Mar. Biol.* 19:183–196.
- FRIEDMAN, G. M. 1965. A fossil shoreline reef in the Gulf of Elat (Aqaba). *Israel J. Earth Sci.* 14:86–90.
- HIRANO, Y. & A. INABA. 1980. *Siphonaria* (pulmonate limpet) survey of Japan. I. Observations on the behavior of *Siphonaria japonica* during breeding season. *Publ. Seto Mar. Biol. Lab.* 25:323–334.
- HOUBRICK, R. S. 1973. Studies on the reproductive biology of the genus *Cerithium* (Gastropoda: Prosobranchia) in the western Atlantic. *Bull. Mar. Sci.* 23:875–904.
- HUGHES, R. N. 1971. Notes on the *Nerita* (Archeogastropoda) population of Aldabra Atoll, Indian Ocean. *Mar. Biol.* 9: 290–299.
- HULINGS, N. C. 1979. Currents in the Jordan Gulf of Aqaba. *Dirasat* 6:21–33.
- HULINGS, N. C. 1985. Activity patterns and homing in two rocky intertidal limpets, Jordan Gulf of Aqaba (Red Sea). *Nautilus* 99:75–80.
- HULINGS, N. C. & A. ABU HILAL. 1983. The temporal distribution of nutrients in the surface waters of the Jordan Gulf of Aqaba. *Dirasat* 10:91–105.
- IRIKI, S., S. NISHIWAKI & T. TOCHIMOTO. 1963. On the peculiar mode of spermatophore transfer in *Nerita albicilla* L. (Prosobranchia, Neritidae). *Venus* 22:290–292.

- JORNÉ, J. & U. N. SAFRIEL. 1979. Linear and non-linear diffusion models applied to the behavior of a population of an intertidal snail. *J. Theor. Biol.* 79:367-380.
- KUMÉ, M. & D. KATSUMA. 1957. Invertebrate embryology. Bai Fukan Press: Tokyo.
- LEVANON-SPANIER, I., E. PADAN & Z. REISS. 1979. Primary production in a desert-enclosed sea—the Gulf of Elat (Aqaba), Red Sea. *Deep-Sea Res.* 26:673-685.
- MAGNUS, D. B. E. & U. HAACKER. 1968. Zum Phänomen der orstsunsteten Ruhrversammlungen der Strandschnecke *Planaxis sulcatus* (Born) (Mollusca, Prosobranchia). *Sarsia* 34:137-148.
- MASTALLER, M. 1978. The marine molluscan assemblages of Port Sudan, Red Sea. *Zool. Meded.* 53:117-144.
- MASTALLER, M. 1979. Beiträge zur Faunistik und Ökologie Mollusken und Echinodermen in den Korallenriffen bei Aqaba, Rotes Meer. Doctoral Dissertation, Ruhr-Universität Bochum, Fed. Republic Germany. 344 pp.
- MERGNER, H. & H. SCHUHMACHER. 1974. Morphologie, Ökologie und Zonierung von Korallenriffen bei Aqaba, (Golf von Aqaba, Rotes Meer). *Helgo. Wiss. Meeresunt.* 26:238-358.
- MORCOS, S. A. 1970. Physical and chemical oceanography of the Red Sea. *Oceanogr. Mar. Biol. Ann. Rev.* 8:73-202.
- PALANT, B. & L. FISHELSON. 1968. *Littorina punctata* (Gmelin) and *Littorina neritoides* (L.), (Mollusca, Gastropoda) from Israel: ecology and annual cycle of genital system. *Israel J. Zool.* 17:145-160.
- PALDOR, N. & D. A. ANATI. 1979. Seasonal variation of temperature and salinity in the Gulf of Elat (Aqaba). *Deep-Sea Res.* 26:661-672.
- RAO, M. B. 1973. Sex phenomenon and reproduction cycle in the limpet *Cellana radiata* (Born) (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* 12:263-273.
- RAO, M. B. 1976. Studies on the growth of the limpet *Cellana radiata* (Born) (Gastropoda: Prosobranchia). *J. Moll. Stud.* 42:136-144.
- RISBEC, J. 1935. Biologie et ponte de mollusques gastéropodes Néo-Calédoniens. *Bull. Soc. Zool. France* 60:387-417.
- ROSEWATER, J. 1970. The family Littorinidae in the Indo-Pacific. Part I. The subfamily Littorininae. *Indo-Pacific Mollusca* 2:417-506.
- SAFRIEL, U. 1969. Ecological segregation, polymorphism and natural selection in two intertidal gastropods of the genus *Nerita* at Elat (Red Sea, Israel). *Israel J. Zool.* 18:205-231.
- SAFRIEL, U. N., A. GILBOA & T. FELSEBERG. 1980. Distribution of rocky intertidal mussels in the Red Sea coasts of Sinai, the Suez Canal and the Mediterranean coast of Israel, with special reference to recent colonizers. *J. Biogeog.* 7:39-62.
- SAFRIEL, U. N. & Y. LIPKIN. 1964. On the intertidal zonation of the rocky shores at Eilat (Red Sea, Israel). *Israel J. Zool.* 13:187-190.
- STEPHENSON, T. A. & A. STEPHENSON. 1949. The universal features of zonation between tidemarks on rocky coasts. *J. Ecol.* 37:289-305.
- THORSON, G. 1940. Studies on the egg masses and larval development of Gastropoda from the Iranian Gulf. *Danish Sci. Invest. Iran* 2:159-238.
- TOKIOKA, T. & T. HABE. 1953. A new type of *Littorina capsula*. *Publ. Seto Mar. Biol. Lab.* 3:55-56.
- WILSON, B. R. & E. P. HODGKIN. 1967. A comparative account of the reproductive cycles of five species of marine mussels (Bivalvia: Mytilidae) in the vicinity of Fremantle, Western Australia. *Aust. J. Mar. Freshwater Res.* 18:175-203.
- ZANN, L. P. 1973. Relationship between intertidal zonation and circa-tidal rhythmicity in littoral gastropods. *Mar. Biol.* 18:243-250.

NOTE ADDED IN PROOF:

Too late for inclusion in the text, information has been obtained on the reproduction of another intertidal gastropod from the Jordan Gulf of Aqaba.

Nerita undata Linnaeus, 1758

(Family NERITIDAE)

Habitat: Only two specimens found, both on boulders above the *Tetraclita* (midlittoral) zone. MASTALLER (1979) reported finding only one specimen.

Specimens examined: One female 19.8 mm long, October 1982; one female 28.0 mm, August 1985.

Reproduction: No spermatophores like those in *Nerita forskalii* and *N. polita* nor any other type were found.

Spawn: The female collected in August 1985 was kept in a seawater table with continuously circulating water. In September 1985 the specimen deposited 11 egg capsules near to and just under the base of a permanently submerged pebble. The capsules are white and composed of mostly round spherulites averaging 0.07 mm in diameter (range, 0.05-0.08). The shape of the capsules is more elliptical than round, averaging 2.7 mm wide × 3.5 mm long (range, 2.4-4.0).

Early development: Development from uncleaved ova to veligers with eyes and opercula occurred in about 3 w. The capsules contained an average of 76 larvae (range, 70-85); the veligers averaged 0.34 mm long. Hatching occurred about 4 w after deposition of the capsules.

NOTES, INFORMATION & NEWS

Consumption of Pelagic Red Crabs by Black Abalone at San Nicolas and San Miguel Islands, California

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Black abalone, *Haliotis cracherodii* Leach, 1817 (Prosobranchia: Haliotidae), are common in rocky intertidal habitats from northern California to southern Baja California Sur, Mexico (MCLEAN, 1978). Black abalone feed primarily on drifting fragments of kelps and other algae (COX, 1962; LEIGHTON & BOOLOOTIAN, 1963; ABBOTT & HADERLIE, 1980). Fragments of foraminiferans, bryozoans, hydroids, sponges, and sea urchins occasionally occur in the guts of black abalone, but ingestion of animal parts is thought to be incidental to consumption of algae (LEIGHTON & BOOLOOTIAN, 1963). Intentional capture and consumption of macroinvertebrates has not been reported, to our knowledge, for any species of abalone.

During a morning low tide on 3 June 1984, VanBlaricom searched for evidence of feeding among several hundred black abalone in a rocky cove (33°16.5'N, 119°33.5'W) at the west end of San Nicolas Island, California. About 15% of the abalone observed were feeding on fragments of kelps. In addition, three abalone were consuming pelagic red crabs (*Pleuroncodes planipes* Stimpson, 1860) (Anomura: Galatheidae). The abalone were all >100 mm in maximum shell diameter, and the crabs were 40-50 mm in total length. The abalone held the crabs against the substratum with the anterior portion of the foot, as they do when consuming algal fragments. When the abalone were removed from the rocks, it was noted that abdominal and posterior thoracic tissues (including the exoskeleton) of the crabs had been rasped away. Crabs held by abalone were dead, but were moist, flexible, and bright red in color. Crabs in the water near black abalone were alive, active, and bright red in color. Dead crabs were only seen high on a nearby beach and were dry, brittle, and bleached. Therefore, it seems likely that abalone captured the crabs alive, although post-mortem capture cannot be ruled out.

Stewart made similar observations on 10 February 1985 while examining a group of approximately 300 black abalone near Otter Harbor (34°3.5'N, 120°25'W) on the north shore of San Miguel Island, California. Many of the abalone were feeding on kelp fragments. Live and dead red crabs and body parts were scattered throughout the rocky intertidal zone. Five abalone held red crabs (dead in all cases) with the anterior part of the foot, and several others held only fragments of crabs. Therefore, it seems likely that some abalone were feeding on crabs captured post-mortem.

During normal oceanographic conditions, pelagic red crabs are common in the coastal waters of Baja California south of 29°N latitude (BOYD, 1967). During El Niño-Southern Oscillation (ENSO) periods, anomalous northward currents carry populations of red crabs to California. As a result, mass strandings of red crabs become common south of Pt. Conception (LONGHURST, 1966), and can occur farther north (GLYNN, 1961). The 1982-83 ENSO was perhaps the strongest of the century (CANE, 1983), producing striking warming of the coastal waters of California (FIEDLER, 1984). Stranded red crabs were observed frequently at San Nicolas Island from January 1983 through November 1984 (STEWART *et al.*, 1984; VanBlaricom & Stewart, personal observations), and at San Miguel Island from January 1983 through February 1985 (STEWART *et al.*, 1984; Stewart, personal observations). Mainland strandings occurred as recently as March 1985 at sites as far north as Monterey Bay (Jameson, Baldrige & Deutsch, personal observations). Strandings and nearshore concentrations of red crabs in California have provided unusual feeding opportunities for gulls (STEWART *et al.*, 1984), sea otters (Deutsch, personal observations), and intertidal sea anemones (VanBlaricom, personal observations), in addition to black abalone.

We thank the Command of the Pacific Missile Test Center, U.S. Navy, for allowing access to San Nicolas Island, and the Superintendent of Channel Islands National Park for allowing access to San Miguel Island. R. Dow, J. Vanderwier, and C. Harrold provided logistic support, and R. Saunders assisted in the field. We thank D. Lindberg for encouragement, J. Estes, R. Jameson, and two anonymous reviewers for comments on the manuscript, and P. Himlan for clerical expertise. GRVB was supported by the Denver Wildlife Research Center of the U.S. Fish and Wildlife Service and BSS was supported by contracts from the U.S. Air Force and the National Marine Fisheries Service.

LITERATURE CITED

- ABBOTT, D. P. & E. C. HADERLIE. 1980. Prosobranchia: marine snails. Pp. 230-307. *In*: R. H. Morris, D. P. Abbott

- & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.
- BOYD, C. M. 1967. The benthic and pelagic habitats of the red crab, *Pleuroncodes planipes*. Pacific Sci. 21:394-403.
- CANE, M. A. 1983. Oceanographic events during El Niño. Science 222:1189-1195.
- COX, K. W. 1962. California abalones, family Haliotidae. Calif. Dept. Fish and Game, Fish Bull. 118:1-113.
- FIEDLER, P. C. 1984. Observations of the 1982-83 El Niño along the U.S. Pacific coast. Science 224:1251-1254.
- GLYNN, P. W. 1961. The first recorded mass stranding of pelagic red crabs, *Pleuroncodes planipes*, at Monterey Bay, California, since 1859, with notes on their biology. Calif. Fish and Game 47:97-101.
- LEIGHTON, D. & R. A. BOOLOOTIAN. 1963. Diet and growth in the black abalone, *Haliotis cracherodii*. Ecology 44:227-238.
- LONGHURST, A. R. 1966. The pelagic phase of *Pleuroncodes planipes* Stimpson (Crustacea, Galatheididae) in the California Current. California Cooperative Oceanic Fisheries Investigation Reports 11, 1 July 1963 to 30 July 1966:142-154.
- MCLEAN, J. H. 1978. Marine shells of southern California. Natur. Hist. Mus. Los Angeles Co., Sci. Ser. 24 (Revised edition):1-104.
- STEWART, B. S., P. K. YOCHER & R. W. SCHREIBER. 1984. Pelagic red crabs as food for gulls: a possible benefit of El Niño. Condor 86:341-342.

Soviet Contributions to Malacology in 1980

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INTRODUCTION

As in past years, herein is provided a listing of malacological papers by Soviet scientists included in, and frequently abstracted by, the 1980 issues of the Referativny Zhurnal (see Veliger 27[3]:339-346 for the last such listing and references to previous ones).

We follow the categorical arrangements as utilized by the Referativny Zhurnal itself, although occasionally we may place selected titles in more appropriate categories.

Certain publications this year are major contributions to the field, the most important of these being Golikov's monograph of the Buccininae of the world in which he treats 93 species and subspecies (several as new) in great detail; this extensive work is illustrated by plates showing the shells as well as enlargements for sculptural detail; also presented are figures of egg capsules, radulae, oper-

cula, and anatomy as well as maps and charts indicating geographical, bathymetric, and ecological ranges and parameters. The bibliography includes nearly 1100 citations.

Although a number of new species were introduced, several papers also established new family-level taxa or revisionary arrangements of previously studied groups. Thus, Starobogatov and Izzatullaev divided the freshwater prosobranch family Thiaridae into three independent familial units: Thiaridae *s.s.*, Melanatriidae, and Melanoididae, new family, on the configuration of the pallial gonoducts; further, they subdivided the widely distributed, often parthenogenetic *Melanoides tuberculatus* into four species, two of which are new. Among "hydrobioid" taxa Izzatullaev discussed the little known pomatiopsid taxa of Tadzhikistan, describing two new species, one in *Kainarella* and another in *Pseudocaspia*.

Special attention to mollusks of the Kuril Islands is reflected in Gul'bin's paper on prosobranchs and Sirenko's on chitons, the latter work considering the chiton fauna off a single island, Simushir; the densities of these animals are high (*e.g.*, 3100/m² for *Juvenichiton albocinnamomeus*). Further, an entire book by Volova, Golikov & Kusakina was devoted to the shelled gastropods of the geographically adjacent Peter the Great Bay; 119 species in 43 families were noted and figures, descriptions, ranges, and ecological notes provided.

Among cephalopods, considerable attention was given to the exploitation of the neritic niche with papers by Nigmatullin on the economically important ommastrephids and by Nesis on sepiids and loliginids. Further, in a short review of the whiplash squids of the family Chiroteuthidae by Nesis, the new genus *Asperoteuthis* was established.

Popov & Skarlato reviewed the bivalve family Cardiidae in the North Pacific, describing a new species of *Cyclocardia*, while Kafanov reconsidered the living cardiids in the Black Sea, making several nomenclatorial alterations. Of particular interest to those working on cardiids is a paper by Zaiko, Zaiko & Krasnov who assert that temperature effects the number of ribs on the shell, rendering narrowly circumscribed rib-counts rather suspect for taxonomic purposes. Izzatullaev examined the five species in the freshwater bivalve family Corbiculidae in Central Asia.

Kuznetsov, Kozaka & Isibasi investigated the relationship of gill-size to palp-size in several bivalves, concluding that the deposit feeding Tellinacea have proportionately much larger palps than suspension feeding bivalves like mytilids or venerids, an adaptation documented earlier by other authors.

For a continental Palearctic freshwater fauna, that of Siberia seems extremely rich: Dolgin & Johansen discussed in some detail 31 species and recorded 65 species of freshwater mollusks from northwestern Siberia, and even in the more isolated Kureyka River, a tributary of the Yenisey above the Arctic Circle, 41 species of fresh-

water mollusks were listed by Gundrizer! For more southern climes, Zatravkin enumerated 55 species of freshwater mollusks, 39 gastropods, and 16 bivalves, from the Il'mensk Preserve in the southern Urals.

ABBREVIATIONS

BMV—Biologiya Morya (Marine Biology, Vladivostok).
 BPGF—Biochim. i populyatsion. genet. rib. (Biochemical and population genetics of fish).
 ES—English summary.
 GZ—Gidrobiologicheskii Zhurnal (Hydrobiological Journal).
 NDVS—Nauch. Dokl. Vyssh. Shkol. Biol. Nauk. (Scientific Reports of the Higher Educational School for Biological Sciences).
 NPS—Nov. probl. zool. nauki i ilk otrazhenie vyzovsk. prepodavani. Tez. Dokl. Nauch. Konf. Zoologov. Ped. in-tov. ch. 1 Stavropol (New problems in zoological science and their effect on university teaching. Thesis Reports on the teaching of science conference. Zoology. Pedagogical Institute, Stavropol).
 PEMZ—Vopr. Evoluts. Morfol. Zhivotnykh. Kazan (Problems of the Evolutionary Morphology of Animals. Kazan).
 PMIN—Paleobiogeokhimiya mor. bespozvonochnykh (Paleobiogeochemistry of Marine Invertebrates, Novosibirsk).
 TIO—Trudy Instituta Okeanologii. Akademiya Nauk SSSR (Transactions of the Institute of Oceanology, Academy of Sciences, USSR).
 ZEBF—Zhurnal Evolyutsionnoi biokhimi i fiziologii (Journal of Evolutionary Biochemistry and Physiology).
 ZZ—Zoologicheskii Zhurnal (Zoological Journal).
 14th PSC—14 Tikhookean. nauch. Kongr. (14th Pacific Science Congress).

GENERAL

ALYAKRINSKAYA, I. O. 1979. On the survival of mollusks under conditions of dehydration. Dikhatel'n Belki Nekotor. Grupp. Sovrem. Zhivotnikh (Respiratory proteins of several groups of Recent animals). Moscow, pp. 151–155.
 [Duration of survival of five aquatic species of snails and ten of clams in an air environment was studied. Though many species survived for several days to over a week, *Planorbis corneus* survived for two months, even in temperatures above 15°C.]
 ALYAKRINSKAYA, I. O. 1979. Dissolution of shell hypostracum in several mollusks. Dikhatel'n Belki Nekotor. Grupp. Sovrem. Zhivotnikh (Respiratory proteins of several groups of Recent animals). Moscow, pp. 155–159.
 [A significant increase in the concentration of calcium in the hemolymph is displayed in the Black Sea bivalve mollusk *Venus gallinae* under conditions of dehydration and in the terrestrial Caucasian mollusk *Caucasotachea atrolabiata* during the summer, the source of which appears to be the internal layers of the shell. Appended is a list of mollusks that utilize dissolution of shell hypostracum during interruptions of normal conditions of respiration.]
 ARTYUSHENKO, O. T. & I. V. MEL'NICHYK. 1979. Paleobotanical and malacofaunistic characteristics of the Quaternary deposits of the basal canyon near Mt. Snyatin (Pre-Carpathians). Ukrainian Botanical Journal 36(6):528–532, 622. (In Ukrainian, with Russian and English Summaries).
 [Palynological and molluscan data showed appreciable differences between forest and plain horizons in neanthropogenic deposits in the Pre-Carpathians.]

BEREZKINA, G. N. 1979. Some data on the biology of *Limnaea atra* in the Smolensk Region. NPS, pp. 49–51.
 BERGER, V. YA. 1979. Euryhaline marine mollusks: morphological and functional aspects. 14th PSC, Sect. F, pp. 5–6.
 DOLGIN, V. I. & B. G. JOHANSEN. 1979. Ecological and morphological characteristics of new and little known freshwater mollusks of northwestern Siberia. Nov. Dannie o Faune i Flore Sibiri (New Contributions on the Fauna and Flora of Siberia). Tomsk, pp. 47–61.
 [The distribution, abundance, and morphological characteristics of 31 mollusks are discussed as is the role of these animals in the diets of fish and birds.]
 DOLGIN, V. I. & B. G. JOHANSEN. 1980. Ecological and geographical characteristics of the mollusks of northwestern Siberia. Nov. Dannie v Prirode Sibiri (New Contributions to the Natural History of Siberia). Tomsk, pp. 30–42.
 [Ecological and zoogeographic data on 65 species of freshwater mollusks are presented.]
 FROLENKOVA, O. A. & N. D. KRUGLOV. 1979. On the morphology of the egg capsules in the molluscan families Acroloxidae, Bulinidae, and Planorbidae. NPS, pp. 181–183.
 GRIDNEY, E. A. & E. A. KAZANNIKOV. 1979. On the maintenance of pond snails (Lymnaeids) under laboratory conditions. NPS, p. 62.
 GUL'BIN, V. V. 1979. Sixth All-Union Meeting on the study of mollusks. Mollusks, principle results of their study. BMV, No. 6, p. 86.
 [96 papers were presented which dealt with various aspects of the ecology, physiology, and biology of marine bivalves, gastropods, and cephalopods as well as freshwater and terrestrial mollusks and their parasites.]
 GUNDRIZER, V. A. 1979. Freshwater mollusks of the Kureyka River (Basin of the Lower Yenisey). Nov. Dannie o Faune i Flore Sibiri (New Contributions on the Fauna and Flora of Siberia). Tomsk, pp. 62–68.
 [The malacofauna of the Kureyka, a right bank tributary of the lower Yenisey, consists of 41 species, 8 recorded for the first time. Information is presented on their ecology, abundance, and role in the diets of fish.]
 KAFANOV, A. I. 1979. On conservatism and variability in growth temperatures in the shells of marine mollusks. BMV, No. 6, pp. 59–69 (ES).
 [Miocene specimens of *Ciliatocardium ciliatum* were shown, using an oxygen isotope method, to have higher average temperatures of growth than contemporary samples, indicating the trend of global cooling over Cenozoic time.]
 KAFANOV, A. I. 1979. On the ecological evolution of the malacofauna of the cool temperate shelf of the Northern Hemisphere and the paleoclimatological significance of marine bivalves. Transactions of the Institute of Biology and Soil Science of the Far Eastern Scientific Center, Academy of Sciences of the USSR, 52/155, pp. 58–72.
 [An hypothesis is proposed to explain the evolution of this fauna since the Neogene, or late Miocene. Ecological parameters such as temperature are reconstructed on the basis of oxygen isotope analyses.]
 KAZANNIKOV, E. A. 1979. Freshwater mollusks of the Stavropol region. NPS, p. 81.
 KHOKHUTKIN, I. M. 1979. Sixth All-Union Meeting for the study of mollusks. 7–9 Feb. 1979. Ekologiya (Ecology), No. 6, p. 104.

[Organized by the Zoological Institute, the conference heard 149 papers dealing with the ecology of mollusks, under the following subheadings: population ecology, species formation, intrapopulation variation in phenotype frequencies, population genetics methodology, evolutionary morphogenesis, co-evolution, radioisotope tracers, growth, development, and other topics.]

KOZLOVA, L. E. & N. T. MANDRIKOVA. 1980. Characteristics of composition of phragmacones of belemnites and shells of bivalve mollusks from Toarcian deposits in Yakut. PMIN, pp. 81–84.

[Data on the mineralogical and chemical compositions of belemnite phragmacones and bivalve shells collected together in the basin of the Vilyuy River were analyzed by infra-red spectroscopy, x-ray diffraction, and determination of specific heat; the mineralogical composition of carbonates was shown to be different.]

KRIVOSHEINA, L. V. 1979. On the zoogeographic characteristics of the freshwater malacofauna of the Upper Irtish River basin. Priroda i Kh-vo Vost. Kazakhstana (Nature and Fisheries of Eastern Kazakhstan), pp. 100–107.

[93 species and subspecies are known from the basin of Upper Irtish, of these 15 have Palearctic distributions, 23 European-Siberian and 8 Siberian; one species is endemic.]

KRUGLOV, N. D. 1979. Reproductive biology and observations on protandry among lymnaeids. NPS, pp. 91–92.

LUR'E, A. A. & S. A. BEYER. 1980. A method for marking mollusks. MS Application, E. I. Marchinovski Inst. of Parasitology and Tropical Medicine.

[Radioactive cobalt and silver were applied, under a layer of water repellent lacquer, to the shells of *Bithynia inflata*, *Biomphalaria alexandrina*, and *Physa acuta*, which were then found to be detectable in the field by scintillation radiometry.]

LUR'E, A. A. & S. A. BEYER. 1980. On a new method of marking freshwater mollusks. ZZ 59(4):609–619 (ES).

[Long-lived isotopes implanted in the shell and covered by a film of nail polish proved to be effective in following populations of *Bithynia inflata* for two years.]

MOSKVICHEVA, I. M. 1979. Studies on the malacofauna of the Upper Zeya (River) Basin. [Amur Province, Western Siberia.] NPS, p. 122.

NATOCHIN, YU. V., V. YA. BERGER, E. A. LAVROVA, O. YU. MIKHAILOVA & V. V. KHLEBOVICH. 1979. The roles of sodium and potassium in the regulation of cell volume in littoral mollusks. 14th PSC, Sect. F, pp. 32–33.

[Marine mollusks are capable of partial regulation of cell volume during changes in the salinity of the environment by regulation of intracellular levels of free amino acids and concentrations of electrolytes (Na, K, Cl).]

NIKOLAEV, V. A. 1979. Clausiliid land snails from the central Russian hills. NPS, pp. 126–127.

POLYAKOV, D. M. 1980. On the choice of a carrier for quantitative spectral analysis of micro-elements in the shells of marine mollusks. PMIN, pp. 139–143.

[The carrier of choice for quantitative analyses of Fe, Mg, Mn, Sr, and Ba by emission spectroscopy was shown to be 10% PbCl.]

REZNIK, Z. V. & N. TIKHOVA. 1979. Terrestrial mollusks of highland pastures in the Urup regions [Western Caucasus] of the Stavropol Territory. NPS, pp. 144–145.

SHAKHMAEV, N. K. 1979. Study of the mechanisms of the accumulation of manganese in freshwater mollusks. Khim. i Biokhim. Okislenne Sistem, Soderzhashch, d-elementy.

(Chemical and biochemical oxidative systems, maintaining d-elements). Chelyabinsk, pp. 38–39.

[Mn accumulates by a variety of mechanisms in different organs, e.g., in gills, 28.8% by metabolism, 17.8% by adsorption, and 4.6% by diffusion; respective values are given for mantle, digestive and gonadal tissue.]

ZATRAVKIN, M. N. 1980. Aquatic malacofauna of the Il'mensk Preserve (Southern Urals). ZZ 59(3):452–455 (ES).

[The 162 samples taken in June–August 1975 were found to contain 55 species (39 gastropods and 16 bivalves). In comparison, Tausson collected 62 species from 1937–1940. Their geographic affinities were: 1 Irtish endemic, 17 European, 1 Siberian, 2 southwestern European, 1 northwestern European, and 40 Euro-Siberian and Palearctic.]

ZATRAVKIN, M. N., E. D. PAVLOVA & V. F. RODIONOV. 1970. Gastropods of the Upper Volga. NPS, p. 74.

POLYPLACOPHORA

SIRENKO, B. I. 1979. Chitons (Polyplacophora) of the coastal waters of Simushir Island. Biology of the shelf of the Kuril Islands. Moscow, pp. 200–208.

[16 species in 11 genera were found to occur in the near-shore waters off Simushir (to 70 m). Highest densities were 3100/m² by *Juvenichiton albocinnamomeus* and 800/m² by *Spongioradsia subaleutica*. *Lepidozona thielei* accounts for the greatest biomass (160 g/m²). The biogeographic composition of the fauna consists of high boreal species 65%, widely distributed boreal species 29%, and boreal-arctic species 6%.]

GASTROPODA, GENERAL

ANDRONNIKOV, V. B. 1980. Threshold temperatures of cellular thermonarcosis of littoral mollusks of coral islands and the temperature conditions of their environment. TIO 90:51–57 (ES).

[Using pedal musculature of snails from supralittoral, littoral, and upper sublittoral zones from the Pacific Ocean, the author established the threshold temperature of thermonarcosis for different species.]

GUL'BIN, V. V. 1979. Distribution of prosobranch gastropod mollusks on the Shelf of the Kuril Islands. Biology of the Shelf of the Kuril Islands, Moscow, pp. 209–221.

[A study of the vertical distribution and relationship to substrate of prosobranch gastropod mollusks of the Shelf of the Kuril Islands showed: more warm-water species dwell in the upper zones of the sea, and their number declines with depth while the opposite is true of cold-water species. A vertical zonation of the shelf results that differs in different parts of the island chain. The most important factor influencing the distribution of mollusks appears to be the temperature of the water. The greatest number of species inhabit rocky substrates, the least gravel substrates; only 20% of gastropod mollusk species are restricted to one type of bottom, while the remainder can inhabit a variety of substrates.]

KORNYUSHIN, A. V. 1980. On the land mollusk fauna of the Black Sea Preserve. Vestnik Zoologii (Zoological Herald), No. 2, pp. 75–78.

[25 species (2 prosobranchs) constitute the fauna, most of which are widely distributed Holarctic species; data on habitat, distribution, and predation by birds are included.]

SIRENKO, B. I. 1980. Gastropods of Scotta Reef. Biol. Korallov. Rifob. Morfol., Sistem., Ekol. (Biology of Coral Reefs; Morphology, Systematics and Ecology). Moscow, pp. 87–112.

[192 species of gastropods are listed with notes on their ecological zonation.]

VOLOVA, G. N., A. N. GOLIKOV & O. G. KUSAKIN. 1979. Shelled gastropod mollusks of Peter the Great Bay. Vladivostok, Dal'nevost. Kn. Isd.-vo. (Far Eastern Book Press), 170 pp.

GASTROPODA, PROSOBRANCHIA

BARSKOV, I. S., M. A. GOLOVINOVA & V. N. GORYACHEV. 1980. On the structure of the nacreous layers of deepwater *Seguenzia* (Mollusca: Gastropoda). Dokl. AN. SSSR (Reports of the Acad. Sci. USSR), 252(4):1015-1017 (ES).

[The structure of the nacreous layer of this genus differ sharply from the columnar nacre of other gastropods, being reminiscent of some bivalves and imparting greater strength to the shell.]

GOLIKOV, A. N. 1980. Fauna of the USSR. Mollusca. Vol. 5, part 2. The molluscan sub-family Buccininae in the World Ocean. Leningrad, Nauka (Science [Press]), 508 pp., 42 pls.

[This monograph is a comprehensive study of the world fauna of Buccininae, including 3 genera, 3 subgenera, 93 species and subspecies, and numerous ecological forms and varieties. A full synonymy, description, figures, and an analysis of ecology and distribution are given for each species. A special section includes tables with species and subspecies diagnoses. Features of adaptive and evolutionary morphogenesis are discussed in the main section. Utilizing data from historical geology and paleontology, the author presents a spatial-temporal scheme of the evolution of the Buccininae, which shows how it coincides with the evolution of ecosystems in the Northern Hemisphere during the Cenozoic. All vertical zones of epicontinental bodies of water of temperate and cold latitudes of the Northern Hemisphere are divided into biogeographic regions based on these data. In the ecology section, quantitative methods were used to examine the relationships between species and different types of substrates, vertical distribution, temperature, including optimal and survivable temperatures, and salinity. Special emphasis was placed on temperatures of growth, life-span, and productivity of the common species. During studies of reproductive ecology, the egg capsules of many species were identified, and conditions optimal to reproduction and artificial propagation clarified.]

IZZATULLAEV, Z. 1979. On new species of gastropod mollusks of the family Pomatiopsidae (Mollusca: Discopoda) from Tadzhikistan. Reports Acad. Sci. Tadzh. SSR 22(10):629-631 (Tadzhik Summary).

[Previously, mollusks from underground springs of central Asia (genera *Kainarella* and *Pseudocaspia*) were included in the family Littorinidae Gray, 1857. Detailed studies of the holotypes allowed the author to clarify the systematic affinities of these species and to include them in the Pomatiopsidae Stimpson, 1865, a group whose representatives are widely distributed in the continental waterways of eastern Asia. Described are *Kainarella likharevi* and *Pseudocaspia rozae*. The former is similar in shell form to *K. minima* from the southeastern region of Turkmenistan, but is distinguished on the basis of its irregular cylindrical shell shape, its round-oval aperture appressed to the wall of the penultimate whorl, the absence of surface sculpture, and by its larger size (holotype: shell 1.5 mm high, 0.65 mm wide; aperture 0.55 mm high, 0.5 mm wide). Number of whorls is 4. *Pseudocaspia rozae* has an egg-shaped to conical, strong, light-brown shell. Dimensions of the holotype: shell 3 mm high, 1.2 mm wide; aperture 1.2 mm high, 1.1 mm wide. Number of whorls 5.]

KANTOR, YU. I. 1980. Species composition and variability of the gastropod molluscan genus *Buccinum* in the White Sea. ZZ 59(4):518-528 (ES).

[Seven species are recorded, two (*B. miltzani*, and *B. finmarchianum*) for the first time. Shell shape and sculpture as well as penial configuration were utilized as distinguishing traits.]

POBEREZHNI, E. S. & V. I. MAKSIMOV. 1979. On unusual forms of the operculum of the mollusk *Benedictia limnaeoides* from Lake Baikal. Hydrobiological and Ichthyological Investigations of Eastern Siberia, Irkutsk, pp. 186-188.

[A triangular rather than an ovate operculum was found in a single female snail of a sample of 330 taken from 5 to 10 m; the authors claim this rare variant is connected to the polyploidy known to occur in *Benedictia*.]

SEMENOV, O. YU. 1979. Experimental studies of the biology of the mollusk *Melanopsis praemorsa* L. Vestn. LGU (Herald of Leningrad State University), No. 15, pp. 9-17 (ES).

[Briefly investigated were the distribution and dispersal of this species, which is not affected by conditions of light, but does prefer warmer areas.]

STAROBOGATOV, YA. I. & Z. I. IZZATULLAEV. 1980. Mollusks of the family Melanoididae (Gastropoda: Pectinibranchia) of central Asia and adjacent territories. ZZ 59(1):23-31 (ES).

[On the basis of the structure of the pallial portion of the female reproductive system, the authors propose to divide the family Thiariidae, as usually accepted, into three independent families: Melanatriidae Thiele, 1929, with a completely open pallial gonoduct, albumen gland in the renal portion, and presence of a bursa; Thiariidae Preston, 1915, with a massive pallial gonoduct reaching to the mid-length of the mantle cavity; and Melanoididae Starobogatov, fam. nov., with the pallial gonoduct represented by two parallel, non-glandular tubes reaching the mid-length of the mantle cavity. Analysis of *Melanoides tuberculatus* from many stations in central Asia and Afghanistan suggests that it can be divided into five species on the basis of shell proportions and sculpture. Doubt is thus cast on the single species concept of *M. tuberculatus* throughout its extensive range of western Africa to Polynesia. There are three species in the territory of the USSR: *Melanoides pamiricus*, *M. kainarensis*, and *M. shahdaraensis*; the last two are described in this paper.]

ZHIRMUNSKIL, A. V., V. L. KAS'YANOV & V. I. LUKIN. 1980. The Mollusk *Haliotis* or sea ear. Priroda (Nature), No. 8, pp. 44-46.

[Moneron Island, off the SW coast of Sakhalin in the Sea of Japan is the only place in the USSR where *Haliotis discus* is found; it also occurs in northern Honshu, Hokkaido, and the islands of Rebun and Rishiri off NW Hokkaido. In 1972 and 1976-77 biologists from the Far Eastern Center studied this population which was noted on cliffs in the *Laminaria* zone at depths of 0.5-2 m. Although population density was high in places, the species was, in general, sparse, and it is unclear whether the population is self-replenishing or whether an influx of larvae on a branch of the Chusumski Current from Rebun and Rishiri islands sustains it. *Haliotis* is fished commercially in many areas of the world, both for its tasty meat and for its beautiful shell. In Japan, the harvest is 5-7 thousand tons per year. It is proposed that the Moneron population be included in "The Red Book of the USSR."]

GASTROPODA, PULMONATA, AQUATIC

KRUGLOV, N. D. 1980. Reproductive biology of freshwater pulmonate mollusks. ZZ 59(7):986-995 (ES).

[The reproductive biology of 27 species of freshwater pulmonates belonging to the families Lymnaeidae, Physidae, Bulinidae, and Planorbidae was found to pass through two stages of gonadal development: male gonadal maturity and hermaphroditic gonadal maturity. The first copulation is always as a male. Products of sperm reabsorption in the spermatheca are humorally transmitted and influence endocrine control over subsequent development of the female portion of the reproductive system.]

SHARKO, N. V. 1980. Adaptations to darkness in the eyes of the pond snail *Lymnaea stagnalis*. ZEBF 16(2):193-196.

[Electrophysiological studies on the adaptation to darkness were conducted on isolated preparations of eyes of adult pond snails. Under stimulation by light flashes, an increase in the amplitude of the electroretinogram was observed with time. Initially the amplitude grows rapidly, later it stabilizes. The dynamics of the response to light stimulation of constant intensity depends on temperature, the optimum being 17-20°C.]

SMIRENINA, L. K. 1979. On the problem of copulation among aquatic gastropods. Biol. Vnutr. Vod. (Biol. Internal Waters), Leningrad, No. 43, pp. 27-29.

[In pairing experiments with *Planorbarius corneus* and *Lymnaea stagnalis*, the latter more easily found each other in aquaria, indicating better long-distance chemoreception in *Lymnaea*.]

STAROBOGATOV, YA. I. & N. D. KRUGLOV. 1979. On two species of pond snail, genus *Lymnaea*, new to the fauna of the Soviet Union. NPS, pp. 162-163.

GASTROPODA, PULMONATA, TERRESTRIAL

AL'MUKHAMBETOVA, S. K. & K. K. UVALIEVA. 1979. Mollusks of the family Vertiginidae (Mollusca: Gastropoda) of south and southeastern Kazakhstan. Izv. AN KazSSR (Proceedings of the Kazakhstan Academy of Sciences). Biol. Ser., No. 4, pp. 35-40 (Kazakh Summary).

[An ecological-faunistic survey of the mountain ranges of south and southeastern Kazakhstan revealed nine species (two described as new) of the family Vertiginidae.]

AL'MUKHAMBETOVA, S. K. & K. K. UVALIEVA. 1980. Mollusks of the family Pupillidae (Mollusca: Gastropoda) from south and southeastern Kazakhstan. Izv. AN KazSSR (Proceedings of the Kazakhstan Academy of Sciences). Biol. Ser., No. 2, pp. 27-32.

[The ecology, biology, distribution, and variability were studied in pupillid species which are separated by features of the reproductive system.]

DAVTOV, S. SH. 1979. Inducers of feeding behavior in *Helix vulgaris* (Stylommatophora: Helicidae). ZZ 58(10):1464-1469 (ES).

[Starch and glycogen always elicit a feeding reaction; less frequently (10-40%) materials of animal origin cause it, suggesting potential carnivory.]

DMITRIEVA, E. F. & YA. S. SHAPIRO. 1979. Studies of non-specific reactions of the reticulated slug to methaldehyde. Nauch. Tr. Leningr. S.-Kh. In-ta. (Scientific Transactions of the Leningrad S. Kh. Institute), No. 374, pp. 59-62.

[The sensitivity of various organs of juvenile slugs to the toxin methaldehyde was investigated histochemically.]

IZZATULLAEV, Z. 1980. On the life cycle of the slug *Lytopelte maculata* (Boch. and Heynemann, 1874) (Mollusca: Gastropoda) in Tadzhikistan. Izv. Acad. Nauk. Tadzh. SSR, Otd. Biol. (Proceedings Acad. Sci. Tadzhikistan SSR, Biological Sciences Section), No. 1, pp. 95-97.

[The structure, coloration, dimensions, and genitalia of *Lytopelte maculata* are described as are the details of reproduction, ecology, and distribution.]

IZZATULLAEV, Z. & A. A. SHILEYKO. 1980. A new species in the terrestrial molluscan genus *Bradybaena* from central Asia and observations on the genus *Ponsadenia*. Dokl. AN Tadzh. SSR (Reports of the Tadzhikistan Academy of Sciences) 23(4): 220-224 (Tadzhik Summary).

[*Bradybaena squamulosa* (type-locality: Cholpon-Ata, near Lake Issyk-Kul in Kirgiz) is described as new based upon features of the reproductive system and upon small, round-triangular periostracal scales that are similar to those on *Ponsadenia hirsuta* from the Terskey Mountains. Diagnoses are given for the subgenera *Tarbagataja* and *Ponsadenia*.]

RIMZHANOV, T. S. 1979. New contributions to the molluscan fauna of the family Bradybaenidae (Mollusca: Gastropoda) of the Zailiysky Mountains. Izv. AN KazSSR (Proceedings of the Kazakhstan Academy of Sciences). Biol. Ser., No. 6, pp. 51-57 (Kazakh Summary).

[One species and one subspecies are described as new based on the morphology of the shell and the structure of the genital system.]

SAMIGIN, F. I. & L. D. KARPENKO. 1980. Motor organization of defensive reflexes in mollusks. NDVS, No. 3, pp. 38-42.

[Bodies of two motor neurons, responsible for contracting the respective right and left columellar muscles, were found in the right and left pedal ganglia of the grape snail.]

SHAPIRO, YA. S. 1979. Terrestrial mollusks of the agrobiocenoses of Leningrad Province (Rept. 1). Nauch. Tr. Leningr. S.-Kh. In-ta. (Scientific Transactions of the Leningrad Institute), No. 374, pp. 62-65.

[16 species of land mollusks representing 7 families were collected on agricultural lands of Leningrad Province.]

SHIKOV, E. V. 1979. Effects of industrial activities of man on the distribution of terrestrial mollusks. The protection of nature in the Upper Volga, Kalinin, pp. 30-50.

[1732 samples with over 60,000 individuals, dating from 1963 to 1979 and taken in the environs of Kalinin, Novgorod, Pskovsk, Leningrad, southern Mirmansk, and Moscow showed that the human factors most responsible for influencing terrestrial mollusks were fire, agriculture, alteration of waterways, and introduction of foreign species of snails.]

SHIKOV, E. V. 1979. Dependence of the distribution of slugs of the genus *Deroceras* Rafinesque, 1820 in the flood-plains of the large rivers of the Valdai Hills on the direction of prevailing winds. Ekologiya (Ecology), No. 5, pp. 97-99.

[In the Staritsk region of Kalinin Province along the flood-plain of the Volga River there occur four species of *Deroceras*: *agreste* which is distributed in exact correspondence with the direction of the prevailing southwesterly winds, *reticulatum* occupies the most protected areas, and *sturanyi* and *laeve* usually co-occur with both species.]

SHILEYKO, A. A. & Z. IZZATULLAEV. 1980. Taxonomic structure of the terrestrial mollusks of the family Pupillidae in the fauna of the USSR and a description of a new species from central Asia. Dokl. AN Tadzh. SSR (Reports of the Tadzhikistan Academy of Sciences) 23(5):282-285 (Tadzhik Summary).

[The diagnoses of three genera and two subgenera of the family are given, as is a description of *Gibbulinopsis (Primipupilla) nansignata*.]

TAVASIEV, R. A. & T. A. TAVASIEVA. 1980. A new species of *Caucasigena* (Gastropoda: Hygromiidae) from the central Caucasus. *ZZ* 59(1):144-146 (ES).

[*Caucasigena schileykoi* is described from limestone cliffs in beech forests at an altitude of 800 m above sea level in the North Ossetian Autonomous Republic; it is distinguished from *C. reingarteni* by a sharp keel and by features of the reproductive system.]

UVALIEVA, K. K. 1980. Ecological faunistic survey of the terrestrial mollusks of the forest-steppe habitat. *Zool. Inst. Acad. Sci. KazSSR, Alma-Ata*, 22 pp., MS No. 2051-2080.

[550 samples of land mollusks were collected on cattle pastures of collective farms in northern and central Kazakhstan and yielded 32 species, representing 17 genera and 13 families; 8 species are first reported from the area and 2 species are described as new.]

ZEIFERT, D. V. & I. M. KHOKHUTKIN. 1979. Experimental studies on natural migrations in populations of autochthonous and introduced species of mollusks. Ecological studies of forest and meadow biocenoses in the Transural Plains. *Info. materials Talitsk. Hospital. Sverdlovsk*, pp. 46-50.

[Marked specimens of *Bradybaena fruticum* and *Eobania vermiculata* were used to show that spatial distribution is determined by the type of plant cover.]

ZHULIDOV, A. V. 1980. On the concentration of gastropods (Mollusca: Pulmonata) on plots of stinging nettles containing increased levels of some chemical elements. *Vestnik Zoologii (Zoological Herald)*, No. 2, pp. 78-79.

[In the Voronezhky Preserve, heterogenous distribution was noted (mainly in *Succinea putris* and *Eulota fruticum*) in thickets of the stinging nettle *Urtica pubescens*; densities varied from zero to 178-211 snails/m² and it was shown that the snails preferred high levels of several trace elements.]

BIVALVIA

ALYAKRINSKAYA, I. O. 1979. On the properties and sizes of shell crystals in bivalve mollusks. *Dikhatel'n Belki Nekotor. Grupp. Sovrem. Zhivotnikh (Respiratory proteins of several groups of Recent animals)*. Moscow, pp. 142-150.

[Dissolution rates of shell crystals were investigated at differing pH's.]

ANGELOV, A. 1976. Revision of the family Pisidiidae in Bulgaria. *Annual Report, Faculty of Zoology, University of Sofia* 69(1):109-119 (Bulgarian; German Summary).

[242 samples from 145 collecting sites yielded three species of *Sphaerium* and ten of *Pisidium*; data include synonymies, descriptions, measurements, habitat characteristics, and distribution.]

DOROFEEVA, L. A. & A. V. KHABAKOV. 1980. Determination of environmental temperatures for Recent and late Quaternary oysters, using the Ca/Mg method. *Byul. Mosk. O-ba. Ispyt. Prirody. Otd. Geol. (Bulletin of the Moscow Naturalists Soc., Geol. Soc.)* 55(4):106-113.

[Accumulation of Mg in calcitic shells of Recent oysters is governed by the temperature regime and is independent of salinity. Average temperatures of surface waters inhabited by late Quaternary oysters from the Karangatsky Horizon of the Kerchensk Peninsula were 22-23°C during the warm period of the year while the average annual temperatures were 15-16°C.]

GERASIMOVA, T. N. 1980. Seasonal changes in the dimensions and biomass of *Didacna trigonoides* (Pall.) in the Caspian Sea. *GZ* 16(2):53-55 (ES).

[Biomass alters significantly with the seasons, being drastically reduced in April-June at the time of the release of gametes.]

GOROMOSOVA, S. A. & A. Z. SHAPIRO. 1979. Physiological and biochemical aspects of adaptations of mussels in normal and in extreme conditions. *Promisl. Dvustvorchat. Mollyuski—Midii i ikh rol' v ekosistemakh (Commercially important bivalve mollusks—mussels and their role in ecosystems)*. Leningrad, pp. 45-47.

[Under hypoxic conditions, the oxidized NAD necessary for glycolysis is produced by malate dehydrogenase.]

GOROMOSOVA, S. A. & V. A. TAMOZHNYAYA. 1980. Seasonal variation of transaminases in tissues of Black Sea mussels. *BMV*, No. 2, pp. 67-68 (ES).

[Intracellular localization and seasonal variation in activity of alanine aminotransferase and aspartate aminotransferase in the tissues of *Mytilus galloprovincialis* were studied. The intracellular distribution of aminotransferases depends on the function of the tissue, being mainly cytoplasmic in muscles and gills and mitochondrial in the hepatopancreas and gonads. Two peaks in activity occur: autumn and spring, both declining during active gametogenesis.]

GREENBERG, M. J. & L. I. DITTON. 1979. Salinity adaptation and probable interdependence between heart muscle physiology, phylogeny, and biogeography of bivalve mollusks: basic directions for future research. 14th PSC, Sect. F, pp. 14-15.

[In the bivalve heart, the auricles appear especially to be the primary filter of urea. The subclasses Pteriomorpha, Heterodonta, and Paleoheterodonta are distinguished by the following physiological characters: the form of the action potential, ionic dependence, excitability, cholinergic systems of the myocardia, as well as by larger structural differences.]

IGNAT'EV, A. V. & E. V. KRASNOV. 1980. Isotopic oxygen composition of water and the growth temperatures of Recent and Quaternary mollusks of the Chukotsk Sea. *PMIN*, pp. 56-60.

[Basing their analysis on living and fossil bivalves from the shores of Wrangel Island in the Chukotsk Sea, the authors show that temperature changes of marine waters in the Northern Hemisphere during Pliocene-Quaternary time can be adequately documented by oxygen isotope paleothermometry.]

IGNAT'EV, A. V. & I. M. ROMANENKO. 1980. Correlation of magnesium content of mussel shells with their mineral composition, structure, and growth temperatures. *PMIN*, pp. 85-91.

[In mussels from Peter the Great Bay, Mg levels increase ontogenetically, show seasonal fluctuations coincident with changes in water temperature, and exhibit sharp increases not correlated with seasonal events.]

IZZATULLAEV, Z. 1980. Bivalve mollusks of the family Corbiculidae in central Asia. *ZZ* 59(8):1130-1136 (ES).

[Of five species of corbiculids found in central Asia, two, *tibetensis* and *ferghanensis* which are ovoviviparous, are allocated to *Corbiculina* Dall, and three, *cor*, *fluminalis*, and *purpurea* which are presumed to be oviparous, to *Corbicula* Mühlfeld.]

KAFANOV, A. I. 1980. On the nomenclature of the Cardiidae (Bivalvia) of the Sea of Azov and the Black Sea. *ZZ* 59(4): 623-626 (ES).

[The nomenclature of three species and one subspecies of cardiids inhabiting the Sea of Azov-Black Sea basin as well as the Mediterranean is discussed. *Cardium hystrix* (Lightfoot, 1786) is considered a synonym of *C. echinatum* Linne, 1758. The following new names are proposed: *C. ciliare* L., 1758, for *C. pauci-*

costatum Sowerby, 1834; *Acanthocardia (Sphaerocardium) ciliaris milaschewitschi* Kafanov, nom. n., for *C. paucicostatum* var. *impedita* Milaschewitsch, 1909, non *C. impeditum* Deshayes, 1860; *Didacna (Pontalmyra) kamyschburunensis* Kafanov, nom. n., for *C. paucicostatum* Deshayes 1838, non Sowerby 1834. The division of *Cerastoderma glaucum* (Poiret, 1789) into four species by Skarlato and Starobogatov (1972, "Guide to the fauna of the Black Sea and the Sea of Azov," pp. 178-249, Kiev) is regarded as correct.]

KARPENKO, A. A. 1980. Avoidance reaction to living starfish in the marine scallop *Patinopecten yessoensis* (Mollusca: Bivalvia). *ZZ* 59(1):146-149 (ES).

[The avoidance reaction, which changes with age of scallops, is a compound, unconditioned reflex, composed of three reactions: an "alert phase," a "response phase," and a "swimming phase."]

KARTAVTSEV, YU. F. 1979. Possible determination of a balanced polymorphism in loci coding for isoenzymes. *BPGF*, pp. 36-40 (ES).

[Either an increase or a decrease in heterozygosity with age was observed in the majority of loci (approx. 70%) of five species of mussels. It is interpreted as being due to some form of balancing selection and indicative of the selective nature of isozyme polymorphisms.]

KRASNOV, E. V., N. A. SIN'KOV, V. O. KHUDOLOZHKIN, A. V. IGNAT'EV, A. A. KARABTZOVA & O. I. NEDAVA. 1980. Complex studies of the shell material in fossil and Recent specimens of *Arctica islandica* L. *PMIN*, pp. 73-80.

[X-ray, spectrophotometric and mass-spectroscopic analyses of Plio-Pleistocene and Recent *Arctica islandica* from eastern Iceland showed that concentrations of Mg, Sr, Na, Fe, and Mn in aragonitic shells increased with geological age. Growth temperatures were investigated by $^{18}\text{O}/^{16}\text{O}$ ratios in glacial and interglacial periods.]

KRASNOV, E. V., V. A. ZAIKO & N. N. ZAIKO. 1979. Biogeochemical indicators of adaptations of marine mollusks to changes in salinity. 14th PSC, Sect. F, p. 27.

[Ontogenetic variation in the incorporation of chlorine into the shells of pectinids was shown, with maximum levels occurring during the autumnal period of rapid growth; sculptural features such as the number of ribs in *Patinopecten yessoensis* and *Swiftopecten swifti* as well as in *Anadara broughtoni* vary with salinity and temperature.]

KUZNETSOV, A. P., M. KOZAKA & I. ISIBASI. 1980. Dimensional characteristics of gills and labial palps of several marine mollusks. *ZZ* 59(2):175-180 (ES).

[Dimensions of gills and palps were measured in *Moerella jedoensis*, a deposit feeder, and in *Ruditapes philippinarum* and *Mytilus edulis*, both suspension feeders; in *M. jedoensis*, about 40% of the total gill-palp area was taken up by the gill and 60% by the palp, while in the other species, over 90% is gill and less than 10% is palp. Thus, the Tellinacea (deposit feeders) should be considered an independent ecological group. Arguments are advanced supporting the origin of the Eulamellibranchia, Pseudolamellibranchia, and Filibranchia from the Protobranchia.]

LUKANIN, V. V. 1979. Roles of cellular and organismic reactions in the accommodation of mussels to changes in salinity. *Promisl. Dvustvorchat. Mollyuski—Midi i ikh rol' v ekosistemakh.* (Commercially important bivalve mollusks—mussels and their role in ecosystems). Leningrad, pp. 82-83.

[Mussels have the ability to undergo adaptive changes in function at cellular and organismic levels during seasonal changes in salinity. Evolutionary pathways of adaptation to low salinities are considered.]

MILEIKOVSKII, S. A. 1979. On the maintenance of the structure and recruitment of spat into the druzes [mats] in the mussel *Crenomytilus grayanus*. *BMV*, No. 5, pp. 39-43 (ES).

[Young larval spat are recruited into the adult attached masses, called *druz* in Russian, of these mussels; such "nursery-like" behavior is apparently caused by an attraction to the byssal strands of adults and also protects the tiny spat.]

NIKIFOROV, S. M. 1979. Genetic and morphometric variability of the far eastern oyster (*Crassostrea gigas*). *BPGF*, pp. 134-138 (ES).

[Electrophoretic study of 46 loci in five populations in Peter the Great Bay showed polymorphism in more than 30% of the loci, an average heterozygosity of 0.07-0.08, and heterozygote deficiencies in most populations.]

NISTRATOVA, S. N., T. M. TURPAYEV, N. N. GODOVIKOV, M. N. GODOVIKOVA & V. I. DANILOVA. 1980. Analysis of the action of several organophosphate inhibitors of cholinesterase on the hearts of bivalve mollusks. *ZEBF* 16(1):30-38 (ES).

[This study investigates the action of organophosphate inhibitors of cholinesterase on isolated ventricles from the hearts of the bivalve mollusks *Crenomytilus grayanus*, *Spisula sachalinensis*, and *Anodonta complanata*.]

POPOV, S. V. 1980. The formation and development of the hinge during the ontogeny of North Pacific bivalve mollusks of the family Carditidae. *ZZ* 59(6):945-948 (ES).

[Hinge formation in six species (*Cyclocardia ventricosa*, *C. crebricostata*, *C. rjabinae*, *C. isaotakii*, *Miodontiscus annakensis*, and *Crassicardia crassidens*) originates in a similar manner. The cardinal teeth of the right valve 3a 3b and the lower lateral tooth AIII appear from the lower primary plate III. The third cardinal tooth appears as a raised edge in the larval stage (nymph). In the left valve, plate IV gives rise to teeth 4b and AIV, the anterior cardinal tooth 2 is newly formed. The complete formula of the hinge is:

$$\frac{AV \ AIII \ 3a \ 3b \ PIII}{AIV \ 2 \ 4b \ PII \ PIV}$$

In species of both *Cyclocardia* and *Crassicardia*, the development of lateral teeth stops in the early stages; in the adult they are barely discernible. In *Miodontiscus*, these teeth are developed in all stages of growth. *Crassicardia crassidens* differs notably in morphology from species of the genus *Cyclocardia* at the early dissoconch stage, supporting the independence of the genus *Crassicardia*.]

POPOV, S. V. & O. A. SKARLATO. 1980. The bivalve mollusks of the family Carditidae in the North Pacific and adjacent seas. *ZZ* 59(7):996-1007 (ES).

[Representatives of the family in the North Pacific, including the Sea of Japan, Okhotsk Sea, Bering Straits, and Chukotsk Sea are: *Crassicardia crassidens*, *Cyclocardia crebricostata*, *C. rjabinae*, *C. isaotakii*, *C. ferruginea*, *Miodontiscus annakensis*, and *M. prolongatus*, the latter three being characteristic of the Bering Straits High Boreal Province, where they occur with *Cyclocardia ventricosa ovata* and *C. ripensis*. Diagnoses of genera and species are included.]

POZDNYAKOVA, L. A. 1980. On the dynamics of the calcium/magnesium ratio in calcitic shells of closely related species of bivalve mollusks in the Sea of Japan. *PMIN*, pp. 92-105.

[Ontogenetic variations of Ca/Mg ratios in three species of pectinids (*Patinopecten yessoensis*, *Chlamys swifti*, and *C. farreri*) reflect seasonal fluctuations of water temperature.]

PROSKURINA, E. S. 1979. On linear and weight growth of the

principle bivalve mollusks of the Aral Sea. GZ 15(5):105-106.

[Studies were conducted on the native *Dreissena polymorpha* var. *aralensis* and *Cerastoderma lamarckii lamarckii* and on the introduced *Abra ovata* collected in 1973-1974. Age was determined by analysis of growth lines; average annual growth was 1.7, 3.5, and 2.06 mm respectively. *Abra* may, in time, become one of the primary components of the benthos in the Aral Sea.]

PRYADKO, V. P. & V. A. KRISAL'NYI. 1980. Histophysiological changes in tissues of several organs of *Anodonta cygnea* under the influence of different calcium concentrations. GZ 16(1): 56-59 (ES).

[Entry of calcium ions into the organism causes a redistribution of the concentrations of K^+ and Na^+ ions in the cells of the glandular apparatus of the gills and in the foot muscle. The overall metabolism of calcium increases with the increase in activity of tissue enzymes. The gills of freshwater mollusks comprise important depots of calcium salts.]

RUSAKOV, YU. I. & V. K. KAZAKOV. 1979. Extraction of an insulin-like substance from mollusks and production of antisera to it. ZEBF 15(6):617-619 (ES).

[An insulin-like substance was extracted from the visceral mass of the freshwater clams, *Unio pictorum* and *Anodonta cygnea*, antisera prepared, and their properties investigated.]

SELIN, N. I. 1980. Coordinating conference for the study of mussels (Mytilidae). Leningrad 12-14 Feb. 1979, BMV, No. 2, pp. 80-81.

[45 papers were presented, including works on systematics, distribution, morphology, ecology, growth, nutrition, and economic importance of mussels.]

SKUL'SKII, I. A., I. V. BUROVINA & N. B. PIVOVAROVA. 1979. Mechanisms of potassium homeostasis in mussels inhabiting seas of varying salinities. 14th PSC, Sect. F, pp. 42-43.

[Two mechanisms are suggested for the maintenance of optimal intracellular concentrations of K in different environmental salinities.]

STANKYAVICHYUS, A. B. 1979. Osmotic and ionic regulation in east Baltic mussels, *Mytilus edulis*, adapted to different salinities of water. Promisl. Dvustvorchat. Mollyuski—Midii i ikh rol' v ekosistemakh (Commercially important bivalve mollusks—mussels and their role in ecosystems). Leningrad, pp. 114-115.

[Under hypotonic conditions, mussels have the ability to maintain elevated osmotic pressure due to the isolation of the mantle cavity from external surroundings.]

YAVNOV, S. V. 1979. Second All-Union Symposium on the morphology, systematics, phylogeny and ecogenesis of bivalve mollusks. Tiraspol, 3-4 Oct. 1978. BMV, No. 5, pp. 93-94.

[The symposium was dedicated to the morphology, taxonomy, paleo- and neo-ecology of oysters (suborder Ostreina) and mactras (superfamily Mactroidea). Twenty-five papers were heard, among these: On the origin and phylogeny of oysters (O. A. Skarlato, Ya. I. Starobogatov & V. A. Sobetskii); Studies on Upper Cretaceous oysters and their habitats (L. A. Dorofeyeva, A. V. Khabakov & V. A. Sobetskii); Species structure, distribution and paleoecology of four subfamilies of Upper Cretaceous oysters (Z. N. Poyarkova); Genetic systematics of contemporary oysters of the southern shore (S. M. Nikiforov); Microstructure of mactrid shells and its implications for systematics (S. V. Yavnov); Development of larval shells in mactrids (L. A. Medvedeva); and Trophic structure of populations (A. P. Kuznetsov).]

YAVNOV, S. V. 1980. Shell structure in mollusks of the family Mactridae. BMV, No. 3, pp. 62-66 (ES).

[Three varieties of crossed-lamellar structures were discerned, with two sublayers in the external layer and a single internal layer, in seven species of this family from Japan, Okhotsk, Black and Barents seas.]

YAVNOV, S. V. & A. V. IGNAT'EV. 1979. Shell structure and growth temperatures in mollusks of the family Mactridae. BMV, No. 5, pp. 44-48 (ES).

[Using layered structures of the shells, the authors determined the maximum ages for three species in the Sea of Japan: *Spisula sachalinensis*, 55 years; *S. voya*, 52 years; and *Mactra sulcataria*, 12 years. Optimum growth temperatures were also determined.]

ZAIKO, V. A., N. N. ZAIKO & E. V. KRASNOV. 1980. Shell sculptures of marine bivalve mollusks as an indicator of the salinity of their habitats. PMIN, pp. 106-112.

[Salinity affects the number of ribs in *Cardium edule*; an equation is given correlating the relationship between the number of ribs and the average salinity.]

ZOLOTAREV, V. N., D. M. POLYAKOV & N. A. SIN'KOV. 1980. Comparison of the chemical composition of the shells of several Recent and subfossil mollusks from the Sea of Japan. PMIN, pp. 61-72.

[Incorporation of Mg, Sr, Fe, Mn, and Ba into the calcium carbonate matrix of shells decreases ontogenetically; Fe and Mn accumulations are initially greater while in larger annulations Ba, Mg, and Sr are found in higher concentrations.]

CEPHALOPODA

DUBININA, T. S. 1980. On the finding of larvae of the squid *Moroteuthis robsoni* (Oegopsida: Onychoteuthidae) in the southwestern Atlantic. ZZ 59(7):1094-1096 (ES).

[The late larval stage of *Moroteuthis robsoni*, a species widely distributed in the southern Atlantic, is described for the first time; its characters closely approach those of *Onychia carriboea*.]

FILIPPOVA, YU. A. & V. L. YUKHOV. 1979. Species composition and distribution of cephalopod mollusks in meso- and bathypelagic Antarctic waters. Antarktika (Moscow), No. 18, pp. 175-187.

[Analysis of sperm whale gut contents and samples taken on various research vessels indicate a high degree of endemism in Antarctic cephalopods.]

KOTELEV'TZEV, YU. V. 1980. Photoaffinity marking of the acetylcholine receptor from optic ganglia of squid. "Materials of the 11th Conference on molecular studies. Faculty of Biology, Moscow State University," Moscow, pp. 103-109, figs.

[Studies were conducted on the binding of the photoaffinity ligand azidocytisine to the nicotine acetylcholine receptor in the optic ganglia of *Loligo*.]

NESIS, K. N. 1979. A short note on the zoogeography of the pelagic fauna of the Australia-New Zealand region. TIO, 106:125-139.

[Based on samples collected by the R/V *S Mendeleev*, *Vityas*, *Obi*, the zoogeographic distributions of 66 species were characterized.]

NESIS, K. N. 1980. Sepiids and loliginids: a comparative survey of the distribution and evolution of neritic cephalopod mollusks. ZZ 59(5):677-688 (ES).

[The horizontal and vertical distributions of the cuttlefish family Sepiidae and the squid family Loliginidae in the Pacific Ocean were analyzed. The greatest generic and species diversities of

lolinids occur in the Indo-Malaysian Province of the Indo-West Pacific; aberrant forms tend to be tropical. Sepiids are absent from the New World; in the Old World, their distributions practically coincide with those of loliginids. Sepiids are more diverse, with endemism and abundance of aberrant forms greatest not in the tropics but in the subtropics (South Africa, Japan, China, southern half of Australia). Species of both families can be divided into upper sublittoral, eurybathic (entire shelf), and lower sublittoral-upper bathyal, but the fraction of "deep water" species is significantly higher in sepiids than in loliginids. The evolution and adaptive radiation of sepiids are discussed in connection with their dominance of the subtropics and relatively greater depths.]

NESES, K. N. 1980. On the systematic position of *Chiroteuthis famelica* Berry (Cephalopoda: Oegopsida). Byul. Mosk. Obshch. Isp. Prir. (Bulletin of the Moscow Naturalists Society), Biology Series, No. 4, pp. 59–66 (ES).

[Studies of a specimen intermediate in dimensions between the holotypes of *Chiroteuthis famelica* Berry, 1909 (postlarval), and *Chiroteuthis acanthoderma* Lu, 1977 (a grown but immature individual), have shown that these taxa are synonymous. A new genus *Asperoteuthis* Nesis is proposed for *C. famelica*, an eastern central Pacific mesobathic species undergoing daily vertical migrations (day 600–1000 m, night 200–400 m). Nine genera are now known in the family Chiroteuthidae; a list of known species is provided.]

NIGMATULLIN, CH. M. 1979. Principle stages in the evolution of the squid family Ommastrephidae (Cephalopoda: Oegopsidae). PEMZ, pp. 210–219.

[Oegopsid squids have evolved as active swimmers (nektonic) with the ommastrephids representing the acme of the lineage. The earliest representatives of this family were probably unspecialized nekto-benthic forms in the transition zone between the shelf and continental slope (100–350 m). The three constituent subfamilies are discussed in terms of presumed evolutionary sequences: the Illicinae with *Illex*, a nearshore nektonic form having originated in the western Atlantic and spread to the eastern Atlantic, with *Todaropsis* diverging from the stem lineage early to occupy a neritic-oceanic niche: the Todarodinae occur over the continental slope and partly open ocean with basically neritic forms (e.g., *Martialia* and *Nototodarus*). Radiation of the todarines occurred in oceanic surface waters above the slope and adjacent parts of the open ocean, especially in high latitudes. The successful exploitation of the open ocean took place within two lineages—the ornithoteuthine and the ommastrephine. The former expanded into the bathyal and middle depths, the latter occupy the epipelagic niche with the larger species occurring in high latitudes. Only *Dosidicus* did not fully adapt to the oceanic epipelagic zone, staying predominantly in comparatively near-shore waters of high productivity. Parallelisms and convergences between the Ommastrephidae and the scombroid fishes in their adaptations to the nektonic oceanic niche are discussed.]

PINCHUKOV, M. A. & YU. V. KORZUN. 1979. On the discovery of a representative of the genus *Nototodarus* (Cephalopoda: Ommastrephidae) in the western portions of the Indian Ocean. Tr. 4th Konf. Mold. Uchenikh, pp. 144–146. (Transactions of the 4th conference of young scientists.)

[This is a preliminary description of a squid of the genus *Nototodarus* first collected on the Saya de Malha Bank and on the southern shelf of Somalia. On the basis of important taxonomic features, these western Indian Ocean squid differ sharply from *N. nipponicus* and are close to *N. sloani*, representing a new subspecies of the latter, or possibly a full species in this genus.

ROZENGART, E. V., A. P. BRESTKIN & YU. I. KAS'YANENKO. 1979. Specific differences in phosphatase activity in optic ganglia of Pacific squid. 4th Internat. Biochem. Meeting. Moscow, p. 166.

[Nerve tissues of the squids, *Beryteuthis magister*, *Ommastrephes bartrami*, *Todarodes pacificus*, and *Nototodarus sloani sloani*, lack alkaline phosphatase and contain acid phosphatases that differ in molecular weight between species.]

ZUEV, G. V., CH. M. NIGMATULLIN & V. N. NIKOL'SKII. 1979. Growth and lifespan of the wing-armed squid *Stenoteuthis pteropus* in the eastern central Atlantic. ZZ 58(11):1632–1641 (ES).

[Growth of linear dimensions and weight was studied. Life-span does not exceed 1–1.5 years.]

ZUEV, G. V., CH. M. NIGMATULLIN & V. N. NIKOL'SKII. 1980. A method for quantitatively surveying oceanic epipelagic squid. Kolichetsv. Metodi v ekol. Zhivotnich. (Quant. Methods in Animal Ecol.). Leningrad, pp. 57–59.

[A method, utilizing the natural attraction of squids to light, was developed to study *Stenoteuthis pteropus* and *S. oualaniensis*.]

Joseph Rosewater, 1929–1985

The malacological community suffered a great loss on March 22 with the passing of Dr. Joseph Rosewater. At the time of his death, Dr. Rosewater, an authority on the taxonomy and evolutionary biology of mollusks, was curator of the mollusk division of the National Museum of Natural History, Smithsonian Institution. The author of more than 80 technical works, Dr. Rosewater was a valued contributor to the pages of our journal, both as an author and as a frequent reviewer of submitted manuscripts. His talents, dedication, and generosity will be missed.

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BOOKS, PERIODICALS & PAMPHLETS

A Review of the Genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea)

by WINSTON F. PONDER. 1985. Records of the Australian Museum, Suppl. 4:221 pp.

A Review of the Genera of the Barleceidae (Mollusca: Gastropoda: Rissoacea)

by WINSTON F. PONDER. 1983. Records of the Australian Museum 35:231-281.

These two major papers are a culmination of many years of work on the small marine gastropods of the superfamily Rissoacea. Ponder has added massively to our knowledge of this group by carefully examining the type specimens of the genera, and by detailed study and analysis of living animals, anatomies, radulae, opercula, and shell morphologies. The illustrations are outstanding. Ponder also discusses in considerable detail taxa that have been previously misassigned to these families. Needless to say, shell morphology provides an imperfect clue to relationships.

These papers, and Ponder's smaller papers on this superfamily, are relevant to students of the American faunas because he discusses and allocates many species from both the western Atlantic and the eastern Pacific.

E. V. Coan

A NEW JOURNAL FOR INDO-PACIFIC ZOOLOGY

Indo-Malayan Zoology

edited by JEAN BOUILLON & MICHEL JANGOUX. A. A. Balkema, Publishers. Lisselein 11, P.O. Box 1675, NL-3000 BR Rotterdam, Netherlands. Annual Subscription price \$25.00 + \$3.50 postage.

Although not a malacological journal, the first number of Volume 1 of *Indo-Malayan Zoology* contains two molluscan papers and has a malacologist on its editorial board (J. L. van Goethem). The journal is published twice a year in two issues of about 160 pages each and accepts manuscripts in either English or French. The emphasis of the journal is strongly marine, and encompasses ecology, systematics, and biogeography of Indo-Malayan and Melanesian animals.

C. S. Hickman

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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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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.

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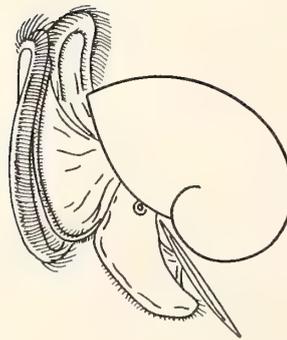
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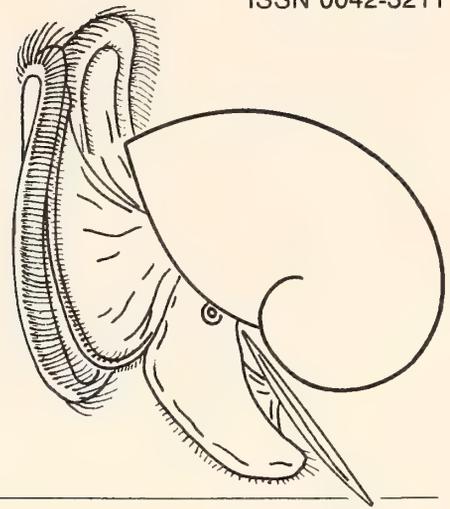
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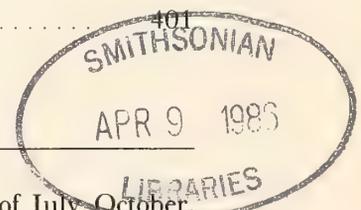
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The *Veliger* (ISSN 0042-3211) is published quarterly on the first day of July, October, January and April. Rates for Volume 28 are \$22.00 for affiliate members (including domestic mailing charges) and \$44.00 for libraries and nonmembers (including domestic mailing charges). An additional \$3.00 is required for all subscriptions sent to foreign addresses, including Canada and Mexico. Further membership and subscription information appears on the inside cover. The *Veliger* is published by the California Malacozoological Society, Inc., % Department of Zoology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.



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Immunological Detection of *Mercenaria mercenaria* in a Predator and Preparation of Size-Class Specific Antibodies

by

ROBERT J. FELLER

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Marine Biology and Coastal Research, University of South Carolina,
Columbia, South Carolina 29208, U.S.A.

Abstract. Successful culture of hard clams (*Mercenaria mercenaria*) requires high survivorship of seed stock during subtidal grow-out. This study was designed to identify natural predators of juvenile clams. Immunological techniques were used to identify *M. mercenaria* proteins in the guts of their natural invertebrate predators and to characterize antigen preparations (whole-organism extracts) of different size classes of clams. The grass shrimp *Palaemonetes vulgaris* was found to eat juvenile *M. mercenaria*. Immuno-electrophoretic separations and immunodiffusion tests of whole-organism extracts of *M. mercenaria* revealed unique antigens in the following size classes: veliger larvae, newly settled spat, juveniles, and adults.

INTRODUCTION

SHELLFISH PRODUCTION on the east coast of the United States is dominated by two commercially important bivalves, the American oyster *Crassostrea virginica* (Gmelin, 1791), and the hard clam, *Mercenaria mercenaria* (Linné, 1758). Because favorable conditions for growth of the hard clam exist in the relatively warm estuarine waters of South Carolina, a pilot scale mariculture facility was established to estimate growth and survivorship of seed clams emplaced subtidally in cages (MANZI *et al.*, 1980). Based on findings reported by numerous workers (*e.g.*, MACKENZIE, 1970, 1977; KRANTZ & CHAMBERLIN, 1978; WHETSTONE & EVERSOLE, 1978, 1981; KRAEUTER & CASTAGNA, 1980), it was reasonable to expect that some seed stock would be lost to predators during grow-out. Unprotected juveniles are known to suffer tremendous mortality soon after settlement in the natural environment (MILEIKOVSKY, 1974; HIBBERT, 1977), but such losses of newly settled spat have never been successfully measured directly in the field. Besides the obvious difficulties of sorting, quantifying, and identifying very small (150–200 μm) post-settlement individuals from sediment samples, the fragile young clams are also not easily identified in the guts of their potential predators. Loss of these small spat to their natural predators, then, is unlikely to be detected with conventional sampling and analytical techniques. This study was conceived to extend the use of an immunological

method capable of detecting soluble proteins of *M. mercenaria* in stomachs of their natural marine predators, to identify heretofore suspected but undocumented predators upon this valuable species, and to characterize antigenic changes in the soluble proteins of *M. mercenaria* during its growth to marketable size.

MATERIALS AND METHODS

Preparation and Characterization of Antibodies

Target specimens (seed clams) were procured from Trident Seafarms Co., Charleston, SC, in eight size classes ranging from 0.6 to 16 mm total shell length (BROWN *et al.*, 1983). Clams that had been growing in tray culture in natural seawater for periods up to several weeks were sorted from their culture debris, separated by size, and immersed live in filtered seawater. The seawater was treated with antibiotics to reduce bacterial contamination, and the clams allowed to empty their stomachs of ingesta for 3 or 4 days at room temperature (20–22°C). Animals from each size class were then solubilized in ice-cold, buffered TES-saline and centrifuged at 3000 \times g for 15 min to remove particulates. The whole-organism-extract supernates of each size class served as antigens for the preparation of antisera in New Zealand white female rabbits, according to the protocol of FELLER *et al.* (1979).

Antibodies were harvested from the rabbits by cardiac

puncture and assayed for titer and specificity in replicate using the double immunodiffusion micro-Ouchterlony technique in agarose gels (OUCHTERLONY, 1968). Further characterization of the antigen-antibody specificities was established using rocket-line and two-dimensional (crossed) immunoelectrophoresis separations in agarose (AXELSEN *et al.*, 1973). In the two-dimensional technique, antigenic components of a given size class are separated according to their electrophoretic mobilities prior to precipitin line formation in the second dimension with all mobilities relative to a bovine serum albumin (BSA) standard (AXELSEN & BOCK, 1972). These methods allow visualization of antigen-antibody precipitin line patterns shared by each size class of clams when antigens are reacted with either their homologous or heterologous antibodies. Immunological distances among the eight size classes of *Mercenaria mercenaria* were assessed by computing a matrix of cross-reactions of each antiserum based upon their relative similarities with the homologous reaction. A hierarchical clustering algorithm (BMDP2M; DIXON, 1981) was used to construct a dendrogram as in FELLER & GALLAGHER (1982).

Detection of Potential Predators

Experimental grow-out cages belonging to Trident Seafarms Co. were examined for macrobenthic predators at their high subtidal (-0.1 m, MLW) sites on Oak Island on 29 October 1980. The cages had been in place for five days and contained juvenile *Mercenaria mercenaria* in the size range 14-18 mm, a size well known to be essentially immune to predation even in open, unprotected sediments. No potential predators were found either on or within the pea gravel of any of the newly emplaced cages. Some other cages in the vicinity of the new ones (in place for approximately one year—Dr. J. Manzi, personal communication) were also examined for potential clam predators by divers. A variety of invertebrates was taken from the cages which, at this time, no longer contained any clams, nor were their containment screens intact. Sediment samples taken in replicate with 2.5-cm diameter cores to a depth of 5 cm were collected at random from the area surrounding both the old and new Oak Island cages and screened through a 250- μ m mesh.

Several small grow-out cages (1 \times 1 \times 0.3 m) were emplaced subtidally in February, 1981 by Dr. J. Manzi near the Trident Seafarms Co. shore facility on Folly Beach, SC. They contained *Mercenaria mercenaria* ranging in size from 3.0 to 7.0 mm. A single cage containing clams was examined on 23 March 1981 for potential predators; the restraining mesh was not completely intact, and the cage contained numerous invertebrates, including the grass shrimp *Palaemonetes vulgaris* (Say, 1818) and the mud snail *Ilyanassa obsoleta* (Say, 1822). All organisms collected from the cage were frozen on dry ice immediately after collection.

Immunological analysis of the stomach contents of sus-

pected predators involved dissection of the gut from individual specimens, microscopic examination for visually identifiable remains, and solubilization of the gut mass in TES-saline using a chilled mortar and pestle (FELLER *et al.*, 1979; FELLER, 1984). The solubilized proteins from within the gut were then analyzed by double immunodiffusion on 25 \times 75 mm glass slides coated with agarose. The fluids (15 μ L) were placed in a central well surrounded by antibody wells, each containing an antiserum to suspected prey—in this case different size classes of *Mercenaria mercenaria*. Antiserum to the predator itself, if available, was also used as a test control to ensure that any precipitin lines formed were due to proteins from the gut contents rather than sloughing of the predator's gut wall proteins. When control antisera were not available, an antiserum to the most closely related taxon was used. If none of these were available, it was assumed that gut wall proteins did not mask the observed reactions. This typically did not cause problems, because very few precipitin lines due to prey were observed in any of the predator guts tested.

RESULTS

Characterization of *Mercenaria mercenaria* Antigens by Immunodiffusion

Antisera were successfully prepared to antigens from eight size classes of *Mercenaria mercenaria* (Table 1). Antibody titer, the reciprocal of the highest dilution of an antiserum that gives a detectable reaction with its homologous antigen, was between 128 and 512 for size classes B and D-H, but only 64 for the two antisera prepared using antigens with the lowest protein concentrations, A and C. The number of precipitin lines produced by double immunodiffusion in replicated homologous double immunodiffusion self-reactions increased with increasing clam shell length, but there was considerable overlap among the size classes in the numbers of self-reaction precipitin lines formed (Figure 1). The veligers (size class A) and spat (B and C) had similar and significantly fewer numbers of homologous precipitin lines than the other size classes of older clams (D-H) which had similar numbers of lines (d.f. = 7,122; $P < 0.001$ by single-classification ANOVA). This immunological overlap reflects the amount of overlap in shell length among the size classes themselves and was entirely expected despite differences in mean weight per individual or protein concentrations among the eight size classes (Table 1). Antisera were unique to the extent that most of the cross-reactions between a given antiserum and antigens from heterologous size classes were not as extensive (did not produce as many precipitin lines) as the identity or self-reaction from that antiserum (Table 2). Exceptions to this include size classes E, F, and G; both E and F contained 6.0-mm individuals, and group G contained individuals similar in size to group F (Table 1). The cross-reactions involving antisera to these three

Table 1
Size-class composition of *Mercenaria mercenaria* antigen preparations.

Sizeclass ¹	No. indiv.	Shell length size range (mm)	Total wet wt. (mg)	TES-buffer (mL)	Protein conc. (mg/mL)	Comments
A ²	10,000	0.2-0.3	300.0	10.0	1.4	veligers
B ²	400	2.0-5.0	100.0	6.0	3.7	starved 3 days
C	1466	0.6-3.5	4.3	6.0	1.3	ground whole
D	484	3.0-5.0	12.5	10.0	2.8	ground whole
E	320	5.0-6.0	11.9	9.5	3.1	ground whole
F	197	6.0-9.9	5.6	9.5	4.1	ground whole
G	53	10.0-16.6	1.3	5.5	4.1	foot muscle
H ³	3	70.0-75.0	7.6	23.0	3.5	foot muscle

¹ A = veligers; B, C = newly set spat; D, E, F, G = juveniles; H = adult.

² Provided by J. W. Ewart, Hatchery Manager, University of Delaware; these veligers had been fed *Isochrysis aff. galbana* (T ISO) and *Thalassiosira pseudonana* 3H.

³ From North Inlet, South Carolina.

groups were strong enough with antigens from adults (size class H) that neither D, E, F, nor G antisera could be considered size class specific. Cross-reactions among the A, B, C, and H size classes were all lower than the homologous reactions based upon maximum numbers of lines observed (Table 2). Thus, it was possible, using double immunodiffusion tests, to distinguish among the following four size classes of *M. mercenaria*: veliger larvae (A), newly settled spat (B, C), juveniles (D, E, F, G), and adults (H) or "chowders." A dendrogram of immunological similarity based on data in the cross-reaction matrix of Table

2 also reflects these differences between size classes (Figure 2).

The presence of cross-reactions among antisera to, and antigens from, *Mercenaria mercenaria* indicated that many of the size classes shared common antigenic proteins. To visualize these antigenic similarities, rocket-line electrophorograms were prepared in 1% agarose gels. These tests essentially confirmed the immunological identities of the size classes discussed above, and in nearly all cases the numbers of precipitin lines observed in double diffusion tests were the same as observed in the rocket-line comparisons. As a further check on the specificity of the separate antisera, two-dimensional (crossed) electrophorograms were prepared on which the precipitin line patterns of both self- and cross-reactions could be visualized.

The existence of both common and unique antigenic components among each of the separate size classes of

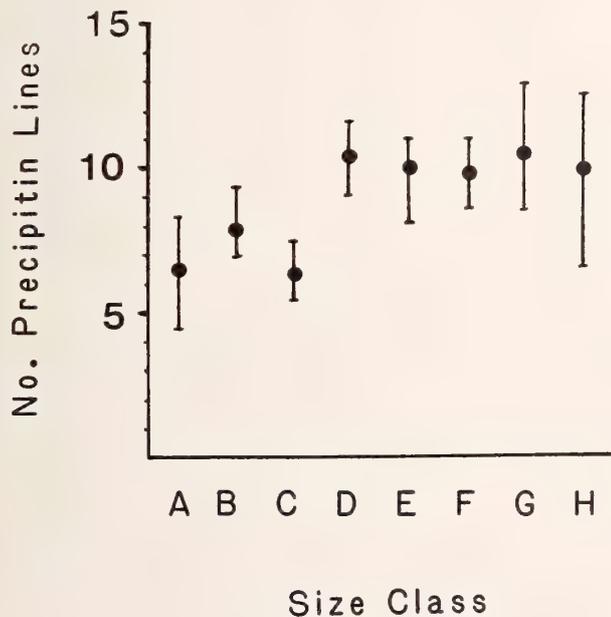


Figure 1

Mean number ($\pm 95\%$ confidence limits) of precipitin lines observed in homologous antigen-antibody reactions for each size class of *Mercenaria mercenaria* defined in Table 1.

Table 2

Maximum number of precipitin lines observed in micro-Ouchterlony double immunodiffusion tests using homologous (on the diagonal) and heterologous reactions between antibodies to and antigens of eight size classes of *Mercenaria mercenaria* (A-H defined in Table 1).

Antisera	Antigens (whole-organism extracts)							
	A	B	C	D	E	F	G	H
(A)	<u>2</u>	7	6	8	7	7	8	7
(B)	7	<u>10</u>	6	8	10	9	5	9
(C)	7	6	<u>9</u>	5	6	4	5	7
(D)	7	11	8	<u>14</u>	13	12	10	10
(E)	7	9	7	11	<u>11</u>	8	11	11
(F)	7	9	9	11	10	<u>12</u>	9	12
(G)	10	11	10	9	12	12	<u>13</u>	13
(H)	8	10	9	9	10	7	12	<u>13</u>

Mercenaria mercenaria was demonstrated using the two-dimensional immunoelectrophoretic separation technique. All possible antigen-antibody reactions were compared, but to illustrate the basic principle, identity and cross-reactions involving the B and G size classes are shown in Figure 3. Not only do the precipitin-line peak patterns show which components are common to both antigens, but the heights of the peaks also reflect the different protein concentrations comprising each antigen-antibody complex (KENNY & FOY, 1975). Comparison of electrophoretic mobilities of each precipitin line relative to BSA's migration in the first dimension (where BSA's migration distance from the antigen well equals unity) also complemented the visual comparisons by establishing which peaks were unique or common to a given antigen-antibody reaction pair. For example, the antiserum for spat produced seven precipitin peaks of identical electrophoretic mobility with both spat and juvenile antigens, indicating that these antigenic components are common to both age classes (Figure 3).

Detection of Potential Predators

Having established the relative specificities and sensitivities of the antisera to individual size classes, it was possible to use them to detect the presence of specific *Mercenaria mercenaria* proteins in the stomachs of potential predators in the field.

Amphipods of the genera *Melita* ($n = 12$) and *Corophium* ($n = 15$) collected from the year-old floating pens at Oak Island on 20 October 1980 did not contain any *Mercenaria mercenaria* protein, nor did any of the snapping shrimp *Alpheus* sp. ($n = 8$) or any of several nereid polychaetes examined. Apparently no clams were available for ingestion in these old cages, and none were visible (as previously noted). Organisms collected by cores from around the newly placed pens (containing 18-mm clams in pea gravel) included a typical assemblage of low intertidal or high subtidal invertebrates in areas of compact oyster shell debris—nereid and phyllodocid polychaetes, turbellarians, nematodes, and a few harpacticoid copepods. The only member of this potential predator community that contained bivalve protein was a single specimen of *Nereis* sp. (12 mm total length), but it was not *M. mercenaria* protein; it was tentatively identified as *Crasostrea virginica* protein. The newly emplaced clams were apparently not accessible to predators, nor were any predators seen in, on, around, or under the new pens.

The Folly Beach cage collections of predators on 23 March 1981 were examined for the presence of *Mercenaria mercenaria* proteins in three specimens of the spionid polychaete *Streblospio benedicti* (Webster, 1879), six *Ilyanassa obsoleta*, two unknown errant polychaetes, and 22 specimens of *Palaemonetes vulgaris*. The *P. vulgaris* stomachs were separated according to total shrimp length (from tip of rostrum to end of telson) into small (<20 cm), medium (20–25 cm), and large (26–27 cm) groups. Each of these groups of potential predators was homogenized

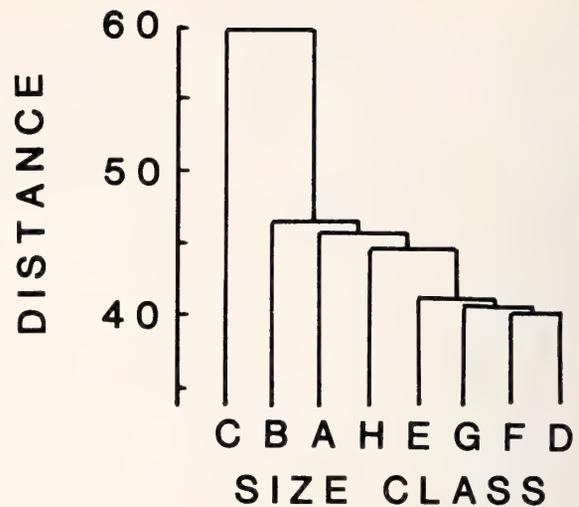


Figure 2

Dendrogram of immunological similarity (based on Euclidean distance) among antisera to the eight size classes of *Mercenaria mercenaria* defined in Table 1.

in saline after visual analysis (dissecting microscope at $50\times$) of individual organism's gut smears revealed only the presence of amorphous material and fluids.

Gut contents from the three groups of *Palaemonetes vulgaris* were tested for the presence of *Mercenaria mercenaria* proteins using antisera to four size classes, C–F inclusive. Because antiserum to *P. vulgaris* was unavailable for use as a control for these immunoassays, antiserum to *P. pugio* was used instead. The control reaction between antiserum to *P. pugio* and antigens from *P. vulgaris* produced eight distinct precipitin lines, whereas the cross-reaction between any one of the four *M. mercenaria* antisera and either *P. pugio* or *P. vulgaris* antigens produced a maximum of only two lines. Presence of *M. mercenaria* in *P. vulgaris* gut contents would thus be indicated by existence of more than two precipitin lines in the immunoassays, as an empty gut would produce the same number of lines as occur in the control cross-reaction.

The combined gut contents of five small *Palaemonetes vulgaris* produced four precipitin lines with anti-D, the antiserum to juvenile *Mercenaria mercenaria* in size class D. The combined gut contents of 13 medium shrimp produced three lines with anti-C, seven lines with anti-D, and three lines with anti-E. No more than two precipitin lines were produced in tests of the four large *P. vulgaris* whose gut contents were combined into one group for analysis. As an additional check that the lines observed were due to the presence of *M. mercenaria* in the shrimp guts, immunoassays were run with antiserum to size class D and known antigens of the same *M. mercenaria* size class adjacent to wells containing the shrimp gut contents. These tests produced lines of identity between the gut contents and the *M. mercenaria* antigens, thus confirming that the grass shrimp had indeed eaten *M. mercenaria*.

Two-dimensional Electrophoresis

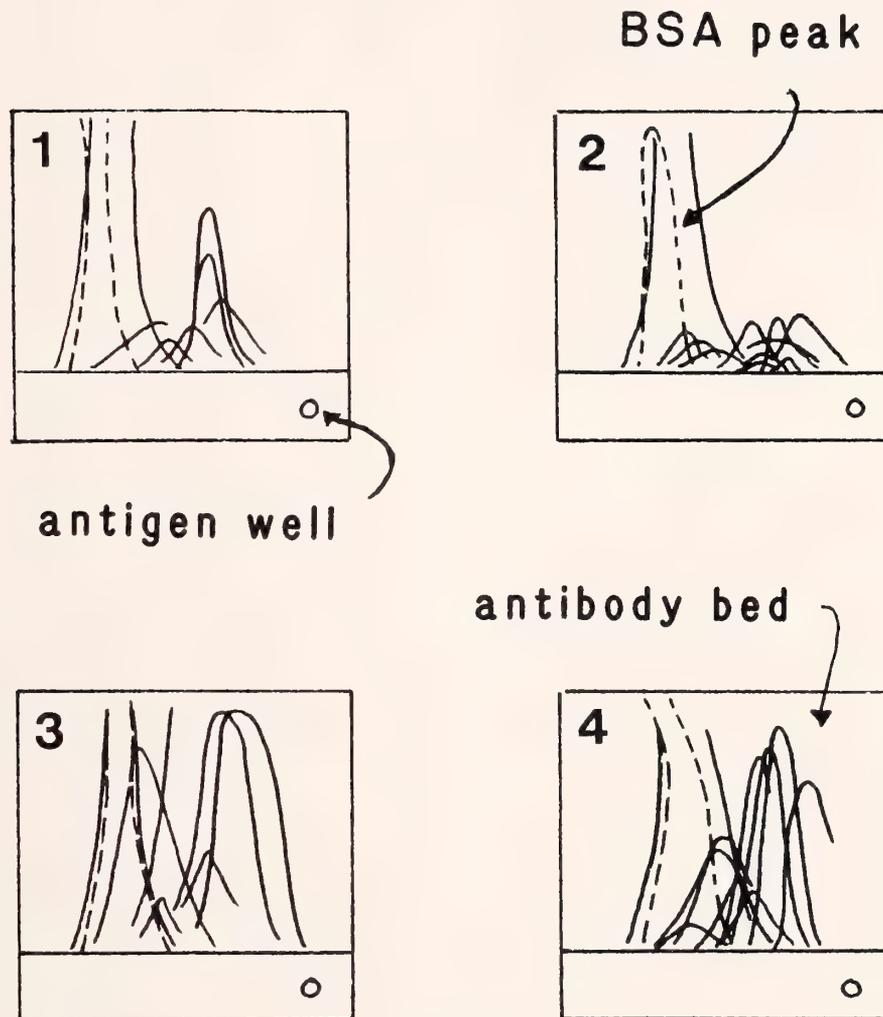


Figure 3

Schematics of two-dimensional immunoelectrophoresis for the homologous (1 and 4) and heterologous (2 and 3) reactions between antigens and antibodies to *Mercenaria mercenaria* size class B (spat) and G (juveniles). Antigens were separated for 1.25 h in the first (horizontal) dimension and then rocketed into a 20% (vol./vol.) antibody gel bed for 6.0 h, all at 2 Volts/cm with constant power at room temperature. Bovine serum albumin (BSA) was used as a marker to which all first dimension migration distances from the antigen well were referenced. Two microliters of anti-BSA (Miles Laboratories) were present in each antibody bed.

- (1) Spat antigen into anti-spat bed (the homologous reaction).
- (2) Spat antigen into anti-juvenile bed (the heterologous reaction).
- (3) Juvenile antigen into anti-spat bed (the heterologous reaction).
- (4) Juvenile antigen into anti-juvenile bed (the homologous reaction).

DISCUSSION

Because separations of antigenic proteins based on Fickian diffusion in agarose gels by double immunodiffusion are not strictly comparable to separations based on electrophoretic mobility, one cannot explicitly equate cross-reactions observed with these two techniques. However, both

immunodiffusion and immunoelectrophoresis (either rocket-line or two-dimensional) are independent methodologies suitable for establishing unique immunological specificities of antisera.

Increasing immunogenicity of *Mercenaria mercenaria* antigens as a function of size reflects the more complex

nature of its antigenic components with increasing age (Figure 1). This ontogenetic phenomenon is reasonably well established for a variety of invertebrate taxa wherein the existence of unique developmental stage-specific or age-specific antigenic components allows immunochemical detection of these taxa in predators (BOREHAM & OHIAGU, 1978). Unique two-dimensional separation patterns seen for antigens from the different size classes of *M. mercenaria* (e.g., Figure 3) point to potential use of the antibodies to detect age-specific predatory mortalities. If antigenic components are also a function of local food resources, then it may even be possible to develop habitat-specific antisera for the veliger age class of *M. mercenaria* and detect the routes of larval dispersal for this species. Notwithstanding the polymorphic traits of natural populations (e.g., PESCH, 1974), such an approach has already been suggested by MENZIES & KERRIGAN (1978) for tracing routes of spiny lobster recruitment on the basis of their biochemical genetics.

The development of antisera capable of detecting minute quantities of *Mercenaria mercenaria* tissue proteins in the predator gut environment is a prerequisite for the use of immunological methods to detect otherwise unknown predators. The technique has been used successfully in both terrestrial and aquatic habitats, and previously unknown predator-prey linkages have usually been identified (BOREHAM & OHIAGU, 1978; CALVER, 1984; FELLER *et al.*, 1985). The immunological study of gastropod predation on oysters by MARSHALL (1977) also attests to the power of this technique for identifying previously unknown predatory species.

Finding that *Palaemonetes vulgaris* had eaten juvenile *Mercenaria mercenaria* was not particularly surprising, as these small shrimp are generalist feeders that typically tear and shred their food upon ingestion, rendering clam tissue visually unidentifiable. A more serious question is whether losses from such a small predator are potentially as great as those posed by other well known predators (drills, xanthiid crabs, asteroids, blue crabs, *etc.*). The Folly Beach cages were not sampled on any other dates; hence, it is unknown whether there were other predators present that could have ingested *M. mercenaria* from them. Casual observations of fauna in the area revealed the presence of several known predators on bivalves (e.g., *Callinectes sapidus* [Rathbun, 1896], *Urosalpinx cinerea* [Say, 1822], birds, and xanthiid crabs), so the potential for additional losses via predation from those small cages did exist.

The impact of large predators (whelks, drills, rays, and crabs) is known to be destructive on *Mercenaria mercenaria* populations (WALKER *et al.*, 1980), and preventive measures may be successful in restricting their access to cultures. A small motile predator such as *Palaemonetes vulgaris*, however, will be much more difficult to exclude, especially if it is small enough to go through protective meshes or screens. It is conceivable that the young of such a predator might gain access to a culture tray and grow

amidst an unlimited food supply. Successful bivalve culture requires not only rapid growth at high stocking densities and absence of pathogens, but also high survivorship and favorable socioeconomic conditions. Most efforts to reduce predatory mortality have been basically physical in nature (mesh cages, gravel burial, *etc.*), but such methods have, in the past, been directed at preventing known predators from gaining access to cultures (e.g., MENZEL & SIMS, 1964; ELDRIDGE *et al.*, 1976; CASTAGNA & KRAEUTER, 1977). Losses that occur in physically protected culture trays are typically assumed to be a result of mechanical damage, handling artifacts, innate morbidity, parasites, disease, or environmental stresses—little consideration had been given to previously unknown predators. Reasons for this are logical and obvious, for if it is not known what all the predators are, it is not possible to design protection from all of them. This is evidenced by the sporadic success of cages in protecting desirable organisms (MENZEL *et al.*, 1976; VIRNSTEIN, 1978). Identification of previously unknown predators enhances the probability that preventive measures can be taken to avoid them, either by emplacing grow-out trays in areas having low predator abundance, by removing specific predators, or by designing more effective enclosure devices.

Preventive measures employed by the Trident Seafarms Co. (mesh and aggregate protection) coupled with emplacement of relatively large individuals for grow-out appears to be effective in reducing predatory losses. Whether optimal growth can occur under these grow-out conditions is still a question (HADLEY & MANZI, 1984).

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LITERATURE CITED

- AXELSEN, N. H. & E. BOCK. 1972. Identification and quantitation of antigens and antibodies by means of quantitative immunoelectrophoresis. A survey of methods. *J. Immun. Meth.* 1:109-121.
- AXELSEN, N. H., J. KROLL & B. WEEKE. 1973. A manual of quantitative immunoelectrophoresis. Methods and applications. *Scandinavian Journal of Immunology*. Vol. 2 (suppl. no. 1): 169 pp. Blackwell Sci. Publ.: Oxford.

- BOREHAM, P. F. L. & C. E. OHIAGU. 1978. The use of serology in evaluating invertebrate prey-predator relationships: a review. *Bull. Ent. Res.* 68:171-194.
- BROWN, J. W., J. J. MANZI, H. Q. M. CLAWSON & F. S. STEVENS. 1983. Moving out the learning curve: an analysis of hard clam, *Mercenaria mercenaria*, nursery operations in South Carolina. *Mar. Fish. Rev.* 45:10-15.
- CALVER, M. C. 1984. A review of ecological applications of immunological techniques for diet analysis. *Aust. J. Ecol.* 9:19-25.
- CASTAGNA, M. & J. N. KRAEUTER. 1977. *Mercenaria* culture using stone aggregate for predator protection. *Proc. Natl. Shellfish Assoc.* 67:1-6.
- DIXON, W. J. (ed.). 1981. Statistical software. BMDP. Univ. of Calif. Press: Berkeley. 725 pp.
- ELDRIDGE, P. J., W. WALTZ, R. C. GRACY & H. H. HUNT. 1976. Growth and mortality rates of hatchery seed clams, *Mercenaria mercenaria*, in protected trays in waters of South Carolina. *Proc. Natl. Shellfish Assoc.* 66:13-20.
- FELLER, R. J. 1984. Dietary immunoassay of *Ilyanassa obsoleta*, the eastern mud snail. *Biol. Bull.* 166:96-102.
- FELLER, R. J. & E. D. GALLAGHER. 1982. Antigenic similarities among estuarine soft-bottom benthic taxa. *Oecologia* 52:305-310.
- FELLER, R. J., G. L. TAGHON, E. D. GALLAGHER, G. E. KENNY & P. A. JUMARS. 1979. Immunological methods for food web analysis in a soft-bottom benthic community. *Mar. Biol.* 54:61-74.
- FELLER, R. J., G. ZAGURSKY & E. A. DAY. 1985. Deep-sea food web analysis using cross-reacting antisera. *Deep-Sea Res.* 32:485-497.
- HADLEY, N. H. & J. J. MANZI. 1984. Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. *Aquaculture* 36:369-378.
- HIBBERT, C. J. 1977. Growth and survivorship in a tidal-flat population of the bivalve *Mercenaria mercenaria* from Southampton water. *Mar. Biol.* 44:77-84.
- KENNY, G. E. & H. M. FOY. 1975. Detection and quantitation of circulating polysaccharide in pneumococcal pneumonia by immunoelectroosmophoresis (counterelectrophoresis) and rocket electrophoresis. *Microbiology (Amer. Soc. for Microbiol.)* 1:97-102.
- KRAEUTER, J. N. & M. CASTAGNA. 1980. Effects of large predators on the field culture of the hard clam, *Mercenaria mercenaria*. *Fish. Bull.* 78:538-541.
- KRANTZ, G. E. & J. V. CHAMBERLIN. 1978. Blue crab predation on cultchless oyster spat. *Proc. Natl. Shellfish Assoc.* 68:38-41.
- MACKENZIE, C. L., JR. 1970. Causes of oyster spat mortality, conditions of oyster setting beds, and recommendations for oyster bed management. *Proc. Natl. Shellfish Assoc.* 60:59-67.
- MACKENZIE, C. L., JR. 1977. Predation on hard clam (*Mercenaria mercenaria*) populations. *Trans. Amer. Fish. Soc.* 106:530-537.
- MANZI, J. J., V. G. BURRELL, JR. & W. Z. CARSON. 1980. A mariculture demonstration project for an alternative hard clam fishery in South Carolina: preliminary results. *Proc. World Maricul. Soc.* 11:79-89.
- MARSHALL, M. J. 1977. Serologically detected patterns of gastropod predation on an intertidal oyster bar. M.S. thesis, Univ. of Florida, Gainesville. 50 pp.
- MENZEL, R. W. & H. W. SIMS. 1964. Experimental farming of hard clams, *Mercenaria mercenaria*, in Florida. *Proc. Natl. Shellfish Assoc.* 53:103-109.
- MENZEL, R. W., E. W. CAKE, M. L. HAINES, R. E. MARTIN & L. A. OLSEN. 1976. Clam mariculture in northwest Florida: field study on predation. *Proc. Natl. Shellfish Assoc.* 65:59-62.
- MENZIES, R. A. & J. M. KERRIGAN. 1978. Implications of spiny lobster recruitment patterns of the Caribbean—a biochemical genetic approach. *Proc. 31st Ann. Gulf and Caribbean Fish. Inst.*, pp. 164-178.
- MILEIKOVSKY, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. *Mar. Biol.* 26:303-311.
- OUCHTERLONY, O. 1968. Diffusion-in-gel methods for immunological analysis. *Ann Arbor Science Publ., Inc.: Ann Arbor.* 215 pp.
- PESCH, G. 1974. Protein polymorphisms in the hard clams (*Mercenaria mercenaria* and *Mercenaria campechiensis*). *Biol. Bull.* 146:393-403.
- VIRNSTEIN, R. W. 1978. Predator caging experiments in soft sediments: caution advised. Pp. 261-273. *In: M. L. Wiley (ed.): Estuarine interactions.* Academic Press: New York.
- WALKER, R. L., M. A. FLEETWOOD & K. R. TENORE. 1980. The distribution of the hard clam *Mercenaria mercenaria* (Linne) and clam predators in Wassaw Sound, Georgia. Georgia Marine Science Center, University System of Georgia, Skidaway Island, Georgia, Tech. Rep. Ser. No. 80-8, 59 pp. (unpublished manuscript).
- WHETSTONE, J. M. & A. G. EVERSOLE. 1978. Predation on hard clams, *Mercenaria mercenaria*, by mud crabs, *Panopeus herbstii*. *Proc. Natl. Shellfish Assoc.* 68:42-48.
- WHETSTONE, J. M. & A. G. EVERSOLE. 1981. Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams, *Mercenaria mercenaria*. *Estuaries* 4:153-156.

How a Clam Builds Windows: Shell Microstructure in *Corculum* (Bivalvia: Cardiidae)

by

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Abstract. *Corculum* is unusual among bivalves because it, like the closely related genus *Fragum* and their distant relative *Tridacna*, possesses endosymbiotic dinoflagellates. But *Corculum* does not expose its algae-laden tissues directly to the sunlight. Instead, the shell of *Corculum* incorporates several unique features that have been interpreted as adaptations to permit passage of incident light through the shell to algae-bearing mantle and gill tissue encased within. These shell modifications in *Corculum* shell include: postero-anterior compression (resulting in a prominently keeled shell with a flattened upper surface), posterior thinning of the shell, and unique transparent "windows" radially arrayed on the shell posterior.

The windows are present only on the posterior (upper) surface, are triangular in outline, and are constructed by expansion and elaboration of the outermost, fibrous prismatic layer of the shell microstructure. A concomitant reduction in pigmentation enhances transparency. Direct measurements of light transmission through the *Corculum* shell show the windows transmit an order of magnitude more light than either the other portions of the shell posterior or the shell's anterior.

INTRODUCTION

TWO BIVALVE lineages, the tridacnids and the Fraginae (including *Corculum*, the heart cockle, and the closely related genus *Fragum*), have independently evolved symbiotic relationships with dinoflagellates, or zooxanthellae (KAWAGUTI, 1950, 1983). Although both bivalve groups are assigned to the Cardiacea, or cockles, they have evolved very different sets of adaptations to accommodate their symbionts. Unlike its distant cousin *Tridacna*, *Corculum* has received little scientific attention. Consequently, its biology is not well known.

Unlike tridacnids, *Corculum* does not gape to expose its zooxanthellae to light. In fact, it cannot employ gaping to expose the algae because the shell's umbos restrict the bivalve's gape to only a few degrees. RAUP (1966) noted the severe valve overlap in *Corculum*, and observed that the two umbos are slightly offset to permit the clam to open. The zooxanthellae are situated within the mantle and gills and are densely packed in the anterior mantle epithelia (KAWAGUTI, 1950, 1966). Under the posterior (upper) valve regions, the algae are stacked in two layers: a thin covering in the posterior mantle and a dense population in the directly subjacent gills (KAWAGUTI, 1966).

Except for the narrow peripheral mantle fringe, the gills and mantle tissue containing the zooxanthellae are

always covered by the shell. Instead of direct exposure, *Corculum* appears to employ a "windows" strategy to culture its symbionts, utilizing a unique set of shell modifications to enhance light penetration through the posterior shell surface (KAWAGUTI, 1950; SEILACHER, 1972, 1973). The animals are noticeably compressed in the antero-posterior direction (Figures 1, 2) and the posterior region of the shell is thin. Located in the posterior region are numerous transparent areas arranged in radial rows. SEILACHER (1972) and VOGEL (1975) suggested that the roughly triangular to dendritic clear areas function not only as transparent windows, but also as optical lenses providing maximum light diffusion.

The purpose of this investigation was to examine the structure and properties of these putative windows and to learn how they might have evolved through modification of pre-existing shell microstructure. Preliminary investigation suggested two possible origins for the windows. Modifications of the aragonite microstructure that constitutes the shells might account for the shape and nature of the windows. Secondly, concomitant changes in shell pigmentation may enhance the transparency of the windows. We also examined the light transmission properties of the shells in order to determine whether the windows afforded any significant increase in light transmitted to the shell interior.

MATERIALS AND METHODS

Specimens of *Corculum cardissa* (Linnaeus, 1758) and *Fragum fragum* (Linnaeus, 1758) were provided by the California Academy of Sciences. Additional specimens of *Corculum* were collected live at the Motupore Island Research Center (9°32'S; 147°16'E) in Papua New Guinea. The shells were in good condition, with clean, unmarred surfaces. For preliminary observations, petrographic slides of radial sections of *C. cardissa* and *F. fragum* were prepared and studied under a polarizing microscope. For scanning electron microscopy (SEM), shells were sectioned and fractured in radial, oblique, and transverse orientations. Sectioned specimens were then polished and etched in dilute hydrochloric acid. Specimens were mounted, coated with gold/palladium, and examined with a Hitachi S-450 Scanning Electron Microscope housed in the Geology Department at the University of California, Davis. Further SEM work was done in the laboratory of J. G. Carter at the University of North Carolina, Chapel Hill.

Two additional techniques were utilized to examine shell microstructure. Pieces of shell were embedded in lucite plugs and sectioned in radial, oblique, and transverse orientations. Acetate peels were then prepared from the polished and etched sections and examined under a light microscope. Embedded sections were also mounted, coated and examined under SEM. These techniques are detailed in CARTER (1980a).

Measurements of light transmission characteristics of different parts of the *Corculum* shell were obtained using a microspectrophotometer. Pieces of shell were mounted on glass slides, with cover slips, in an embedding wax. The percent light transmission was then measured for the anterior region of the shell, the posterior non-window portion, and the windows. Measurements were taken every 10 nm at wavelengths from 420 to 700 nm. Measurements are given as percent of incident light at the specified wavelength transmitted through the shell, relative to that transmitted through the glass slide, cover slip, and mounting medium.

RESULTS

Anterior Shell Microstructure of *Corculum*

The region of the *Corculum* shell anterior to the pronounced medial keel is composed of three types of microstructure arranged in layers. (Terminology for microstructure employed here follows CARTER, 1980a.) The relatively thin outer layer of the shell consists of fibrous prismatic crystals (Figure 3). Previous workers (TAYLOR *et al.*, 1973) have found cardiacean shells to be entirely aragonitic, and the morphology of the fibrous prismatic crystals and of crystals forming the other shell layers is consistent with that observation (for comparisons, see CARTER, 1980a). The prisms are oriented in a plumose

pattern, running parallel to the shell surface and then radiating away from the central axis toward the interior and exterior surfaces of the shell. The central plane of this layer tends to form a natural breakage plane parallel to the surface of the shell. Throughout the layer, the prisms have identical ratios of length to width.

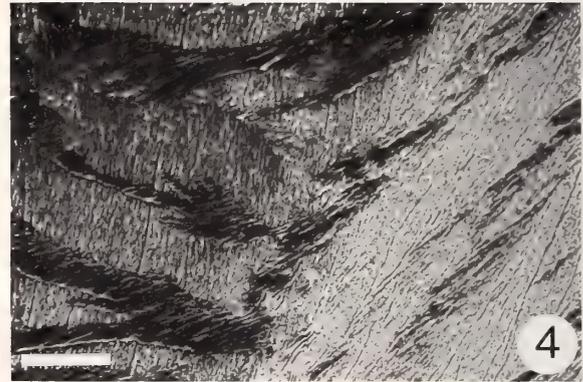
Directly underlying the fibrous prismatic layer is a thick layer of irregular complex crossed-lamellar shell material. This microstructure is an irregular three-dimensional arrangement of aragonite crystals with three or more crystal orientations. In radial section, the pattern produced by the different orientations resembles dendritic striping (Figure 4).

The innermost shell layer consists of an interdigitating cone-complex crossed-lamellar structure (Figure 5). Aragonite crystals are arranged in a pattern of stacked cones, with the crystals radiating downward from the apices of the cones. This pattern presents nearly identical appearances when viewed in any direction normal to the shell surface, thus distinguishing it from the irregular complex crossed-lamellar structure. In some places, especially where the shell is flexed by formation of a plication, the cone-complex crossed-lamellar structure grades upward into the irregular complex crossed-lamellar structure.

Posterior Shell Microstructure of *Corculum*

The shell is thinner posterior to the medial keel than in the anterior portion. Also, the microstructure is strikingly different. The outer fibrous prismatic layer is in places greatly thickened, extending through the underlying layers to the interior surface of the shell. Where the fibrous prismatic layer penetrates to the interior shell surface, the crystals are greatly elongated and oriented perpendicular to the shell surface. These elongated prisms constitute the features previously described as windows (Figure 6). Small topographic highs form on the interior shell surface where the fibrous prismatic layer reaches to the shell surface. Figure 8 presents a block diagram showing the geometric arrangement of fibrous prismatic crystals within the shell.

The non-window matrix of the shell posterior is composed of irregular complex crossed-lamellar microstructure and a very reduced layer of cone-complex crossed-lamellar structure. Our observations of petrographic slides of *Corculum* under polarized light indicate windows contain unpigmented growth lines. In contrast, non-window areas do contain pigment, suggesting pigmentation is suppressed during window formation. The combination of pigmentation and type of microstructure undoubtedly contributes to the visually obvious variation in translucency of the *Corculum* shell posterior. Interestingly, there are also relatively translucent areas in the shell anterior, though these areas are not as pronounced as the windows. There is no variation in microstructure associated with these patches, suggesting the effect is due entirely to pigmentation.



Shell Microstructure of *Fragum fragum*

There is no significant differentiation of the microstructure in the anterior and posterior parts of the *Fragum fragum* shell. The shell is also less compressed, thicker, and visibly more opaque. The *Fragum* shell contains a more diverse suite of microstructure; four types of microstructure are found in contrast to the three occurring in *Corculum* (Figure 7). The outermost shell layer is composed of relatively thin, fibrous prismatic aragonite. Underlying this layer is a thin, irregular complex crossed-lamellar layer. Subjacent to this is a relatively thick, extensive layer of simple crossed-lamellar microstructure. This microstructure, not found in *Corculum*, consists of laths of aragonite arranged in two orientations within parallel primary sheets, with adjacent sheets having alternate lath orientations. The innermost layer is a relatively thick layer of cone-complex crossed-lamellar structure that occurs dorsal to the pallial line and is separated from the overlying layer by a thin pallial myostracum.

Light Transmission Characteristics of the *Corculum* Shell

Windows transmit as much as 40% of incident light, and a full order of magnitude more light than either posterior shell matrix or anterior portions of the shell. Light transmission is relatively poor in the shorter wavelengths, but increases rapidly through the greens, yellows, and reds (Figure 9). At the long end of the spectrum, transmission is again reduced. The windows provide significant increases in light transmission at wavelengths important for photosynthesis.

Compared with the anterior part of the shell, the relatively thin posterior shell matrix transmits more light, but the maximum transmission is only a few percent of incident light (Figure 9).

DISCUSSION

Our results indicate that a combination of pigmentation and shell microstructure greatly increases the intensity of light transmitted to the shell interior of *Corculum*. Presumably, this is an adaptation for the benefit of the symbiotic dinoflagellates inhabiting the clam's tissues. The evolutionary pathways followed in development of the unique windows of *Corculum* can be inferred from com-

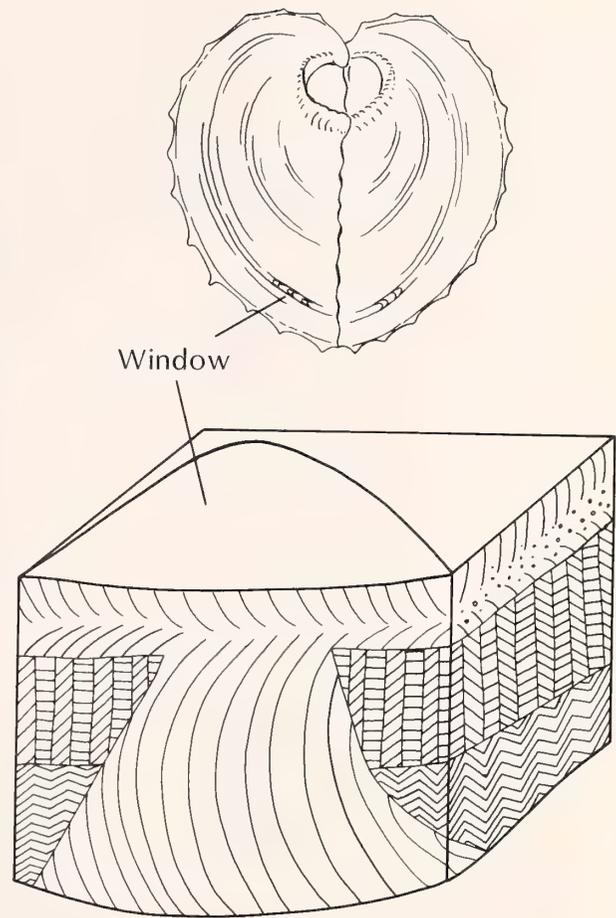


Figure 8

Block diagrams showing the geometric arrangement of the three microstructural layers that constitute the posterior portion of the shell of *Corculum*. Expansion of the fibrous prismatic layer and penetration of the prisms to the inner shell wall form light-transmitting structures, or windows. Drawn approximately to scale.

parison of character states present in *Corculum* and *Fragum*.

The role of pigmentation in enhancing shell transparency is not entirely clear from our results, nor is the general phenomenon of shell pigmentation well understood. Research to date (for review, see CRENSHAW, 1980) sug-

Explanation of Figures 1 to 7

- Figure 1. Ventral view of *Corculum cardissa*. Scale bar = 2 cm.
- Figure 2. Posterior view of *C. cardissa*. Scale bar = 2 cm.
- Figure 3. Outermost, fibrous prismatic microstructural layer of anterior shell of *C. cardissa*. Scanning electron micrograph of fractured radial section. Scale bar = 50 μ m.
- Figure 4. Irregular complex crossed-lamellar microstructure of anterior shell of *C. cardissa*. Scanning electron micrograph of polished and etched oblique section. Scale bar = 50 μ m.

- Figure 5. Innermost cone-complex crossed-lamellar microstructure layer of posterior portion of *C. cardissa* shell. Scanning electron micrograph of fractured radial section. Scale bar = 5 μ m.
- Figure 6. Expanded, window-forming fibrous prismatic microstructure of posterior shell of *C. cardissa*. Scale bar = 5 μ m.
- Figure 7. Simple complex crossed-lamellar microstructure of *Fragum fragum*. Scanning electron micrograph of fractured transverse section. Scale bar = 50 μ m.

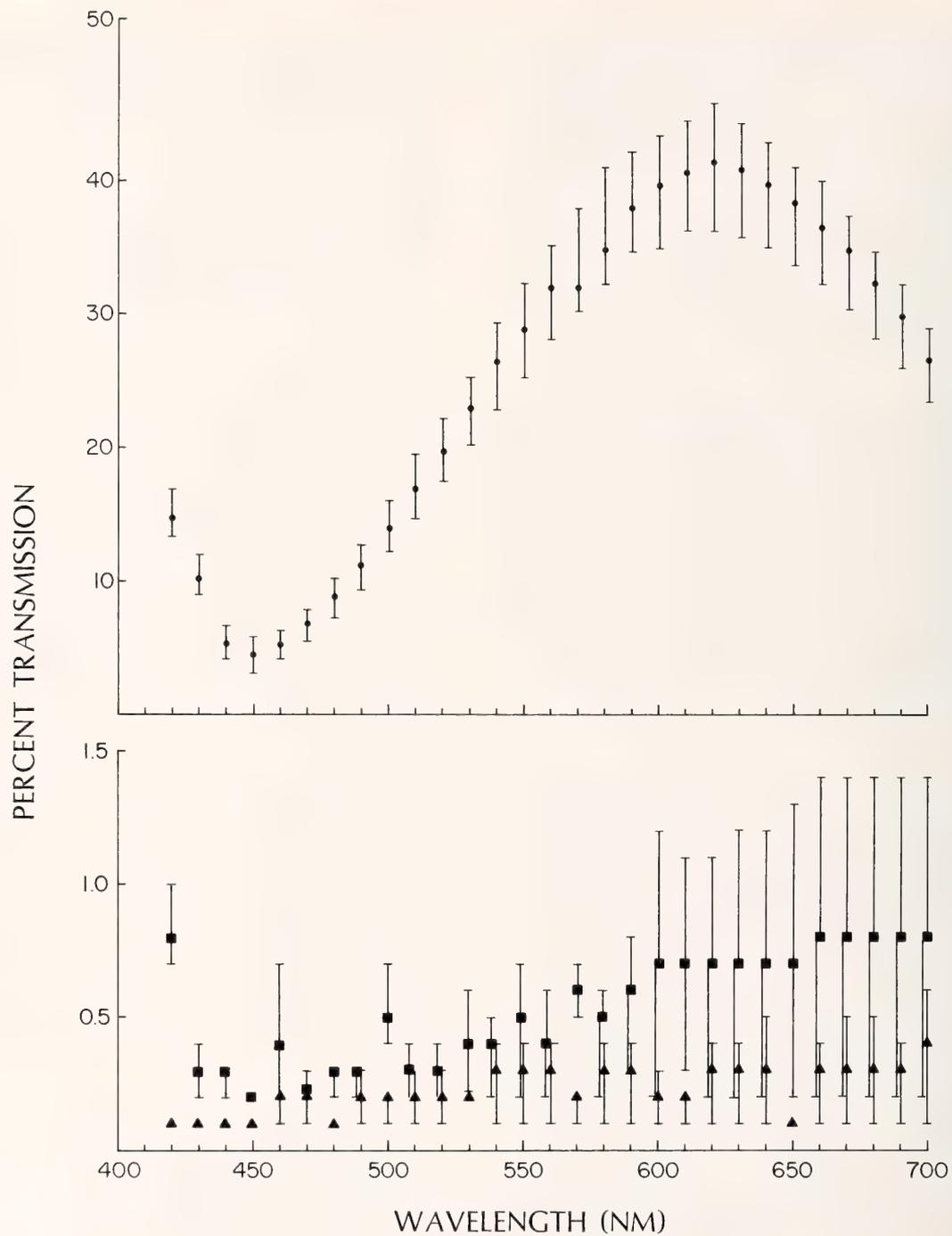


Figure 9

Transmission characteristics of the shell of *Corculum cardissa*. Circles indicate mean value for four windows, lines indicate range of readings. Squares indicate values for four readings on the shell matrix of the shell posterior, and triangles indicate percent transmission for four areas of the anterior shell of *Corculum*. Lines above and below squares and triangles represent ranges of values obtained.

gests changes in organic content and concentration are linked to salinity fluctuations, mantle irritation, and anaerobiosis during shell deposition. It is perhaps suggestive that the prismatic layer of both the anterior and posterior

portions of *Corculum* and *Fragum* contain no pigmented growth lines. Thus, simple expansion of the prismatic layer may be sufficient to cause an increase in light transmission.

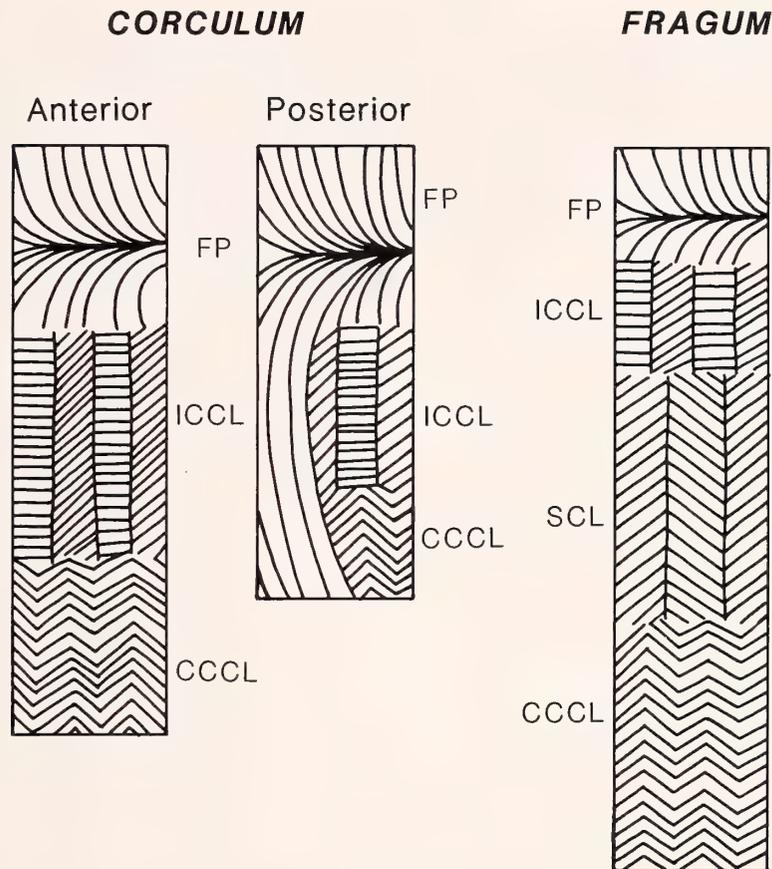


Figure 10

Comparison of shell architecture of *Fragum* and *Corculum*. Layers indicated as follows: FP, fibrous prismatic; ICCL, irregular complex crossed-lamellar; CCCL, cone-complex crossed-lamellar; and SCL, simple crossed-lamellar. Not drawn to scale.

On the other hand, several modifications of the *Corculum* shell occurred, leading to the present combination of gross morphology and the presence of windows. These include antero-posterior flattening of the shell (with a concomitant increase in the ratio of surface area to shell volume), thinning of the posterior portion of the shell through reduction in the number of shell layers and thinning of the remaining layers, and differential expansion of the fibrous prismatic layer resulting in triangular, clear windows in the posterior region of the shell. The peculiar, flattened shell of *Corculum* and the windows are unique among modern bivalves, but reduction in the numbers of microstructural layers is a common occurrence in the evolution of bivalve clades (TAYLOR *et al.*, 1973; TAYLOR, 1973; CARTER, 1980b).

Comparison of the shell microstructure of *Fragum* and *Corculum* reveals several evolutionary modifications (Figure 10). Both *Fragum* and *Corculum* have an outermost fibrous prismatic layer. However, this layer is relatively thin in *Fragum* and well developed in *Corculum*. Underlying the fibrous prismatic layer in both *Corculum* and *Fragum* is an irregular complex crossed-lamellar layer. In *Fragum* the irregular complex crossed-lamellar layer is

thinner and more variable in extent than in *Corculum*, where it represents a major microstructural component of the shell. Whereas *Corculum* lacks a simple crossed-lamellar structure, in *Fragum* it is a major component of the shell. The inner shell layer of cone-complex crossed-lamellar structure occurs in both *Fragum* and *Corculum*, but is much reduced in the posterior portion of the latter. In *Fragum*, a noticeable prismatic myostracum separates the inner cone-complex crossed-lamellar layer from the simple crossed-lamellar layer, but in *Corculum* the myostracum separating the inner cone layer from overlying irregular complex crossed-lamellar structure is prominent only in the anterior portion of the shell. Thus, the major evolutionary modifications apparent in the transition from the typical *Fragum* shell structure to that of *Corculum* are an elimination of the simple crossed-lamellar layer, an elaboration of the fibrous prismatic layer, and a differentiation of patterns of deposition between the anterior and posterior portions of the *Corculum* shell.

The absence of a pallial myostracum and reduction in the extent of the cone-complex crossed-lamellar layer in the posterior region of the *Corculum* shell suggests a significant change in the pattern of shell deposition by the

mantle. Because the cone-complex crossed-lamellar layer lies below the myostracum, the region of the mantle depositing this layer must be the mantle surface inside the pallial line. The lack of this layer and any appreciable myostracal prisms in the posterior region of the *Corculum* shell indicates that deposition by this part of the mantle must be suspended. The mantle edges of *Corculum*, which deposit the fibrous prismatic layer, must at times greatly increase the rate of deposition to form windows, while deposition continues normally at other parts of the mantle margin. This demonstrates an extreme flexibility in patterns of deposition and greatly increases the range of structures that potentially could be formed by the mantle.

CARTER (1980b) has found that expansion or contraction of shell microstructural layers during ontogeny occurs in at least three bivalve genera. *Mercenaria*, *Cerastoderma*, and *Spisula* show either occasional inter-tonguing of the outer and middle shell layers, or periodic expansion and contraction of the area of deposition of the outer shell layer in response to environmental stresses such as seasonal climatic changes and thermal shock or in response to spawning.

Observations of shell structures in *Corculum cardissa* and *Fragum fragum* reveal a greater diversity, both in variety and arrangement, of microstructure than described by earlier workers. TAYLOR *et al.* (1973) described cardiacean microstructure in general, and *Fragum unedo* (Linnaeus, 1758) in particular, as consisting of two concentric layers: an outer aragonite crossed-lamellar structure and an inner complex crossed-lamellar layer usually separated by a thin prismatic myostracum. The surprising diversity of shell microstructure now known to be present in *Corculum* and *Fragum* suggests the possibility of undiscovered diversity and variation in the microstructure of other molluscan taxa.

Photosymbiosis in *Fragum*

KAWAGUTI (1983) has recently reported the presence of symbiotic dinoflagellates in *Fragum fragum* and *F. unedo*. In the latter species, the photosymbionts are primarily concentrated in the enlarged mantle tissues around the siphons and in the gills. Kawaguti reports that this species lives buried shallowly in the sediment, with enlarged mantle tissues around the siphons spread over the sediment. In contrast, Kawaguti reports that *F. fragum* lives with the posterior side of the shell above the sediment. This species lacks the enlarged mantle tissues and does not gape widely. (PWS confirms these observations on *F. fragum* from field and laboratory work in Guam.) In *Fragum fragum* the zooxanthellae are distributed throughout the animal, and are concentrated in the gills and mantle. In this species, light transmitted through the shell apparently sustains the enclosed zooxanthellae, as in *Corculum*. Thus, these three species seem to constitute an evolutionary series from *Fragum unedo*, which uses a *Tridacna*-like strategy of directly exposing zooxanthellae-laden tissue to light,

to *Corculum*, where the shell encloses the animal at all times (KAWAGUTI, 1983).

Life Habits of *Corculum*

One remaining question is how *Corculum* keeps the posterior surface of its shell clear of fouling and boring organisms. Surfaces in shallow marine environments do not remain unfouled in the Indo-Pacific for long (more than a few days) unless there is some mechanism to deter organisms from settling or to remove organisms that have settled.

Corculum occurs in shallow intertidal to subtidal areas throughout the Indo-Pacific region (BARTSCH, 1950). KAWAGUTI (1950) reported that *Corculum* occurs around reefs, often resting half obscured by filamentous algae and rubble. (This report would appear to contradict the suggestion that the posterior surface of the *Corculum* shell serves to conduct light to algae living within the clam's tissues.) Other authors have reported *Corculum* occurring in shallow sandy or muddy areas (Franco in BARTSCH, 1950; CERNOHORSKY, 1972). One of us (PWS) recently was able to observe living *Corculum cardissa* and *C. monstrosum* (Gmelin, 1791) at Motupore Island in Papua New Guinea. At Motupore Island, the two species occur intertidally. *Corculum monstrosum* was found living free on a sand and grass flat; *C. cardissa* was found living in a sheltered area on sandy mud among intertidal rocks on the lee side of Motupore Island. In each case, the shell posterior was exposed to the sunlight and was free of algae or fouling organisms.

Corculum maintained in aquaria will migrate within the tank from shady to sunny areas. If overturned, they will right themselves by planting the foot in the substrate and rotating the entire shell onto its anterior surface. The foot also occasionally sweeps the posterior surface of the shell, and may be the mechanism for keeping that area free of fouling organisms.

Comparison of *Corculum* and *Notoacmea*

There is an interesting morphological parallel between the *Corculum* windows and the limpet *Notoacmea persona*. LINDBERG *et al.* (1975) noted the presence of light-transmitting spots in the anterior shell of *N. persona*, and demonstrated that these spots play a role in the limpet's negatively phototropic reaction to light. The *Corculum* windows might also facilitate the bivalve's positive response to light noted above, but that was not tested. Nevertheless, the structures documented in the limpet windows by LINDBERG *et al.* (1975) and in *Corculum* (this paper) are quite distinct.

Recognition of Photosymbiosis in Fossil Bivalvia

Depending on the degree of preservation, shell modifications such as those seen in *Corculum* could be recognized in the fossil record. Unusual shell thinness, indica-

tive of translucency, would be especially obvious. Recognition of other modifications such as prismatic windows or layers would depend upon the degree of preservation, especially for aragonitic structures. Even though only two Recent bivalve lineages, tridacnids and the Fraginae, are known to maintain symbiotic algal associations, given the broad spectrum of Recent organisms that harbor algae we should expect to find other examples of paleophotosymbiosis in the fossil record. For example, YANCEY (1982) has recently interpreted an unusual Permian myalinid bivalve group, the Alatoconchidae, as the earliest photosymbiont-bearing bivalves. Alatoconchids resemble tridacnids in size and shell thickness, yet resemble *Corculum* in terms of antero-posterior compression, life position, and prismatic microstructure. COWEN (1983) has reviewed the evidence for photosymbiosis in bivalves and other fossil clades.

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During the course of this investigation, we learned that an independent study of *Corculum* microstructure was being conducted by Mr. Clement Counts, III, at the University of Delaware (Counts, 1981). We thank Mr. Counts for outlining his project for us, sharing his ideas on cardiacean microstructure and providing suggestions on techniques employed here.

LITERATURE CITED

- BARTSCH, P. 1950. The little hearts (*Corculum*) of the Pacific and Indian Oceans. *Pacific Sci.* 1:221-226.
- CARTER, J. G. 1980a. Guide to bivalve shell microstructures. Pp. 645-673. *In*: D. C. Rhoads & R. A. Lutz (eds.), *Skeletal growth of aquatic organisms*. Plenum Press: New York.
- CARTER, J. G. 1980b. Environmental and biological controls of bivalve shell mineralogy and microstructure. Pp. 69-113. *In*: D. C. Rhoads & R. A. Lutz (eds.), *Skeletal growth of aquatic organisms*. Plenum Press: New York.
- CERNOHORSKY, W. O. 1972. Marine shells of the Pacific. Volume II. Pacific Publications: Sydney. 411 pp. + 68 pl.
- COUNTS, C. L., III. 1981. Shell ultrastructure of *Corculum* spp. (Roeding) (Bivalvia: Cardiacea). *Bull. Amer. Malacol. Union Conv. Proc.*, Ft. Lauderdale, Florida. p. 35.
- COWEN, R. 1983. Algal symbiosis and its recognition in the fossil record. Pp. 431-478. *In*: M. J. S. Tevesz & P. I. McCall (eds.), *Biotic interactions in the fossil record*. Plenum Press: New York.
- CRENSHAW, M. A. 1980. Mechanisms of shell formation and dissolution. Pp. 115-132. *In*: D. C. Rhoads & R. I. Lutz (eds.), *Skeletal growth of aquatic organisms*. Plenum Press: New York.
- KAWAGUTI, S. 1950. Observations on the heart shell, *Corculum cardissa* (L.) and its associated zooxanthellae. *Pacific Sci.* 4: 43-49.
- KAWAGUTI, S. 1966. Electron microscopy on zooxanthellae in the mantle and gill of the heart shell. *Biol. J. Okayama Univ.* 141:81-92.
- KAWAGUTI, S. 1983. The third record of association between bivalve molluscs and zooxanthellae. *Proc. Japan Acad., Ser. B*, 59:17-20.
- LINDBERG, D. R., M. G. KELLOGG & W. E. HUGHES. 1975. Evidence of light reception through the shell of *Notoacmea persona* (Rathke, 1833). *Veliger* 17:383-386.
- RAUP, D. M. 1966. Geometric analysis of shell coiling: problems. *J. Paleontol.* 40:1178-1190.
- SEILACHER, A. 1972. Divaricate patterns in pelecypod shells. *Lethaia* 5:325-343.
- SEILACHER, A. 1973. Fabricational noise in adaptive morphology. *System. Zool.* 22:451-465.
- TAYLOR, J. D. 1973. The structural evolution of the bivalve shell. *Palaeontology* 16:519-534.
- TAYLOR, J. D., W. J. KENNEDY & A. HALL. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea, Conclusions. *Bull. Brit. Mus. (Natur. Hist.)* 22:253-294.
- VOGEL, K. 1975. Endosymbiotic algae in rudists? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 44:63-69.
- YANCEY, T. E. 1982. The alatoconchid bivalves: Permian analogs of modern tridacnid clams. *Third North American Paleontological Convention, Proc.* 2:589-592.

Rates and Processes of Compensatory Buoyancy Change in *Nautilus macromphalus*

by

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Abstract When faced with sudden buoyancy gain or loss, specimens of *Nautilus macromphalus* undergo compensatory buoyancy change. Rates of compensatory buoyancy change (as measured by weight gain or loss in seawater) depend upon animal size and the amount of initial buoyancy change; the higher the initial buoyancy gain or loss, the higher the compensatory buoyancy change rates. For the experiments described here, the mean rate of compensatory buoyancy change during the first 10-h period following the initiation of the experiment was 0.15 g/h of weight gain for those mature *N. macromphalus* made suddenly more buoyant, and 0.10 g/h of weight loss for the nautilus made suddenly less buoyant. During subsequent 10-h periods, the rates of weight gain for the initially buoyant animals dropped to less than 0.05 g/h, while rates for the initially heavy animals stayed approximately the same. The ultimate amount of weight change for highly buoyant nautilus was limited to about 5 g of in-seawater weight increase, whereas the weight loss in the animals made artificially heavy was unlimited, as long as there was cameral liquid in the chambers to be removed. Positive buoyancy of as little as -5 g was sufficient to trap a mature *N. macromphalus* at the surface, so that no amount of swimming would allow resubmergence.

INTRODUCTION

THE PHRAGMOcone of an ectocochliate cephalopod serves to reduce the overall density of shell and animal to approximately that of seawater (DENTON & GILPIN-BROWN, 1966). It has been proposed that an additional function of the phragmocone is to produce buoyancy change on demand, either for vertical migration or for compensatory buoyancy change (HEPTONSTALL, 1970; MUTVEI & REYMENT, 1973). The latter, compensatory buoyancy change, can be defined as density change or buoyancy change brought about by the animal in response to some sudden addition or reduction in the animal's specific gravity. HEPTONSTALL (1970) used, as an example, the case of the ammonoid *Buchiceras bilobatum*, which, during life, became covered with oysters (first described by SEILACHER, 1960). Heptonstall showed that the overgrowth of oysters on the shell of the living ammonite would have required compensatory action by the ammonite, in this case a reduction of overall shell density, to maintain neutral buoyancy. Other, perhaps more common examples requiring compensatory buoyancy change can be readily observed in living *Nautilus*. *Nautilus* shells of all species commonly exhibit healed breaks. In some cases, the scars

of what must have been very large breaks are visible, indicating that at some time during the life of the nautilus, many grams of shell material were suddenly lost (Figure 1). Another type of buoyancy change common in nautilus would come from windfall feeding. Nautilus appear to be opportunistic feeders. In New Caledonia, specimens of *Nautilus macromphalus* are known to eat lobster molts (WARD & WICKSTEN, 1980). The ingestion of molt material makes the nautilus more dense. In both of these examples, the action produces rather sudden changes in the buoyancy of the animal, in the first place making it lighter or less dense, in the second, heavier or more dense. The purpose of this paper is to describe experiments conducted with specimens of *Nautilus macromphalus*, designed to test the potentiality and characteristics of compensatory buoyancy change in *Nautilus* under these types of conditions.

MATERIALS AND METHODS

Specimens of *Nautilus macromphalus* (the only species used in this study) were captured in baited traps at 150 to 400 m in New Caledonia and then immediately trans-

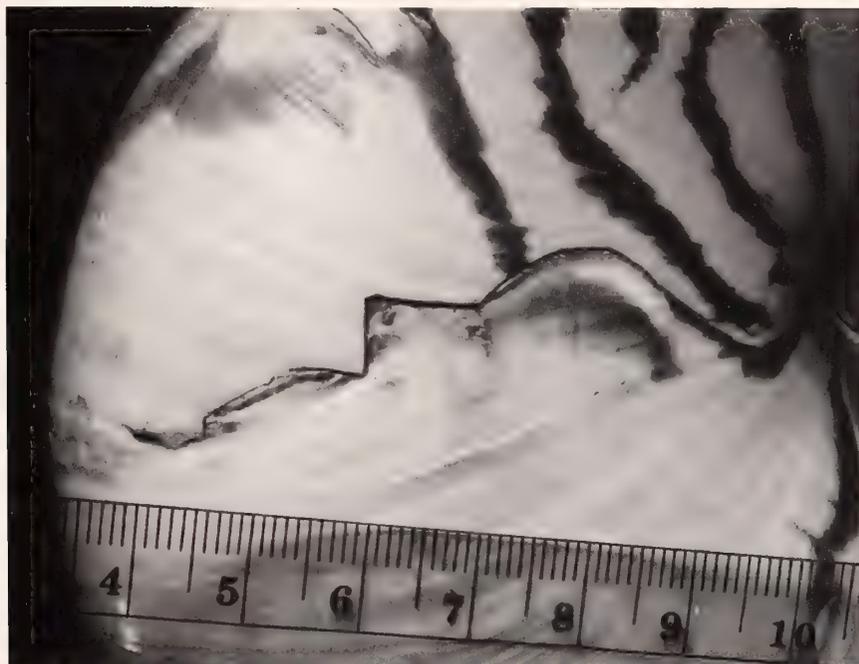


Figure 1

Shell break in *Nautilus* that would have resulted in a sudden loss of buoyancy. Causes of such shell breaks are unknown, but probably result from mechanical impact, predatory attacks, or intraspecific competition.

ported in cooled seawater to a nearby refrigerated seawater system, maintained at 17–18°C. To determine weight in seawater (which will serve as a quantitative descriptor of buoyancy), the nautilus were tightly wrapped in a piece of cheesecloth of known seawater weight, and while still being held underwater, transferred to a submerged rigid plastic box of known seawater weight, suspended by a wire from a modified, electronic top-loading balance (Ohaus Brainweight model 1500). The balance had a sensitivity of 0.1 g. *Nautilus* specimens with densities higher than that of seawater gave positive readings on the balance, while those lighter than seawater gave negative readings. Neutral buoyancy (a nautilus with the density of seawater) zeroed the balance.

Even using the wrapping procedure, the respiratory movements of the nautilus within the closed plastic box sometimes caused sufficient movement to produce a range of weight values. Under these conditions, the balance gave a stream of values, with those considered significant (by the balance) marked by a “g” after the reading. Each data point used in this study is the mean value of 10 stable “g” readings recorded on the balance. The mean standard deviation of 100 randomly selected data points used in this study (1000 balance measurements) was found to be 0.132 g.

Prior to each experiment, the nautilus were fed and radiographed. Except on very long-term experiments (more than 100 h), the nautilus were not fed during the course of the experiments, because feeding significantly increased

weight (both in air and in water). To observe rates of liquid movement into the phragmocone, the last three to five chambers in each specimen were drilled and the cameral liquid volume in each chamber measured or removed using methods described by WARD & GREENWALD (1982). The holes drilled in the chambers were resealed with tapered, hard-rubber stoppers, earlier determined to be leakproof using this procedure (WARD & GREENWALD, 1982). The buoyancy of the experimental animals was then suddenly either increased (by removing shell material from the apertural region with needle-nosed pliers, and in some cases by removing cameral liquid from the first three chambers as well) or decreased (by adding new liquid to chambers, or by adding weights cemented to the side of the shell). To ensure that the drilling procedure was not in some unknown way affecting experimental results, one animal (No. 10) was made more buoyant through shell breakage, but not drilled. This animal showed compensatory weight change similar to those in the drilled animals.

The term buoyancy is used throughout this paper. However, the measures used in this study are weights in seawater and density (specific gravity, determined from weight in seawater and weight in air). In this paper, weight in seawater is used as a descriptor of buoyancy, for lack of a better method of attempting to quantify a qualitative term. A nautilus referred to as 5 g positively buoyant, or 20 g negatively buoyant, refers to specimens weighing –5 or +20 g respectively on the zeroed balance. Animals

showing increasing buoyancy were undergoing reductions of seawater weight and density.

RESULTS

Control Experiments: No Induced Buoyancy Change

The weights in seawater of freshly captured nautilus have been previously measured by DENTON & GILPIN-BROWN (1966), WARD *et al.* (1977), and WARD & MARTIN (1978). In every case, the computed densities of the observed specimens have been equal to, or slightly higher than, seawater density (therefore, most display negative buoyancy). In the one study in which weights in seawater were followed through time in aquarium-maintained animals (WARD & MARTIN, 1978), all animals eventually showed increasing buoyancy. In this latter study, however, the weighings were conducted on animals anaesthetized in a 2% solution of urethane in seawater, and maintained in water temperatures of 23 to 26°C. The observations listed here are on unanaesthetized animals kept at cooler temperatures.

The weights in seawater of four freshly captured *Nautilus macromphalus* used in this study are shown in Figure 2. These animals showed a seemingly random fluctuation near neutral buoyancy (0 g). Error bars showing the amount of experimental error (three standard deviations) in each direction of a reading) are shown on this graph. No pattern of day versus nighttime weight patterns could be detected. These four animals, without experimentally produced buoyancy change, serve as control animals against which the following experiments and observations can be compared.

Induced Buoyancy Change: Compensatory Buoyancy Change in Reaction to Increased Buoyancy

To test for the possibility of compensatory change in nautilus made artificially more buoyant, specimens were made suddenly more buoyant by either the removal of cameral liquid, the removal of shell material, or both. This latter procedure mimics the effect of shell breakage, which could occur through either mechanical action (such as impact in shallow water, high energy environments) or predation. Following the episode of increased buoyancy, the nautilus specimens were weighed periodically (generally at 15–30-min intervals during the first 2 h, followed by every one to two hours).

The results of these experiments are shown in Figure 3. In most cases significant weight increases occurred after the initiation of the experiment. Increase in weight (decrease in buoyancy) was usually apparent within the first hour, and sometimes in as little as 30 min. The rate of weight increase was highest during the first 10 h following the initiation of the experiments, and then tapered off, so that most curves of buoyancy change can be seen to descend steeply during the first 10 to 20 h, and then level off after about 30 to 40 h. This suggests that the rate of

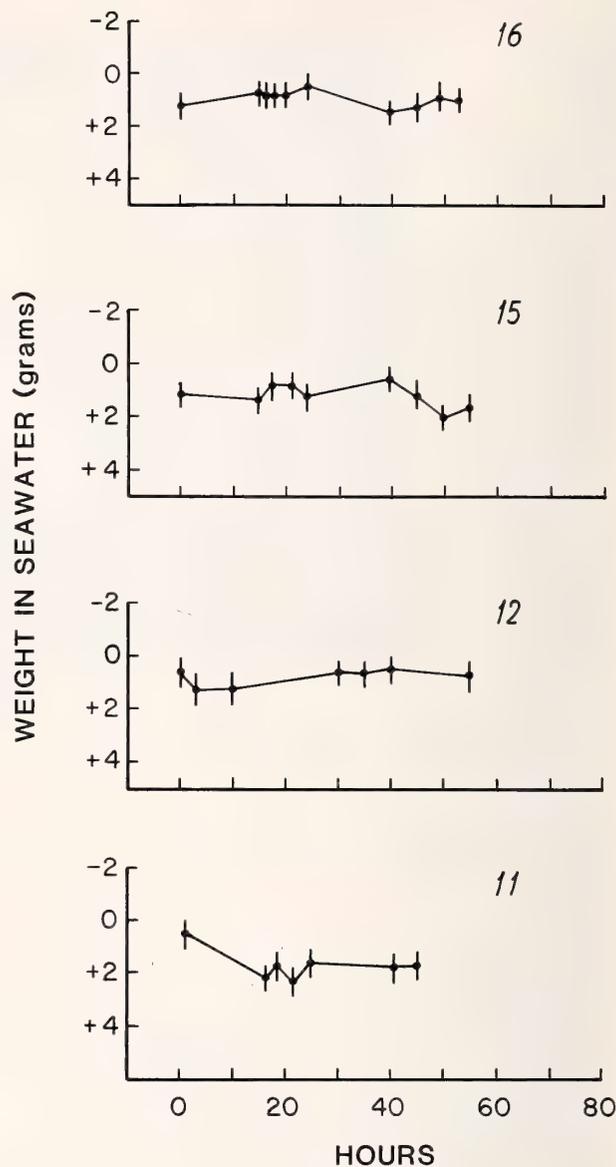


Figure 2

Weight in seawater of four freshly captured *Nautilus macromphalus* (specimens No. 82-16, 15, 12, and 11). The sizes of these animals can be found in Table 2. None of these animals was manipulated in terms of its buoyancy; these measures can, therefore, serve as controls against which the following experiments, involving sudden buoyancy change, can be compared. The vertical bars on the graphs refer to estimated experimental error (0.3 g). Experimental error comes from sensitivity of the balance (0.1 g) and the weighings themselves. Although no subsequent graphs show the error bars, all points listed on subsequent graphs have similar estimated error ranges.

compensatory buoyancy change decreases with time, or has a limit to the amount of change. To test this, mean values for aggregate weight change during 10-h increments following the initiation of the experiments were

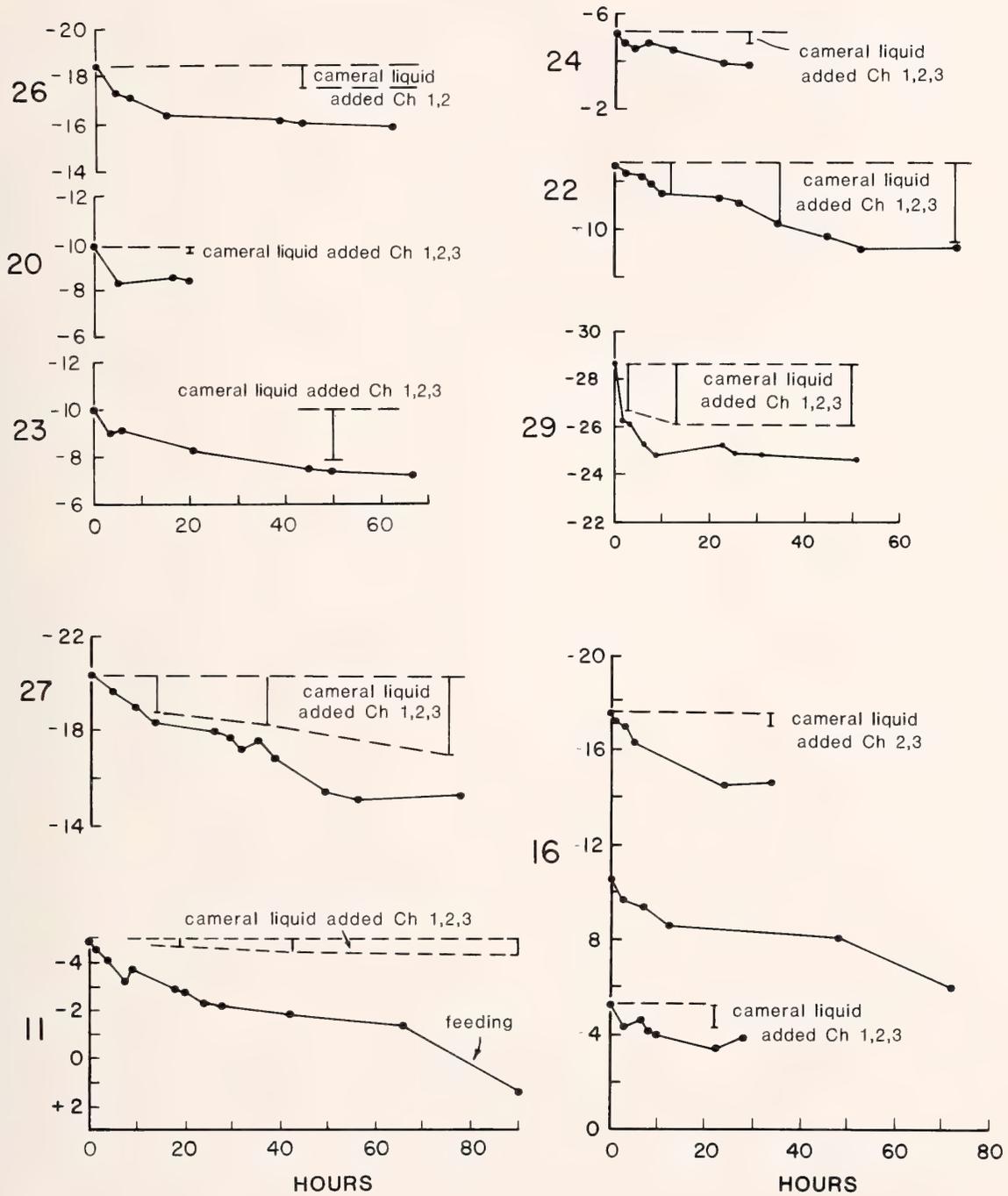


Figure 3

Compensatory buoyancy change in nine *Nautilus macromphalus* made positively buoyant through cameral liquid removal, apertural shell removal, or both. The vertical axis in each graph refers to weight in seawater; the horizontal axes show the number of hours after the initiation of each experiment. The portion of each graph labeled "cameral liquid added" shows the amount of buoyancy change that can be attributed to measurable chamber refilling with cameral liquid.

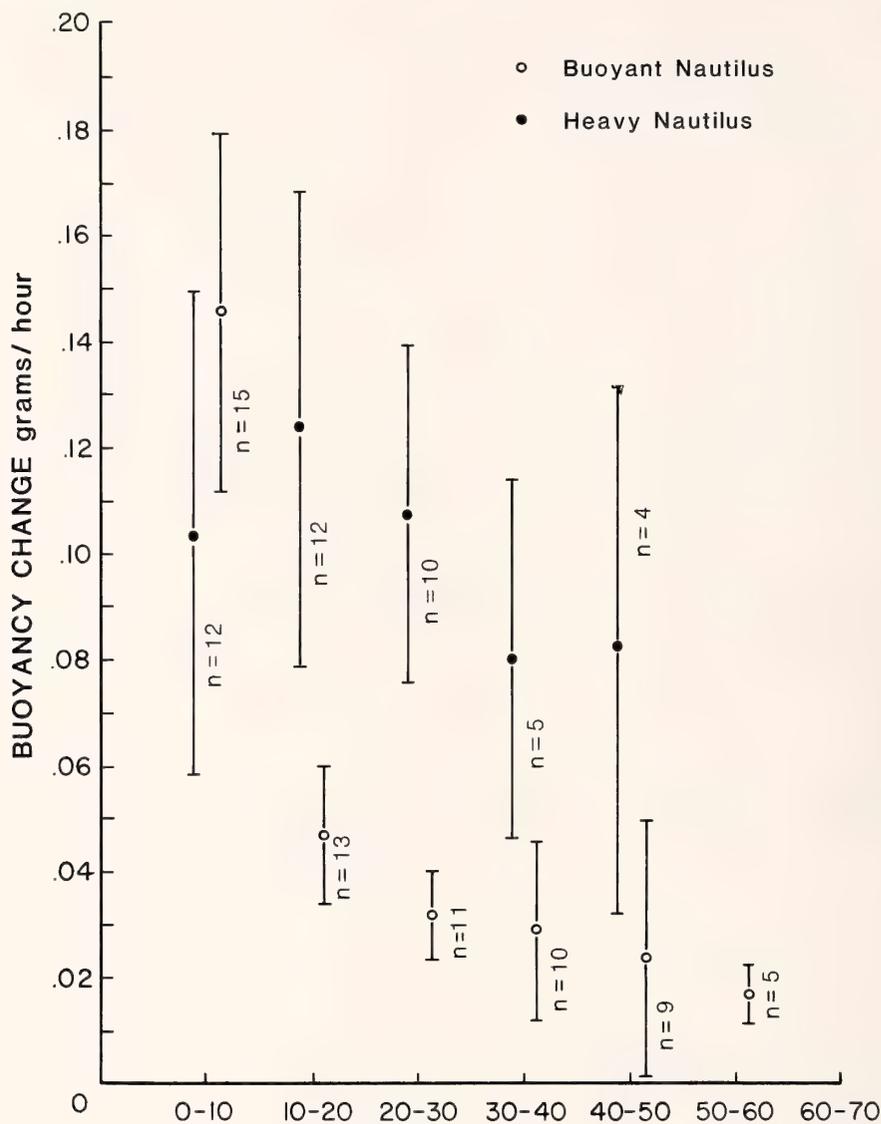


Figure 4

Mean seawater weight changes in 10-h increments for *Nautilus macromphalus* made suddenly positively buoyant (open circles) and negatively buoyant (closed circles). Error bars indicate 95% confidence limits using two-tailed tests for significance; "n" refers to the number of experiments used to compute means. Mean rates of compensatory buoyancy change are not significantly different for positive and negative animals during the first 10-h intervals, but then change. Animals made positively buoyant appear to have a limited compensatory response, as indicated by the significant drop in buoyancy change during the second and later 10-h increments.

computed. These figures are shown in Figure 4 along with the number of observations for each value. The highest rate of weight change occurred during the first 10 h (0.15 g/h) for the 15 specimens used in the experiment. The following 10-h increments had significantly lowered rates of weight change; the second 10-h period showed rates of about 0.05 g/hour. Subsequent 10-h periods showed similarly lowered rates. These experiments suggest that the greatest amount of compensatory buoyancy change will

occur within the first 10 h, and that subsequent change will be far less.

A second group of experiments was designed to examine the relationship between rates of compensatory buoyancy change in response to increased buoyancy and the amount of buoyancy change initiating the response: does an ever higher initial buoyancy change produce ever faster compensatory changes in response? To test this, the initial amount of induced weight change was plotted against

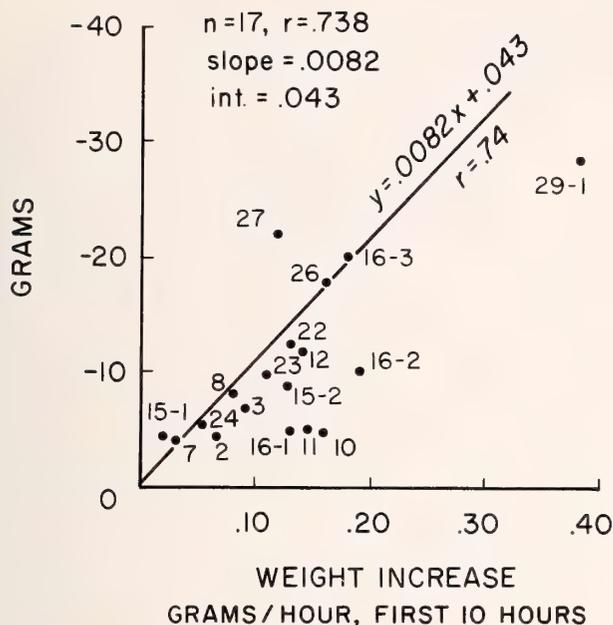


Figure 5

Relationship between rate of compensatory buoyancy change in animals made suddenly positive, against amount of positive buoyancy initiating the experiment. There does appear to be some positive correlation between the rate of compensatory refilling response and the amount of buoyancy increase at the start of the experiment. Previously, GREENWALD *et al.* (1980) and WARD (1982) have shown that a similar relationship exists between the opposite conditions, *i.e.*, liquid emptying rates and initial *negative* buoyancy.

compensatory response for the first 10 h (Figure 5). The correlation coefficient for the linear regression is 0.738. Apparently the initial amount of buoyancy change does affect the rate of compensatory response.

The ultimate amount of compensatory buoyancy change was limited. The maximum weight change observed was an increase of 6.5 g (No. 27), and the mean amount was slightly less than 4 g. From these experiments, it appears that the compensatory response to suddenly increased buoyancy is, at least at surface pressure, extremely limited, and in this species probably never reaches as much as 10 g, regardless of the initiating buoyancy change.

Induced Buoyancy Change: Decreased Buoyancy

Experiments examining liquid emptying rates in response to buoyancy change have previously been made by GREENWALD *et al.* (1980) and WARD (1982a). Compensatory buoyancy change in nautilus specimens made heavy by the addition of cameral liquid to partially or completely emptied chambers, or through the addition of weights to the side of the shell, was monitored in a fashion similar to that used for nautilus made artificially less dense. The heavy nautilus were weighed in seawater at 30-min to 2-h intervals, and the aggregate amount of weight change

recorded. The results of these experiments are shown in Figures 6-7.

As in the case of artificially increased buoyancy, the animals made suddenly heavier than seawater showed compensatory buoyancy change. The rates of weight change during the first 10 h for the nautilus made heavy were not significantly different from the rates of decreasing buoyancy change for the nautilus made light, as described above (-0.10 g/h for the first 10 h, as compared to 0.15 g/h for the nautilus made light). Unlike the experiments with nautilus made lighter, however, these specimens showed roughly similar rates of weight change during the following 10-h intervals (Figure 4). During the second 10-h period, rates were higher than during the first 10 h (0.13 g/h). Subsequent rates per 10-h increments were variable, but never significantly different. Compensatory buoyancy change following sudden buoyancy decrease thus seems different from that following sudden buoyancy increase.

The Mode of Buoyancy Change

In both cases described above, the question of the mechanism involved must be considered. It has been demonstrated that buoyancy change can be effected in a nautilus through the movement of liquid out of, as well as into, chambers (WARD & MARTIN, 1978; GREENWALD *et al.*, 1980; WARD & GREENWALD, 1982). The nature of the weight-change curves in the experiments described here, however, suggests that the mechanism is more complex than the simple removal or addition of liquid from reservoirs of liquid pooled at the bottoms of the last several chambers.

To examine the nature of the buoyancy change system, the amount of cameral liquid in each experimental animal was measured prior to the initiation of each experiment. Each nautilus was radiographed, and those specimens with visible pooled liquid within their chambers were drilled. As in previously reported cases with mature nautilus specimens, the presence of pooled water was usually found only in the last one or two chambers; it has been shown that mature nautilus characteristically contain little or no cameral liquid (COLLINS *et al.*, 1980). In the cases where nautilus specimens were made heavier through the addition of new cameral liquid into the last one or two chambers, the original chamber volume was also noted, so that the new chamber volume at the start of the experiment was known. Through repeated experiments of adding or removing liquid into chambers, it was found that experimental error in volume measurement using this technique was within 0.2 ml of the originally implied volume.

If 1 ml of cameral liquid or seawater is assumed to weigh 1 g, then the change of cameral liquid volume should be the same as the change of weight. It soon became apparent, during the course of the experiments, that the weight change of most of the experimental animals ex-

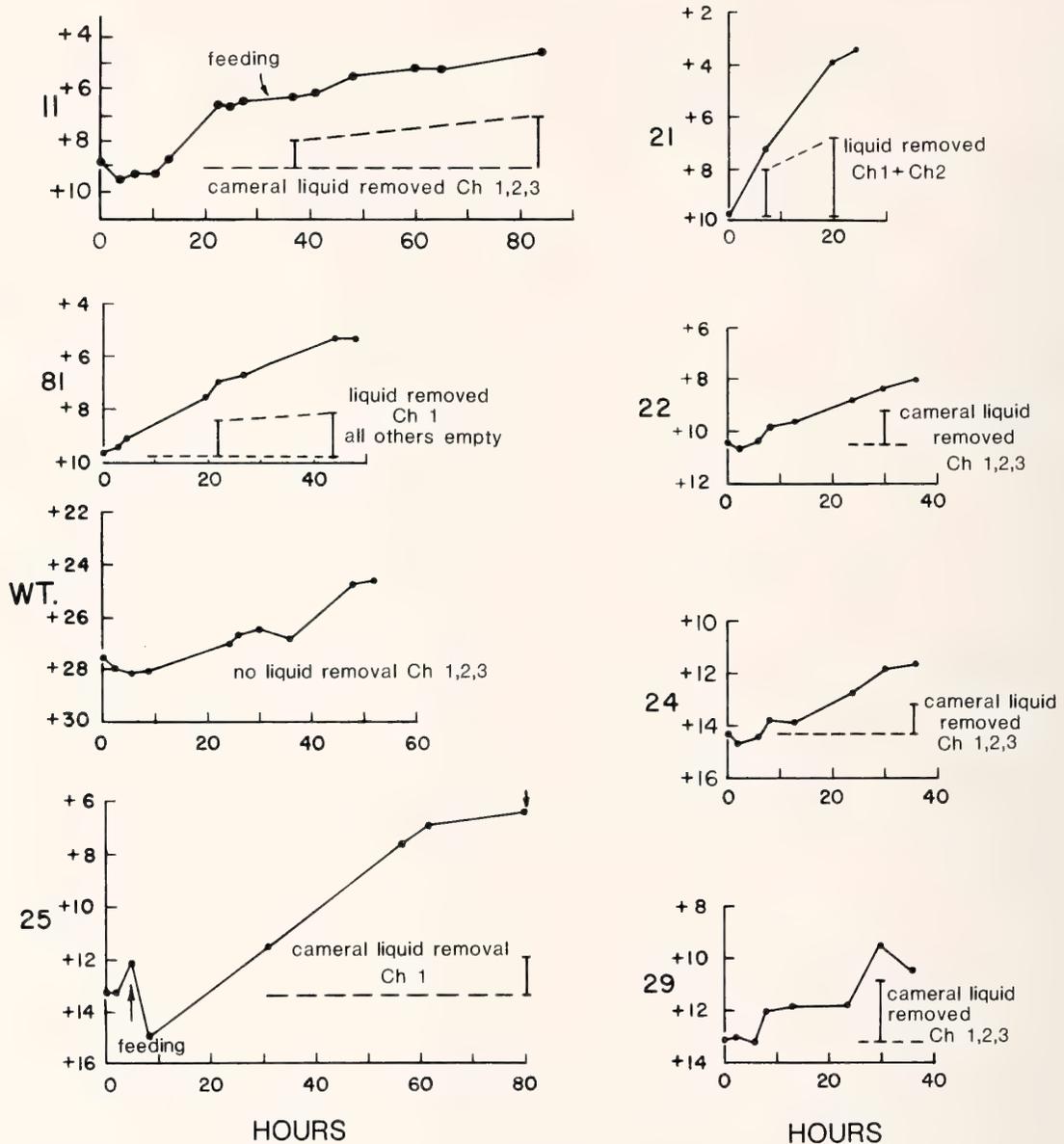


Figure 6

Compensatory buoyancy change in eight *Nautilus macromphalus* made artificially less buoyant by addition of seawater into chambers or addition of metal weights to the shell. The "liquid removed" part of the graph refers to the amount of compensatory buoyancy change that can be attributed to measurable cameral liquid removed.

ceeded the measurable volume change of liquid moving into, or out of, chambers. This is best illustrated in the figures showing experimental results. In these figures, known weight change and volume change are shown on the same graph. The figures have been plotted so as to show the amount of weight change attributed to measurable liquid removal or addition in the last two or three chambers. In almost every case, initial weight change was not caused by addition or removal of pooled liquid; instead, changes in the volumes of these liquids within the

last two or three chambers were only seen *after* a duration of several hours. Only two possibilities exist to explain the observed buoyancy change. Either buoyancy change is being affected by density changes within the soft parts of the animal, or density change is occurring within the phragmocone, but in a manner not observable either with radiographs or in chamber volume determinations.

To test for the possibility of density changes occurring in the body chamber, specimens of *Nautilus macromphalus* were made either lighter or heavier in a manner used in

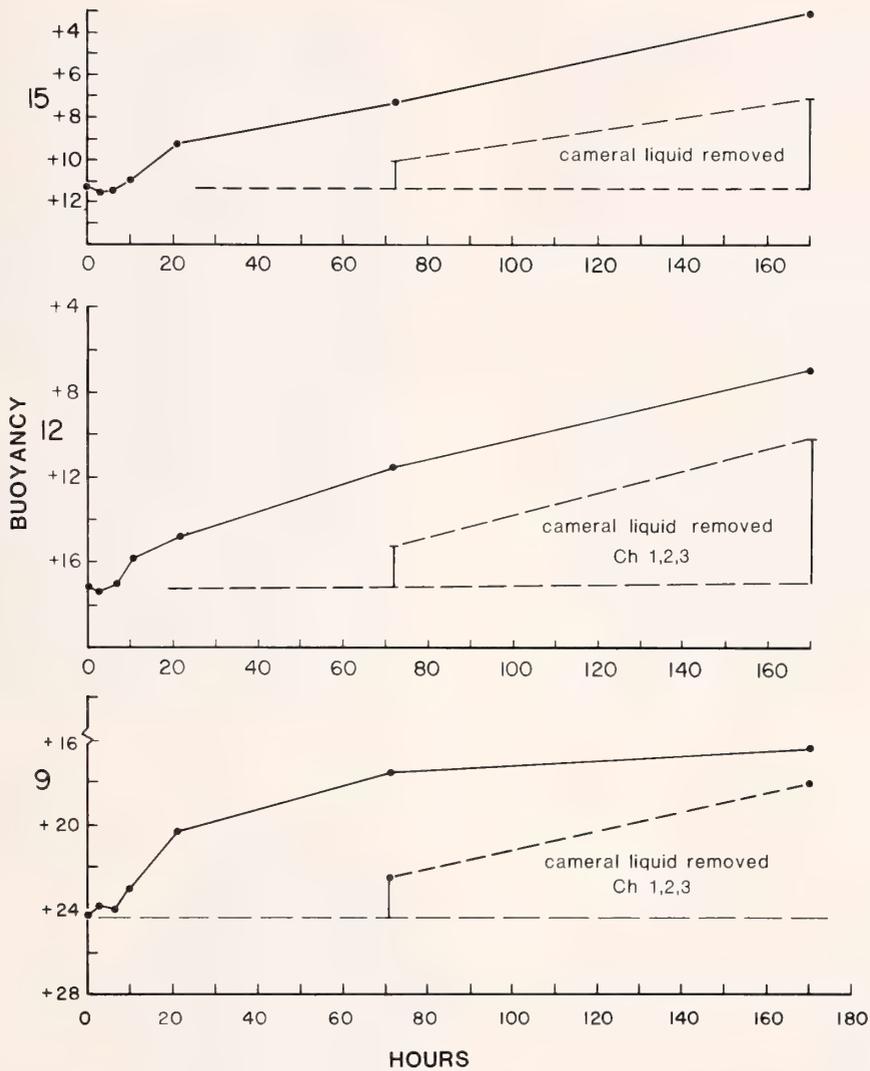


Figure 7

Compensatory buoyancy change in three *Nautilus macromphalus* made less buoyant.

the previous experiments. After the confirmation of weight change (through balance measurements) these animals were sacrificed. Samples of blood, coelomic fluid (from the liver region), and a variety of tissue samples were taken (Table 1). In no case could accurate density measurements (± 0.002) show tissue or fluid densities suggestive of soft-part compensatory response sufficient to account for the observed but unaccounted for weight change. For example, in those animals made heavy, the observed volumes and densities of blood, liver, and coelomic fluid do not appear to be agents of compensatory buoyancy change.

Another possibility is that buoyancy change was occurring within the phragmocone, but not only through the addition or removal of *pooled* liquid (liquid observable on a radiograph as a distinct volume of liquid at the bottom of a chamber) from the last five or so chambers. This

possibility is harder to test for, but is considered to be the cause of the buoyancy change. By breaking open individual chambers, visual observations of the chamber walls indicated that significant volumes of non-pooled water were trapped within the nautilus shell. Most of this appears to be within the pellicle, a hydrophilic membrane that lines the inside of the chambers and covers the outer region of the siphuncle. The chalky layer of the siphuncle could also be a significant reserve of liquid. Also, the use of high-energy radiographic techniques (in contrast to the small, low kv portable machines used in my previous studies) allowed the first observations of the interiors of chambers in the early whorls. Previously, chamber liquid could only be radiographically observed in the last-formed 10 or 11 chambers (chambers of the last whorl). By combining high-energy exposures with high-contrast screens,

technicians at the Radiographic Facility of the Magenta Hospital, New Caledonia, succeeded in penetrating and observing earlier chambers. These chambers showed small but significant liquid volumes, usually trapped at the septal wall-shell wall intersections (the sutures), rather than occurring as pools of liquid at the bottoms of the chambers. These early chambers thus show small volumes of water, long after emptying, in seemingly gravity-defying orientations (Figure 8).

In the event of rapid buoyancy change, it appears that the liquid is moved to or from the pellicle and sutural regions (perhaps in concert with the reservoir contained within the chalky tube of the siphuncle). These volumes are so small (less than 0.2 ml) that movement would not be detected by changes in the volume of "pooled" liquid within the chamber, if any were present. By acting in concert over many chambers, however, this reservoir could produce a significant volume of cameral liquid. For instance, the movement of just 0.1 ml into, or out of, a single chamber would not be measurable by volume determination methods. Produced over 32 chambers, however, over 3 g of buoyancy change would be effected. If this system acts in this way, it may answer the question posed by WARD *et al.* (1980) as to why the siphuncle remains unblocked in life long after earlier chambers have been emptied, and seemingly would be of no further use to the animal's buoyancy system. The chambers, with their thin linings of hydrophilic membrane, may remain active and useful throughout life as a means of allowing "rapid" buoyancy change through admission or removal of small volumes of liquid.

Size and Buoyancy Change

If the pellicle system is indeed the source of the rapid, "unaccounted" buoyancy change observed in the experimental animals, it should become increasingly important in increasingly larger nautilus. The amount of buoyancy change allowed by the pellicle system would be dependent on the surface area of the chambers, and thus would be dependent on the number of chambers present. Larger nautilus should be expected to show larger amounts of buoyancy change.

To examine the rates of compensatory buoyancy change

Table 1

Soft-part densities for *Nautilus macromphalus* undergoing compensatory buoyancy change.

Number	Initial buoyancy	Soft-part density (± 0.002)	Digestive gland density (± 0.002)	Coelomic fluid density (± 0.01)
81	negative	1.064	1.073	1.06
21	negative	1.064	1.090	1.03
Wt	negative	1.063	1.070	1.06
25	negative	1.067	1.069	1.06
20	positive	1.068	1.089	1.02
15	positive	1.059	1.081	—
83	positive	1.063	—	—
24	positive	1.062	1.066	1.03
Flt	positive	1.063	1.068	1.04

in differently sized specimens of *Nautilus macromphalus*, immature specimens of various sizes were made between 4 and 7 g positive, and the rate of buoyancy change then was monitored as in the previous experiments. Unfortunately, during these experiments it proved impossible to capture very small *N. macromphalus* (less than 15 chambers); almost all of the specimens used in this study were mature or within one or two chambers of final size.

The list of animals and experiments in which liquid movement was monitored is shown in Table 2. Only three specimens, No. 82-7, 14, and 22, had fewer than 30 or 31 chambers. All three of these specimens showed lowered amounts of "unaccounted" weight change. The two smallest, No. 7 and 14, showed virtually no weight changes. However, it could be that smaller animals were more stressed by the experimental procedures.

Buoyancy Change and Depth Equilibrium

The last question examined here relates to the amount of positive buoyancy necessary to drive a nautilus to the surface and block it there, so that no amount of swimming effort allows resubmergence. Six mature or near mature specimens of *Nautilus macromphalus* were made between 6 to 8 g lighter than seawater. With these buoyancies, all

Figure 8

Radiographs of four freshly captured specimens of *Nautilus macromphalus*. These specimens were radiographed with a high-energy hospital radiograph unit, with the use of high-contrast radiograph film in an image enhancement screen. These radiographs provide the first glimpse into the interior whorls. On normal radiographic exposures of nautilus shells, the interiors of only the last ten or so chambers can be observed; earlier chambers are screened from view by shell (whorl) overlap. The high energy radiographs penetrate two separate shell walls, and clearly show the presence of small volumes of liquid in early chambers. Previously, liquid in *Nautilus* was thought to be present in measurable volumes only in the last formed 4 or 5 chambers in juveniles, and one or two chambers in matures. Note the orientations of the liquid in these chambers, at the top of the chambers, caught between the shell and septal walls, rather than at the bottom of the chambers (the radiographs were taken in the living orientation of the specimen and rotated 90% counterclockwise in the figure, so that "up" is to the left).



Table 2

Buoyancy change in *Nautilus macromphalus*. "Unaccounted" buoyancy change refers to buoyancy change that cannot be attributed to water movement into or out of the last 2 chambers.

Specimen number	Total weight (g)	Number of septa	Starting buoyancy	Total buoyancy change (g)	"Unaccounted for" buoyancy change (g)	Percentage of buoyancy change due to "unaccounted"
7	369	26	-4.5	0.5	0	0
9	665	30	+24.0	7.8	4.4	56
12	756	31	+17.0	10.0	3.6	36
14	219	25	-5.0	0.0	0	0
15	705	31	+11.0	8.2	3.5	43
15	—	—	-4.2	0.9	0	0
15	—	—	-8.5	2.0	1.0	50
16	569	30	-5.0	1.7	1.0	59
16	—	—	-17.5	2.8	2.3	82
20	807	31	-9.8	1.0	0.8	80
21	658	31	+10.0	6.4	3.0	47
22	458	28	+10.5	2.5	0.8	32
22	—	—	-12.8	3.6	0.2	05
23	709	30	-10.0	2.9	0.4	14
24	688	30	-5.0	1.3	0.7	54
24	—	—	+14.0	2.4	1.2	50
27	739	31	-20.2	4.8	1.6	33
29	541	30	-29.0	4.0	1.4	35
29	—	—	+13.1	3.5	1.2	34
81	780	30	+9.6	4.6	2.6	56
w+	708	31	+27.5	3.0	3.0	100

$\bar{X} = 1.15$, $SD = 1.1$, $n = 7$, for unaccounted buoyancy change, with starting buoyancy positive.*

$\bar{X} = 2.81$, $SD = 1.1$, $n = 8$, for unaccounted buoyancy change, with starting buoyancy negative.*

* Excluding immature animals No. 7, 14, 22.

were trapped at the surface. Each of these animals was then periodically weighed, and its position (on the surface, or submerged) noted. All showed buoyancy reduction. Each nautilus was weighed the first time it was found to be either attached to the wall or swimming so that the entire shell was submerged; the weights at first submergence varied between -3.5 and -5.0 g. It appears that more than about 5 g excess buoyancy is sufficient to isolate a mature *Nautilus macromphalus* on the surface.

DISCUSSION

The experiments and observations reported in this paper suggest that compensatory buoyancy change occurs in specimens of *Nautilus macromphalus*. The following points are also raised:

(1) Rates of compensatory weight change for positive and negatively buoyant *Nautilus macromphalus* specimens (surface held animals) are not significantly different (although the directions of change are opposite, with one being an increase in weight, the other a decrease in weight) during the first 10 h, but then change. Those animals originally made negatively buoyant (heavier than seawater) continue to reduce buoyancy at approximately constant rates. Those animals made positively buoyant (light-

er than seawater) show marked reduction in buoyancy change after the first 10-h period.

(2) Because of the change in rates in the positively buoyant specimens, the *potential* for buoyancy change is limited in buoyant animals. For the nautilus made more than 5 g positively buoyant, the range in total buoyancy change was found to be from 1.4 to 6.5 g \pm 0.3 g ($\bar{X} = 3.8$ g). There was no limit of buoyancy change for animals made negatively buoyant. This indicates that the cameral liquid refilling system (in a compensatory response) allows replacement of a limited volume of water in emptied chambers (at the surface), whereas the cameral liquid *emptying* system has no limitation, as long as there is liquid within the chambers to remove. In mature animals, however, with small volumes of pooled cameral liquid, compensatory responses would be ultimately limited to liquid pooled and liquid tied up in the pellicle, and hence be quite limited as well.

(3) Positive buoyancy of more than 5.0 g is sufficient to trap mature *Nautilus macromphalus* at the surface, so that no amount of swimming allows resubmergence. Negative buoyancy of 5 g, however, does not trap a mature *N. macromphalus* at the bottom. This is probably due to the position and anatomy of the hyponome, which produces water jet propulsion. The hyponome, located beneath the

Table 3

Liquid refilling rates in single chambers at the surface and at depth.

Specimen no.	Depth (m)	Chamber number	Liquid refilling rates $\mu\text{L}/\text{h}$
83-2	0	1	8.3
83-16	0	1	16.6
83-15	0	2	5.0
83-15	0	2	13.7
83-22	0	1	125
83-27	0	1	93
83-24	0	1	12.5
(From WARD & GREENWALD, 1982)			
81-5	0	1	63
81-5	250	1	100
81-5	250	1	21
81-10	0	1	70
81-10	250	1	75
81-20	0	2	54
81-20	250	2	38

tentacles and head region, is not long enough to direct jets of water directly upward, which would push the animal down. The hyponome is much more efficient at pushing the animal off the bottom, as it can jet directly downward.

(4) Compensatory refilling or emptying appears to occur over many chambers, not just the last two or three. There appear to be significant reserves of liquid within the chambers (perhaps mostly maintained in the pellicle) that allow for removal of liquid from chambers that do not have pooled liquid. Conversely, *Nautilus* specimens appear capable of replacing liquid into the phragmocone system, and thus increasing density, without accumulating volumes of "pooled" liquid at the bottoms of the chambers. Also, in contrast to previous observations, significant volumes of liquid exist in early-formed chambers.

In some respects the experiments listed here are artificial. For instance, the rates of liquid removal for nautilus held at the surface are always much faster than those for animals held at depth (WARD & MARTIN, 1978), and, hence, the rate figures found and listed above would probably not be equivalent to those of a naturally occurring nautilus undergoing compensatory buoyancy change at depths greater than 50 to 100 m. The deeper the depth, the slower the emptying. On the other hand, specimens of *Nautilus macromphalus* are commonly encountered at near-surface depths (WARD, 1982b), and in these cases the surface rates found in this study would probably be quite similar. In the case of positively buoyant nautilus, those animals having sufficient shell removed would be forced to the surface. In this case, the experiments performed here would directly model the case in nature. For those animals experiencing sudden positive buoyancy at depth, but still maintaining depth even though positively buoyant, it could be argued that the added force of ambient

pressure would force water into the chambers and, hence, allow more rapid compensatory buoyancy change than found in this study. Unfortunately, the logistics of producing in-water experiments on emptying and refilling are extremely difficult. No data are available about the rates of in-water buoyancy change. However, data about the amount (volume) of liquid volume change through time in positively buoyant nautilus held at depth are available (WARD & GREENWALD, 1982). In five specimens of *Nautilus macromphalus* held at a depth of 250 m for periods of 4, 24, or 168 h after artificially induced positive buoyancy, rates of liquid refilling ranged between 21 and 100 $\mu\text{L}/\text{hour}$. Similar rates of refilling for single chambers at surface pressure in this study ranged between 5 and 125 $\mu\text{L}/\text{h}$, while rates listed by WARD & GREENWALD (1982) for surface-held specimens ranged between 54 and 70 $\mu\text{L}/\text{h}$ (Table 3).

Perhaps the most unexpected result of this study was the finding that variable but significant fractions of the ultimate amount of buoyancy change could not be attributed to measurable liquid volume change within the last-formed two or three chambers in most specimens. Non-pooled liquid is that liquid within a chamber that is trapped by the pellicle and within porous calcareous layers of the siphuncular neck and connecting ring. It cannot be shown experimentally that the removal of this liquid (and also the addition of liquid into this system) is the cause of unexplained density change. However, because it can be demonstrated that density changes are not being produced from within the soft parts, there remain only the small-volume early chambers, and the pellicle and other porous regions within the chambers, that could conceivably be acting for liquid storage. During emptying (following initiation of compensatory buoyancy change in response to increased density) liquid must first be removed from the chalky layers of the connecting ring and siphuncular neck, passing quickly and directly into the siphuncular epithelium. As these regions become emptied of liquid, more liquid will be drawn onto them from the contiguously attached pellicle of the septal face. The pellicle itself then draws up liquid from any pooled liquid volume present at the bottom of the chamber. In those chambers where no pooled liquid is still present, the pellicle will apparently be emptied until it is essentially dehydrated. At this time the chamber is no longer of any use in density change. Through simultaneous removal of liquid from the pellicles of many chambers, relatively rapid density change occurs prior to the observable removal of pooled liquid reserves, which in mature animals can only be found in the last one or two chambers if present at all.

The pellicle system must have some equilibrium volume. However, it appears to be able to take up and store additional liquid if necessary. In the experiment in which animals were made suddenly less dense, significant proportions of the density change observed could not be accounted for by the accumulation of pooled liquid in the chambers. Again, because density increase through soft-

part tissue change could not be demonstrated, the observed density change must have been through the movement of liquid from the siphuncle onto the pellicle, where it was stored. Continued addition of liquid onto the pellicle results in saturation and the initiation of pooling at the base of the chamber. Apparently, as much as 2 g of weight increase can occur before measurable accumulation can be noted.

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LITERATURE CITED

- COLLINS, D., P. WARD & G. WESTERMANN. 1980. Function of cameral water in *Nautilus*. *Paleobiology* 6(2):168-172.
- DENTON, E. & J. GILPIN-BROWN. 1966. On the buoyancy of the pearly *Nautilus*. *J. Mar. Biol. Assoc. U.K.* 46:723-759.
- GREENWALD, L., P. WARD & O. GREENWALD. 1980. Cameral liquid transport and buoyancy control in chambered nautilus. (*Nautilus macromphalus*). *Nature* 286:55-56.
- HEPTONSTALL, B. 1970. Buoyancy control in ammonoids. *Leithaia* 3:317-328.
- MUTVEI, H. & R. REYMENT. 1973. Buoyancy control and siphuncle function in ammonoids. *Palaeontology* 16(3):623-636.
- SEILACHER, A. 1960. Epizoans as a key to ammonoid ecology. *J. Paleontol.* 34:183-193.
- WARD, P. 1982a. The relationship of siphuncle size to emptying rates in chambered cephalopods: implications for cephalopod paleobiology. *Paleobiology* 8(4):426-433.
- WARD, P. 1982b. Have shell, will float. *Natur. Hist. (Oct)*: 64-69.
- WARD, P. & L. GREENWALD. 1982. Chamber refilling in nautilus. *J. Mar. Biol. Assoc. U.K.* 62:469-475.
- WARD, P. & W. MARTIN. 1978. On the buoyancy of the pearly *Nautilus*. *J. Exp. Zool.* 205:5-12.
- WARD, P. & A. MARTIN. 1980. Depth distributions of *Nautilus pompilius* in Fiji and *Nautilus macromphalus* in New Caledonia. *Veliger* 22(3):259-264.
- WARD, P., R. STONE, G. WESTERMANN & A. MARTIN. 1977. Notes on animal weight, cameral fluids, swimming speed, and color polymorphism of the cephalopod *Nautilus pompilius* in the Fiji Islands. *Paleobiology* 3:377-388.
- WARD, P. & M. WICKSTEN. 1980. Food sources and feeding behavior of *Nautilus macromphalus*. *Veliger* 23(2):119-124.

A Model for Shell Patterns Based on Neural Activity

by

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Abstract. The patterns of pigment on the shells of mollusks provide one of the most beautiful and complex examples of animal decoration. Recent evidence suggests that these patterns may arise from the stimulation of secretory cells in the mantle by the activity of the animal's central nervous system. We present here a mathematical model based on this notion. A rather simple scheme of nervous activation and inhibition of secretory activity can reproduce a large number of the observed shell patterns.

INTRODUCTION

THE GEOMETRICAL patterns found on the shells of mollusks comprise some of the most intricate and colorful patterns found in the animal kingdom. Their variety is such that it is difficult to imagine that any single mechanism can be found. Adding to their mystery is the disturbing fact that, since many species hide their pattern in the bottom mud, or beneath an opaque outer layer, it is doubtful they could serve any adaptive function. Perhaps these wonderful patterns arise as an epiphenomenon of the shell secretion process. This may account for the extreme polymorphism exhibited by certain species—a phenomenon characteristic of traits shielded from selection.

Several authors have attempted to reproduce some of these patterns using models that depend on some assumed behavior of the pigment cells in the mantle that secrete the color patterns (WADDINGTON & COWE, 1969; COWE, 1971; WANSHER, 1972; HERMAN & LIU, 1973; HERMAN, 1975; LINDSAY, 1982a, b; WOLFRAM, 1984; MEINHARDT, 1984). These models have generally been of the "cellular automata" variety, and the postulated rules were chosen

so as to give interesting patterns, rather than to correspond to known physiological processes (WADDINGTON & COWE, 1969; LINDSAY, 1982a, b; WOLFRAM, 1984). In the most recent attempt, MEINHARDT (1984) modeled the growing edge of the shell as a line of cells subject to activator-inhibitor kinetics and a refractory period. He was able to obtain a variety of shell-like patterns, suggesting that an activator-inhibitor mechanism is likely to be involved in the actual process.

Recently, CAMPBELL (1982) proposed a novel explanation for the shell patterns. He reasoned that the pigment cells of the mantle behaved much like secretory cells in other organisms; that is, they secreted when stimulated by nervous impulses. Therefore, the shell patterns could be a recording of the nervous activity in the mantle. Because the phylogeny of mollusks is well represented in the fossil record, the implications of this view for the study of the evolution of a nervous system are obvious.

Building on Campbell's notion, and the suggestive simulations of Lindsay, Meinhardt, and Wolfram, we have constructed a model for the shell patterns based on nerve-

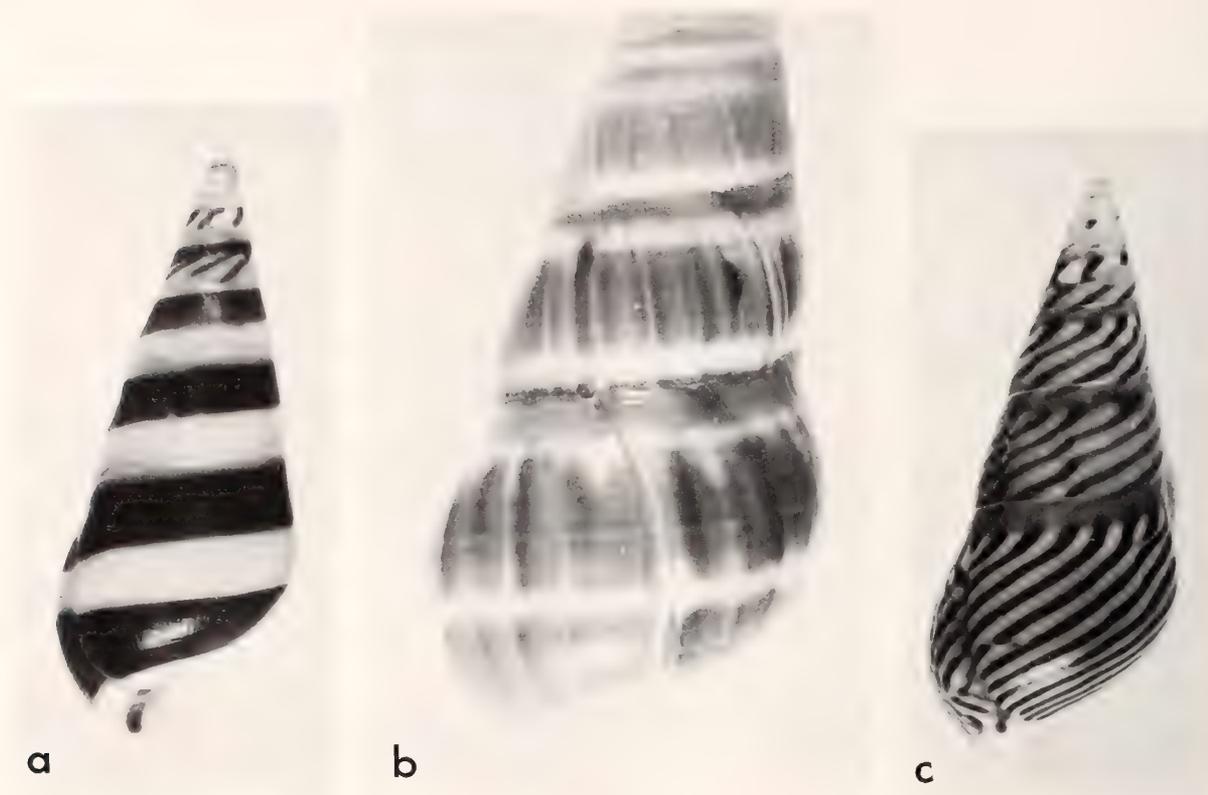


Figure 1

Three fundamental classes of shell pigment markings on *Bankivia fasciata*: a, longitudinal bands; b, incremental lines; c, oblique stripes.

stimulated secretion of the mantle epithelial cells. This model differs from previous models in at least one important aspect: it depends on the "nonlocal" property of nerve nets. That is, because innervations may connect secreting cells that are not nearest neighbors, the possibility of cooperative, long-range interactions is present. This greatly enlarges the pattern-generating repertoire over nearest-neighbor models, and has the virtue of relating directly to the anatomy of the mantle. Despite its simplicity, the model is remarkably successful in mimicking a wide variety of shell patterns.

The paper is organized as follows. First, we catalog a number of regularities in the shell pattern that bear on the neural hypothesis. In particular, those phenomena that implicate a global organizer and preclude strictly local interactions. Second, we sketch the model equations and discuss their behavior. Third, we present patterns generated by simulations of the model and compare them to actual shell patterns. Fourth, we discuss some experiments the model suggests and some generalizations of the model. The Appendices contain the mathematical details of the model and a discussion of how it relates to other models of shell patterns.

OBSERVATIONS ON SHELL PATTERNS

The variety of shell patterns is so enormous that it appears that any attempt to classify them will inevitably leave out many special cases. However, we do not hope to explain all of the patterns; rather, we seek to model the global features shared by all patterns in a restricted class. In particular, we shall focus mostly on the patterns exhibited by *Nerita turrata* and *Bankivia fasciata* (Figures 1, 2, 3). These animals exhibit a representative variety of shell patterns from which we can draw some inferences.

Many pigment patterns of gastropod shells are composites of three basic types of patterns: (a) longitudinal bands that run perpendicular to the lip of the shell, (b) incremental patterns arranged parallel to the growing shell edge, and (c) oblique patterns that run at an angle to the lines of the shell. Some mollusk taxa have more specialized types of patterns, such as the circular eye-spots on some cowry shells, or the intricate tent-like patterns on cone shells. Species differ in the categories of patterns that they display. *Nerita turrata* shells are always dominated by oblique patterns without longitudinal bands, whereas other members of the genus have shells with bands as well



Figure 2

a, an incremental alternation in zebra stripes across the entire whorl of *Bankivia fasciata*; b, simultaneous termination of stripes in *B. fasciata*.

as modified oblique lines. Shells of *Bankivia fasciata* are highly polymorphic, with various combinations of these pattern types, as illustrated in Figure 1.

Longitudinal bands require only simple developmental controls. They could result from a mosaic mantle in which regions continuously deposit pigment, along with shell, separated by mantle zones that do not synthesize pigment. In general, the number and position of bands appears to be a genetic characteristic of the species, or of the individual in a polymorphic species. A second possibility—which we shall illustrate with the model—is that the band width and spacing are characteristic of the neural activity in the mantle. The two mechanisms are not mutually exclusive, as we shall discuss. Banding indicates that variation can be a permanent (*e.g.*, programmed) feature of the mantle edge.

Incremental markings have several sources. Some appear to result from haphazard physiological stresses or environmental factors that temporarily affect the activities of the mantle as a whole. In addition, some species of snails (other than the ones we shall consider here) show regular periodic incremental shell patterns, indicating that they are programmed in a deterministic and cyclic manner. One of the most important incremental features seen on shells of the two species we have chosen for analysis are varices: time periods during which shell synthesis was halted (Figures 2, 3). In general, mollusks do not produce shell continuously, but go through cyclic periods of shell

building (producing about one-third to one-half whorl of shell in the case of *Bankivia fasciata*), followed by “rest” periods during which no shell is secreted. Shell patterns often are reorganized at these major interruptions in shell synthesis, and many sculptured shells produce flamboyant ridges or spines along varices.

Oblique patterns are the most intricate, and have the most implications for our theoretical model. They imply that the activities involved in pigment secretion are coordinated laterally and proceed dynamically across the mantle. For example, the oblique lines shown in most of the shell illustrations in this paper represent a patch or domain of secretory activity that sweeps across the mantle, eventually migrating to its edge. These mobile domains of activity in the mantle behave in a variety of ways to produce the diverse appearance of the patterns.

EVIDENCE IN FAVOR OF LONG-RANGE COORDINATION OF PATTERNS

The neural network model we propose here allows for interactions and coordination beyond nearest neighbors. As we shall demonstrate in the next section, this generalization enormously enlarges the possible types of patterns over previous models, which employ short range, or “nearest neighbor” interactions. What evidence do we have that pigment secretion is indeed a neurally controlled process? We can offer no direct experimental support, for we

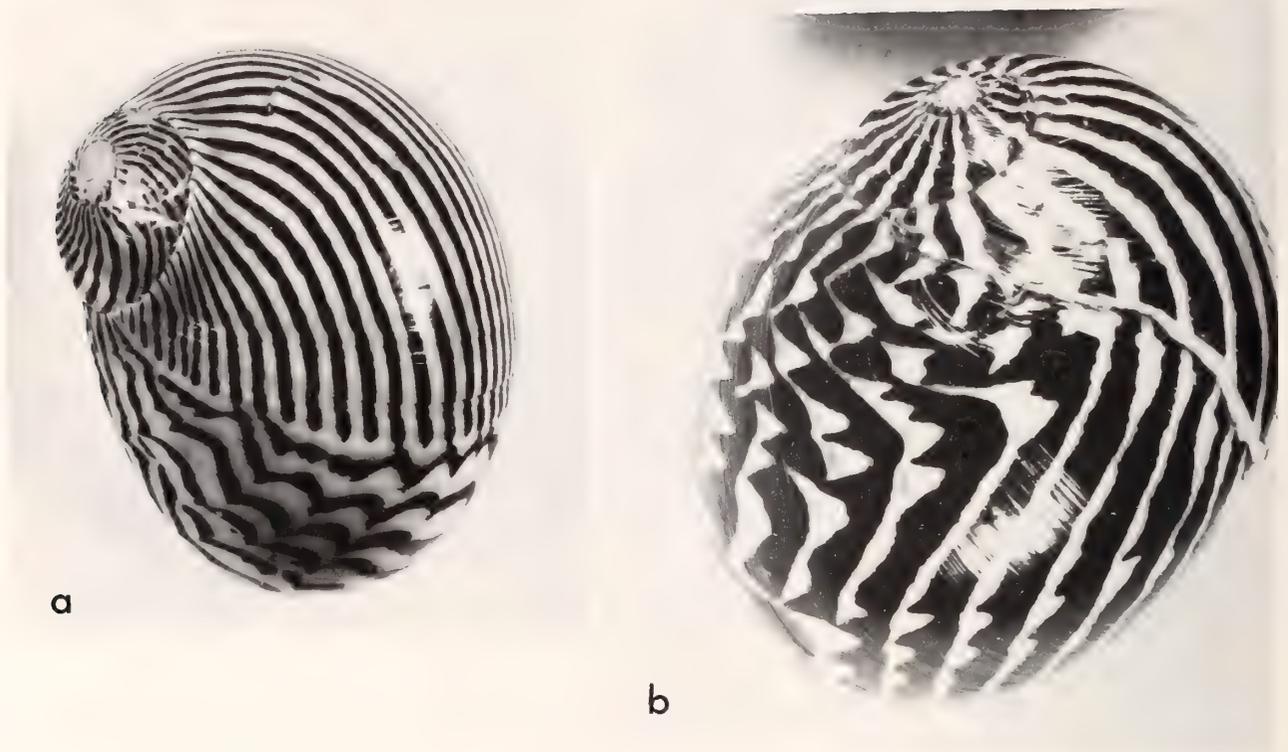


Figure 3

Abrupt reorganization of patterns on shells of *Nerita turrita* (a), and after a break in a shell (b).

have not been able to find any anatomical studies of mantle innervation patterns nor of secretory cell physiology. Therefore, aside from the general observation that secretory cells in most organisms are influenced by neural activity, we can offer only the following indirect evidence in support of the neural activation hypothesis of shell patterns.

Global reorganizations. At a varix, a shell pattern may become systematically and simultaneously reorganized across an entire shell (*cf.* Figures 2a, b), sometimes into an entirely different sort of pattern (Figure 3a). A variety of new patterns may arise in this manner, rather than arising locally and propagating as a wave across the shell. Such changes in the "state" of the pattern can also be initiated by a break in the shell (Figure 3b). It is hard to see how such local perturbations could have such global effects by means other than nervous activity.

It should be noted that physiological and (or) environmental factors can influence the entire mantle simultaneously. Indeed, it has been demonstrated that changes in diet can alter not only the color of the pattern, but the pattern itself (D. Lindberg, personal communication). This fact does not argue for or against the neural hypothesis, for it is relatively common for dietary factors to affect nervous activity, as well as other physiological systems.

However, because diet and other environmental factors affect the pattern formed on a shell, there must be some physiological mechanism that relates the two. That is, there must be some mechanism whereby a systemic effect allows two separated regions of mantle tissue to manifest coincidental patterning. The two main avenues for transmitting stimuli from the environment to the mantle cells are soluble chemical factors (especially hormones) and nervous connections. Both may modulate patterns, but influences that differentially affect discrete parts of the mantle simultaneously seem more plausibly mediated by the nervous system.

Entrainment of lines. Shells in which oblique lines become entrained in the middle of a longitudinal band also suggest coordination of pattern across sizable distances, measured in cell diameters. A particular example of this is the shell in Figure 4a, on which a band appears spaced equidistant from the neighboring bands.

Termination of lines. On the shell in Figure 4b three oblique lines terminated anomalously at about the same time. These events occurred in regions of shell separated by uninterrupted oblique bands. If these changes were due to a signal that propagated from one locale to another, that signal would have to have migrated cryptically past the unaffected domains in the mantle. The simpler inter-

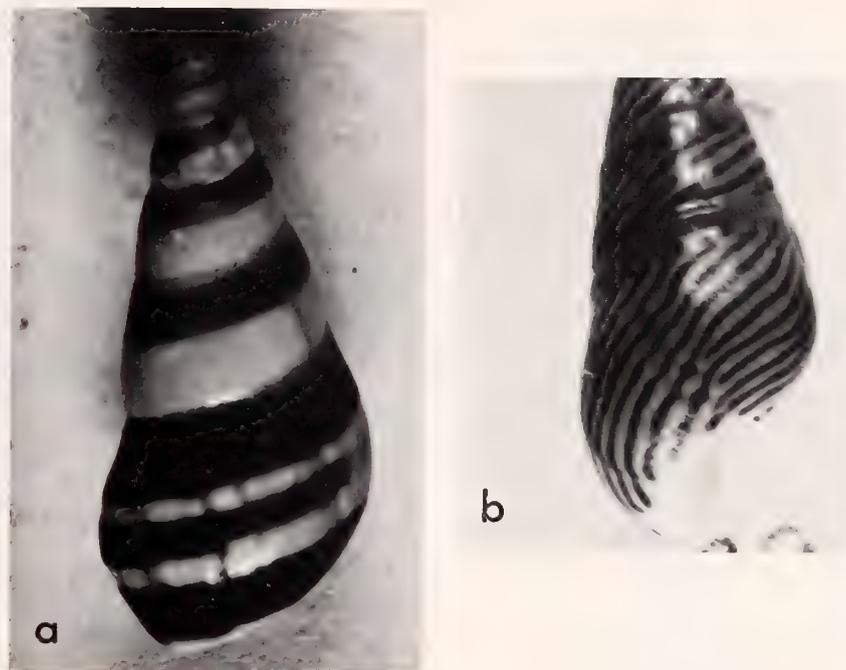


Figure 4

a, appearance of a band spaced equidistantly between adjacent bands; b, simultaneous termination of several separated zebra stripes without noticeable concurrent alteration of the stripes in between.

pretation is that the three separate areas were acted upon by a signal that could be conveyed to multiple local regions simultaneously.

Blotching. A polymorphism (not otherwise described here) among *Bankivia fasciata* shells is blotching (Figure 5). On blotched shells areas of pigmentation abruptly disappear or appear incrementally across large blocks of shell. Alternatively, various segments of the mantle can be affected simultaneously by blotching. Also, for some blotched shells the zone of pigment deposition did gradually spread along the mantle, indicating that blotching can be controlled in a variety of ways.

Global appearance of patterns. On some shells a general type of pattern gradually develops across the entire mantle, but with no indication that the change sweeps across the mantle; the saw-tooth pattern in Figure 6 illustrates this phenomenon.

Checkerboard patterns. (Figure 7) It is possible to create a checkerboard pattern from two sets of colliding waves that propagate by strictly local interactions. However, it is remarkable that the checkerboard as a whole can stay in register without drifting in alignment. This synchronicity implies that a substantial segment of the mantle cycles back and forth between an active and inactive state in precise coordination. Adjacent subzones switch states of activity simultaneously, but in opposite directions.

THE NEURAL MODEL

In this section we present a qualitative description of the shell pattern model. The mathematical discussion is given in the Appendices. The model we shall present here is the simplest possible neural model, and we do not expect to reproduce every shell pattern, even those observed on the two species we have selected for study. However, the model is capable of producing sufficiently diverse patterns that we consider it a reasonable first approximation; we shall suggest a number of improvements which will enlarge the class of patterns, but at the expense of computational simplicity.

BIOLOGICAL ASSUMPTIONS OF THE MODEL

The basic assumption of the model is that the secretory activity of the epithelial cells that generate shell patterns is regulated by nervous activity. Specifically, we assume that the secretory cells are enervated from the central ganglion and secrete or not as they are activated and inhibited by the neural network that interconnects them with the ganglion. Although arguments in favor of this hypothesis were presented above, the issue can only be settled empirically, and experiments are under way to test the neural hypothesis directly. Figure 8 shows a schematic of the



5



6



7

Explanation of Figures 5 to 7

Figure 5. Blotched patterns on *Bankivia fasciata* shells.

Figure 6. Sawtooth patterns on *Nerita turrata*.

Figure 7. Checkerboard patterns on *Bankivia fasciata*.

mantle and the secreting cells (EMBERTON, 1963; KAPUR & GIBSON, 1967; NEFF, 1972; KNIPRATH, 1977).

The specific assumptions that underlie the model are:

(1.) Cells at the mantle edge secrete in intermittent (*e.g.*,

daily) bursts of activity. At the beginning of each session the mantle aligns with the previous pattern and extends it by a small amount. This alignment process probably depends on the ability of the mantle to sense (taste) the pigmented and (or) non-pigment-

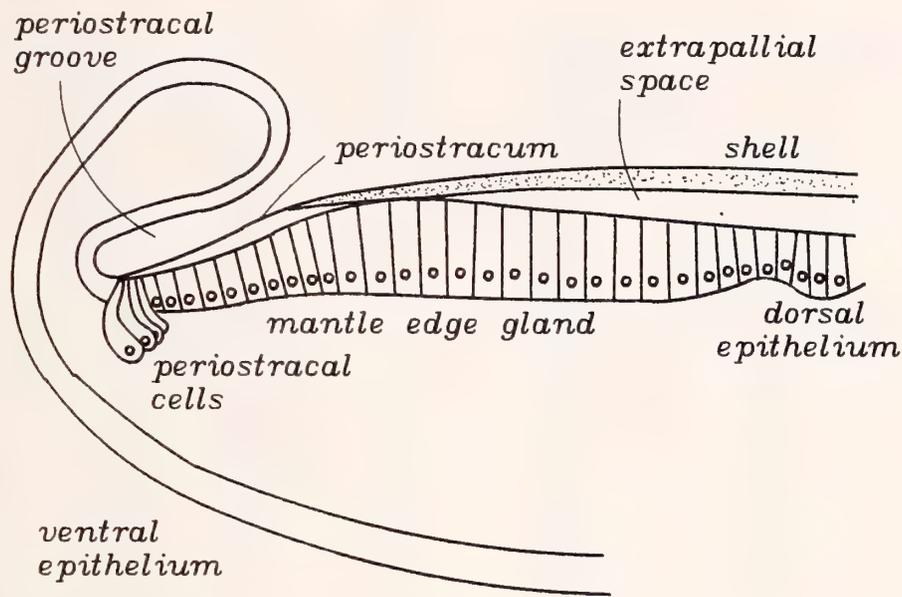


Figure 8

Diagram of the anatomy of the mantle region.

ed regions from the previous period of secretion. Equivalently, a section of pigmented shell laid down during the previous period will stimulate the mantle neurons locally to continue the pattern.

- (2.) The secretion during a given period depends on two factors:
 - (a) the neural stimulation, S , from surrounding regions of the mantle.
 - (b) the buildup of an inhibitory substance, R , within the secretory cell.
- (3.) The net neural stimulation of the secretory cells is the difference between excitatory and inhibitory inputs from surrounding tissue.

We incorporate these assumptions into the model as follows.

Secretion of Pigment Depends on Current Neural Activity

Consider a line of secretory cells whose position along the mantle edge is located by the coordinate x (Figure 9). Let

- $P_t(x)$ = the amount of pigment secreted by a cell at x during the time period t (*e.g.*, one day).
- $A_t(x)$ = the average activity of the mantle neural net at position x on the mantle edge during one secretion period, t .
- $R_t(x)$ = the amount of inhibitory substance produced by cells at location x in day t .
- $S[P]$ = the net neural stimulation at location x during

period t . This will depend on sensing the pigment secreted during the previous period, $P_{t-1}(x)$.

Then the equation governing the neural activity in the mantle during period $t + 1$ is related to the pigment secretion during period t by the equation

$$A_{t+1}(x) = S[P_t(x)] - R_t \quad [1]$$

Equation [1] says that the average neural activity, $A_{t+1}(x)$, at location x on the mantle during day $t + 1$ depends on the net neural stimulation at that location, which is stimulated by sensing the previous day's pigment $S[P_t(x)]$. In the absence of stimulation, this nervous activity decays as the inhibitory substance $R_t(x)$ builds up. The inhibitory substance, R , builds up as pigment, P , is manufactured, and is degraded at a constant rate ($\delta < 1$):

$$R_{t+1}(x) = \gamma P_t(x) + \delta R_t(x) \quad [2]$$

Finally, we assume that secretion of pigment will only occur if the mantle activity is above a threshold value, A^* :

$$P_t(x) = H(A - A^*) \quad [3]$$

where $H(A - A^*)$ is a threshold function for pigment secretion: it is zero for $A < A^*$, and one for $A > A^*$. Equations [1] and [2] describe how the activity, A , and refractory substance, R , evolve in time; having computed A , the actual pigment secretion is given by [3]. In the computer simulations we have simplified the model even further by incorporating equation [3] into equation [1], and writing equations for P directly (*cf.* Appendix A). This modification makes little difference in the computed

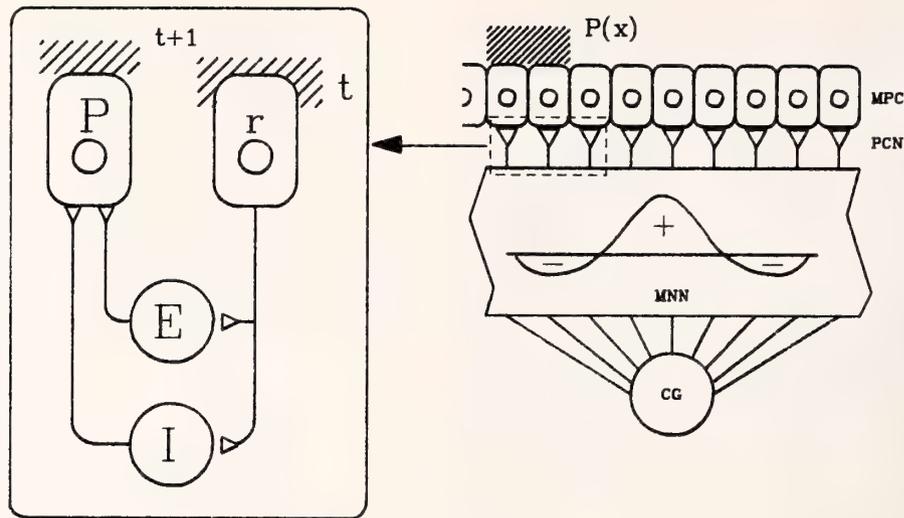


Figure 9

Diagram of the model: MPC, mantle pigment cells; PCN, pigment cell neurons; MNN, mantle neural net; CG, central ganglion; r, receptor cells sensing pigment laid down in time period t ; P, pigment cells secreting pigment in time period $t + 1$; E, excitatory neurons; I, inhibitory neurons.

patterns, but is somewhat simpler to simulate. Figure 9 shows a schematic of the model's structure.

Neural Activity Depends on the Difference Between Excitatory and Inhibitory Stimulation

Next, we must model the process of neural stimulation that regulates the secretion of the pigment. We regard the net stimulation of a cell at x to be the difference between excitatory and inhibitory stimulations from nearby cells. The situation is illustrated in Figure 10a: a cell located at a position x on the mantle edge received excitatory inputs and inhibitory inputs. The inhibitory signals are generally more "long range" than the excitatory inputs; that is, the mantle edge exhibits the property of short-range excitation and long-range inhibition characteristic of neural nets (BERNE & LEVY, 1983; ERMENROUT & COWAN, 1979). Moreover, we assume that the response of a nerve cell is a saturating function of its inputs; that is, both excitation and inhibition are sigmoidal functions of their arguments, as shown in Figure 10b. The mathematical form of the neural stimulation term we have employed is given in the Appendix.

When these assumptions are incorporated into the model equations there results a set of functional difference equations that determines the pigment pattern, $P_i(x)$ (cf. equations [A1, 2]). In Appendix A we perform a linear analysis on these equations. This gives some idea of the repertoire of patterns the model can generate, and provides a guide to the numerical simulations presented below.

The Model Parameters

Any model contains adjustable parameters, and equations [1]-[3] contain several. These parameters fall into

two categories: (A) those controlling the shape of the neural stimulation function, and (B) the production and degradation rates of the inhibitory substance. Each parameter corresponds to a definite physiological quantity, and so is measurable, at least in principle.

Neural parameters. The neural stimulation function, S , in equation [1] contains the curves for excitation, inhibition, and firing threshold shown in Figure 10. Each of these functions must be described by formulae that contain parameters to control their shapes. The functions we have employed in our simulations are described in Ap-

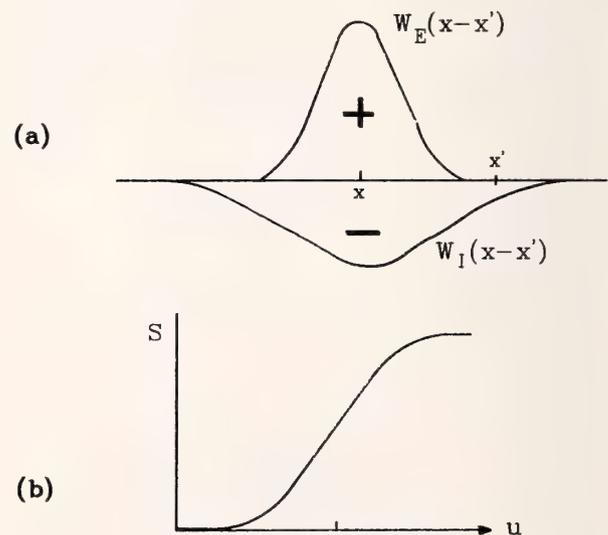


Figure 10

Diagram of the neural influence function and threshold function.

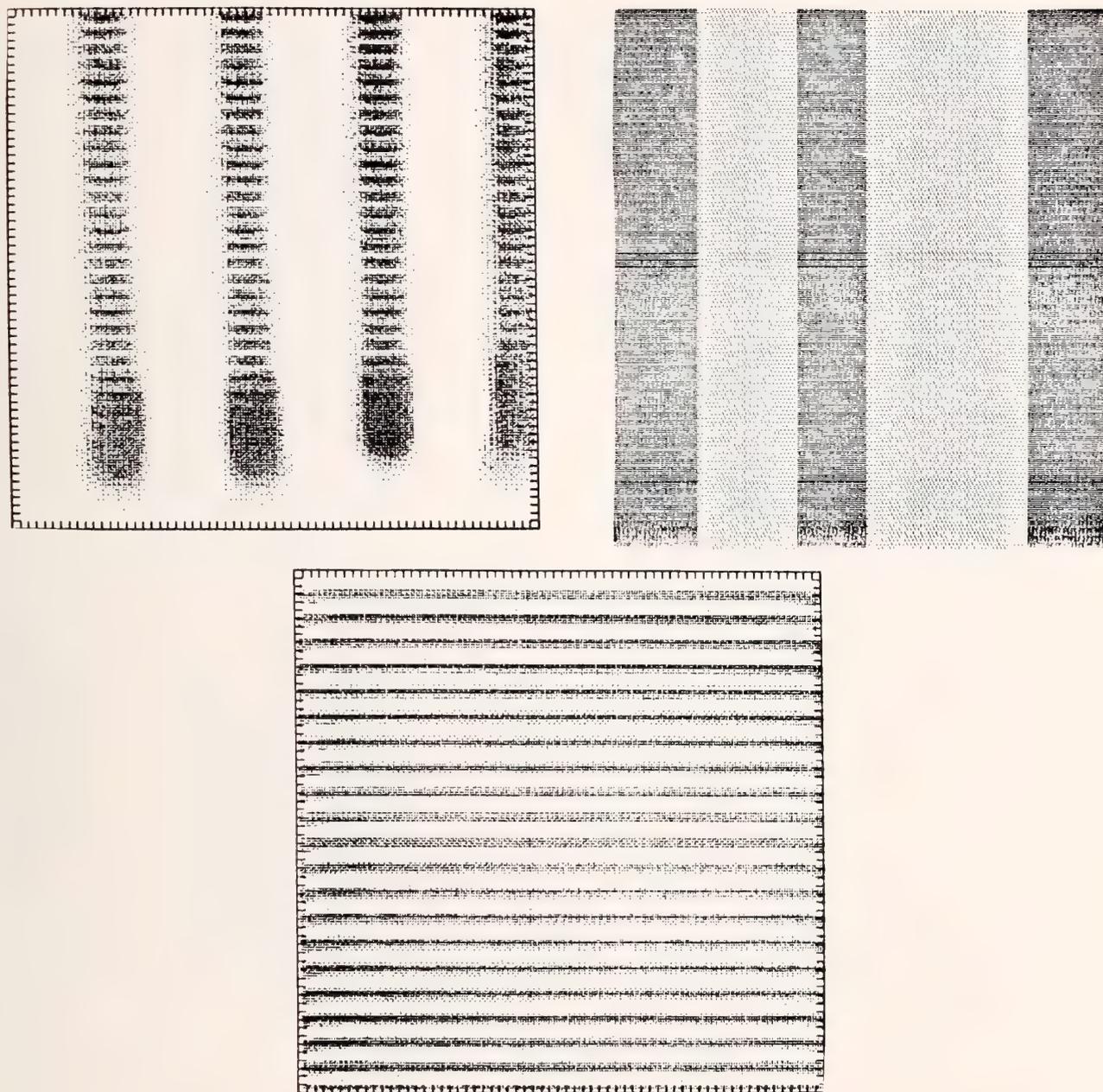


Figure 11

Simulations of: a, vertical stripes of constant width; b, vertical stripes of variable width; c, horizontal stripes.

pendix A; however, experience has shown that the qualitative predictions of the model depend only on the general shapes of the functions, not on their particular algebraic form.

Cellular parameters. Each secretory cell is characterized by its production rate of pigment under neural stimulation and its production and degradation of refractory substance, R . The production rate of pigment is controlled entirely by the neural stimulation, S , and so no new parameters are required to describe it. The refractory sub-

stance, however, requires the two parameters: γ to regulate the growth rate of R , and δ to control the decay rate of R .

Even though each of the model parameters has a direct physiological interpretation, with enough parameters one might feel that any variety of patterns is possible. However, this is not true. For a fixed neural structure, there are but two adjustable parameters: γ and δ . Varying the neural interactions involves changes in their shape-controlling parameters, and analysis and simulation studies

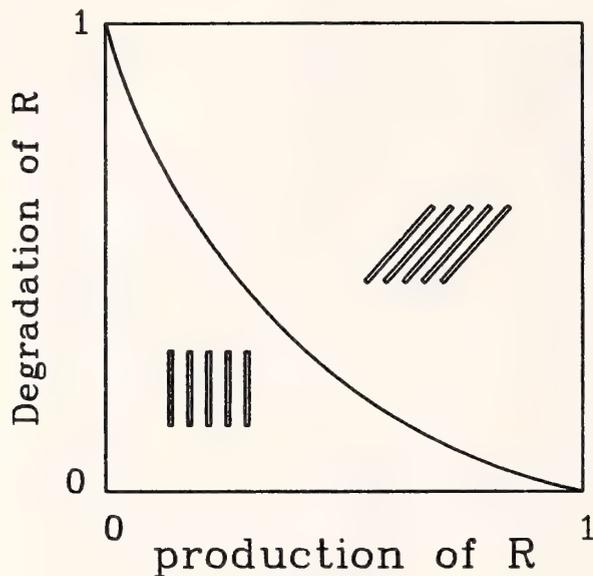


Figure 12

γ - δ parameter plane showing domain of stripes and obliques.

show that the resulting patterns can be classified into a relatively small number of types. Within each distinct type, variations of the parameters merely alter the relative dimensions of the pattern, and not its qualitative appearance. However, parameter variations that exceed certain thresholds, cause the pattern to shift not just its scale, but its qualitative type as well. This "bifurcation" behavior will be discussed further below.

PATTERNS GENERATED BY THE MODEL

In this section we describe the patterns generated by the neural model. We shall present numerical simulations of the neural model which mimic certain patterns observed on the shells of *Bankivia fasciata* and *Nerita turrata*.

Basic Patterns

Equations [1]–[3] constitute the simplest possible model for a neural net; consequently, we cannot hope to reproduce all of the known shell patterns. However, we can reproduce all of the basic patterns; moreover, it is easy to see how the model can be elaborated to incorporate a wider variety of patterns. We shall briefly discuss these modifications here, and present a more detailed study in a subsequent paper.

The three fundamental patterns exhibited by *Nerita turrata* and *Bankivia fasciata* are longitudinal bands, incremental lines, and oblique stripes (Figure 1). The parameter values that realize these patterns are given in Table 2 in Appendix A. Qualitatively, the conditions that yield these patterns are as follows.

Vertical stripes (Figures 1a, 11) occur when refrac-

toriness is very low and the neural influence functions are strong and thresholds small. There are two mechanisms for producing stripes: one is similar to the Turing mechanism in diffusion-reaction models. That is, short-range activation creates a laterally spreading zone of activity, which is eventually quenched by the longer range inhibitory activity. This produces stripes whose width is constant, as shown in Figure 11a. The stripe width is a function of the parameters (being roughly the width of the activation-inhibition zone), and the locations of the stripes are determined by the width of the domain (*i.e.*, the size of the mantle). A different mechanism produces stripes of unequal widths, as shown in Figure 11b. It is also possible to produce vertical stripes by simply activating certain regions of the mantle permanently, so that secretion is always turned on. Only experiments can distinguish between these two possibilities.

Horizontal stripes, or incremental lines (Figures 1b, 11c), are produced when the refractory parameters are small and thresholds are high. This results from a synchronized, or homogeneous oscillation along the entire mantle (not to be confused with the incremental pattern associated with the episodic nature of shell deposition).

Diagonal stripes, or zebra bands (Figures 1c, 2, 3, 4), are characterized by very low thresholds and gradual cut-offs. These arise as waves of activity propagate along the mantle. If the neural structure is constant, the presence of oblique stripes or vertical bands depends on the values of the two parameters controlling the refractoriness, γ and δ . Figure 12 shows the parameter domain that characterizes each pattern type.

The direction of the stripes produced by the model depends on the parameter values. However, downward oriented stripes (*i.e.*, away from the apex of the shell) are more common in *Bankivia fasciata* and *Nerita turrata* and exhibit far fewer irregularities. Moreover, upward-directed stripes appear to be more unstable, reverting to downward stripes after a short progression. This points to a consistent inhomogeneity in the mantle. Indeed, superimposing a parameter gradient (*e.g.*, in δ and [or] γ) on the model equations strongly biases the direction of striping in one direction. Interestingly, the direction of stable striping is in the same direction as the spiral of the shell. Because shell patterns are associated with shell construction, this could indicate a physiological (anatomical) correlation between the direction of shell growth and the pattern direction, such as an asymmetry in the muscle mass of the mantle. The direction of the zebra stripes can switch at certain times, especially—but not exclusively—at a varix.

Divaricate patterns. Zebra patterns may reverse directions giving a herring-bone pattern. We have used the observation that synchronous switching of the direction of stripes indicates a global coordinating mechanism for the pattern. In terms of the model, switching of the direction of obliques involves a jump in a parameter value. The model does not address what the underlying signal for

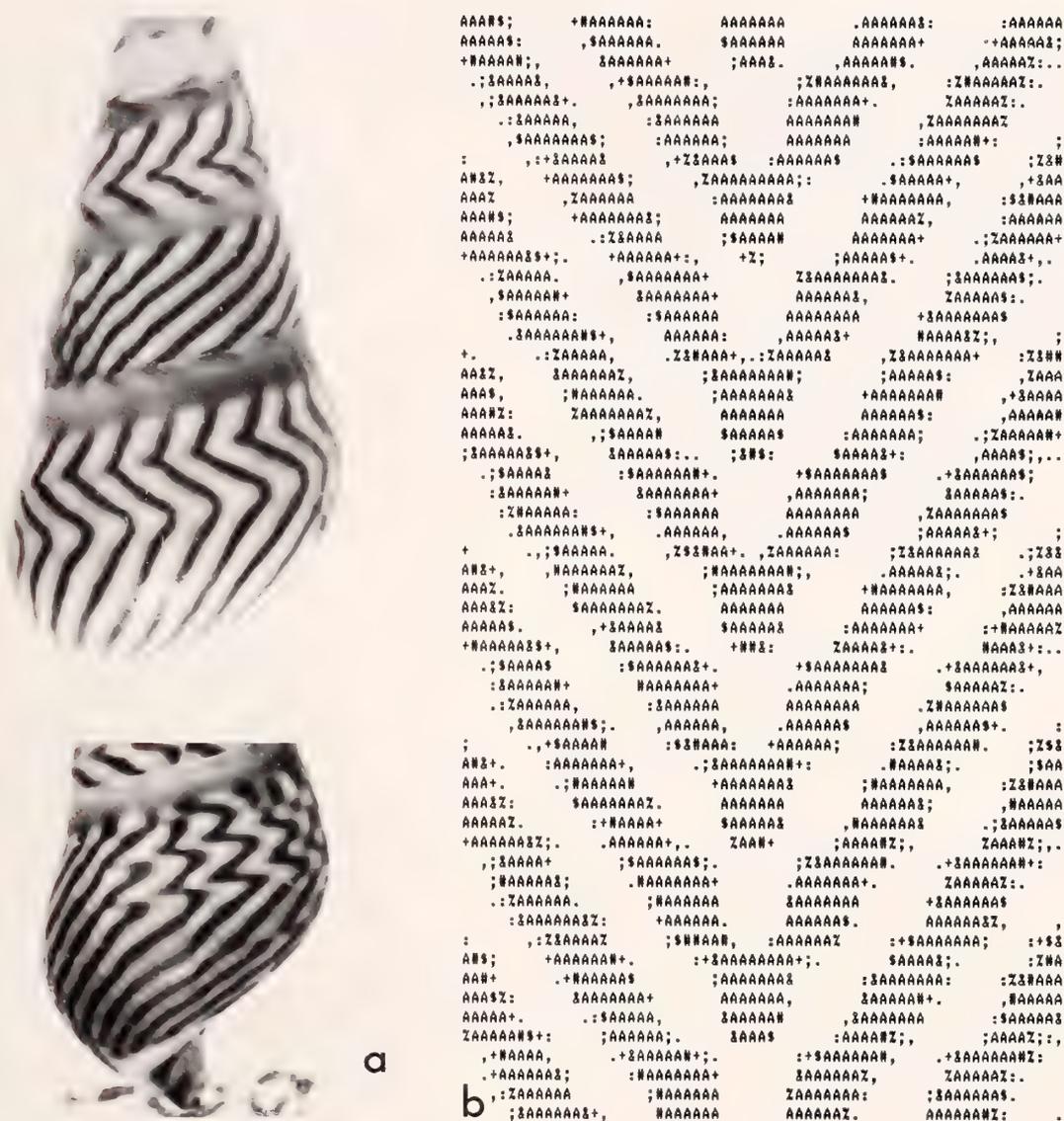


Figure 13

a, divaricate patterns on *Bankivia fasciata* showing open and closed V's; b, simulation of V's.

such an event is, but does provide a mechanism for generating a coordinated reversal of the pattern orientation (Figure 13). Lines that converge as the shell grows will be called "closed V's"; those that diverge as the shell grows are "open V's." Pattern reversals that produce a "closed V" frequently extend beyond the intersection a small amount, forming a "snout" on the V. This is also a feature of the simulations, because a collision of two obliques admits a small overlap of the activation region extending beyond the collision apex. Note also that the upward stripes are shorter than the downward stripes, suggesting a mantle inhomogeneity. This has been suggested previously by WRIGLEY (1948).

Wavy stripes (Figure 14). These are characterized by very sharp cutoffs of the excitatory and inhibitory thresholds, small thresholds, and large turnover of refractory substance ($\gamma, \delta \approx 1$). Note the "shocklike" discontinuities in the stripes that the simulation reproduces.

Streams (Figure 15) are irregular striped patterns that occur when the sharpness of the cutoff is quite large and refractoriness is persistent ($\delta \approx 0.8$).

Interaction Patterns

In addition to the basic patterns, additional designs emerge from the interaction of the basic patterns. Typi-



Figure 14

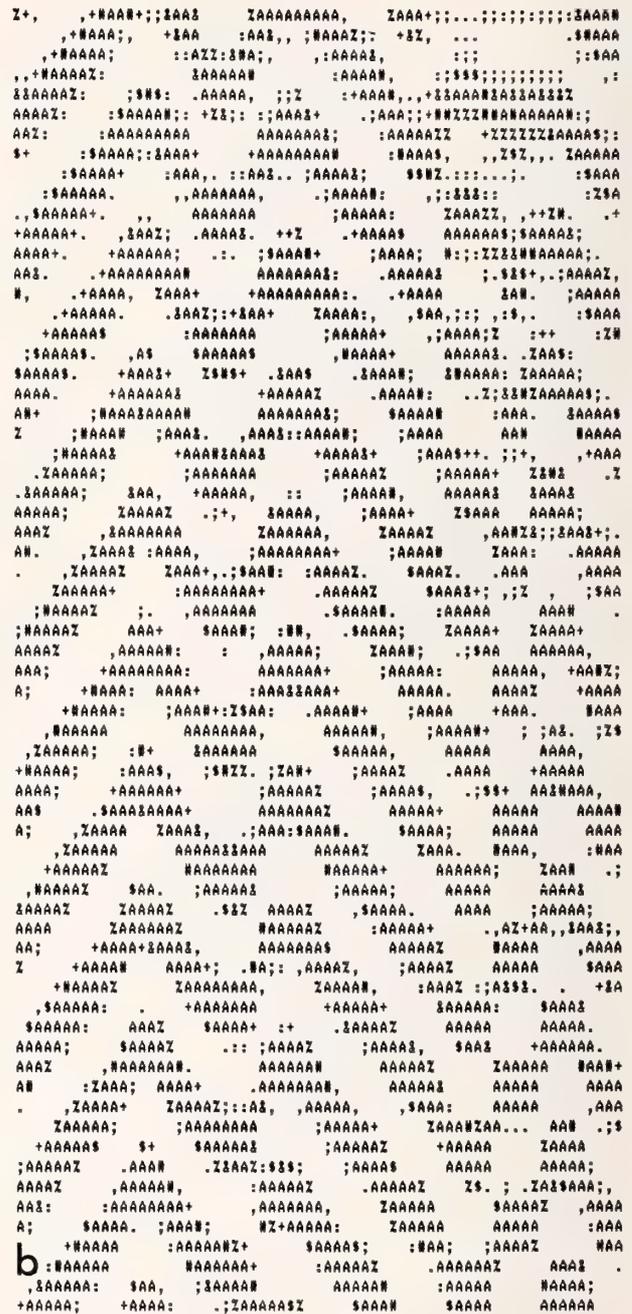
a, divaricate patterns (wavy bands) on *Nerita turrit*; b, simulation.

cally, when two diagonals collide one of several things happen.

Checks (Figures 7, 16) occur when the range of neural interaction is large. As the sharpness of the excitatory and inhibitory thresholds increases, the checks become more stable and persistent.

On some shells, colliding diagonals pass through one another. This cannot happen in our two-variable model. In order to obtain this effect one must add a third variable; this implies that the secretory activity of the mantle is associated with more than one pigment, or that the mantle can sustain several coexisting and independent patterns of neural activity. We will deal with this phenomenon in a subsequent publication.

Tents. These patterns are not observed on *Nerita turrit* or *Bankivia fasciata*, but are common on the cone shells. We include them here because the model also can produce a wide variety of tent patterns, examples of which are illustrated in Figure 17. These patterns most easily arise when the concentration of refractory substance, R, is very low ($\delta, \gamma \ll 1$), the nonlinearities are extremely sharp, and the range of neural interaction small. In this limit the model resembles the "nearest neighbor" cellular automata models of WOLFRAM (1984) and others (cf. Appendix C). Indeed, the tent patterns appear to arise from more localized interactions ("nearest neighbors" in the cellular automata models) than the other patterns described herein. In this regard, the models of Wolfram are able to mimic a remarkable variety of these kinds of "local" patterns, and the model presented here can do little better in pro-



ducing tents. However, where tent patterns are overlain with other patterns, which is frequently the case, then the local nature of the automata models is insufficient (cf. WRIGLEY, 1948).

One point worth mentioning about the tent patterns is the apparent role that stochastic processes play in their evolution. In the neural model we have not included such stochastic features—although it would be trivial to do so—because we were primarily interested in the patterns that



Figure 15

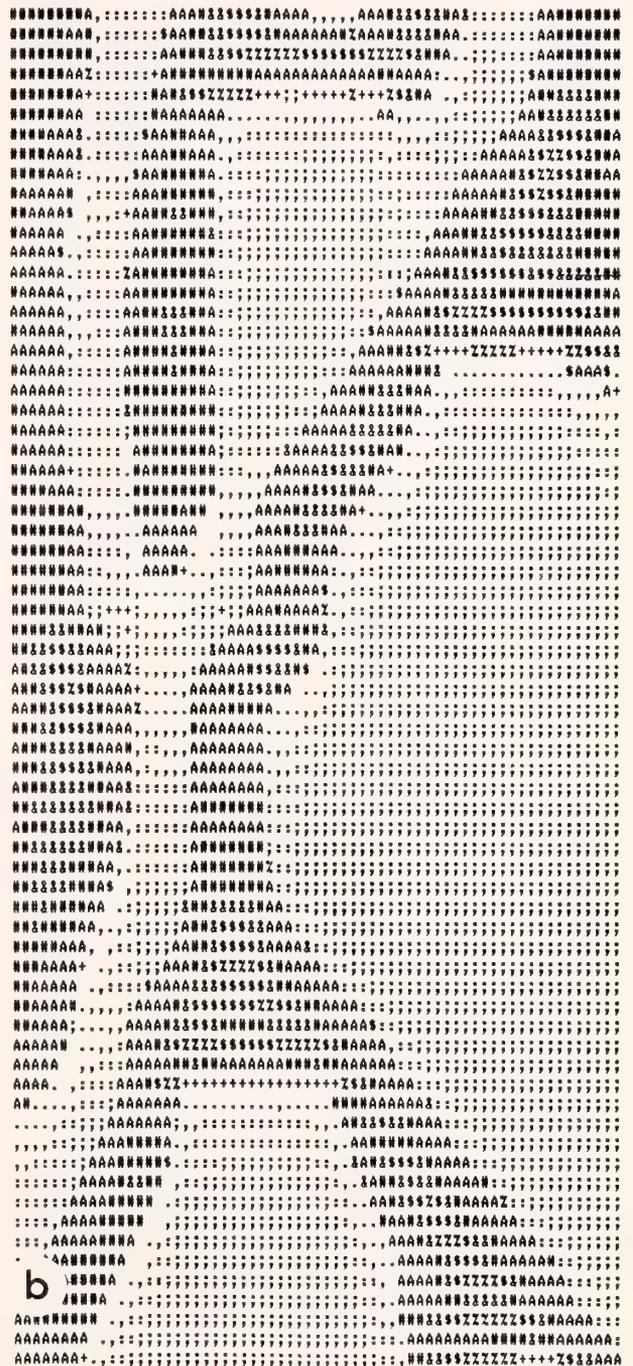
a, wandering stripes on *Bankivia fasciata*; b, simulation.

could be produced in a deterministic fashion. In a subsequent study we shall demonstrate the role of stochastic influences on the structure of the patterns.

DISCUSSION

We have constructed a model for shell patterns based on the hypothesis that the secretion of pigment is stimulated by neural activity. Our model postulates the simplest possible neural interactions: local activation and lateral inhibition, such as is found in the retina. Despite its simplicity the model is able to reproduce a variety of observed shell patterns, such as bands, diagonal stripes, and various divaricate interference patterns that arise from the interaction of propagating bands.

The type of pattern generated by the model depends on the nature of the neural interaction, its range, persistence,



and threshold for activation. Very short-range interactions and strong nonlinearities produce tentlike patterns characteristic of the cone shells, and which resemble the patterns generated by the automata models of Lindsay and of Wolfram and his coworkers. Longer range interactions produce interference patterns, such as checks and wandering streams seen on *Bankivia fasciata* and other shells.

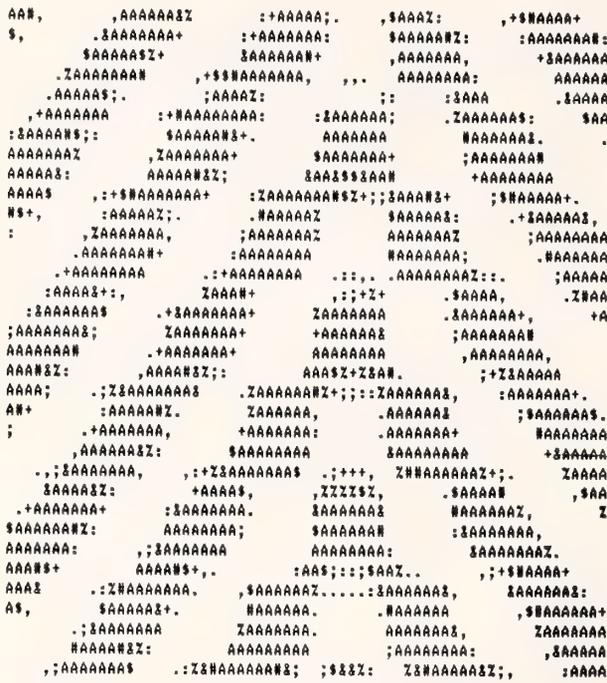


Figure 16

Checkerboard patterns.

We have mapped out many, but not all, of the possible patterns that arise from the neural hypothesis. The model can be elaborated in several directions. For example, what is the effect of postulating a more complex neural structure (such as long-range activation)? Many shells secrete several kinds of pigments; including more than one pigment into the neural model would increase enormously the possible patterns it could generate, including the characteristic of stripes passing through one another—a common phenomenon that the simple neural model presented here cannot reproduce. It is clear from many studies (e.g., WRIGLEY, 1948) that the mantle is not a homogeneous tissue as we have assumed here. By adding to the model spatial gradients and periodic variations in the parameters (e.g., refractoriness or density of innervation) a far greater variety of patterns can be produced than from the homogeneous mantle we have assumed here. We shall present simulations of more complex mantle structures elsewhere. In addition to spatial variations, a variety of transition patterns can be produced if parameter values evolve slowly as the simulation proceeds. These are distinct from the discontinuities and V-patterns that may involve a sudden, global perturbation of a system parameter. In particular, shell size is an important determinant of pattern. Small, or young animals will typically exhibit less complex designs, because fewer stripes will “fit” into a smaller domain. Moreover, as shell size (i.e., domain size in the model) increases with growth, stripes widen until a threshold is reached, whereupon another stripe interca-

lates, a phenomenon commonly observed, especially in *Nerita turrata*. Such sudden shifts in behavior triggered by smoothly varying a parameter are typical of models with strong nonlinear terms (MAY & OSTER, 1976; GUCKENHEIMER *et al.*, 1976).

The cowries have a mantle that imprints a pattern over a large expanse of shell, rather than just at the growing edge. To model this, one must employ a two-dimensional version of the neural model. Two-dimensional automata models with very local interactions can produce patterns that bear a striking resemblance to those found on the map cowrie (N. Packard & S. Wolfram, personal communication), and preliminary analysis of the neural model indicates that the eye-spot pattern found on many cowries can be easily obtained.

The neural model also touches on the problem of shell construction, for as WRIGLEY (1948) and others have pointed out, there is a correlation between the color patterns and the geometrical features of the shell (e.g., pigments may concentrate in the grooves between ridges, and spines tend to be colorless). This is hardly surprising, because the same mantle that deposits the color is busy building the shell. However, this correlation between pattern and form suggests that the neural model might be extended to investigate the diversity of shell shapes and their mode of construction.

If the neural hypothesis is correct, the shell is a hard-copy record of the neural activity in the mantle. The fossil record for these creatures is as complete as for any known lineage. What can such an electroencephalogram tell us about the evolution and ecology of mollusks? We shall not speculate here, but the model suggests an explanation for the diversity of patterns found on the same species in different environments, and the similarity of different species in the same environment. Moreover, the enormous diversity of pattern within certain species may reflect the fact that the patterns in those species are not visible during the animal's life. Being invisible to selection generally leads to increased genotypic variance, and so we should expect the color patterns in such species to be highly polymorphic.

The usefulness of any model stems not only from its specific predictions and its ability to unify disparate experimental observations, but also from its fertility in suggesting further experiments. If the neural hypothesis is correct experiments that intervene with mantle neural activity, without disrupting shell construction, need to be devised. Perhaps the topical application of neuroactive substances such as xylocaine, lysergic acid, or various kinds of neurotransmitters can provide information. Probably electrophysiological measurements will interrupt mantle activity, but perhaps the neural connections between pigment cells can be explicated in sufficient detail to determine the range of neural interactions characteristic of each pattern type. It is a rich field for neurobiology and anatomy which will have a direct impact on larger issues of evolution and adaptation.

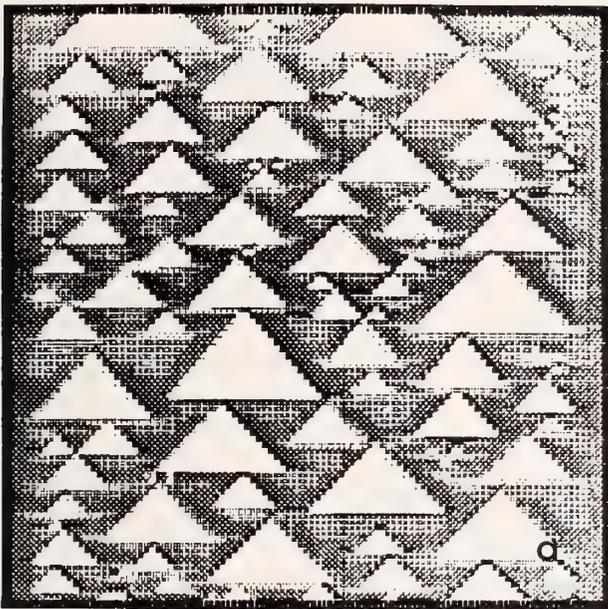


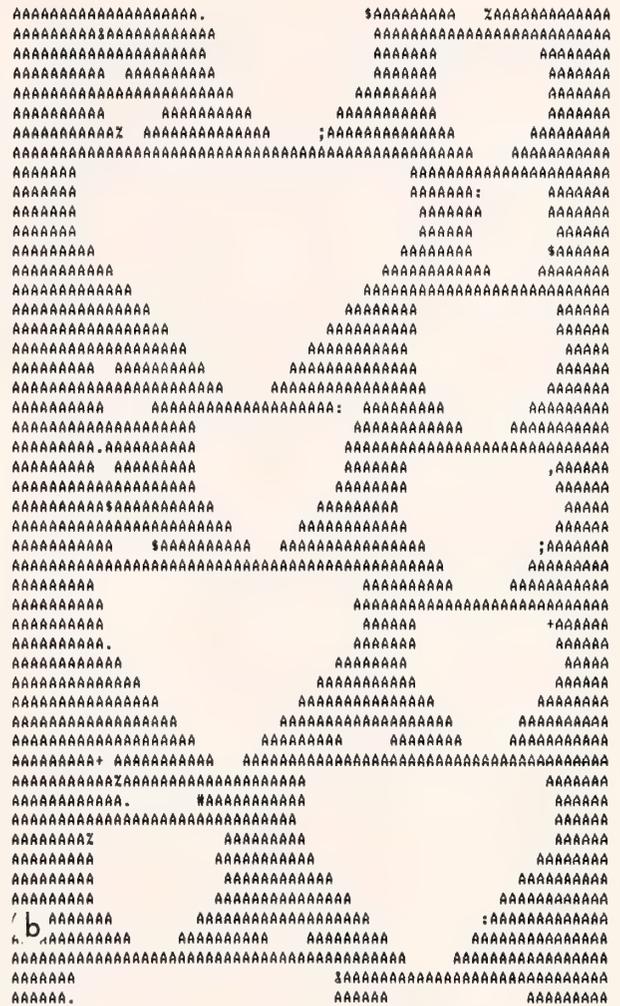
Figure 17

a, tent patterns characteristic of olive snails (*e.g.*, tent olive or royal purple olive (*Oliva porphyria*); b, tent patterns characteristic of the textile or range cones—these patterns differ from (a) by slightly longer range neural interactions.

Finally, we should mention the issue of the uniqueness of the model. It would be gratifying if we could claim that our model can reproduce the observed patterns better than all competing models; however, this is not the case. Using a model based on diffusion and reaction of chemical morphogens, H. Meinhardt has produced simulations that are equally as convincing in reproducing the shell patterns as the neural model. The reason is clear: one can model the phenomenon of local activation and lateral inhibition characteristic of neural nets in a variety of ways. Any number of diffusion-reaction mechanisms can produce this effect by a slowly diffusing autocatalytic reaction that is quenched by a fast diffusing inhibitor molecule (MEINHARDT, 1982). Even the mechanical models that OSTER *et al.* (1985) have employed to model the regular patterns of microvilli on cells can be viewed as a mechanical implementation of this neural-like property. Therefore, we are left with the disappointing conclusion that it may be quite difficult to infer mechanism from pattern alone, because several quite distinct cellular mechanisms can produce identical patterns. Thus the issue of whether the patterns on mollusk shells arise from neural activity as we have suggested here will be settled only by experiments. Theory can provide only a shopping list of possible mechanisms.

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LITERATURE CITED

BERNE, R. & M. LEVY. 1983. Physiology. Pp. 116-118. Mosby: St. Louis.
 CAMPBELL, J. 1982. Proposal submitted to the National Science Foundation (Grant No. PCM-20923).
 COMFORT, A. 1951. Pigmentation of molluscan shells. *Biol. Rev.* 26:285.
 COWE, R. J. 1971. Simulation of seashell pigment patterns using an interactive graphics system. *Computer Bull.* 15: 290.
 EMBERTON, L. 1963. Relationships between pigmentation of

shell and of mantle in the snails *Cepaea nemoralis* (L.) and *Cepaea hortensis* (Mull). Proc. Zool. Soc. Lond. 140:273.

ERMENROUT, B. & J. COWAN. 1979. A mathematical theory of visual hallucination patterns. Biol. Cybernetics 34:137-150.

GUCKENHEIMER, J., G. OSTER & A. IPAKCHI. 1976. Density dependent population models. J. Math. Biol. 4:101-147.

HERMAN, G. T. & W. H. LIU. 1973. The daughter of Celia, the French flag, and the firing squad. Simulation 21:33.

HERMAN, G. T. 1975. Developmental systems and language. North-Holland: Amsterdam.

KAPUR, S. & M. GIBSON. 1967. A histological study of the development of the mantle-edged gland and shell in the freshwater gastropod *Helisoma durvi endiscus*. Can. J. Zool. 45:1169.

KNIPRATH, E. 1977. Ontogeny of the shell field in *Lymnaea stagnalis*. Roux. Arch. Dev. Biol. 181:11.

LINDSAY, D. 1982a. Simulating molluscan shell pigment lines and states: implications for pattern diversity. Veliger 24: 297-299.

LINDSAY, D. 1982b. A new programmatic basis for shell pigment patterns in the bivalve mollusc *Lionconcha castrensis* (L.). Differentiation 21:32-36.

MAY, R. & G. OSTER. 1976. Bifurcation and dynamic complexity in simple ecological models. Amer. Natur. 110:573-599.

MEINHARDT, H. 1984. A model for positional signalling, the threefold subdivision of segments and the pigmentation patterns of molluscs. J. Embryol. Exp. Morphol. 83(Suppl.): 289-311.

NEFF, J. 1972. Ultrastructure of the outer epithelium of the mantle of the clam *Mercenaria mercenaria* in relation to calcification of the shell. Tissue Cell 4:591.

OSTER, G., J. MURRAY & G. ODELL. 1985. The formation of microvilli. In: G. Edelman (ed.), Molecular Determinants of Animal Form. UCLA Sympos. Molec. Cell. Biol. (in press).

TIMMERMANS, L. 1969. Studies on shell formation in molluscs. Neth. J. Zool. 19:417.

WADDINGTON, C. & R. COWE. 1969. Computer simulation of a molluscan pigmentation pattern. J. Theo. Biol. 25:219-225.

WAUSHER, J. 1972. Considerations on phase-change and decorations in snail shells. Hereditas 71:75-94.

WILBER, K. 1972. Shell formation in mollusks. In: M. Florin & B. Scheer (eds.), Chemical zoology. Vol. 7. Academic Press: New York, p. 113.

WOLFRAM, S. 1984. Cellular automata as models of complexity. Nature 311:419-424.

WRIGLEY, A. 1948. The color patterns and sculpture of molluscan shells. Proc. Malacol. Soc. Lond. 27:206.

APPENDICES

A. The Model Equations

In this Appendix we give the complete mathematical expression for the model equations given in the text, as well as the functional forms employed in the numerical simulations.

The model consists of the three difference-integral equations

$$A_{t+1}(x) = S[P_t(x)] - R_t \tag{1}$$

$$R_{t+1}(x) = \gamma P_t(x) + \delta R_t(x) \tag{2}$$

$$P_t(x) = H(A - A^*) \tag{3}$$

where $0 < \gamma < 1$ is the rate R increases and $0 < \delta < 1$ is its degradation rate.

We can further simplify the model by assuming that the pigment secretion, P, is simply proportional to the activity, A, and let the function S take care of the threshold for secretion. This does not affect the patterns significantly, and is somewhat easier to treat numerically and theoretically. Thus the equations we shall deal with are

$$P_{t+1}(x) = S[P_t(x)] - R_t \tag{4}$$

$$R_{t+1}(x) = \gamma P_t(x) + \delta R_t(x) \tag{5}$$

The neural stimulation function, $S[P_t(x)]$ in equation [4] is composed of excitatory and inhibitory effects. Note that the pigment secretion on day $t + 1$ can depend only on the excitation during day $t + 1$; however, according to the assumptions of the model, each day's pattern of excitation is stimulated by "tasting" the previous day's pigment pattern. We can safely assume that the time constants for neural interactions are much shorter than those of shell growth, so that we need deal only with the daily average, or steady state firing rate of the neurons in the mantle. Therefore, we define the following functionals:

Excitation:

$$E_{t+1}(x) = \int_{\Omega} W_E(x' - x) P_t(x') dx' \tag{6}$$

Inhibition:

$$I_{t+1}(x) = \int_{\Omega} W_I(x' - x) P_t(x') dx' \tag{7}$$

Here the kernels $W_E(x' - x)$ and $W_I(x' - x)$ weight the effect of neural contacts between cells located at position x' and a cell at x ; they effectively define the connectivity of the mantle neuron population. In general, the inhibitory kernel, $W_I(x' - x)$ is broader than the excitatory kernel, $W_E(x' - x)$; i.e., activation has a shorter range than inhibition. Ω is the domain of the mantle; for most shells this is a finite interval, but may be circular in the case of mollusks such as limpets and planar in cowries.

The particular connectivity functions we have employed in our simulations are:

$$W_j = 0 \quad \text{for } |x| > \sigma_j, \quad j = E, I$$

$$W_j = q_j [2^p - (1 - \cos(\pi x / \sigma_j))^p] \tag{8}$$

for $|x| \leq \sigma_j, \quad j = E, I$

where q_j is chosen so that

$$\int_{\Omega} W_j(x) dx = \alpha_j, \quad j = E, I \tag{9}$$

Table 1

Neural influence function parameters	
α_E	= amplitude of the excitatory influence function.
α_I	= amplitude of the inhibitory influence function.
σ_E	= range of the excitatory influence function.
σ_I	= range of the inhibitory influence function.
p_E	= sharpness of the excitatory influence cutoff, or the "flatness" of the influence function.
p_I	= sharpness of the inhibitory influence cutoff.
Firing threshold functions	
ν_E	= steepness of the excitatory cutoff (nonlinearity).
ν_I	= steepness of the inhibitory cutoff.
θ_E	= location of the excitatory threshold; <i>i.e.</i> , the midpoint of the sigmoidal curve (threshold).
θ_I	= location of the inhibitory threshold.
Refractory parameters	
γ	= production rate of refractory substance.
δ	= decay rate of refractory substance.

The shape of the connectivity functions is controlled by p : for p very small the W_j are sharply peaked, for p large, the W_j become nearly rectangular. In our simulations p is in the range of 4–8. The range for lateral inhibition is made greater than the excitation by choosing $\sigma_I > \sigma_E$, and since the local excitation strength is generally greater than the inhibition, we choose $\alpha_E > \alpha_I$.

The responses of the secretory cells to neural stimulation are assumed to be sigmoidal functions of their inputs:

$$S[P_i(x)] = S_E[E_{i+1}(x)] - S_I[I_{i+1}(x)] \quad [10]$$

For simulation purposes, we have employed the following function for both S_E and S_I

$$S_j(u) = \frac{1}{1 + e^{\nu_j(u - \theta_j)}}, \quad j = E, I \quad [11]$$

The parameter ν_j controls the sharpness of the nonlinearity, and θ_j the location of the threshold.

Thus the raw parameter list consists of the 12 quantities:

$$[\alpha_E, \alpha_I, \sigma_E, \sigma_I, p_E, p_I, \nu_E, \nu_I, \theta_E, \theta_I, \gamma, \delta]$$

This list can be reduced to nine because some parameters enter only as products, and some may be rescaled. Table 1 summarizes the model parameters.

B. Analysis and Simulation of the Model

A linear stability analysis of the model equations gives some idea of the patterns the model will generate. Therefore, we proceed as follows.

The pair of equations [4, 5] are equivalent to the single second order equation

$$P_{i+2} = S[P_{i+1}] + \delta P_{i+1} - \gamma P_i - \delta S[P_i] \quad [12]$$

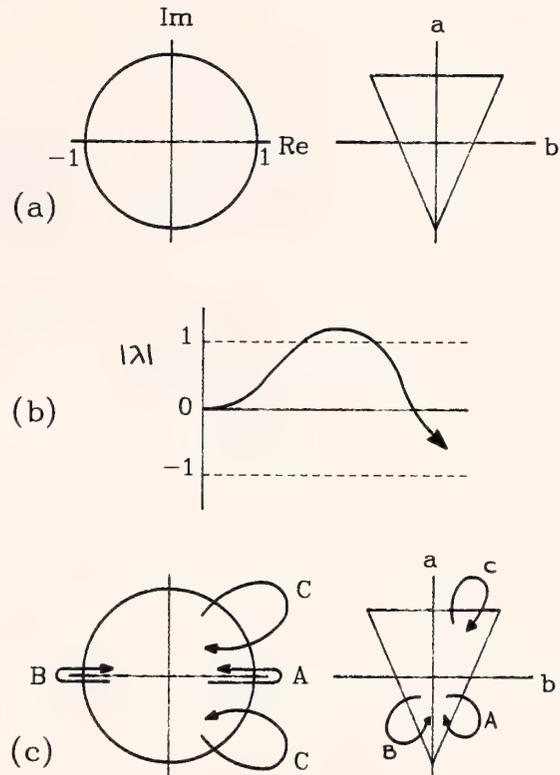


Figure A1

a, the unit circle and the stability triangle on the coefficient (a, b) plane; b, dispersion relation $\lambda(k)$ for spatial instability; c, trajectories for each type of bifurcation.

where we have suppressed the dependence on x for notational simplicity.

Let P_o be a homogeneous equilibrium, *i.e.*,

$$P_o = S[P_o] + \delta P_o - (\gamma P_o + \delta S[P_o]) \quad [13]$$

or

$$P_o = S[P_o] \frac{1 - \delta}{1 - \delta + \gamma} \quad [14]$$

If we shift the sigmoid S so that $S_E(0) = S_I(0) = 0$, then we can linearize about $P_o = 0$ to obtain the linear difference equation:

$$P_{i+2} + L_o P_{i+1} + \delta P_i - [\gamma P_i + \delta L_o(P_i)] = 0 \quad [15]$$

where $L_o(\cdot)$ is the linear (convolution) operator

$$L_o[u](x) = S'_E(P_o) \int_{\Omega} W_E(x' - x) u(x') dx' - S'_I(P_o) \int_{\Omega} W_I(x' - x) u(x') dx', \quad [16]$$

where $S'_j(P_o)$ are derivatives of S_j .

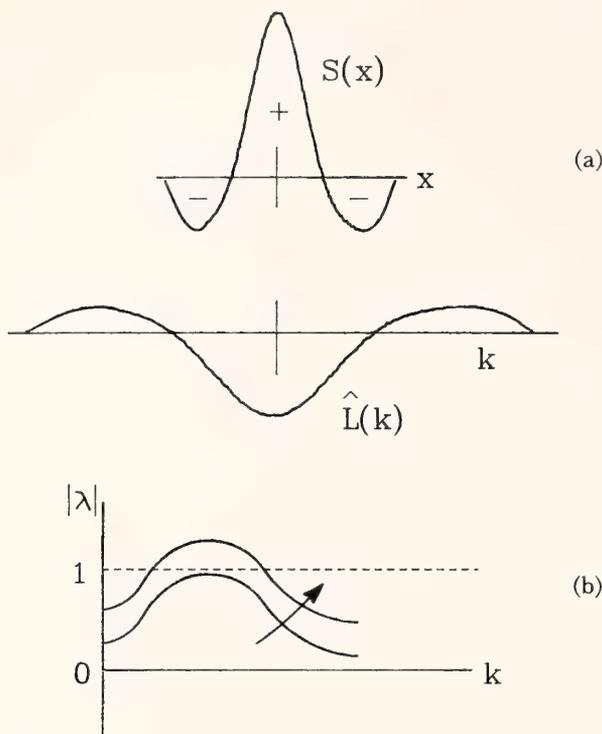


Figure A2

a, the shapes of $S(x)$ and $L(k)$; b, the dispersion relation.

On a periodic domain of length L (e.g., the limpet), the eigenfunctions for L_o are $\exp(2\pi i n x/L)$, $n = 1, 2, \dots$; on a finite linear domain these are approximate eigenfunctions, since the domain size, L , is much greater than the range of the connectivity functions W .

The characteristic equation for the spatially homogeneous system is obtained by substituting $P_i(x) \approx \lambda \exp(2\pi i k x/L)$ into the linearized equation:

$$\lambda^2 + (L^*(k) + \delta)\lambda - [\gamma + \delta L^*(k)] = \lambda^2 + a(k)\lambda + b(k) = 0 \quad [17]$$

Here

$$L^*(k) \equiv S'_E(P_o)\hat{W}_E(k) - S'_I(P_o)\hat{W}_I(k) \quad [18]$$

where the \hat{W}_j are (close to) the Fourier cosine transforms of the W_j :

$$\hat{W}_j(k) \approx \int_0^L \cos(2\pi k x/L) W_j(x) dx \quad [19]$$

The spatially homogeneous solution is stable if and only if the roots of the characteristic equation lie within the unit circle on the complex plane: $|\lambda| < 1$ for every $k = 0, 1, 2, \dots$. This condition can be plotted on the coefficient plane (a, b), as shown in Figure A1a, where stability requires that a and b lie within the shaded triangle.

Spatial instability requires that (i) the homogeneous solution be stable: $|\lambda|(k=0) < 1$, and (ii) there exists a

finite range of unstable modes: $|\lambda|(k) > 1$ for $0 < k_1 < k < k_2 < \infty$. That is, the dispersion relation $\lambda(k)$ should look qualitatively as shown in Figure A1b.

Such an instability can arise in three qualitatively different ways: as one of the model parameters is varied the unstable eigenvalue can pass out of the unit circle through $+1$, -1 or at a complex value (Figure A1c). Which one of these instabilities occurs depends on which parameter is varied and on the shape of the connectivity kernels, W_j .

The neural connectivity function, $W(x)$ we have employed is the usual "short-range excitation/long-range inhibition" type shown in Figures 9 and 10. The linear operator $L^*(k)$ is essentially the Fourier transform of $W(x)$. By the properties of the Fourier transform, $L^*(k)$ has the shape shown in Figure A2a. Because only positive values of k are physically relevant, the dispersion relation looks qualitatively as sketched in Figure A2b.

The three paths to spatial instability shown in Figure A1c correspond to violating the following three inequalities:

(a) Bifurcation through $+1$ will occur if $L^*(k) > (1 - \gamma)/\delta$ (path a in Figure A1c). This is a so-called "equilibrium" bifurcation because in the spatially homogeneous case ($k=0$) such a bifurcation creates a new equilibrium point (cf. MAY & OSTER, 1976; GUCKENHEIMER *et al.*, 1976). When $k > 0$ this creates a stationary spatial pattern of regularly spaced stripes as shown in Figure A3a.

(b) Bifurcation through -1 will occur if $L^*(k) < -(1 + \gamma/(1 + \delta))$ (path b in Figure A1c). From Figure A2b we see that this can occur only at $k=0$, so that homogeneous instability results. (This can only happen in this model for the kernel shown providing $\theta_E \gg \theta_I$, since we have assumed that $\alpha_E > \alpha_I$.) The pattern resulting from this bifurcation consists of fine horizontal stripes, as shown in Figure A2b.

(c) Bifurcation through $\lambda = e^{i\theta}$ ($\theta \neq 0, \pi$) occurs if $L^*(k) > 1 + \gamma/(1 - \delta)$ (path c in Figure A1c). This generates periodic spatio-temporal patterns, as shown in Figure A3c (e.g., stripes and checks).

Note that $(1 - \gamma)/\delta < 1 + \gamma/(1 - \delta)$ if and only if $\delta > 1 - \sqrt{\gamma}$. Thus $+1$ bifurcations occur first when $\delta < 1 - \sqrt{\gamma}$; otherwise the bifurcation is via a complex eigenvalue.

When $\gamma = 0$, so that the refractory substance cannot build up, the model can take a particularly simple form. If we make p large, and σ_E, σ_I equal, and ν large, then the model is approximated by the rule:

$$P_{i+1}(x) = 1 \text{ if } \theta_E < \int_{-\sigma}^{\sigma} P_i(x+x') dx' < \theta_I \\ = 0 \text{ otherwise} \quad [20]$$

This is essentially a continuous space analog of Wolfram's Class-3 cellular automata rule (WOLFRAM, 1984). This type of rule leads to "chaos" and the "tent" patterns.

The linear analysis was employed to guide the numer-

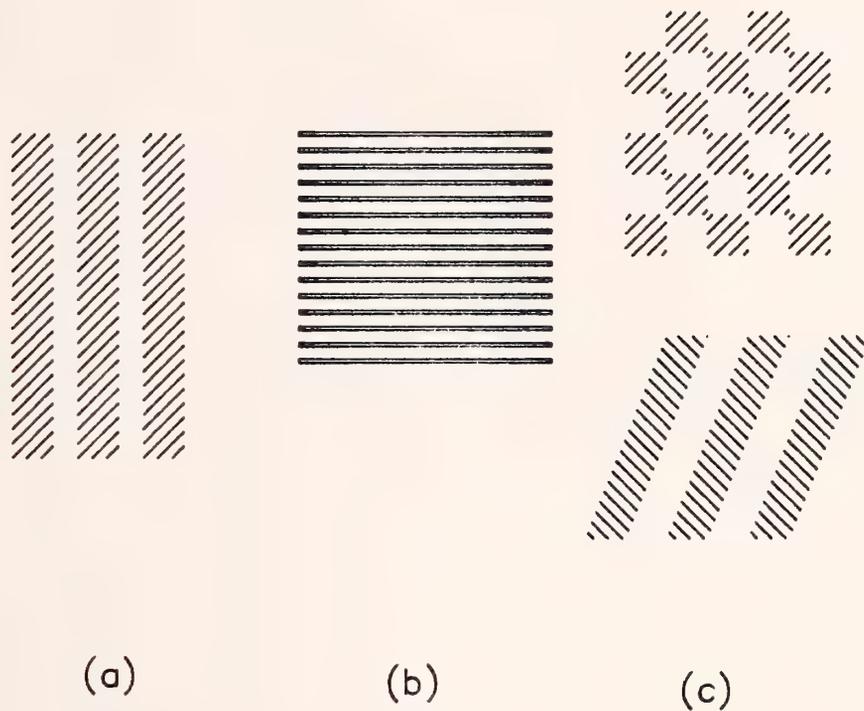


Figure A3

a, spatial pattern arising from +1 bifurcation; b, spatial pattern arising from -1 bifurcation; c, spatial pattern arising from complex bifurcation.

ical simulations. The model equations were converted to a single second order difference equation and the integrals approximated by

$$\int W(x' - x)P(x') dx' \approx \frac{1}{N} \sum_{j=0}^N W_{(i-j)/N} P_j \quad [21]$$

Generally, N was taken to be 64, although when unusual patterns were encountered N was set to 128 or 256 to check that they were not numerical artifacts. Initial conditions were random, or small regions of the domain were excited. Typically, long transients generated complicated patterns which gradually simplified as the transients damped out.

Table 2

Fig.	θ_E	θ_I	α_E	α_I	σ_E	σ_I	γ	δ	ν
11a	0.0	0	6	8	0.1	0.2	0.0	0.0	1
11b	5.5	0.22	15	0.32	0.1	0.15	0.0	0.0	8
11c	4.5	0	15	0.5	0.1	0.12	0.05	0.6	8
14b	1	100	5.0	4.0	0.05	0.2	0.8	0.4	2
15b	4.5	0.32	15	0.5	0.1	0.15	0.1	0.8	8
16	0	0	8.8	6.6	0.1	0.2	0.4	0.6	1
17a	3	4	8.0	4.0	0.1	0.2	0	0	8
17b	5.5	5.5	10	4	0.1	0.2	0.3	0.2	8

C. Alternative Formulations

The behavior of the model equations can be illuminated by examining their continuous time limit. If we subtract P and R from both sides of [4] and [5], respectively, we obtain

$$P_{t+1} - P_t = S[P_t] - R_t - P_t \quad [22]$$

$$R_{t+1} - R_t = (\delta - 1)R_t + \gamma P_t \quad [23]$$

By an appropriate choice of time scale, t, we can divide

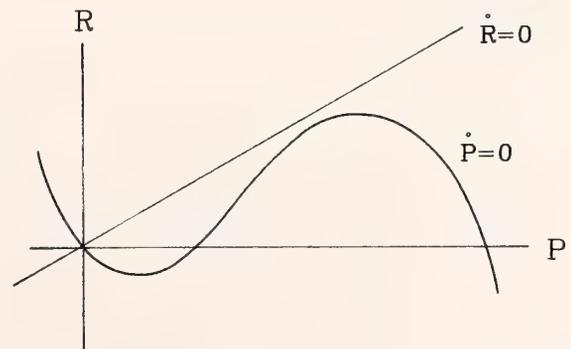


Figure A4

Phase plane for the differential equations [A24] and [A25].

both sides by t and replace the differences by derivatives to obtain:

$$\frac{\partial P}{\partial t} = S[P] - R - P \quad [24]$$

$$\frac{\partial R}{\partial t} = (\delta - 1)R + \gamma P \quad [25]$$

Now let us examine the phase plane of this system at a fixed $x = x_0$. The operator S is sigmoidal in P , and so the right-hand side is a cubic-shaped curve (a sigmoid minus a linear term). The (P, R) phase plane is shown in Figure A4; it is qualitatively similar to the FitzHugh-Nagumo model for excitable media. That is, each volume element is excitable, and the volume elements are spatially coupled by the activation-inhibition operator W .

If only nearest neighbor cells interact inhibitorily, then W can be expanded in a Taylor series about x , and only lowest order terms retained. Then a familiar diffusion-reaction model emerges:

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial x^2} + F(P, R) \quad [26]$$

$$\frac{\partial R}{\partial t} = \gamma P + (\delta - 1)R \quad [27]$$

where D is a diffusion coefficient that can be expressed in terms of the expansion coefficients of the integrand.

If activation-inhibition is to be retained in the model, then fourth order terms must be retained (odd order terms dropping out by symmetry), and we obtain the biharmonic diffusion-reaction system:

$$\frac{\partial P}{\partial t} = -D_1 \frac{\partial^2 P}{\partial x^2} - D_2 \frac{\partial^2}{\partial x^2} \left[\frac{\partial^2 P}{\partial x^2} \right] + F(P, R) \quad [28]$$

$$\frac{\partial R}{\partial t} = \gamma P + (\delta - 1)R \quad [29]$$

Here the negative sign in D_1 corresponds to short-range activation, and the negative sign in D_2 corresponds to long-range inhibition.

A model quite similar to this was arrived at by J. Keener (personal communication) by defining a net neural firing rate, $f(x, t)$ according to the equation

$$\frac{\partial f}{\partial t} = (aP - bf) + \int_{\alpha} W(x' - x) f(x') dx' \quad [30]$$

where $W(x - x')$ is the activation-inhibition kernel shown in Figure 9. Coupling to the secretion is obtained by defining the secretion rate to be a bistable function:

$$\frac{\partial P}{\partial t} = F(P, f) \quad [31]$$

where $F(P, f)$ is an S-shaped curve whose intercept is regulated by f . By expanding the convolution to fourth order, this model can also be reduced to a biharmonic diffusion-reaction model:

$$\frac{\partial r}{\partial t} = -D_1 \frac{\partial^2 f}{\partial x^2} - D_2 \frac{\partial^2}{\partial x^2} \frac{\partial^2 f}{\partial x^2} + (aP - bf) \quad [32]$$

$$\frac{\partial P}{\partial t} = F(P, f) \quad [33]$$

Somewhat different approaches were employed by WADDINGTON & COWE (1969), MEINHARDT (1984), and WOLFRAM (1984). They modeled the shell patterns by an automata wherein the activation-inhibition effect was represented by nearest neighbor interactions via diffusion. Meinhardt's model employed two substances with different diffusion constants ($D_I > D_A$). He obtained some of the same patterns we obtain here by assuming that each cell of the automata could periodically fire and become refractory for a while. In a more recent simulation, Meinhardt and Klingler (to appear) included longer range interactions by allowing morphogens to diffuse beyond nearest neighbors. These simulations resemble ours and it appears that most patterns can be created by either mechanism. However, it is not clear how the diffusion-reaction model handles the problem of pattern alignment between episodes of shell secretion, whereas this is intrinsic to the neural model. Wolfram's simulations mimic to a remarkable extent the "tent" patterns observed on many cone shells. However, his rules were rather arbitrary, and have no obvious physiological interpretation. The neural net model, in the limit of short-range interactions and sharp threshold functions, reduces to the automata model, and can also reproduce the tent patterns.

All of these models have a similar structure: a locally excitable activator-inhibitor system that is coupled spatially to nearby points. In order to obtain spatial patterns, the activation-inhibition is essential. Moreover, it appears that many of the patterns depend on the long-range (*i.e.*, beyond nearest neighbor) interactions characteristic of neural nets. Also, the episodic nature of the secretion process dictated our choice of a discretized model in time; this feature also appears essential to the formation of certain pattern types. In a subsequent publication we shall investigate a broader class of neural models, including kernels with long-range activation and two-dimensional mantles, such as are found in cowries.

Predation-Induced Changes in Growth Form in a Nudibranch-Hydr oid Association

by

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Abstract. The estuarine hydr oid *Cordylophora lacustris* was cultured under controlled laboratory conditions and several growth parameters were measured, including stolon growth rate, stolon budding rate, interstalk distance, and polyp budding rate. Young colonies of *C. lacustris* were subjected to experimental removal of polyps to determine whether physical and(or) chemical cues from predation by the nudibranch *Tenellia fuscata* induced any changes in growth form. Nudibranch predation and polyp removal with chemical stimuli from both direct and indirect exposure to nudibranch mucus caused decreased stolon growth rate and increased stolon budding. The result of these changes in growth should be a hydr oid colony of greater density than without predation. Polyp removal without a chemical stimulus inhibited stolon budding, which would cause a more dispersed colony form. The results suggest that the hydr oid responds differently to physical damage alone than to physical damage combined with the chemical stimulus of the mucus of its predator.

INTRODUCTION

NUDIBRANCH PREDATION on cnidarians has been documented numerous times and the feeding behavior of many nudibranchs described (see TODD, 1981). Less well known are defensive mechanisms utilized by their cnidarian prey. The defensive behaviors of a number of anemone species have been reported (ROSIN, 1969; HARRIS, 1973; EDMUNDS *et al.*, 1976; TODD, 1981), but little is known about possible responses by hydr oids to nudibranch predation. Certainly nematocysts are released and polyps may contract, but are there any more subtle responses such as changes in growth form? Growth forms for a number of hydr oid species have been described (see BRAVERMAN, 1974), but no studies to date have discussed the effect of predation on growth rate and form in a hydr oid.

Herbivore attacks have been shown to induce changes in growth in plants (BOSCHER, 1979). HARVELL (1984) reported that nudibranch predation stimulated spine formation in the bryozoan *Membranipora membranacea* (Linnaeus, 1767), but no changes in growth form were observed. An arborescent hydr oid might be expected to respond in one of three ways to a loss of tissues from nudibranch predation: (1) to grow slower with no change in colony form; (2) to grow more densely, paralleling the response of trees to pruning; and (3) to spread out the

colony by elongation of stolons to "run away" from the predator.

The purpose of the present study is to determine whether nudibranch predation on the hydr oid *Cordylophora lacustris* (Allman, 1844) would induce changes in growth form. *Cordylophora lacustris* is common in the euryhaline portions of rivers emptying into the Great Bay Estuary, and it is easily cultured under controlled laboratory conditions. The dendronotacean nudibranch *Tenellia fuscata* (Gould, 1870) is a natural predator of *C. lacustris* in the Great Bay Estuary and adapts well to laboratory conditions (HARRIS *et al.*, 1980). This study describes the results of short-term experiments testing for the effect of nudibranch predation on hydr oid growth.

MATERIALS AND METHODS

The animals used in this study were collected from the Great Bay Estuary in New Hampshire and maintained in laboratory cultures in the Zoology Department of the University of New Hampshire. Colonies of the hydr oid *Cordylophora lacustris* were collected from floats and pilings in the Lamprey River at Newmarket, New Hampshire, and both hydr oids and the nudibranch *Tenellia fuscata* were obtained from floats in the Salmon Falls River at Stratham, New Hampshire.

Table 1

A summary of results of growth rate parameters measured under a series of control and experimental treatments testing for the effects of physical and chemical stimuli associated with polyp removal on growth rate in *Cordylophora lacustris*. The parameters measured were stolon growth (mm per day), stolon budding (buds per stolon per day), polyp budding (polyps per stolon per day), and interstalk distance (mm). The experimental treatments of polyp removal were (1) direct predation by *Tenellia fuscata* for 6 h, (2) removal of three polyps by forceps (no chemical stimulus), (3) removal of three polyps by forceps and rubbing a nudibranch over the wounds (direct chemical stimulus), and (4) removal of three polyps by forceps and presence of a nudibranch nearby but not in contact with the hydroid (indirect chemical stimulus). * Each experimental treatment differed from the control value to at least $P = 0.05$ level using ANOVA.

Growth parameters	Control	Direct feeding	Forceps only	Forceps & mucus (direct)	Forceps & mucus (indirect)	df	F-ratio	Significance
Stolon growth* (mm·day ⁻¹)	1.06	0.61	0.88	0.42	0.07	4/103	5.89	$P < 0.001$
Stolon budding* (buds·stolon ⁻¹ ·day ⁻¹)	0.1	0.37	0.00	0.46	0.23	4/45	5.19	$P < 0.005$
Polyp budding (polyp·stolon ⁻¹ ·day ⁻¹)	0.32	0.23	0.691	0.21	0.44	4/56	2.36	NS
Interstalk distance (mm)	3.25	3.04	3.0	2.61	2.76	4/42	0.43	NS

The hydroids were maintained in aerated aquaria at a constant temperature of 23°C and salinity of 20‰. Salinity was checked daily to eliminate the possibility that any changes in growth form were induced by abiotic factors. Experimental colonies were established by attaching fragments of colony containing stolon and one or two polyps to glass slides with nylon fishing line. The slides were suspended in an aquarium to which freshly hatched brine shrimp nauplii were added daily in order to maintain a constant food supply. Each slide was examined daily. Once a colony had attached and begun growing, it was utilized for one of several experiments.

Growth parameters in each colony were determined by placing the glass slide onto a plastic coated sheet of graph paper with a 1-mm² grid in a water-filled dish. The colony was then observed under a dissecting microscope and the colony was mapped on another piece of graph paper. All measurements were then made from the daily sequence of diagrams for each colony. Four growth parameters were consistently measured: (1) stolon growth rate; (2) stolon budding rate; (3) interstalk distance per stolon; and (4) polyp budding rate per stolon.

Tenellia fuscata was maintained in aquaria at the same temperature and salinity as the hydroids and fed colonies of *Cordylophora lacustris*. There were periods when a second hydroid, *Bougainvillea* sp., was used as food due to decreased availability of *C. lacustris*.

In order to determine the feeding rate of adult nudibranchs, specimens of *Tenellia fuscata* were allowed to feed on hydroid colonies of known size for 24 h. The number of polyps consumed was counted and an hourly polyp consumption rate was calculated. Nudibranchs were also allowed to feed on colonies for 6 h to verify the feeding rate. All experiments for growth responses to nudibranch predation in *Cordylophora lacustris* were based on this 6-h time period.

The impact of polyp removal on hydroid growth was tested using four variations. (1) A nudibranch was allowed to feed on a colony for 6 h and then removed. (2) Polyps were removed by forceps to mimic predation without a chemical stimulus. (3) Polyps were removed by forceps and then a nudibranch was rubbed over the wounds to mimic predation including a direct chemical stimulus. (4) Polyps were removed by forceps and the colonies were maintained in an aquarium where a nudibranch was held in a mesh container to provide only an indirect chemical stimulus. Regeneration rates of removed polyps were also monitored using the same four treatments.

All experiments involved three or more replicates per treatment and each experiment was run at least two times. Colonies were followed for approximately a week after the treatments. Analysis of variance was used to test for the statistical significance of various results in each experiment.

RESULTS

Growth rate measurements, made during the early phases of colony formation by newly attached fragments of colonies, are given in Table 1. Colony formation during the early stages of establishment on glass slides involves extensive stolon growth and limited upward growth of stalks, so that most stalks contain only one or two polyps. This pattern appears to change only after stolons begin to regularly overlap each other and most of the slide is colonized; then growth shifts to production of branching stalks containing many polyps.

Tenellia fuscata is an active and fast growing nudibranch (HARRIS *et al.*, 1980). Individual nudibranchs were seen feeding in two ways during observations to determine feeding rates. The most common method was for *Tenellia* to crawl up a hydroid stalk to the base of the polyp, grasp

it in the jaws, and rasp away tissue until the hydranth was consumed. Nudibranchs were also observed to make a hole in the perisarc of a stalk and to consume tissue and fluids by a combination of rasping and pumping movements of the radula and buccal mass. Direct consumption of polyps was the primary feeding method observed when nudibranchs were on growing hydroid colonies with an abundance of polyps. The mean feeding rate determined for 6- and 24-h tests was 0.48 polyp per hour or 11.52 polyps per day. In all experiments in which forceps were used to mimic predation, three polyps were removed to represent approximately 6 h of feeding by a nudibranch. All hydroid colonies used had been recently established on slides. Three polyps constituted a loss of no more than 10% of the polyps in a colony.

The most obvious change in growth following polyp removal was a decrease in stolon growth rate and a change in stolon budding rate (Table 1). Stolon growth rate might be expected to decrease along a stolon where polyps and, therefore, feeding capability were reduced. The increase in stolon budding may have accounted for the slowdown in stolon growth rate and represented a shift in growth form.

The decrease in stolon growth was least where no chemical stimulus from a nudibranch was present; stolon budding actually ceased in the portions of those colonies that were monitored. Stolon growth was least in colonies that were exposed to only indirect chemical cues, but the stolon budding rate did not change as dramatically as in the cases where mucus directly contacted the colonies. A major difference between treatments, though, was that in cases of direct mucus contact, the contact lasted no more than 6 h (direct predation) and often only a few minutes (forceps and mucus), while the colonies used in the indirect chemical stimulus tests remained in culture with a nudibranch for several days and were, therefore, presumably exposed to low levels of chemical stimulus for the duration of the experiment.

The different treatments caused decreased or increased rates of polyp budding. In the two cases where nudibranch mucus directly contacted the damaged portion of the colonies, polyp production decreased. In contrast, polyp production increased in the two tests where mucus was not present or was not in direct contact with the hydroid. Slight decreases in interstalk distance occurred along stolons where polyps were removed, but such changes did not correlate with decreases in stolon growth rates.

The net result of the observed responses to polyp removal was predicted to be a denser colony form with more stolon branching and decreased interstalk distance. The one exception may be where no chemical stimulus was present, because a continuation of the observed sharp decrease in stolon budding would produce a very diffuse colony form.

Cordylophora lacustris showed a consistent pattern of polyp regeneration following removal of several polyps (Table 2). Polyps regenerated in a sequential fashion along

Table 2

A summary of polyp regeneration rates and totals following the four methods of removal. Polyps were removed using the following treatments: (1) direct predation by *Tenellia fuscata*, (2) forceps alone, (3) forceps and application of nudibranch mucus, and (4) forceps and nudibranch in the same bowl but no direct contact.

Treatment	Regeneration rate (day ⁻¹)	Percent regenerated
Nudibranch predation	0.8	12.5
Forceps only	0.734	64.0
Forceps and mucus (direct)	0.429	68.0
Forceps and mucus	0.482	68.0

the stolon, beginning with the proximal or oldest polyp and progressing distally along the stolon. In all treatments, the regeneration rate of removed polyps was less than one polyp per day (Table 2), but this was faster than the polyp production rate for new polyps on a stolon. The quickest regeneration occurred in those polyps removed by nudibranch predation (Table 2), but the number of polyps that regenerated was small. The results were not statistically significant so they are at best suggestive that actual nudibranch predation of a polyp may affect the hydroid differently from removal by forceps.

DISCUSSION

The growth form and rates of colony growth for *Cordylophora lacustris* are well studied (FULTON, 1961, 1962, 1963; OVERTON, 1963). BRAVERMAN (1974) has clearly documented the value of using hydroids for modeling growth in colonial organisms, plant and animal. Although it has been shown that herbivory can alter growth form in plants (BOSCHER, 1979), no similar work has been conducted on hydroids. The results of this study suggest that nudibranch predation does induce changes in rates of stolon growth and budding, which may alter growth form, and that there may be a chemical component involved in the induction process.

The colony morphology described in this study is similar to that reported for laboratory cultures of *Cordylophora lacustris* by previous workers (FULTON, 1961; OVERTON, 1963). Our stolon growth rate of 1.06 mm/day is slower than the approximately 3 mm/day reported by FULTON (1963), but the interstalk distances of about 3 mm were the same, suggesting that while growth form was similar, growth rate was about one-third the maximum rate achieved by FULTON (1963). The culture techniques we used could certainly have been refined, but our primary concern was in determining whether nudibranch predation affected growth rates and(or) form. Therefore, once we determined that our culture techniques produced healthy colonies with a consistent growth form similar to that described in the literature, we focused our efforts on the experiments described.

The experiments showed that predation either by *Tenellia fuscata* or by polyp removal by forceps, accompanied by direct or indirect exposure to *T. fuscata* mucus, induced increased stolon budding rates. Enhanced stolon budding results in a denser colony form. This change could be caused by removal of three polyps, using forceps, and an application of mucus to the wounded portion of the colony lasting only a few minutes. In fact, removal by forceps and direct contact with mucus stimulated a greater response, lower stolon growth rate, and higher stolon budding rate than actual predation by a nudibranch. The greater impact on the hydroid may have resulted from the removal of three polyps in a minute or two rather than from a nudibranch feeding on the same number of polyps over a 6-h period. HARRIS & HOWE (1979) found that mucus from the nudibranch *Aeolidia papillosa* (Linnaeus, 1767) induced a behavioral response in its prey, the anemone *Anthopleura elegantissima* (Brandt, 1835), but this appears to be the first evidence of predator-induced growth changes in a cnidarian.

It is interesting that removal of polyps independent of a chemical stimulus had a negative impact on stolon budding and thus alters colony morphology in an opposite way to that induced by polyp removal accompanied by a chemical cue from the nudibranch predator. Polyp budding increased when forceps were used alone, but without stolon budding there would be only a higher density of polyps along non-branching stolons growing away from the point of colony initiation—similar to a hedgerow instead of a grove. One of us (Harris) had hypothesized that a hydroid might respond to predation by a nudibranch by sending out stolons to disperse the colony as occurred when forceps were used alone. However, the opposite occurred, suggesting that *C. lacustris* grows away from areas of abiotically caused injury, whereas predation induces a growth response that leads to a denser colony.

Tenellia fuscata has a short life-span of about 30 days (HARRIS *et al.*, 1980). A single individual, even if it were able to feed at the maximum rate for its entire life-span, would consume less than 360 polyps. FULTON (1962) reported that a *Cordylophora lacustris* polyp might live more than 100 days and his colonies, in limited space, produced well over 2000 polyps. Therefore, a healthy colony could easily survive limited nudibranch predation, but would be swamped by numerous individuals as described by CHAMBERS (1943). A denser colony form induced by nudibranch predation may benefit the hydroid by making it more difficult for larvae, including the veligers of *T. fuscata*, to pass through the canopy of predatory polyps to settle within the colony. STANDING (1976) reported that *Obelia* sp. inhibited barnacle settlement by eating settling cyprids, thereby prolonging the persistence of the colony in the community. However, limited predation might have a positive effect on a hydroid as has been suggested for some host-parasite associations (CHENG, 1971; LINCICOME, 1971).

In conclusion, the predator-prey association between

Tenellia fuscata and *Cordylophora lacustris* is more complex than the simple physical act of polyp removal by the nudibranch. It is a dynamic process involving rates of polyp addition and replacement to counter their loss through predation and changes in growth form induced by both physical damage as well as the combination of physical and chemical stimuli. The fact that both species adapt well to laboratory culture suggests that this system could be useful for studies relating to (1) chemical induction and (2) the dynamics of predator-prey associations.

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LITERATURE CITED

- BOSCHER, J. 1979. Modified reproduction strategy of leek *Allium porrum* in response to a phytophagous insect, *Acrolepiopsis assectella*. *Oikos* 33:451-456.
- BRAVERMAN, M. 1974. The cellular basis of morphogenesis and morphostasis in hydroids. *Oceanogr. Mar. Biol. Ann. Rev.* 12:129-221.
- CHAMBERS, L. A. 1943. Studies on the organs of reproduction in the nudibranchiate mollusks, with special reference to *Embletonia fuscata* Gould. *Bull. Amer. Mus. Natur. Hist.* 66:599-641.
- CHENG, T. C. 1971. Enhanced growth as a manifestation of parasitism and shell deposition in parasitized molluscs. Pp. 103-138. In: T. C. Cheng (ed.), *Aspects of the biology of symbiosis*. University Park Press: Baltimore, MD.
- EDMUNDS, M., G. W. POTTS, R. C. SWINFEN & V. L. WATER. 1976. Defensive behavior of sea anemones in response to predation by the opisthobranch mollusc *Aeolidia papillosa* (L.). *J. Mar. Biol. Assoc. U.K.* 56:65-83.
- FULTON, C. 1961. The development of *Cordylophora*. Pp. 287-295. In: H. M. Lenhoff and L. Loomis (eds.), *The biology of Hydra and of some other coelenterates*. University of Miami Press: Coral Gables, FL.
- FULTON, C. 1962. Environmental factors influencing the growth of *Cordylophora*. *J. Exp. Zool.* 151:61-78.
- FULTON, C. 1963. The development of a hydroid colony. *Devel. Biol.* 6:333-369.
- HARRIS, L. G. 1973. Nudibranch associations. Pp. 213-314. In: T. C. Cheng (ed.), *Current topics in comparative pathobiology*. Academic Press.
- HARRIS, L. G. & N. R. HOWE. 1979. An analysis of the defensive mechanisms observed in the anemone *Anthopleura elegantissima* in response to its nudibranch predator *Aeolidia papillosa*. *Biol. Bull.* 157:138-152.
- HARRIS, L. G., M. POWERS & J. RYAN. 1980. Life history studies of the estuarine nudibranch *Tenellia fuscata* (Gould, 1870). *Veliger* 23:70-74.
- HARVELL, C. D. 1984. Predator-induced defense in a marine bryozoan. *Science* 224:1357-1359.
- LINCICOME, D. R. 1971. The goodness of parasitism: a new

- hypothesis. Pp. 139-228. *In*: T. C. Cheng (ed.), Aspect of the biology of symbiosis. University Park Press: Baltimore, MD.
- VERTON, J. 1963. Intercellular connections in the outgrowing stolons of *Cordylophora*. *J. Cell Biol.* 17:661-671.
- ROSIN, R. 1969. Escape responses of the anemone *Anthopleura nigrescens* (Kerrill) to its predatory aeolid nudibranch *Heroviella* (Baba). *Veliger* 12:74-77.
- STANDING, J. D. 1976. Fouling community structure: effects of the hydroid, *Obelia dichotoma*, on larval recruitment. Pp. 155-164. *In*: G. O. Mackie (ed.), Coelenterate ecology and behavior. Plenum Publishing Corp.: New York.
- TODD, C. D. 1981. The ecology of nudibranch molluscs. *Oceanogr. Mar. Biol. Ann. Rev.* 19:141-234.

Avoidance and Escape Responses of the Gastropod *Nucella emarginata* (Deshayes, 1839) to the Predatory Seastar *Pisaster ochraceus* (Brandt, 1835)

by

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Abstract. The gastropod *Nucella emarginata* (Deshayes, 1839) exhibits both avoidance and escape responses to the predatory seastar *Pisaster ochraceus* (Brandt, 1835). When exposed to water "scented" by *P. ochraceus*, *N. emarginata* demonstrated a strong avoidance response that was absent when exposed to normal (control) seawater. *Nucella emarginata* also responded rapidly to the touch of a tube foot from *P. ochraceus* by changing direction and increasing mobility. Little or no response was elicited by the touch of a glass rod.

INTRODUCTION

MANY GASTROPOD mollusks exhibit defensive behaviors in response to predatory animals. These have been considered to be of two types: avoidance and escape behaviors (PHILLIPS, 1977). Avoidance behavior is exhibited when a prey species, responding to substances that have diffused from a predator through the water, reacts to the presence of the still distant predator (FEDER & ARVIDSSON, 1967; MACKIE, 1970). Escape behavior is a response to actual contact with the predator. There are many documented examples in the literature of escape responses and chemically mediated avoidance responses by marine gastropods to predatory asteroids, crabs, and gastropods (BULLOCK, 1953; EDWARDS, 1969; FEDER, 1963, 1967; GELLER, 1982; GONOR, 1965; MACKIE, 1970; MARGOLIN, 1964; MENGE, 1972; PHILLIPS, 1975, 1976, 1977, 1978).

Nucella emarginata (Deshayes, 1839) and *Pisaster ochraceus* (Brandt, 1835) are two species that overlap both in spatial distribution and dietary composition. They are also linked in prey-predator interactions, as *N. emarginata* is one of the species preyed upon by *P. ochraceus* (BERTNESS, 1977; FEDER, 1959). *Nucella emarginata* is found on rocky shores ranging from Alaska to Mexico (RICKETTS & CALVIN, 1968) and has been previously

shown to demonstrate a weak defensive response to the predatory seastar *Leptasterias hexactis* (MENGE, 1972).

The purpose of the present study is to determine if *Nucella emarginata* exhibits avoidance and escape responses to the predatory seastar *Pisaster ochraceus*. (Henceforth *Nucella emarginata* and *Pisaster ochraceus* will be referred to by their generic names only.)

MATERIALS AND METHODS

Study Sites

Specimens of *Nucella* were collected from Dillon Beach and Doran Rocks, two locations near Bodega Bay, Sonoma County, California. Both sites are boulder-strewn beaches supporting abundant populations of this gastropod.

Experimental Methods

Snails from both sites were maintained at the nearby Bodega Marine Laboratory (BML) in running seawater in a partitioned aquarium. A separate aquarium housed a seastar, collected from the coast adjacent to the BML.

The apparatus for testing both escape and avoidance responses consisted of four open-top boxes constructed of 0.32-cm thick plexiglas with dimensions 30.5 × 30.5 × 2.54 cm. A grid of 28 × 28 cm in 1-cm gradations was drawn on the base. Gradations were identified along one side by numbers and along the perpendicular side by letters of the alphabet in order to record the displacement of the snail without disturbance.

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Table 1

Avoidance response of *Nucella emarginata* from two sites, Dillon Beach and Doran Rocks, and the combined results from both locations. Fifty snails were used in each trial. The test criteria for a positive response were shell lifting behavior, changing direction, or a combination of both behaviors. A response was scored as negative if there was no apparent change in activity. χ^2 values resulted from comparing the control with the seastar run by means of a 2×2 contingency table corrected for continuity. ** = $P < 0.001$.

Site	Posi- tive re- sponses	Nega- tive re- sponses	χ^2
Dillon Beach			
Control	1	49	
<i>Pisaster</i> -scented water	49	1	88.36**
Doran Rocks			
Control	5	45	
<i>Pisaster</i> -scented water	47	3	67.35**
Dillon Beach and Doran Rocks			
Control	6	94	
<i>Pisaster</i> -scented water	96	4	158.48**

In the avoidance response test procedure, the seastar was weighed and placed in a 4-L beaker containing 3 L of seawater. After 2 h water from the beaker containing the seastar was poured into a 250-mL beaker for use in the experiments. The plexiglas boxes were filled to a depth of 1 cm with fresh seawater. Snails were measured with calipers (apex to end of siphonal canal), and placed, one per box, at the center of the grid. Once the snail's foot was extended, 1 mL of fresh seawater or 1 mL of scented water was allowed to flow freely from a pipette 2 cm from the anterior end of the snail. Responses were closely observed and recorded for 5 min. The position of the snail, based upon the location of the apex of the shell, was recorded at the end of 5, 10, and 15 min. Fifty snails were tested from each site. Control and experimental trials were conducted on consecutive days.

In the escape response test procedure, the plexiglas boxes were each filled to a depth of 1 cm with fresh seawater. Snails were measured and placed, one per box, at the center of the grid. Once the foot was extended, the snail was touched anteriorly either with the tip of a glass pipette or a tube foot that had been removed from a seastar and was held with forceps. Responses were closely observed and recorded for 5 min. Displacement of the snails was recorded at the end of 5, 10, and 15 min. Fifty snails were tested from each site. Control and experimental trials were conducted on consecutive days.

Between each trial the boxes were rinsed in running seawater. The pipette was also rinsed between each trial in the escape response procedure. A tube foot was used

Table 2

Escape response of *Nucella emarginata* from two sites, Dillon Beach and Doran Rocks, and the combined results from both beaches. Fifty snails were used in each trial, and the test criteria were as in Table 1. χ^2 values resulted from a comparison of control with seastar trial data by means of a 2×2 contingency table corrected for continuity. ** = $P < 0.001$.

Site	Posi- tive re- sponses	Nega- tive re- sponses	χ^2
Dillon Beach			
Control	5	45	
<i>Pisaster</i> tube foot touch	42	8	52.02**
Doran Rocks			
Control	4	46	
<i>Pisaster</i> tube foot touch	44	6	60.93**
Dillon Beach and Doran Rocks			
Control	9	91	
<i>Pisaster</i> tube foot touch	86	14	115.80**

four times before being discarded and replaced. In all trials, a positive response was defined as a change in behavior from that observed prior to the stimulus.

RESULTS

Nucella responded to the scent of *Pisaster* (Table 1). A total of 96 of 100 snails responded to the *Pisaster*-scented water, while only 6 of 100 responded to fresh seawater, a highly significant difference ($\chi^2 = 158.5$, $P < 0.001$). The behavior exhibited by *Nucella* when exposed to the *Pisaster*-scented water was remarkably different from activity prior to exposure. Some snails (2.1%) were observed only to lift their shells repeatedly and extend upward the body mass between the head and foot. They appeared to be rocking back and forth. Others moved in circles (21.9%), while many others combined both responses (76.0%).

Nucella exhibited an escape response when contacted by the tube foot of *Pisaster* (Table 2). A total of 86 of 100 snails responded to the tube foot touch compared to only 9 of 100 responding to the touch of the tip of a glass pipette. Trials involving tube foot touch were significantly different from control trials ($\chi^2 = 115.8$, $P < 0.001$). The escape response by *Nucella* was similar to the avoidance response, but it was not as pronounced. Snails were observed to lift up only initially, and then make 180° change of direction from the point of stimulus. Snails were observed to lift up (2.3%), change direction (64.0%), and to change direction and lift up (33.7%).

DISCUSSION

The present study confirms that the gastropod *Nucella emarginata* does exhibit both avoidance and escape re-

sponses to the predatory seastar *Pisaster ochraceus*. The primary response of the snail was to change direction and increase its activity. It must be kept in mind, however, that laboratory studies, such as the test procedure used here for avoidance responses, are subject to the criticism that laboratory conditions do not duplicate those normally found in the natural habitat. For example, high concentration of seastar scent, minimal water disturbance, and smooth substrate are not naturally found in the intertidal zone. Assuming that the behaviors elicited in the laboratory also occur in the field, they would be advantageous to an organism such as *Nucella* whose habitat overlaps that of a predator, in this case, *Pisaster*.

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LITERATURE CITED

- BERTNESS, M. D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* 58:86-97.
- BULLOCK, T. H. 1953. Predator recognition and escape responses of some intertidal gastropods in the presence of starfish. *Behavior* 53:130-140.
- EDWARDS, D. C. 1969. Predators on *Olivella biplicata*, including a species-specific predator avoidance response. *Veliger* 11:326-333.
- FEDER, H. M. 1959. Food of the starfish *Pisaster ochraceus* along the California coast. *Ecology* 40:721-724.
- FEDER, H. M. 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. *Ecology* 44:505-512.
- FEDER, H. M. 1967. Organisms responsive to predatory seastars. *Sarsia* 29:371-394.
- FEDER, H. M. & J. ARVIDSSON. 1967. Studies on a seastar (*Marthasterias glacialis*) extract responsible for avoidance reactions in a gastropod (*Buccinum undatum*). *Arkiv For Zoologi* 19:369-379.
- GELLER, J. B. 1982. Chemically mediated avoidance response of a gastropod, *Tegula funebris* (A. Adams), to a predatory crab, *Cancer antennarius* (Stimpson). *J. Exp. Mar. Biol. Ecol.* 65:19-27.
- GONOR, J. J. 1965. Predator-prey relations between two marine prosobranch gastropods. *Veliger* 7:228-232.
- MACKIE, A. M. 1970. The escape reactions of marine invertebrates to predatory starfish. *J. Exp. Mar. Biol. Ecol.* 5:63-69.
- MARGOLIN, A. S. 1964. A running response of *Acmaea* to seastars. *Ecology* 45:191-193.
- MENGE, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.* 42:25-50.
- PAINE, R. T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology* 50:950-961.
- PHILLIPS, D. W. 1975. Distance chemoreception-triggered avoidance behavior of the limpets *Acmaea (Collisella) limatula* and *Acmaea (Notoacmea) scutum* to the predatory starfish *Pisaster ochraceus*. *J. Exp. Zool.* 191:359-368.
- PHILLIPS, D. W. 1976. The effect of species-specific avoidance response to predatory starfish on the intertidal distribution of gastropods. *Oecologia (Berlin)* 23:83-94.
- PHILLIPS, D. W. 1977. Avoidance and escape responses of the gastropod mollusc *Olivella biplicata* (Sowerby) to predatory asteroids. *J. Exp. Mar. Biol. Ecol.* 28:77-86.
- PHILLIPS, D. W. 1978. Chemical mediation of invertebrate behaviors and the ability to distinguish between foraging and inactive predators. *Mar. Biol.* 49:237-243.
- RICKETTS, E. F. & J. CALVIN. 1968. *Between Pacific Tides*. 4th ed., rev. by J. W. HEDGEPEETH. Stanford University Press: Stanford, California. 614 pp.

Oxygen Production and Consumption in the Sacoglossan (=Ascoglossan) *Elysia chlorotica* Gould

by

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Abstract. A naturally occurring population of *Elysia chlorotica* Gould (Opisthobranchia: Sacoglossa) composed of a mixture of individuals ranging from dark green to non-green in color was found in the Minas Basin, Nova Scotia, Canada. This species is usually dark green in color because of endosymbiotic chloroplasts derived from their food alga *Vaucheria* sp. Individuals from this population were examined for O₂ production and consumption. A correlation between chlorophyll content and O₂ production was found.

INTRODUCTION

SINCE THE FIRST identification of sacoglossan endosymbionts as chloroplasts (KAWAGUTI & YAMASU, 1965), many such associations have been described, especially in reference to plastid origin (TAYLOR, 1968; TRENCH *et al.*, 1969; GREENE, 1970a; TRENCH, 1975) and functional capacity, including carbon fixation (GREENE, 1970b; TRENCH, 1973; STIRTS & CLARK, 1980; CLARK *et al.*, 1981) and oxygen production (Brandt, 1883, *in* TAYLOR, 1968; KAWAGUTI & YAMASU, 1965; TRENCH *et al.*, 1969; TRENCH, 1975; GRAVES *et al.*, 1979). These authors have demonstrated a net O₂ production under illumination and attributed it to the presence of endosymbiotic chloroplasts.

Sacoglossans are herbivorous and feed by slitting or piercing a food plant with their radula and suctorially removing plant sap and chloroplasts (TRENCH *et al.*, 1969; JENSEN, 1983). The chloroplasts are phagocytized by the slug's digestive cells (MUSCATINE *et al.*, 1975; MCLEAN, 1976) in which they are maintained for variable periods of time depending upon the sacoglossan and algal species (TAYLOR, 1968; TRENCH *et al.*, 1969; HINDE & SMITH, 1972; CLARK *et al.*, 1981).

The presence of chloroplasts in the digestive diverticula typically colors the slug identically to the plastid source, and comparison of pigment spectra of the slug and possible food choices is commonly used to determine the actual food plant (TAYLOR, 1968; TRENCH *et al.*, 1969; GREENE, 1970a; TRENCH, 1975). Chlorophyll content has been shown to be indicative of chloroplast functional capacity, often decreasing with starvation of the sacoglossan (GREENE, 1970b; CLARKE & BUSACCA, 1978).

In the summers of 1983 and 1984, three salt marshes

in the Minas Basin, Nova Scotia, contained populations of *Elysia chlorotica* Gould, 1870 (Opisthobranchia: Sacoglossa) ranging from light green to non-green in color, instead of the usual rich dark green that results from the presence of endosymbiotic chloroplasts derived from the food alga *Vaucheria* sp. (BAILEY & BLEAKNEY, 1967; GRAVES *et al.*, 1979). A survey of the literature indicated that a naturally occurring population of symbiotic elysiid sacoglossans not strongly pigmented by chloroplasts had never been reported.

The aim of this study was to use the above population as the basis for an examination of sacoglossan color and chloroplast function as related to chlorophyll content, oxygen production, and oxygen consumption.

MATERIALS AND METHODS

Collection and Maintenance of Animals

Elysia chlorotica individuals were collected from salt marshes located at Kingsport, Pickett's Wharf, and Porter's Point in the Minas Basin. They were usually found on exposed mats of an undetermined *Vaucheria* species along the edges of pools and creeks, on pool bottom sediments, or on an assortment of submersed algae, including *Rhizoclonium*, *Cladophora*, and *Ectocarpus* species.

The slugs were divided into three study groups by comparison with MUNSELL (1977) color charts. Color groupings used were as follows: Group 1 (dark green) ranged in color from 7.5GY 4/4, 4/6 to 5GY 7/6, 7/8, Group 2 (light green) from 5GY 7/6, 7/8 to 2.5GY 7/4, 7/6, and Group 3 (non-green) from 2.5GY 7/4, 7/6 to 5Y 8/4, 8/6. All specimens were used as soon as possible after

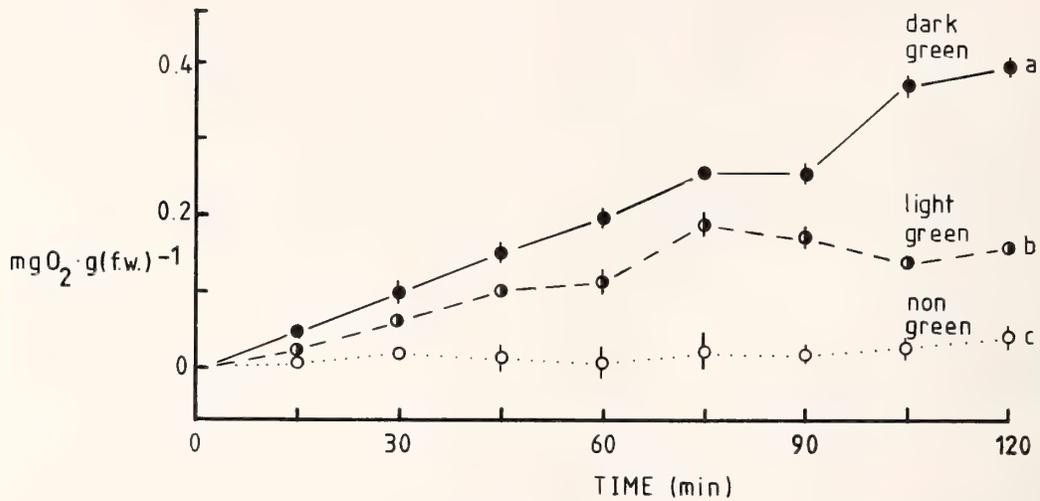


Figure 1

Gross O₂ production of each *Elysia chlorotica* study group. Mean values are plotted, and SE bars included where the standard error is greater than the area covered by the mean symbol. n = 6 for each group. a, Group 1; b, Group 2; c, Group 3.

collection and were maintained in the dark at 9°C and at 28‰ salinity without food between tests.

Measurements of Oxygen Production and Consumption

Photosynthetic and respiratory activity were compared between study groups by measuring light-dark O₂ production and consumption. Control tests without slugs were also conducted. Slugs were gently blotted to remove excess water, weighed, and placed in a stoppered 12-mL flask filled with O₂-saturated (PO₂ = 155 mm Hg) seawater (28‰ salinity). Changes in oxygen pressure were measured at 15-min intervals for 2 h with a Radiometer O₂-electrode system. Illumination was provided by a 120-Volt American Optical fluorescence lamp with two bulbs positioned at right angles to each other and at a 1-cm distance from the flask. During the dark trials, the flask was wrapped in aluminum foil and continuous illumination was maintained to eliminate the possibility of light-induced temperature changes (1.2–2.0°C) affecting the electrode characteristics and O₂ solubility. The water was mixed with a small magnetic stirrer and the electrode allowed to stabilize before each reading was taken. PO₂ was converted to mg O₂ with the following equation (adapted from HOAR & HICKMAN, 1975):

$$\text{mg O}_2 \cdot \text{g(fw)}^{-1} \text{ h}^{-1} = \frac{\text{PO}_2 \text{ mm Hg} \cdot 1000\alpha \cdot 1.43}{\text{BP} \cdot \text{g(fw)} \cdot \text{h}}$$

where g(fw) = fresh weight of the slug in grams, h = time (in hours), α = the appropriate O₂ solubility coefficient alpha for a specific temperature, 1.43 = a conversion factor to change mL O₂ to mg O₂, and BP = barometric pres-

sure. Gross O₂ production was determined by adding the amount of O₂ consumed in the dark to that produced in the light. Rates of respiration (O₂ consumed in the dark) were compared using a Mann-Whitney U test.

Measurement of Chlorophyll Content

Animals were gently blotted to remove excess water, weighed, anaesthetized at -9°C for 2–3 min, and homogenized in 2 mL of absolute methanol. The suspension was centrifuged in a IECHE centrifuge at 8000 rpm for 10 min. The centrifuged pellet was washed twice with absolute methanol and the extracts combined for a total volume of 5 mL. Samples were stored temporarily (less than 1 h) in the dark at 9°C to prevent bleaching. Chlorophyll content (chlorophylls a and c inclusive) was determined with a Varian Techron model 635 spectrophotometer using the following equation (after MACLACHLAN & ZAHLIK, 1963):

$$\text{mg chl g(fw)}^{-1} = 25.5(A_{650}) + 4.0(A_{655}) \cdot V / (\text{g(fw)} \cdot 1000)$$

where g(fw) = fresh weight of slug in grams, A = absorption at the indicated wavelength, and V = total volume (5 mL) of methanol extract.

OBSERVATIONS

The three study groups showed some gross O₂ production (Figure 1). Group 1 (dark green slugs) have both the greatest O₂ production and the highest chlorophyll content (Table 1), Group 2 (light green slugs) showed less O₂ production and a lower chlorophyll content, while Group 3 (non-green slugs) showed almost no O₂ production and a very low chlorophyll content. Groups 2 and 3 consumed O₂ at a greater rate than O₂ was produced, in contrast to

Table 1

Chlorophyll content, O₂ production, and O₂ consumption for each *Elysia chlorotica* study group. Values given are means \pm SE. n = 6 for each group.

Group	Group 1 (dark green)	Group 2 (light green)	Group 3 (non-green)
Chlorophyll content mg chl g (fw) ⁻¹	1.83 \pm 0.16	0.59 \pm 0.05	0.16 \pm 0.01
mg O ₂ g(fw) ⁻¹ h ⁻¹			
O ₂ produced in light	0.0775 \pm 0.0095	-0.0193 \pm 0.0073	-0.0828 \pm 0.0097
O ₂ consumed in dark	-0.1109 \pm 0.0029	-0.1060 \pm 0.0082	-0.0913 \pm 0.0038
Gross O ₂ production	0.1884 \pm 0.0119	0.0883 \pm 0.0125	0.0122 \pm 0.0125
mg O ₂ g(fw) ⁻¹ g chl ⁻¹ h ⁻¹	0.1029	0.1500	0.0762

Group 1. O₂ produced per unit chlorophyll was greatest in Group 2, and lowest in Group 3. The three study groups displayed similar rates of respiration (O₂ consumption in the dark).

DISCUSSION

Although a naturally occurring non-green elysiid population has not previously been reported, the relationship between chlorophyll content, an indicator of chloroplast functional capacity (GREENE, 1970b), and sacoglossan starvation has been studied by several authors (TRENCH *et al.*, 1969; CLARK *et al.*, 1981). Results vary with species. Chlorophyll levels have been found to decrease after a 24-h starvation period in *Elysia hedgpethi*, accompanied by a parallel decrease in chloroplast functional capacity (GREENE, 1970b). In the same study, Greene observed that chlorophyll levels in *Placobranchus ianthobapsus* remained unaffected throughout a 27-day starvation period, while the photosynthetic ability of the chloroplasts decreased. In *Elysia viridis*, chlorophyll levels increased over a 93-day starvation period and chloroplasts remained functional for 3 months (HINDE & SMITH, 1972). CLARK & BUSACCA (1978) found that chlorophyll content decreased with starvation in four sacoglossan species: *Elysia tuca*, *Tridachia crispata*, *Oxynoe antillarum*, and *Elysia cauzei*.

It could not be determined whether or not starvation had occurred before collection of the naturally pale *Elysia chlorotica* specimens examined in this study, and if it did, for what length of time. However, there is a relationship between chlorophyll content and chloroplast functional capacity. *Elysia chlorotica*, from all three study groups, showed some gross O₂ production. Group 1 (dark green slugs) had both the greatest chlorophyll content and the largest O₂ production. Although less O₂ was produced by the animals in Group 2 (light green slugs), each unit of chlorophyll produced 31% more O₂ than in Group 1. Animals in Group 3 (non-green slugs) showed almost no gross O₂ production, the chlorophyll content decreased to 9% of that of Group 1, and each unit of chlorophyll produced 26% less O₂ than in Group 1. The increased O₂ production per unit of chlorophyll in Group 2 is of inter-

est, although difficult to explain. Possibly as chlorophyll is lost, more light is able to penetrate the sacoglossan tissue, or some means of regulating chlorophyll activity occurs. However, it appears that *E. chlorotica* can maintain a high level of O₂ production while chlorophyll levels are starting to decline. As chlorophyll levels continue to fall, this ability is lost, as shown in Group 3.

All three study groups had equivalent rates of respiration (Groups 1 and 3 compared: Mann-Whitney U = 48.5, $P > 0.05$, $n_1 = 9$, $n_2 = 9$). This is indicative of the tissues being in a similar physiological condition, regardless of color. Variations observed might have been influenced by several factors. Specimens used were selected from a certain size range (4–12 mm) but the variation within this range would result in differing rates of respiration (SANDER & MOORE, 1978). Respiration rates may also be affected by the small temperature changes that occurred (SANDER & MOORE, 1978) as well as by the change in O₂ tension in the experimental chamber as O₂ was consumed during each test (MANDAN MOHAN DAS & VENKATACHARI, 1984).

The cause for the appearance of the naturally pale *Elysia chlorotica* population is not known. Field records for the salt marshes of the Minas Basin (Bleakney, 1966–1982, unpublished data), report that only two light green *E. chlorotica* individuals have been previously collected (May 1, 1969). Field records for 1983 indicate that almost all of the algae in and around the marsh pools were dead by late May, probably as a result of heavy rainfall throughout the month. In 1984, *Vaucheria* mats did not appear until the end of June. Perhaps the loss of green pigment was related to the inability of the slugs to locate sufficient *Vaucheria*. This would either result in starvation or force the slugs to find another food source, presumably without compatible chloroplasts. However, starvation of this species does not usually produce a loss of green pigment. Dark green *E. chlorotica* collected in other years have remained healthy and green for at least 4 months in a 9°C refrigerator. S. K. Pierce (1984, *in litt.*) was also unable to bleach out the chlorophyll through starvation of this species. Dark green slugs collected in the Minas Basin

in the summers of 1983 and 1984 did lose chlorophyll when starved for 2 to 3 wk. Non-green slugs fed freshly collected *Vaucheria* sp. turned green within 4 days. Perhaps the *Vaucheria* ingested during this period was in some way debilitated, causing the chloroplasts to bleach more rapidly.

Examination of a naturally occurring green and non-green *Elysia chlorotica* population indicates that there is a relationship between declining chlorophyll content (reflected in slug color) and the photosynthetic ability of the endosymbiotic chloroplasts. The functional capacity of the total amount of chlorophyll present seems to vary as pigment is lost. Regardless of color, the rate of O₂ consumption does not appear to change.

ACKNOWLEDGMENTS

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LITERATURE CITED

- BAILEY, K. H. & J. S. BLEAKNEY. 1967. First Canadian report of the sacoglossan *Elysia chlorotica* Gould. *Veliger* 9:353-354.
- CLARK, K. B. & M. BUSACCA. 1978. Feeding specificity and chloroplast retention in four tropical Ascoglossa, with a discussion of the extent of chloroplast symbiosis and the evolution of the order. *J. Moll. Stud.* 44:272-282.
- CLARK, K. B., K. R. JENSEN, H. M. STIRTS & C. FERMIN. 1981. Chloroplast symbiosis in a non-elysiid mollusc, *Costasiella liliana* (Marcus) (Hermaidae: Ascoglossa) (=Sacoglossa): effects of temperature, light intensity, and starvation on carbon fixation rate. *Biol. Bull.* 160:43-54.
- GRAVES, D. A., M. A. GIBSON & J. S. BLEAKNEY. 1979. The digestive diverticula of *Alderia modesta* and *Elysia chlorotica* (Opisthobranchia: Sacoglossa). *Veliger* 21:415-422.
- GREENE, R. W. 1970a. Symbiosis in sacoglossan opisthobranchs: symbiosis with algal chloroplasts. *Malacologia* 10:357-368.
- GREENE, R. W. 1970b. Symbiosis in sacoglossan opisthobranchs: functional capacity of symbiotic chloroplasts. *Mar. Biol.* 7:138-142.
- HINDE, R. & D. C. SMITH. 1972. Persistence of functional chloroplasts in *Elysia viridis* (Opisthobranchia, Sacoglossa). *Nature New Biology* 239:30-31.
- HOAR, W. S. & C. P. HICKMAN. 1975. A laboratory companion for general and comparative physiology. 2nd ed. Prentice-Hall Inc.: New Jersey.
- JENSEN, K. R. 1983. Factors affecting feeding selectivity in herbivorous Ascoglossa (Mollusca: Opisthobranchia). *J. Exp. Mar. Biol. Ecol.* 66:135-148.
- KAWAGUTI, S. & T. YAMASU. 1965. Electron microscopy on the symbiosis between an elysioid gastropod and chloroplasts of a green alga. *Biol. J. Okayama Univ.* 11:57-65.
- MACLACHLAN, S. & S. ZAHLIK. 1963. Chlorophyll mutant of barley. *Can. J. Bot.* 41:1053-1062.
- MADAN MOHAN DAS, V. & S. A. T. VANKATACHARI. 1984. Influence of varying oxygen tension on the oxygen consumption of the freshwater mussel *Lamellidens marginalis* (Lamarck) and its relation to body size. *Veliger* 26:305-310.
- MCLEAN, N. 1976. Phagocytosis of chloroplasts in *Placida dendritica* (Gastropoda: Sacoglossa). *J. Exp. Zool.* 197:321-329.
- MUNSELL. 1977. Colour charts for plants tissues. 2nd ed. Kollmorgen Corporation: Baltimore.
- MUSCATINE, L., R. R. POOL & R. K. TRENCH. 1975. Symbiosis of algae and invertebrates: aspects of the symbiont surface and the host-symbiont interface. *Trans. Amer. Microsc. Soc.* 94:450-469.
- SANDER, F. & E. A. MOORE. 1978. Comparative respiration in the gastropods *Murex pomum* and *Strombus pugilis* at different temperatures and salinities. *Comp. Biochem. Physiol.* 60:99-105.
- SKIRTS, H. M. & K. B. CLARK. 1980. Effects of temperature on products of symbiotic chloroplasts in *Elysia tuca* Marcus (Opisthobranchia: Ascoglossa). *J. Exp. Mar. Biol. Ecol.* 43:39-47.
- TAYLOR, D. L. 1968. Chloroplasts as symbiotic organelles in the digestive gland of *Elysia viridis* (Gastropoda: Opisthobranchia). *J. Mar. Bio. Ass. U.K.* 48:1-15.
- TRENCH, R. K. 1973. Further studies on the mucopolysaccharide secreted by the pedal gland of the marine slug, *Tri-dachia crispata* (Opisthobranchia, Sacoglossa). *Bull. Mar. Sci.* 23:299-312.
- TRENCH, R. K. 1975. Of 'leaves that crawl': functional chloroplasts in animal cells. *Soc. Exp. Biol. Cambridge Symposium* 29:229-266.
- TRENCH, R. K., R. W. GREENE & B. G. BYSTROM. 1969. Chloroplasts as functional organelles in animal tissues. *J. Cell Biol.* 42:404-417.

Environmental Perturbations Reflected in Internal Shell Growth Patterns of *Corbicula fluminea* (Mollusca: Bivalvia)¹

by

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Abstract. Anthropogenic and natural seasonal environmental perturbations were reflected in shell growth patterns of specimens of *Corbicula fluminea* living at the northernmost extent of their range along the east coast of North America (Raritan River, New Jersey). Growth of organisms in experimental cages was monitored from August 1981 to January 1982 and from July to December 1982 at stations located upstream (controls: 2 stations) and immediately downstream (perturbed: 1 station) from a combined industrial-sewage effluent. In 1981, the growing shell margin of each clam was notched with a small drill before each was placed in a cage; these marked organisms were sacrificed after various lengths of time. In 1982, specimens were not notched, but a growth cessation mark in the shell microstructure of all caged organisms marked the beginning of the monitored growth period. Growth patterns in shell microstructure were examined in acetate peels and polished thin sections. Microgrowth increments in the outer crossed-lamellar layer were deposited at an average rate of approximately one increment per day. A growth cessation mark found in all specimens sampled in 1981 ($n = 53$) was dated to within two days of a major storm using increment counts, revealing the accuracy of their use to date shell regions. Lack of growth in winter resulted in a growth discontinuity in the inner complex crossed-lamellar layer and an associated growth cessation mark in the outer layer. Increment counts suggested that growth resumed in late March or early April each year as water temperatures rose above approximately 10°C. Growth rates of 1+ year old individuals during spring and early summer (before entering experimental cages) averaged 65 and 45 $\mu\text{m}/\text{increment}$ in 1981 and 1982 respectively. In 1981, growth rates at each site were significantly slower during the monitored growth period than before it, which was probably due to injury inflicted by notching the ventral shell margin. In 1982, growth rates of unnotched clams at the control sites were similar before and after entering the experimental cages (after an initial two-week decrease in growth rates). However, unnotched specimens moved to the perturbed site in 1982 subsequently grew at significantly slower rates and had fewer increments during the monitored period than those collected from cages at control sites.

INTRODUCTION

AQUATIC ECOLOGISTS are frequently concerned with assessing effects of environmental events, such as chronic, periodic, or accidental additions of a pollutant, on growth

of organisms after the event has occurred. In the absence of information about pre-disturbance growth rates, the ecologist, like the paleontologist, is confronted with the problem of after-the-fact data acquisition. Detailed analyses of growth patterns in molluscan shell structure provide a tool for addressing this problem. Records of an organism's dynamic environment are capable of being preserved as structural, morphological, or chemical changes in the shell. Research into these relationships has been largely to reconstruct paleoenvironments (PANNELLA & MACCLINTOCK, 1968; RHOADS & PANNELLA, 1970; BERRY

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& BARKER, 1975; PANNELLA, 1976; JONES, 1980; RYE & SOMMER, 1980; LUTZ, 1981; DODD & CRISP, 1982). However, implications of this approach for ecological work have also interested many neontologists (RHOADS & PANNELLA, 1970; KENNISH & OLSSON, 1975; KENNISH, 1980).

Present knowledge of the relationship between the environment and bivalve shell structure is limited. However, studies of shell growth patterns of *Mercenaria mercenaria* (Linné) by KENNISH & OLSSON (1975) and KENNISH (1980) have demonstrated the application of shell analytical techniques to *in situ* environmental monitoring studies. In the present study, microstructural shell growth patterns of the freshwater Asiatic clam *Corbicula fluminea* (Müller) were analyzed to assess effects on clam growth of the combined effluents of an organic chemical plant and a sewage treatment facility in a freshwater, non-tidal segment of the Raritan River, New Jersey. *Corbicula fluminea* was chosen as the test organism because it maintains a large population within the river (TRAMA, 1982), has rapid rates of shell growth (BRITTON *et al.*, 1979; BRITTON & MORTON, 1982), and because it is an opportunistic, pest species (BRITTON & MORTON, 1982). In order to discern the effects of environmental perturbations in shell microstructure, it was necessary to first document the natural, seasonal shell growth pattern of the species.

The shell of *Corbicula fluminea* is composed of three calcareous layers when viewed in radial section. These are, from exterior to interior: the outer fine crossed-lamellar layer, a pallial myostracum, and the inner complex crossed-lamellar layer (TAYLOR *et al.*, 1973; COUNTS & PREZANT, 1982; PREZANT & TAN-TIU, 1985). cursory examination of thin radial sections (or acetate peels) of the aragonitic outer and inner layers reveals bands or lines within the shell (Figure 1A, B). A single pair of dark lines within the outer layer that delineates a lighter band of shell between them is defined as a microgrowth increment. A growth cessation mark is an irregularity in the periodic deposition of microgrowth increments, often resulting in a V-shaped notch in the shell exterior, an unusually thick microgrowth increment boundary, or an abrupt change in the depositional surface, caused by a loss of mantle attachment to the ventral margin (KENNISH & OLSSON, 1975; RICHARDSON *et al.*, 1980). Furthermore, growth lines within the inner layer, which are often associated with microgrowth increments or growth cessation marks in the outer layer, may also reflect the growth history of the animal.

TRAMA (1982) first reported the occurrence of *Corbicula fluminea* in the Raritan River from collections made in March 1981. He estimated the year of introduction as not later than 1978 based on an age of between 3 and 4 years for the largest specimen collected, which had a shell length of 25 mm. Little is known about the population ecology of *C. fluminea* in the Raritan River. Based on other studies in North America and Asia (see reviews of BRITTON &

MORTON, 1979, 1982), *Corbicula* can aptly be described as opportunistic, but also well adapted, especially in its reproductive biology, to lotic environments. Density-independent factors, such as weather and reservoir draw-down, have been shown to cause catastrophic mortalities of *Corbicula* in streams, lakes, and reservoirs, but due to early maturation and high fecundity, the organism has been able to maintain populations in many such systems (BRITTON & MORTON, 1979). The temperature ranges for survival and growth of *C. fluminea* are not precisely known, but RODGERS *et al.* (1979) reported a minimum of 10°C for growth. Low winter temperatures and their duration are suspected of limiting the spread of the species to generally south of latitude 40°N on the North American continent. Maximum shell lengths of *Corbicula* in North America vary from a low of 18 mm in San Luis Reservoir, California, to between 40 and 50 mm in other systems in Texas and California, suggesting that factors other than low winter temperatures are involved in controlling ultimate shell size (BRITTON & MORTON, 1982). The relatively small maximum size of *Corbicula* attained in the Raritan River, New Jersey, then may indicate that this population is "dwarfed," and possibly stressed by factors other than low winter temperatures.

To study shell growth during known periods, caged populations of *Corbicula fluminea* were established near the effluent discharge and at two control stations in the Raritan River in summer 1981 and sampled, along with the natural population, during the next one and one-half years (Figure 2). Through comparisons of microstructural shell growth of caged *C. fluminea* at the three locations and uncaged specimens at one site, we (1) analyzed effects of chronic exposure to the effluent on growth, (2) determined effects of notching the ventral shell margin and caging on growth, (3) documented the natural annual pattern of shell growth (from which changes caused by the effluent, notching and/or caging had to be distinguished), and (4) determined the periodicity of microgrowth increment formation.

MATERIALS AND METHODS

Sampling Methods

Caged populations of *Corbicula fluminea* were established at three stations in the Raritan River, New Jersey (Figure 2). The experimental station, AC, received the combined effluents of the American Cyanamid Organic Chemical Plant and the Somerset-Raritan Valley Sewage Authority. Composition of the effluent varied considerably on a daily basis (B. Ruppel, NJ Department of Environmental Protection, personal communication). Consequently, we did not determine the specific effects on shell growth of high nutrient loadings or organo-chlorine compounds in the effluent, but rather the integrated results of chronic exposure to a broad spectrum, sublethal alteration of water quality. Only a small population of *C. fluminea*

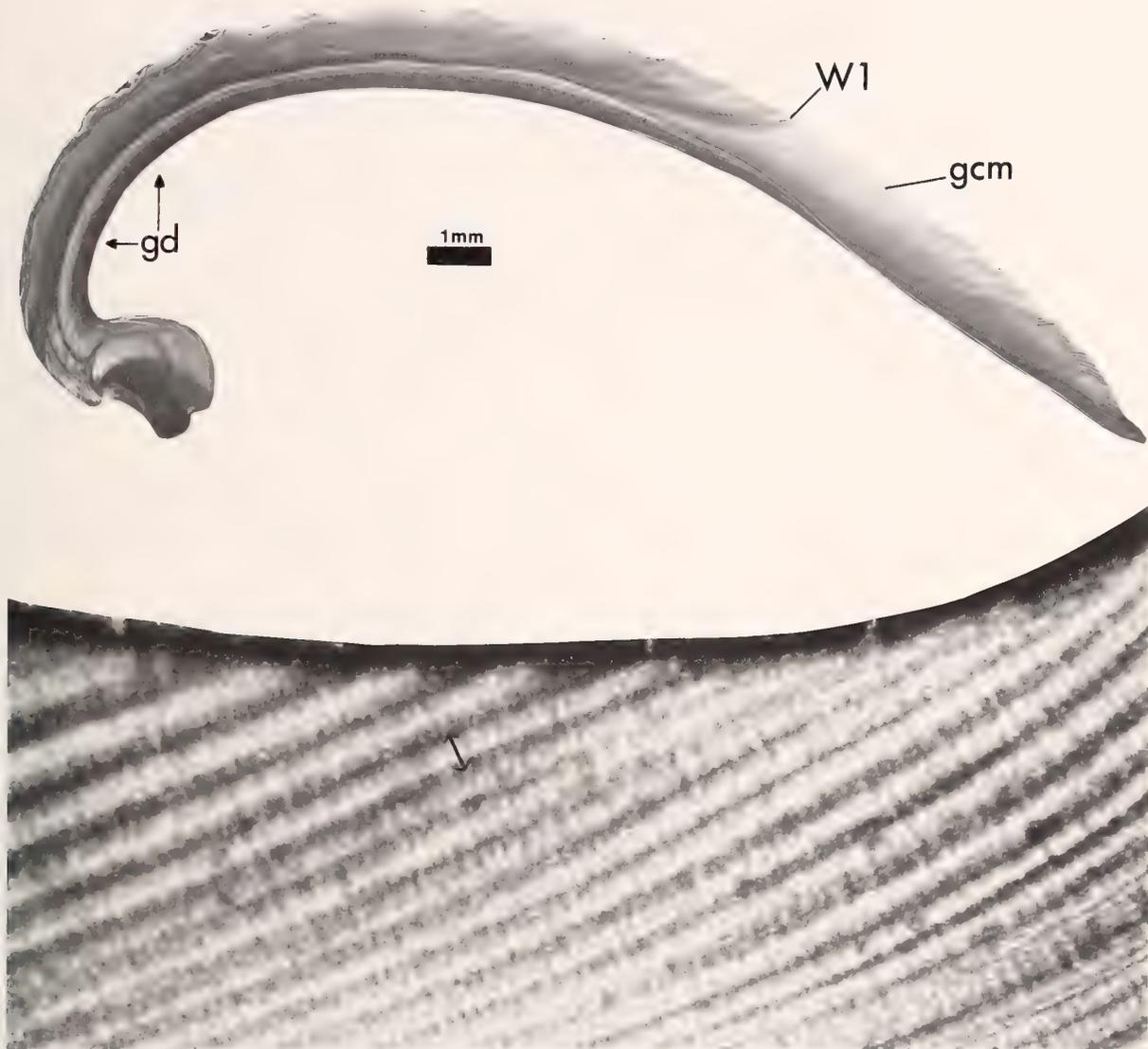


Figure 1

A (above). Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected on 13 July 1981 from the natural population at station C (see Figure 2). Print was made by placing thin shell section in an enlarger and exposing photographic paper directly; thus, the enlargement is a negative image of the section. The winter 1980-1981 growth cessation (W1) and the growth cessation mark (gcm) in the outer fine crossed-lamellar layer, and the growth discontinuity (gd) in the inner complex crossed-lamellar layer are labelled. Total shell height is 18.1 mm and growth is to the right. B (below). Light micrograph of the outer fine crossed-lamellar layer of a specimen of *Corbicula fluminea* showing a series of microgrowth increments. Arrows delineate one increment. Micrograph is a positive image of the section. Growth is to the right and the horizontal field width is 0.7 mm.

was present at station AC, but a large population, with shell lengths ranging from 2 to 20 mm, was located at the confluence of the Millstone and Raritan rivers (TRAMA, 1982; this study), approximately 1.6 km upstream from station AC. This site was one of the controls (station C) and was the source of all animals placed in cages at the three stations. The other control station, DI, located 12

km upstream from station AC, was selected because there were no direct inputs to the site from sewage treatment plants, industries, or landfills. Station DI in 1981 did not have a natural population of *C. fluminea* associated with it. In 1982, the station was moved approximately 500 m upstream where clams were found in numbers similar to those at station AC.

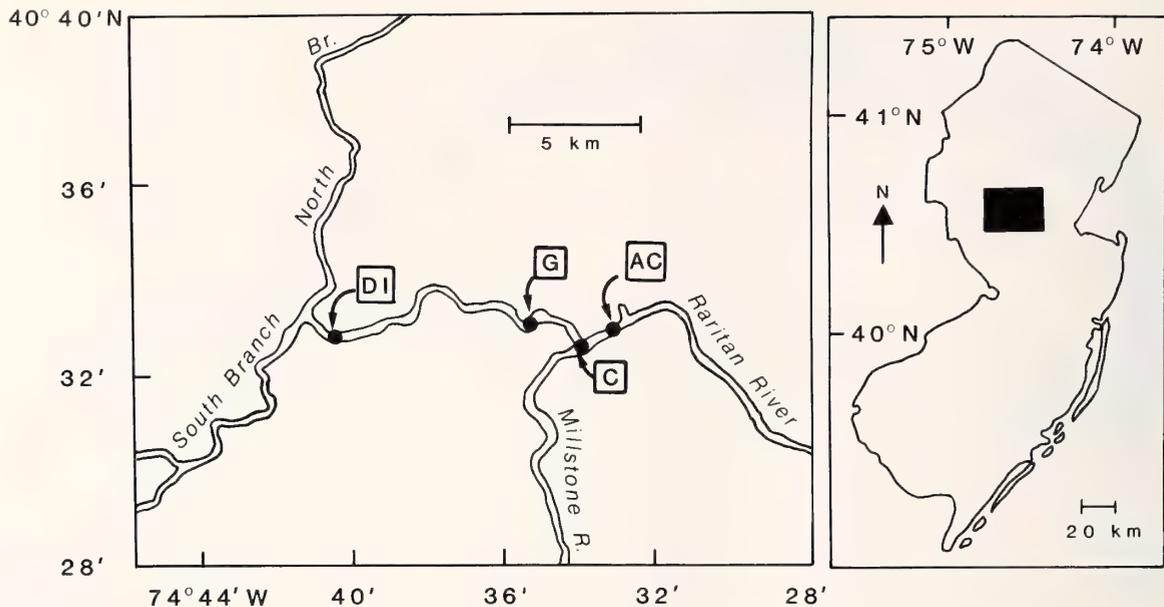


Figure 2

Map of New Jersey, U.S.A. (right); shaded area is enlarged on the left. Stations: AC, experimental site; C, control site and location of natural population; DI, control site; G, United States Geological Survey (USGS) gauging station at Manville, NJ.

Two groups of caged specimens of *Corbicula fluminea* (shell lengths ranging from 8 to 20 mm) were established and sampled in 1981. The first group, Notch I, consisted of animals collected on 17 August 1981. The ventral margin of each animal was notched with a drill (bit size of 1.6 mm) to provide a reference point on the shell prior to planting in cages at stations DI and AC (one cage per station). Cages were 0.3 × 0.3 × 0.15 m open wood frames lined with 1 mm galvanized steel mesh. Substratum from each site was placed in the cage to a depth of approximately 10 cm and 50 specimens of *C. fluminea* were planted in each cage, a density of 530 clams per m⁻². The second group, Notch II, was composed of animals collected on 16 September 1981 and notched as described for Notch I. For this group, cages consisted of plastic mesh (1.6 mm) bags filled with substratum from each station and anchored to the bottom. Fifty clams were placed in each bag, yielding the same cage densities as the Notch I group. One cage with Notch II specimens was placed at the two control stations (DI and C) and one perturbed (AC) station. Samples of Notch I and II animals were collected and sacrificed on five and three occasions, respectively, through January 1982. There were massive mortalities of *C. fluminea* in spring 1982 in all cages, as well as in the natural population at station C. To continue the experiment, new animals were collected from the rejuvenated population at station C.

In 1982, cages were constructed and sampled by Dr. Angela Cristini as part of a study of the use of adenylate

energy charges to detect stress (CANTELMO-CRISTINI *et al.*, 1983). Shells of caged and uncaged specimens were supplied to us by Dr. Cristini. Cages were 0.9 × 0.9 × 0.25 m wood frames, with the top, bottom, and a portion of two opposing sides (0.9 × 0.1 m openings) composed of 1.6-mm mesh cloth. Two cages were placed at each site. Substratum from station C was placed in each cage to a depth of 0.2 m. On 19 July 1982, approximately 200 clams were placed in each cage, a density of 250 clams per m⁻². The ventral shell margin of these animals was not notched. Three animals were sampled from the cages at each station and the natural population at station C on six dates through December 1982.

Examination of Shell Growth Patterns

A single valve from each specimen was embedded in epoxy resin and radially sectioned (along the height axis from umbo to ventral margin). The two cross-sectional surfaces were finely ground with 600-grit carborundum powder, polished with diamond compounds on lapidary wheels, etched for 30 secs in 0.9 N HCl, rinsed in distilled water, and air-dried; one was used to prepare an acetate peel replica of the microstructural growth patterns (KENNISH *et al.*, 1980) while the other was used to prepare a thin shell section (CLARK, 1980).

To determine the periodicity of microgrowth increment formation, the number of microgrowth increments (mean of three counts) in specified regions of the shell was de-

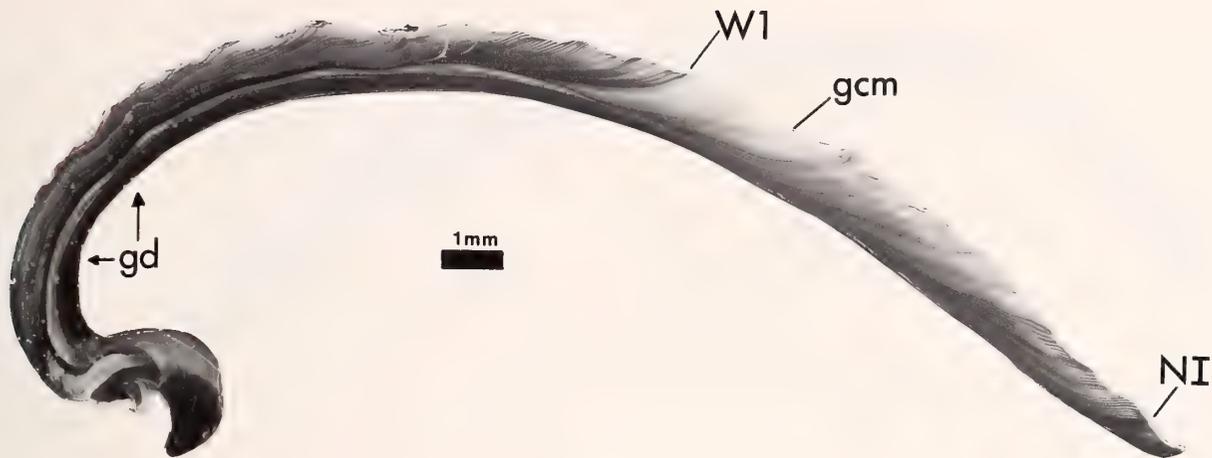


Figure 3

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* from the Notch I group collected from station DI on 19 September 1981. Clam was notched on 17 August 1981 (NI). Total shell height is 19.6 mm. All other features are as in Figure 1A.

terminated using the acetate peel under a compound microscope at $100\times$ magnification. Counts were made in shell regions in which the dates at the beginning or end of the count, or both, were known. The distance (in μm) between the two points was measured along the shell exterior surface, which is the surface of maximum growth (SMG) (PANNELLA & MACCLINTOCK, 1968) in radial shell sections. Measurements were made from either the peel or thin section using a compound microscope (at $40\times$) equipped with a calibrated ocular reticle. The shell height corresponding with the beginning and/or endpoints of an increment count was measured to the nearest 0.1 mm using either (1) a pair of calipers using the unembedded valve of each specimen, or (2) an ocular reticle at $40\times$ using the acetate peel or thin section. Height measurements were chord distances from the umbo to the shell exterior surface along a straight line between the two points and not along the shell exterior surface. Statistical procedures used (analysis of variance, least-squares linear regression, Student's *t*-test and Kruskal-Wallis test) were those of SOKAL & ROHLF (1969).

RESULTS

Natural Shell Growth Patterns

Collections in 1981

Notching the ventral shell margins of clams on 17 August (Notch I) or 16 September 1981 (Notch II) produced a growth cessation mark, NI or NII, in each radial section (Figures 3–5). The notch divided each shell section into regions deposited before (toward the umbo, or dorsal) and after (toward the shell margin, or ventral) it. Exact location of the growth cessation mark caused by notching was aided by the location of the V-shaped notch on the exterior shell surface.

In 25 of 44 Notch I and 28 of 32 Notch II clams (or 53 of 76 clams sectioned in 1981), there was a recognizable series of microgrowth increments in the outer layer and two growth lines within the inner layer (Figure 3; see also Figure 1A). A growth cessation mark (W1) formed the ventral boundary of the group of microgrowth increments, and was associated with one growth line in the inner layer. Another growth cessation mark (GCM) in the outer layer, located between 1.2 and 3.7 mm ventral from W1, was associated with the other growth line. The growth lines within the inner layer will hereafter be referred to as discontinuities, because, as it will be shown, each resulted from a period of little or no shell growth.

There are two lines of evidence supporting the hypothesis that the series of microstructures described above was formed between late fall 1980 and spring 1981. First, Notch I and II clams without growth discontinuities in the inner layer were an average of 6.9 and 4.2 mm smaller in shell height, respectively, at the time of notching than those with discontinuities (Table 1A). Mean shell heights of clams without discontinuities, 9.1 mm in mid-August (Notch I) and 12.4 mm in mid-September (Notch II), could be attained by young-of-the-year, or the spring 1981 brood (BRITTON & MORTON, 1979). These shell heights were similar to those at mark W1 in clams with discontinuities (Table 1B). These data suggest that clams with the series of microgrowth increments in the outer layer and growth discontinuities in the inner layer were members of the 1980 year-class. Winter 1980–1981 was represented as growth cessation mark W1 and an associated discontinuity in the inner layer. No clams in either the Notch I or II groups had other growth discontinuities in the inner layer or growth cessation marks in the outer layer that would correspond with winter 1979–1980; thus, all clams were most likely either members of the 1980 (1

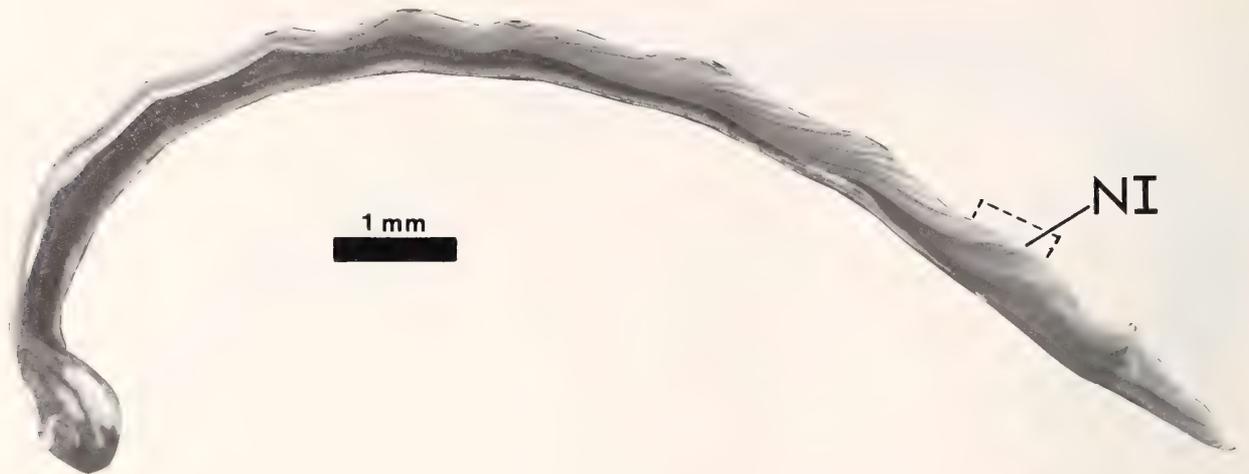


Figure 4

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* from the Notch I group collected from station DI on 14 November 1981. Clam was notched on 17 August 1981 (NI). Total shell height is 10.2 mm. Dashed lines mark portion enlarged in Figure 5. All other features are as in Figure 1A.

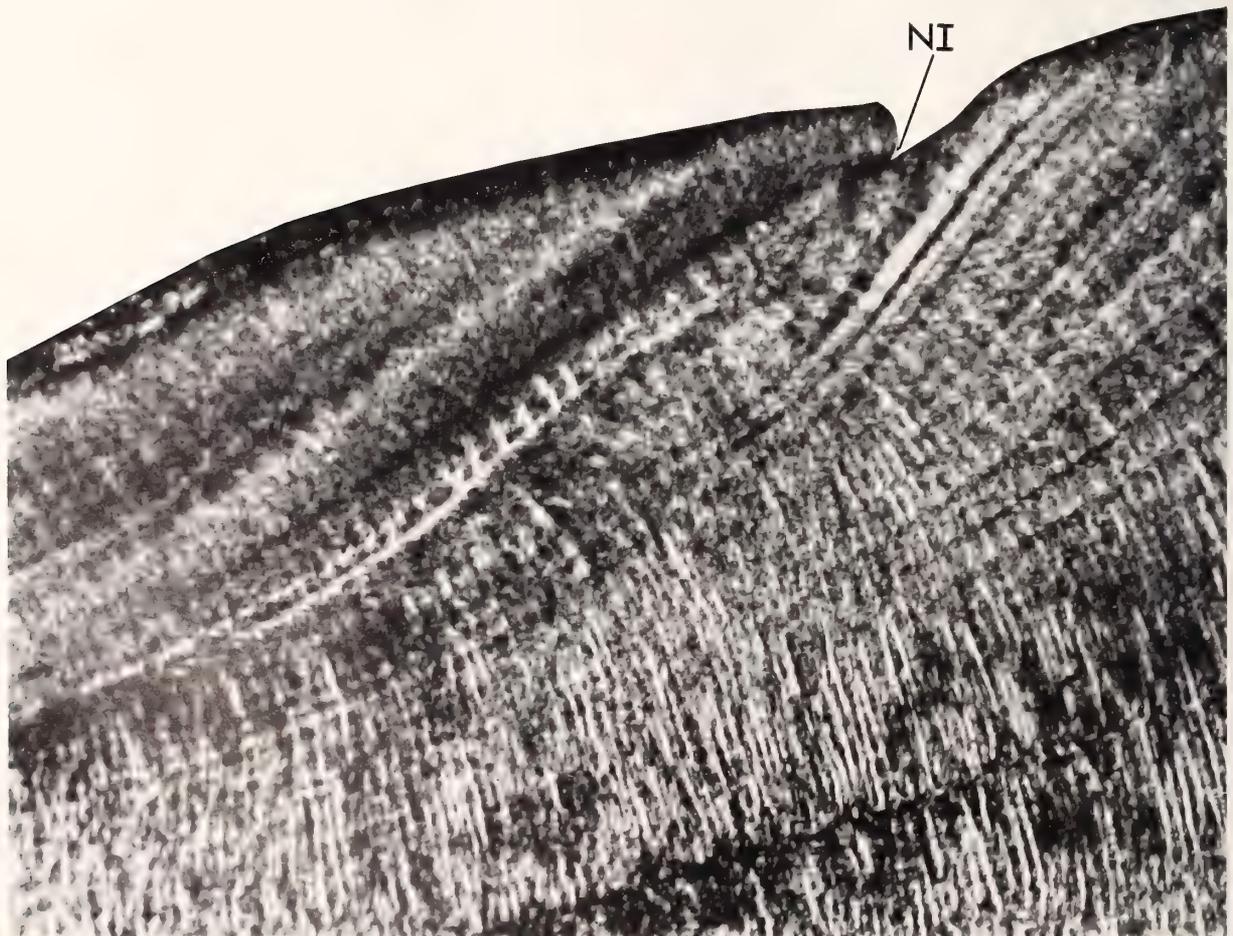


Table 1

Shell height (mm) at the notch (Table 1A) and at the winter 1980–1981 growth cessation (W1; Table 1B) in Notch I (notched on 17 August 1981) and Notch II (notched on 16 September 1981) groups of *Corbicula fluminea* with and without growth discontinuities (GD) in the inner shell layer. Collections from all dates and stations were pooled.

Group	With GD			Without GD		
	N	Mean	Range	N	Mean	Range
A. Shell height (mm) at notches						
Notch I	25	16.0	12.3–19.1	19	9.1	6.3–12.3
Notch II	28	16.6	13.1–19.2	4	12.4	11.1–13.5
B. Shell height (mm) at W1						
Notch I	25	8.8	4.2–12.3			
Notch II	28	9.0	5.0–11.3			
Total	53	8.9	4.2–12.3			

year old; Figure 3) or 1981 year-class (young-of-the-year; Figure 4).

The second group of data that aids in dating the microstructures described above was microgrowth increment counts and measurements of shell growth between W1 and NI or NII. Data obtained from these shell regions (and from clams sampled in 1982) suggest that microgrowth increments were periodically deposited, because the number of increments was independent of the amount of shell deposited by both Notch I ($r^2 = 0.02$) and Notch II ($r^2 = 0.18$) clams (Figure 6). The mean number of increments from W1 to NI or NII in each group suggested an average deposition rate of approximately one increment per day. Data obtained from clams moved to the three stations and notched on the same day were pooled because there were no significant differences in shell growth (Kruskal-Wallis test: Notch I: $H = 0.71$, $P > 0.1$; Notch II: $H = 4.18$, $P > 0.1$) nor in the mean number of increments counted (Notch I: $t = 0.01$, $P > 0.9$; Notch II: $F = 2.35$, $P > 0.1$) among clams in each group (Table 2). In Notch I clams, the grand mean ($\pm 95\%$ confidence interval) number of increments from W1 to the notch was 136.3 (± 6.2). If one increment were formed each day, the "mean" date of growth resumption after W1 would be 3 April, or 136 days before 17 August. Similarly, the grand mean number of increments in Notch II clams was 160.5

(± 5.5), placing the "mean" date of growth resumption on 9 April, or 160 days before 16 September. These two independent estimates of the date of growth resumption are quite similar, and for purposes of this discussion, the grand "mean" date of growth resumption in spring 1981 is 6 April, or halfway between the two dates. Further support for an average daily deposition rate of microgrowth increments was seen in the difference in mean number of increments from W1 to each notch (24.2), which was similar to the number of days between notch dates (30; Figure 6).

Resumption of growth in early April 1981 might also have been predicted on the basis of the water temperature record for the Raritan River and the reported temperature tolerances of *Corbicula fluminea* (RODGERS *et al.*, 1979). From late November 1980 to late March 1981, water temperatures near station C were 7°C or below (U.S. Geol. Survey Water-Data Report NJ-81-1, 1982). A prolonged period of valve closure and inactivity could be reflected in the shell as a growth discontinuity and cessation mark as in Figures 1A and 3 (see LUTZ & RHOADS, 1977). Between 25 March and 7 April 1981, water temperatures near station C increased from 7 to 12°C (Figure 7), which could have stimulated shell deposition. The close agreement between the estimated date of growth resumption from increment counts and the water temperature record supports both of the following hypotheses: (1) discontinuance of growth in winter 1980–1981 was reflected in shell microstructure as a discontinuity within the inner layer and W1 in the outer layer, which followed deposition of a recognizable series of microgrowth increments in fall 1980, and (2) microgrowth increments in the outer layer were formed at an average rate of one per day from W1 to each notch.

Assuming that winter 1980–1981 was reflected in shell microstructure as in hypothesis (1) above, then GCM was formed subsequently, possibly during spring 1981 (Figures 1A, 3). As can be seen in Figure 7, the mean daily discharge of the Raritan River near station C increased over 50-fold, from 6.3 to 342.6 $\text{m}^3 \cdot \text{sec}^{-1}$, from 10 to 12 May 1981 as a result of 10 cm (4 inches) of rain in the Raritan River watershed. This was the highest mean daily flow recorded during the two-year study period. Based on increment counts from W1, GCM could have resulted from the increase in turbidity and high flow rates associated with this storm. As in the shell region from W1 to each notch, the number of increments from W1 to GCM was independent of the amount of shell deposited ($r^2 =$

Figure 5

Light micrograph of the portion of outer fine crossed-lamellar layer outlined in Figure 4 showing the growth cessation mark resulting from notching on 17 August 1981 (NI). Note the narrow microgrowth increments deposited after (to the right of) the growth cessation mark, as well as the greater proportion of "crossed-lamellar" microstructures. Growth is to the right and the horizontal field width is 0.7 mm.

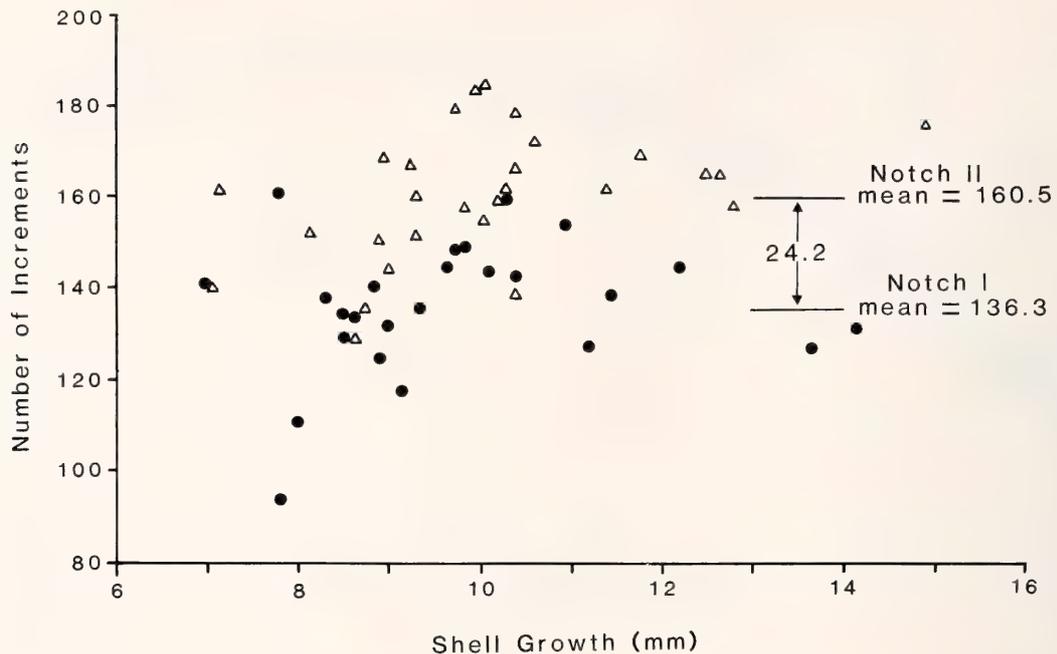


Figure 6

Number of microgrowth increments in the outer layer of Notch I (solid circles) and II (open triangles) groups of *Corbicula fluminea*, from W1 (see Figure 1) to the notch, as a function of shell growth (see Table 2). The mean numbers of increments in each group are shown, along with the difference between the two means.

0.0003; Figure 8). There were no significant differences in the mean number of increments from W1 to GCM in both of the following groups of tests (Table 3): (1) among clams collected from different stations within each notched group (Notch I: $t = 1.02$, $P > 0.2$; Notch II: $F = 0.09$, $P > 0.75$), and (2) between separately pooled Notch I and II clams ($t = 1.82$, $P > 0.05$). Pooling increment counts from the 53 Notch I and II clams resulted in a grand mean of $34.3 (\pm 0.9)$ increments, which placed the date of GCM formation on 10 May 1981, or only two days before the date of highest mean flow.

Average growth rates along the SMG (shell height axis) from W1 to Notch I and II were 69 and 62 $\mu\text{m}/\text{increment}$ (day), respectively, with a total range of 44–108 $\mu\text{m}/\text{increment}$. Individual shell length increases from W1 to Notch I and II, when divided by the mean number of increments in each group (136 and 160 respectively) yielded mean daily growth rates of 63 and 55 $\mu\text{m}/\text{day}$ along the length axis, respectively, with a total range of 41–87 $\mu\text{m}/\text{day}$. These rates were calculated from clams with initial (at W1) shell heights ranging from 4.2 to 12.3 mm (Table 1), and lengths ranging from 5.6 to 13.6 mm. Post-

Table 2

Shell growth and number of microgrowth increments from W1 to the notch in Notch I and II groups of *Corbicula fluminea* (see Table 1). Collections from all dates were pooled.

Group	Station	N	Shell growth (μm)		Number of microgrowth increments		
			Median	Range	Mean	$\pm 95\%$ CI	Range
Notch I	DI	12	9500	8300–12,200	136.3	129.7–142.8	118.0–154.0
	AC	13	8830	7000–14,150	136.2	125.1–147.3	93.7–160.7
	Total	25	9350	7000–14,150	136.3	130.1–142.5	93.7–160.7
Notch II	DI	12	9840	7150–14,920	166.5	157.5–175.5	135.7–185.0
	C	5	8960	8140–10,240	152.3	134.2–170.4	129.3–168.7
	AC	11	10,400	7040–12,800	157.7	149.4–166.0	138.7–178.3
	Total	28	10,000	7040–14,920	160.5	155.0–166.0	129.3–185.0

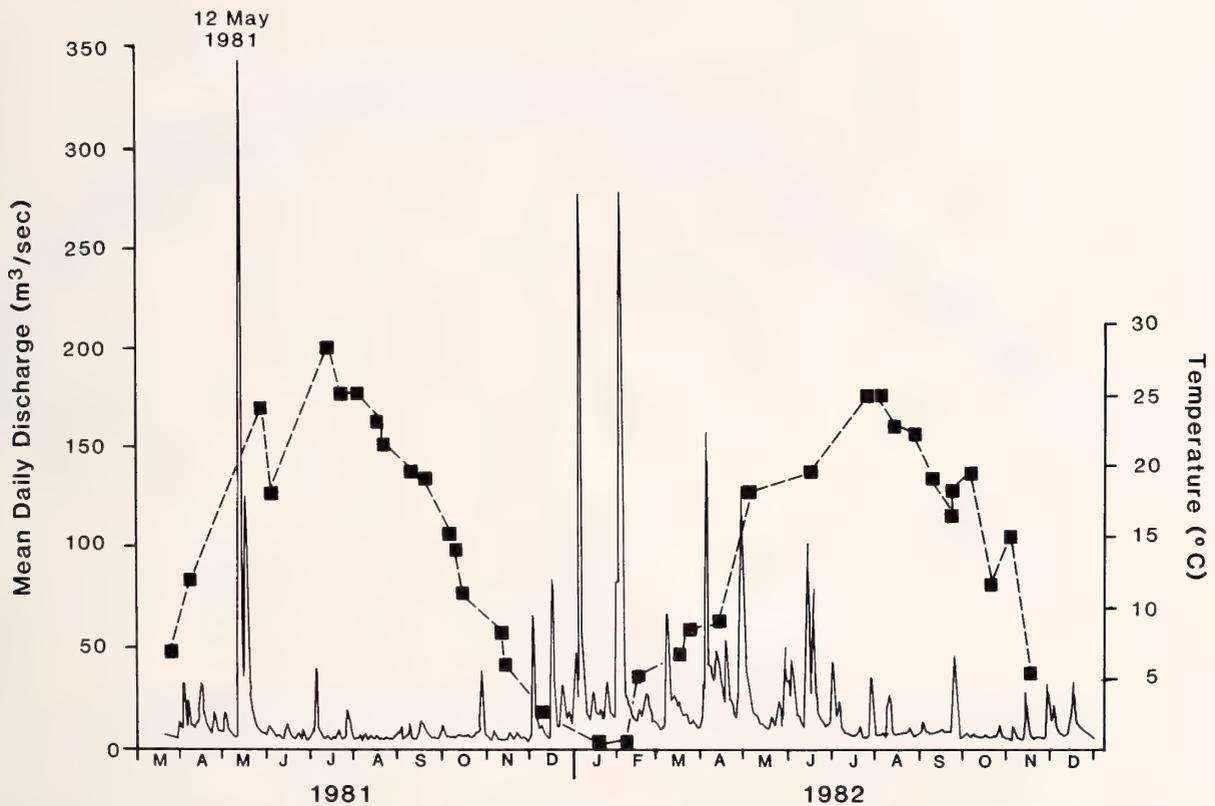


Figure 7

Mean daily discharge (solid line) and water temperature (symbols and dashed line) of the Raritan River at the gauging station at Manville, NJ (see Figure 2). Data from U.S. Geological Survey Water-Data Reports NJ-81-1 and NJ-82-1, and from USGS-WRD, 418 Federal Building, 402 E. State St., Trenton, NJ 08608. Some water temperatures were measured at station C during this study.

notch growth rates along the SMG of Notch I clams declined to a mean of $25 \mu\text{m}/\text{increment}$ (range of $14\text{--}44 \mu\text{m}/\text{increment}$), a decline of over 60% from pre-notch rates regardless of the station to which each clam was moved or the date of collection. Post-notch growth rates of Notch II clams were negligible at all stations and from all collection dates. As will be shown with reference to collections of unnotched clams in 1982, the large decline in post-notch growth rates in 1981 was most likely a result of notching and not an effect of the cage or station to which clams were moved.

Collections in 1982

The growth disturbance mark in shell microstructure caused by moving clams from the natural population at station C to cages at the three stations on 19 July 1982 was less distinct than that caused by notching the ventral margin in 1981. The move was reflected in microstructure as a growth cessation mark (M) that was translucent in thin section. In all specimens moved to control stations DI and C, an opaque region in the outer shell layer was

deposited ventral to M (Figure 9). This opaque region was generally not observed in post-move shell growth of clams moved to station AC (Figure 10). Identification of the move disturbance in clams moved to stations DI, C, and AC was based on shell growth measurements and counts of microgrowth increments in shell regions ventral and dorsal to M, as well as its absence in clams collected from the wild population at station C (Figure 11).

Analyses of shell dorsal to M revealed the presence of a single discontinuity in the inner shell layer associated with a recognizable series of two or three growth cessation marks in the outer shell layer of 45 of 50 clams moved to experimental or control stations (Figures 9, 10). This growth pattern was also observed in 14 of 17 clams sampled from the natural population at station C (Figure 11). As with the Notch I and II clams collected in 1981, it will be shown that this series of microstructures was caused by a growth discontinuity in the winter of 1981–1982; clams without this series of microstructures were members of the spring brood of 1982. The ventral-most growth cessation mark in the series of two or three will hereafter be referred to as W2.

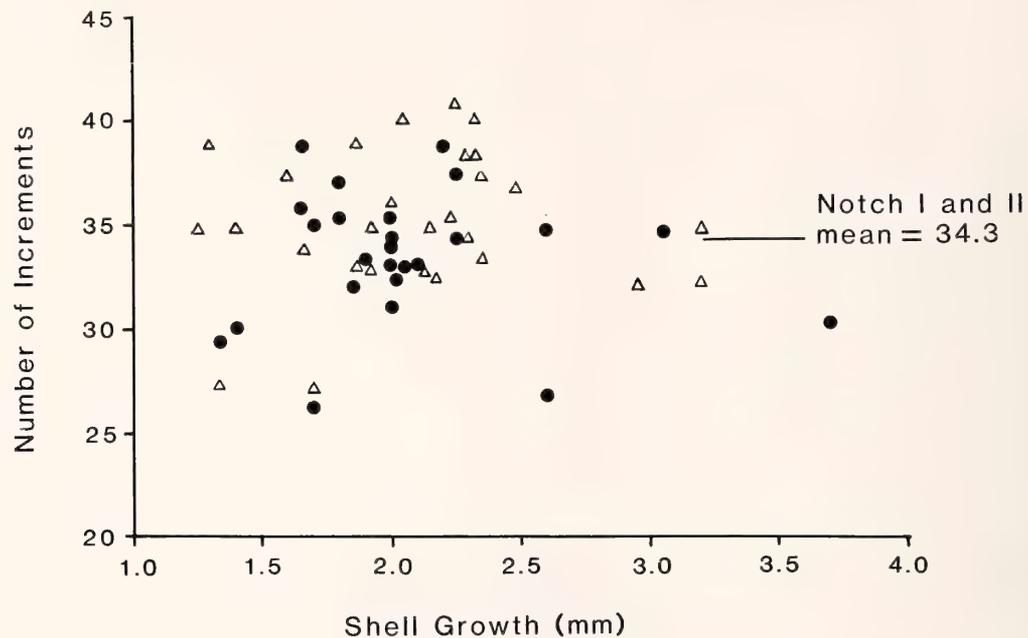


Figure 8

Number of microgrowth increments in the outer layer of Notch I (solid circles) and II (open triangles) groups of *Corbicula fluminea*, from W1 to the growth cessation mark (gcm; see Figures 1B and 3), as a function of shell growth (see Table 3). The mean number of increments for the two groups combined is shown.

Measurements of shell growth and counts of microgrowth increments from W2 to M yielded results similar to those from collections in 1981: (1) there was no correlation between the number of increments and the amount of shell growth ($r^2 = 0.21$; similar in pattern to Figure 6), suggesting that microgrowth increments were periodically deposited, and (2) the mean number of increments from W2 to M suggested an average deposition rate of one increment per day. Data obtained from clams moved to the three stations were pooled because there were no sig-

nificant differences in shell growth (Kruskal-Wallis test: $H = 1.06$, $P > 0.5$) nor in the mean number of increments counted ($F = 0.07$, $P > 0.75$) among clams in each group (Table 4). Thus, prior to entering the period of monitored growth (or before 19 July 1982), there were no significant differences in growth among the one experimental and two control groups of clams. Using the grand mean of $113.9 (\pm 5.6)$ increments from W2 to M, placed the "mean" date of growth resumption after winter on 27 March 1982 (114 days before 19 July). Resumption of

Table 3

Shell growth and number of microgrowth increments from W1 to growth cessation mark, GCM (see text), in Notch I and II groups of *Corbicula fluminea* (see Table 1). Collections from all dates were pooled.

Group	Station	N	Shell growth (μm)		Number of microgrowth increments		
			Median	Range	Mean	$\pm 95\%$ CI	Range
Notch I	DI	12	2000	1700–2600	34.1	32.1–36.1	26.3–38.7
	AC	13	2000	1350–3700	32.8	30.8–34.8	26.7–38.7
	Total	25	2000	1350–3700	33.4	32.1–34.7	26.3–38.7
Notch II	DI	12	2280	1250–3200	35.4	33.1–37.7	27.0–40.7
	C	5	1660	1300–2350	34.7	31.8–37.6	33.0–38.7
	AC	11	2130	1350–3200	34.9	32.4–37.4	27.3–40.0
	Total	28	2140	1250–3200	35.0	33.7–36.3	27.0–40.7
Grand total		53	2000	1250–3700	34.3	33.4–35.2	26.3–40.7

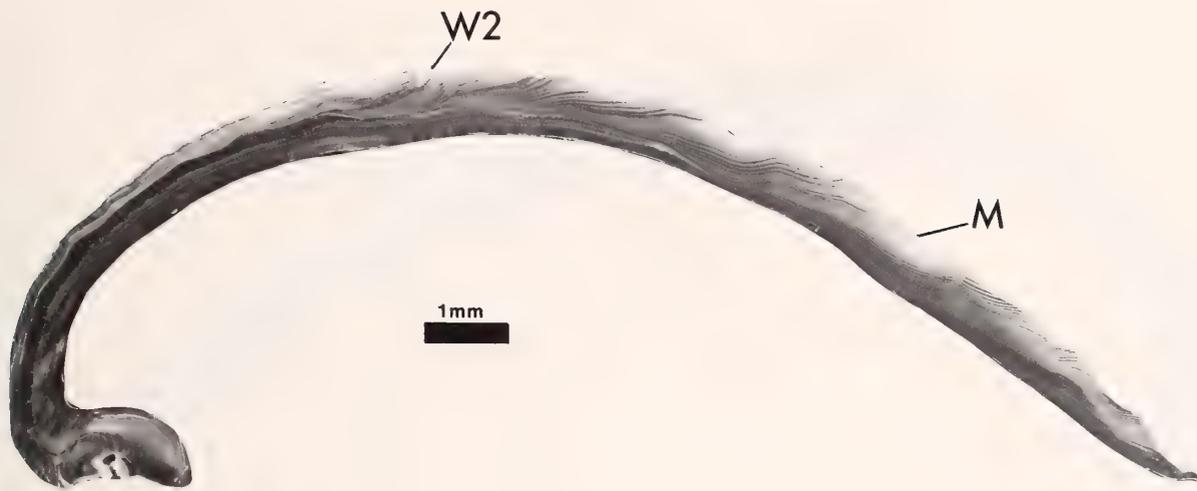


Figure 9

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected from the cage at station C on 20 October 1982. Growth cessation caused by moving clam from the natural population to the cage on 19 July 1982 is labelled (M), as is the winter 1981–1982 growth cessation (W2). Total shell height is 14.9 mm; growth is to the right.

growth in late March could also have been predicted from the water temperature record (Figure 7).

The average growth rate along the SMG from W2 to M for the 45 clams was $45 \mu\text{m}/\text{increment}$ (day), with a range of $25\text{--}94 \mu\text{m}/\text{increment}$, or approximately $20 \mu\text{m}/\text{increment}$ less than in 1981. Dividing individual increases in shell length from W2 to M by the mean number of increments (114) yielded a mean daily shell length in-

crease of $46 \mu\text{m}/\text{day}$, with a range of $28\text{--}78 \mu\text{m}/\text{day}$. These rates were calculated from clams with initial (at W2) shell heights ranging from 4.8 to 10.4 mm and lengths ranging from 6.2 to 11.7 mm.

Shell Growth during Monitored Periods in 1982

Because growth of clams during spring and early summer 1982 was similar in the groups moved to the three

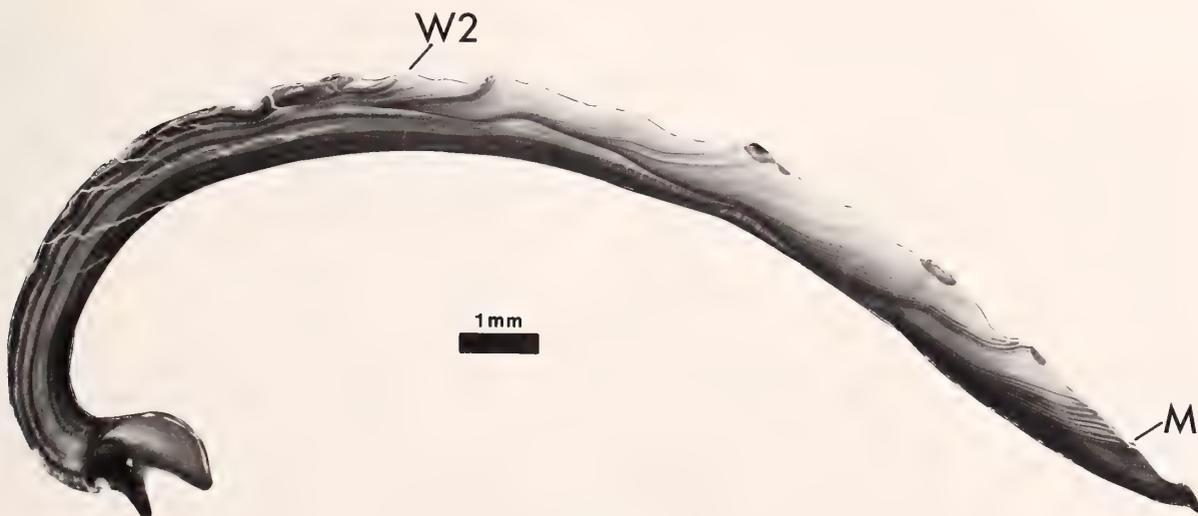


Figure 10

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected from the cage at station AC on 20 October 1982. Growth cessation marks are labelled as in Figure 9. Note differences in post-move shell growth between this clam and the one collected from the control station (Figure 9). Total shell height is 15.7 mm; growth is to the right.

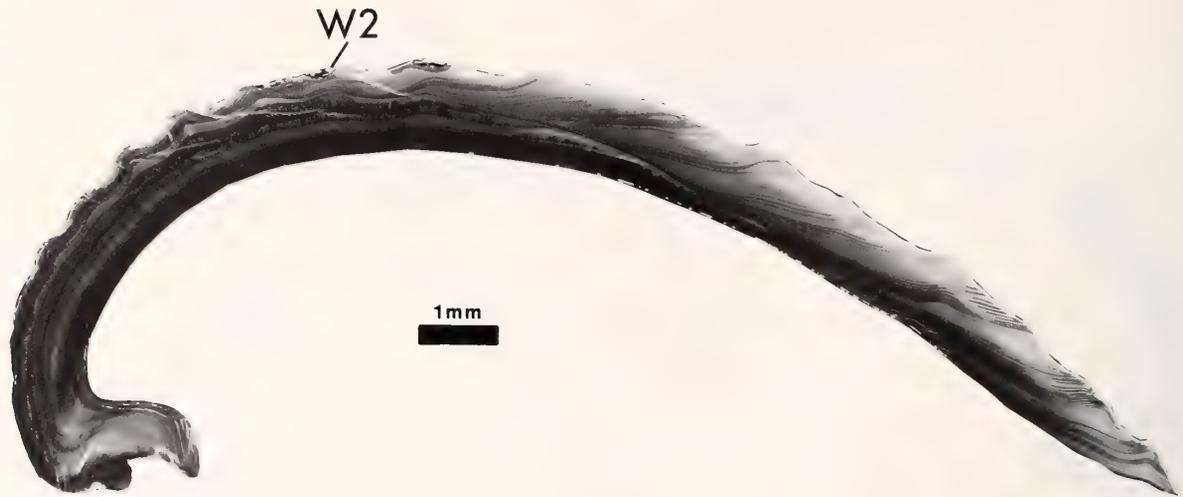


Figure 11

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected from the natural population at station C on 20 October 1982. Growth cessation mark is labelled as in Figure 9. Total shell height is 15.5 mm; growth is to the right.

stations, any differences in shell growth between groups subsequent to the move would most likely be due to site-specific factors. As previously stated, the growth disturbance associated with the move and placement in cages in 1982 had a much less deleterious effect on subsequent growth than did notching the ventral shell margins in 1981 (compare Figure 9 with Figures 3–5). Shell deposited after the notch resembled the immediate post-move shell in that both were relatively opaque in thin section and growth rates ($\mu\text{m}/\text{increment}$) were depressed. Median shell growth from W2 to the shell margin in three of the six collections (30 July, 27 August, and 17 November) was considerably greater in wild clams than those from control stations, but this was most likely a result of the smaller mean shell height at W2 in the wild clams collected on these dates (Table 5). Counts of microgrowth increments from W2 to the shell margin in clams from control stations DI and C were not significantly different

from counts in the same shell region in clams from the natural population ($F = 1.11$, $P > 0.25$; Table 5; Figure 12). Furthermore, the number of increments counted from W2 to the shell margin in the four collections through October (or those collections before which water temperatures were greater than 10°C) suggests an average deposition rate of one increment per day. A linear regression of the pooled counts from wild and control clams against days since 19 July 1982 resulted in a slope (1.18) that was not significantly different from 1.00 ($t_s = 1.52$, $P > 0.2$; $n = 28$, $r^2 = 0.86$; see Figure 12).

From 19 July 1982 to the date of collection, clams moved to experimental station AC grew slower and deposited fewer increments than caged clams at control stations (Table 6). A linear regression of increments from M to the shell margin against days since 19 July in clams collected from the control stations through October resulted in a slope (0.97) which was not significantly different from

Table 4

Shell growth and number of microgrowth increments from the winter 1981–1982 growth cessation mark (W2) to the growth cessation mark caused by the move (M) on 19 July 1982 in specimens of *Corbicula fluminea*. Collections from all dates were pooled.

Station	N	Shell growth (μm)		Number of microgrowth increments		
		Median	Range	Mean	$\pm 95\%$ CI	Range
DI	17	5390	3640–9290	115.0	108.6–121.4	99.3–139.3
C	15	5260	3210–6810	112.6	101.1–124.1	79.7–162.3
AC	13	3880	2015–9940	114.1	100.0–128.2	81.7–150.3
Total	45	5150	2015–9940	113.9	108.3–119.5	79.7–162.3

Table 5

Shell growth and number of microgrowth increments from W2 (see Table 4) to the shell margin in specimens of *Corbicula fluminea* collected on six dates in 1982. Collections from stations DI and C were from cages, while those from NP were from the natural population at station C.

Date of collection	Station	N	Mean shell height at W2 (mm)	Shell growth (μm)		Number of microgrowth increments	
				Median	Range	Mean	Range
30 Jul	DI	3	7.6	5310	4280-5680	125.1	112.0-137.3
	C	3	8.7	3585	3560-5640	110.4	94.3-132.0
	NP	2	6.1	7000	6310-7690	120.7	115.7-125.7
27 Aug	DI	2	8.0	7300	5960-8650	147.5	142.7-152.3
	C	2	8.7	5740	5350-6140	145.8	142.0-149.7
	NP	2	2.9	12,530	11,310-13,750	149.0	142.3-155.7
23 Sep	DI	3	8.8	8740	8440-8820	171.8	165.3-175.7
	C	2	8.6	8390	7900-8880	186.0	176.7-195.3
	NP	1	6.6	7620		138.7	
20 Oct	DI	3	8.1	10,280	7460-12,340	220.7	213.0-235.7
	C	2	6.2	10,720	10,690-10,740	193.5	193.0-194.0
	NP	3	6.9	10,060	9250-12,250	231.4	218.7-238.3
17 Nov	DI	3	8.4	9430	9400-9450	222.9	214.3-230.3
	C	3	9.0	9380	8380-10,440	221.9	211.7-231.7
	NP	3	5.9	12,000	10,000-13,120	234.6	215.7-271.7
15 Dec	DI	3	6.6	11,010	10,320-14,150	246.5	234.7-268.7
	C	3	8.0	9310	8750-11,120	256.1	217.3-290.3
	NP	3	6.3	11,250	10,620-13,250	247.0	232.0-266.3

1.00 ($t_s = -1.36$, $P > 0.2$; $n = 24$, $r^2 = 0.98$). However, a similar linear regression based on counts from clams collected from station AC had a slope (0.79) that was significantly lower than 1.00 ($t_s = -3.03$, $P < 0.02$; $n =$

10, $r^2 = 0.94$; see Figure 13A). This strongly suggests that, on the average, clams at station AC were growing on fewer days than those at stations DI and C. Furthermore, both the absolute amount of shell growth (Figure 13B)

Table 6

Shell growth and number of microgrowth increments from M (see Table 4) to the shell margin in specimens of *Corbicula fluminea* collected from cages at the three stations on six dates in 1982.

Date of collection	Station	N	Shell growth (μm)		Number of microgrowth increments	
			Median	Range	Mean	Range
30 Jul	DI	3	450	390-550	14.3	12.3-18.0
	C	3	350	220-380	14.3	13.3-15.0
	AC	3	230	170-310	15.1	14.7-15.3
27 Aug	DI	3	2320	2300-3220	41.3	40.0-42.3
	C	3	2080	1800-5720	38.7	38.0-39.7
	AC	2	440	160-570	29.5	22.7-36.3
23 Sep	DI	3	3340	3120-3530	68.6	61.3-76.7
	C	3	2750	2700-3560	64.2	63.3-65.0
	AC	2	1520	1310-1740	60.0	56.3-63.7
20 Oct	DI	3	3580	3320-4080	94.5	91.3-96.3
	C	3	4620	4090-5810	94.0	90.7-96.0
	AC	3	1530	820-2000	78.1	67.0-84.0
17 Nov	DI	3	4060	3960-4390	99.4	91.3-105.3
	C	3	3500	3370-3620	108.0	104.7-110.3
	AC	1	1660		88.3	
15 Dec	DI	3	5220	4910-5330	129.6	128.0-131.0
	C	3	3880	3500-4620	123.2	119.3-128.0
	AC	3	950	870-1000	58.8	53.0-61.7

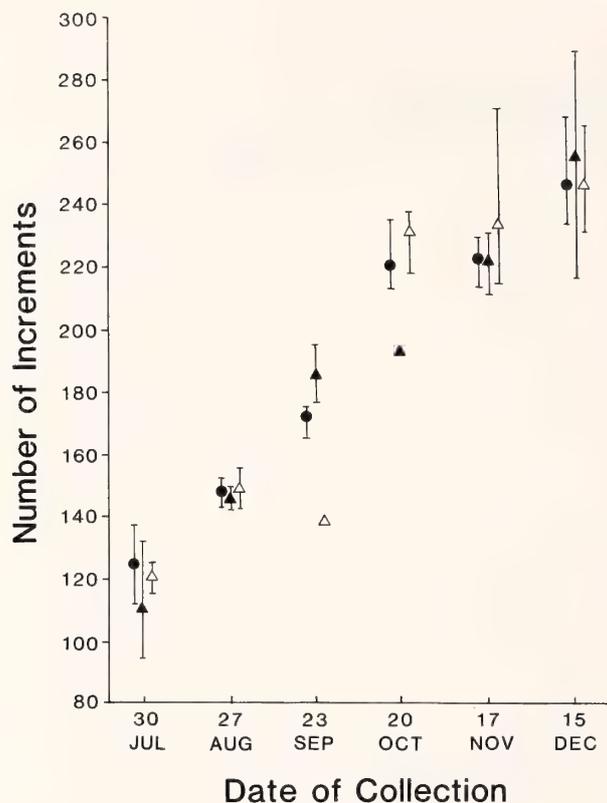


Figure 12

Mean (symbols) and range (vertical lines) of the number of microgrowth increments from the winter 1981-1982 growth cessation mark (W2; see Figures 9-11) to the shell margin in specimens of *Corbicula fluminea* collected from cages at stations DI (solid circles) and C (solid triangles) and from the natural population at C (open triangles) in 1982. Date of collection is plotted three days before actual date for station DI and three days after for the natural population to permit plotting (see Table 5).

and growth rate (Figure 13C) were lower in clams at AC than at the control stations. Post-move growth rates during the first 11 days (or through 30 July) at all stations were lower than pre-move rates. This may have been due to a period of acclimation to the site and/or cage, and may also be related to deposition of the opaque region immediately ventral to M by control clams. Growth rates at control stations DI and C returned to pre-move levels by the August sample, while those at AC were lower than pre-move rates in all subsequent samples (Figure 13C). Evidence strongly suggests that the effluent discharged near station AC decreased the number of days of growth as well as growth rates of specimens of *Corbicula fluminea* relative to those at control stations.

DISCUSSION

In the present study, we have shown that microgrowth increments in the outer fine crossed-lamellar shell layer

of *Corbicula fluminea* (described previously by PREZANT & TAN-TIU [1985]) were formed at the rate of approximately one per day and can be used to date shell regions. Furthermore, cessation of growth in winter resulted in a growth discontinuity within the inner complex crossed-lamellar layer and a growth cessation mark in the outer layer. Periodically deposited growth patterns in the two shell layers and evidences of growth cessations were used to reconstruct the growth history of groups of *C. fluminea* exposed to natural and anthropogenic environmental perturbations. Other methods, such as examination of external shell growth lines or serial measurements of shell axes (length or height) may not have been sensitive enough to document these changes in such short-term monitoring studies.

The periodicity of formation of microgrowth increments in outer prismatic or crossed-lamellar layers of several other bivalve species has been investigated previously by a number of researchers (see LUTZ & RHOADS, 1980). In the most commonly analyzed species, *Mercenaria mercenaria*, several investigators have documented a solar daily periodicity of formation in subtidal populations (PANNELLA & MACCLINTOCK, 1968; KENNISH & OLSSON, 1975; THOMPSON, 1975; KENNISH, 1980; FRITZ & HAVEN, 1983), but there is also evidence that suggests a closer correlation with the lunar day in intertidal specimens (PANNELLA, 1976). Tidally deposited growth increments have also been observed in intertidal populations of *Cerastoderma edule* (RICHARDSON *et al.*, 1979) and *Clinocardium nuttalli* (EVANS, 1972). Longer cycles, such as seasonal changes in temperature, are often reflected (and most easily discerned) in middle and inner shell layers, such as those of *M. mercenaria* (FRITZ & HAVEN, 1983), *Mya arenaria* (MACDONALD & THOMAS, 1980), and *Mytilus edulis* (LUTZ, 1976). Similarly, in *Corbicula fluminea*, short cycles (days) are reflected in outer layer microgrowth increments and long cycles (seasons) in inner layer growth discontinuities.

Caution must be exercised in using growth patterns to reconstruct life histories of individual specimens. This is due to both subjectivity in the method of detecting and counting increments (CRABTREE *et al.*, 1979/1980; HUGHES & CLAUSEN, 1980) and natural variability within a bivalve population in growth rate (*i.e.*, number of increments deposited and their width in a specified time) due to age and individual differences in sensitivity to environmental stresses (KENNISH & OLSSON, 1975; CRABTREE *et al.*, 1979/1980; RICHARDSON *et al.*, 1980; FRITZ & HAVEN, 1983). This does not imply, however, that attempts to interpret growth patterns in bivalve shell structures should be avoided. On the contrary, use of growth patterns in carbonate and proteinaceous secretions to determine age, growth rates, and aspects of life history of both vertebrates and invertebrates is well founded in studies of population dynamics and ecology (see RICKER, 1975). One strives to be as accurate as possible by analyzing large numbers of shells, applying objective criteria to the defi-

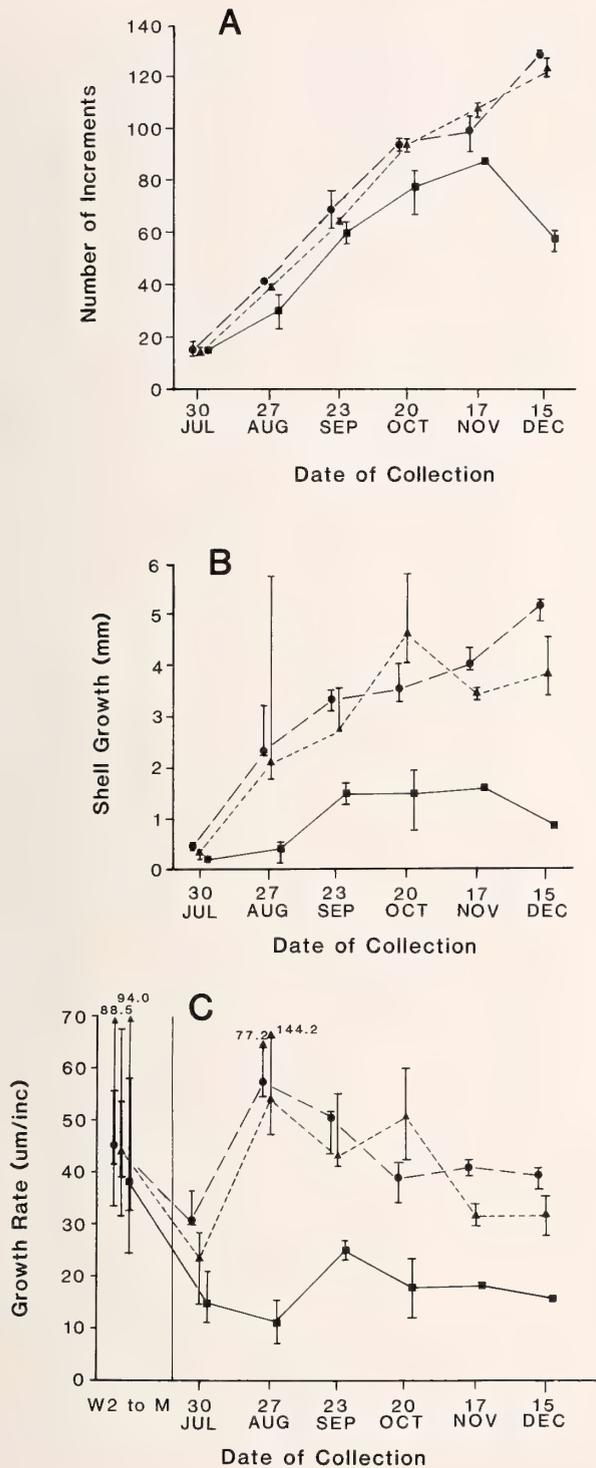


Figure 13

Analyses of shell growth of specimens of *Corbicula fluminea* at stations DI (circles and long dashed lines), C (triangles and short dashed lines), and AC (squares and solid lines) from the growth disturbance mark caused by the move on 19 July 1982 (M; see Figures 9 and 10) to the shell margin (date of collection). Offset on X-axis is the same as in Figure 12 (see Table 6). A. Mean

number of increments and patterns in shell sections (such as those of CRABTREE *et al.*, 1979/1980), and being consistent in interpretation and analysis.

KENNISH & OLSSON (1975) were the first to use bivalve shell growth patterns to monitor environmental perturbations. Growth cessation marks, a decrease in microgrowth increment width, and "replacement" of prismatic with "crossed-lamellar" microstructures in the outer layer of specimens of *Mercenaria mercenaria* were directly correlated with increased exposure to elevated water temperatures from a nuclear power plant. In the present study, the number of days of growth and shell growth rates of specimens of *Corbicula fluminea*, as measured through analyses of microstructural banding patterns, decreased (relative to controls) with exposure to the combined effluents from chemical and sewage treatment plants. Results of a concurrent *in situ* study of physiological responses to the effluent (CANTELMO-CRISTINI *et al.*, 1983) support these observations. In 1982, CANTELMO-CRISTINI *et al.* (1983) measured total adenylates and calculated adenylate energy charge of each of the specimens whose shells were sectioned for growth analysis in the present study. Energy charge of specimens was lower at station AC than at the control sites on 7 of 9 sampling dates during the monitored period, an indication of a site-specific stress at AC which was, most probably, chronic exposure to the effluent.

It is common in shell growth studies of this nature (*e.g.*, RICHARDSON *et al.*, 1980; FRITZ & HAVEN, 1983) to notch the ventral shell margin to induce a size-time benchmark in shell microstructure. As shown in the present study, notching should be avoided because it caused a decrease in growth rate and alteration of shell microstructure in the 1981 group. Alternative methods of inducing a growth cessation mark in shell microstructure, such as thermal shock (RICHARDSON *et al.*, 1979; FRITZ & HAVEN, 1983) or moving the animal to a new location (FRITZ & HAVEN, 1983; this study) cause less alteration to shell microstructure and apparently less damage to mantle tissue.

Size-specific growth rates of *Corbicula fluminea* in the Raritan River, New Jersey, were slower than those measured in Lake Benbrook, Texas, for periods of similar duration (BRITTON *et al.*, 1979). In the present study, mean growth rates along the length axis in spring and summer of 1981 and 1982 (periods of 136 and 160 days in 1981 and 114 days in 1982) were 63 and 55 µm/day, and 46 µm/day, respectively, for uncaged clams with ini-

(symbols) and range (vertical lines) of number of microgrowth increments. B. Median (symbols) and range (vertical lines) in shell growth. C. Median (symbols) and range (thin vertical lines) in growth rate (µm/increment). Also shown are distributions of growth rates from W2 to M (or prior to the monitored growth phase) in each group. Top and bottom of heavy bar are 75th and 25th percentiles, respectively, of the distributions of pre-move growth rates.

tial shell lengths ranging from 4.2 to 12.3 mm. In Lake Benbrook, the mean growth rate of specimens held in containers for 107 days was 54 $\mu\text{m}/\text{day}$, but initial shell lengths ranged from 10 to 25 mm. Measured growth rates in the two studies were similar, but the larger initial shell lengths of clams in the Texas study, and the fact that smaller clams tend to grow faster than larger clams (BRITTON *et al.*, 1979) indicated that size-specific growth rates were slower in the Raritan River. This difference may actually be greater because container-held specimens tend to grow slower than uncaged individuals (BRITTON *et al.*, 1979).

The largest specimen of *Corbicula fluminea* collected to date from the Raritan River is 25 mm in shell length and was found dead in March 1981 (TRAMA, 1982). The largest specimen analyzed in the present study was 20.8 mm in shell length at the end of its second growing season (age 1+ years). Consequently, it is likely that the 25 mm specimen was between 2 and 3 years old at the time of death, and not 3 to 4 years old as concluded by TRAMA (1982), which changes the latest possible year in which the species became established in the Raritan River system to 1979 instead of 1978. The relatively small maximum size and slow size-specific growth rates may result from low temperatures and/or their duration in winter, because the Raritan River is the northernmost extension of the recorded range of *C. fluminea* along the Atlantic seaboard (TRAMA, 1982). However, other factors such as food supply and quality, bottom type, and flow regime may also be involved in creating a "dwarfed" population. Causes of the catastrophic mortalities of *C. fluminea* observed in the Raritan River (and in other lotic systems [BRITTON & MORTON, 1982]) are also not known. Research into causes of "dwarfism" and mortalities would be a logical direction for future studies of the population dynamics of *C. fluminea* in the Raritan River.

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LITERATURE CITED

- BERRY, W. B. N. & R. M. BARKER. 1975. Growth increments in fossil and modern bivalves. Pp. 9-25. *In*: G. D. Rosenberg & S. K. Runcorn (eds.), Growth rhythms and the history of the earth's rotation. John Wiley & Sons: London.
- BRITTON, J. C., D. R. COLDIRON, L. P. EVANS, JR., C. GOLIGHTLY, K. D. O'KANE & J. R. TENYCK. 1979. Re-evaluation of the growth pattern in *Corbicula fluminea* (Müller). Pp. 177-192. *In*: Proceedings of the First International *Corbicula* Symposium, Fort Worth, Texas.
- BRITTON, J. C. & B. MORTON. 1979. *Corbicula* in North America: the evidence reviewed and evaluated. Pp. 249-287. *In*: Proceedings of the First International *Corbicula* Symposium, Fort Worth, Texas.
- BRITTON, J. C. & B. MORTON. 1982. A dissection guide, field and laboratory manual for the introduced bivalve *Corbicula fluminea*. Malacol. Rev., Suppl. No. 3. 82 pp.
- CANTELMO-CRISTINI, A., F. HOSPOD & R. LAZELL. 1983. *In situ* studies on the adenylate energy charge of populations of *Corbicula fluminea* in a freshwater system. International Council for the Exploration of the Sea Publication No. CM 1983/E:53. 18 pp.
- CLARK, G. R., II. 1980. Study of molluscan shell structure and growth lines using thin sections. Pp. 603-606. *In*: D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms: biological records of environmental change, Vol. 1, Geobiology Series. Plenum Press: New York.
- COUNTS, C. L., III & R. S. PREZANT. 1982. Shell microstructure of *Corbicula fluminea* (Bivalvia: Corbiculidae). Nautilus 96:25-30.
- CRAFTREE, D. M., C. D. CLAUSEN & A. A. ROTH. 1979/1980. Consistency in growth line counts in bivalve specimens. Palaeogeography, Palaeoclimatology, Palaeoecology 29:323-340.
- DODD, J. R. & E. L. CRISP. 1982. Non-linear variation with salinity of Sr/Ca and Mg/Ca ratios in water and aragonitic bivalve shells and implications for paleosalinity studies. Palaeogeography, Palaeoclimatology, Palaeoecology 38:45-56.
- EVANS, J. W. 1972. Tidal growth increments in the cockle, *Clinocardium nuttalli*. Science 176:416-417.
- FRITZ, L. W. & D. S. HAVEN. 1983. Hard clam, *Mercenaria mercenaria*: shell growth patterns in Chesapeake Bay. Fish. Bull. 81:697-708.
- HUGHES, W. W. & C. D. CLAUSEN. 1980. Variability in the formation and detection of growth increments in bivalve shells. Paleobiology 6:503-511.
- JONES, D. S. 1980. Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecological significance. Paleobiology 6:331-340.
- KENNISH, M. J. 1980. Shell microgrowth analysis: *Mercenaria mercenaria* as a type example for research in population dynamics. Pp. 255-294. *In*: D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms: biological records of environmental change, Vol. 1, Geobiology Series. Plenum Press: New York.
- KENNISH, M. J., R. A. LUTZ & D. C. RHOADS. 1980. Preparation of acetate peels and fractured sections for observations of growth patterns within the bivalve shell. Pp. 597-601. *In*: D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms: biological records of environmental change, Vol. 1, Geobiology Series. Plenum Press: New York.
- KENNISH, M. J. & R. K. OLSSON. 1975. Effects of thermal discharges on the microstructural growth of *Mercenaria mercenaria*. Environ. Geol. 1:41-64.
- LUTZ, R. A. 1976. Annual growth patterns in the inner shell layer of *Mytilus edulis* (L.). J. Mar. Biol. Assoc. U.K. 56: 723-731.
- LUTZ, R. A. 1981. Electron probe analysis of strontium in mussel (Bivalvia, Mytilidae) shells: feasibility of estimating water temperature. Hydrobiologia 83:377-382.
- LUTZ, R. A. & D. C. RHOADS. 1977. Anaerobiosis and a theory of growth line formation: micro- and ultrastructural growth patterns within the molluscan shell reflect periodic respiratory changes. Science 198:1222-1227.

- LUTZ, R. A. & D. C. RHOADS. 1980. Growth patterns within the molluscan shell: an overview. Pp. 203-254. *In*: D. C. Rhoads & R. A. Lutz (eds.), *Skeletal growth of aquatic organisms: biological records of environmental change*, Vol. 1, Geobiology Series. Plenum Press: New York.
- MACDONALD, B. A. & M. L. H. THOMAS. 1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. *Mar. Biol.* 58:105-109.
- PANNELLA, G. 1976. Tidal growth patterns in Recent and fossil mollusc bivalve shells: a tool for the reconstruction of paleotides. *Naturwissenschaften* 63:539-543.
- PANNELLA, G. & C. MACCLINTOCK. 1968. Biological and environmental rhythms reflected in molluscan shell growth. *J. Paleontol.* 42:64-80.
- PREZANT, R. S. & A. TAN-TIU. 1985. Comparative shell microstructure of North American *Corbicula* (Bivalvia: Sphaeriacea). *Veliger* 27:312-319.
- RHOADS, D. C. & G. PANNELLA. 1970. The use of molluscan shell growth patterns in ecology and paleoecology. *Lethaia* 3:143-161.
- RICHARDSON, C. A., D. J. CRISP & N. W. RUNHAM. 1979. Tidally deposited growth bands in the shell of the common cockle, *Cerastoderma edule* (L.). *Malacologia* 18:277-290.
- RICHARDSON, C. A., D. J. CRISP & N. W. RUNHAM. 1980. Factors influencing shell growth in *Cerastoderma edule*. *Proc. Roy. Soc. Lond.* 210:513-531.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Bd. Canada*, Bull. No. 191: 382 pp.
- RODGERS, J. H., JR., D. S. CHERRY, K. L. DICKSON & J. CAIRNS. 1979. Invasion, population dynamics, and elemental accumulation of *Corbicula fluminea* in the New River, VA. Pp. 99-110. *In*: *Proceedings of the First International Corbicula Symposium*, Fort Worth, Texas.
- RYE, D. M. & M. A. SOMMER, II. 1980. Reconstructing paleotemperature and paleosalinity regimes with oxygen isotopes. Pp. 169-202. *In*: D. C. Rhoads & R. A. Lutz (eds.), *Skeletal growth of aquatic organisms: biological records of environmental change*, Vol. 1, Geobiology Series. Plenum Press: New York.
- SOKAL, R. R. & F. J. ROHLF. 1969. *Biometry. The principles and practice of statistics in biological research*. W. H. Freeman, Co.: San Francisco. 776 pp.
- TAYLOR, J. D., W. I. KENNEDY & A. HALL. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea. *Conclusions*. *Bull. British Museum (Natur. Hist.)* 22:255-294.
- THOMPSON, I. 1975. Biological clocks and shell growth in bivalves. Pp. 149-162. *In*: G. D. Rosenberg & S. K. Runcorn (eds.), *Growth rhythms and history of the earth's rotation*. John Wiley & Sons: London.
- TRAMA, F. B. 1982. Occurrence of the Asiatic clam *Corbicula fluminea* in the Raritan River, New Jersey. *Nautilus* 96: 6-8.

Reproductive Cycle in the Freshwater Mussel *Diplodon chilensis chilensis* (Mollusca: Bivalvia)

by

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Abstract. The reproductive cycle of the freshwater mussel *Diplodon chilensis chilensis* (Gray, 1828) was investigated between March 1982 and April 1983 by monthly examination of gonad sections and inspection of demibranchs in the females. The gonad is active throughout the year in both sexes, suggesting the existence of an annual cycle with continuous gametogenesis. A spawning phase occurs during the spring-summer months. Spawning is partial and asynchronous in the specimens of the Chilean population studied from Lake Villarrica. No regression in gametogenic activity or rest period was observed.

INTRODUCTION

SEVERAL ASPECTS of reproduction in freshwater mussels show a number of marked differences and specializations among the species that have been studied. Much of the available information concerns unionids of North America and Europe. Virtually all members of the Sphaeriidae are hermaphroditic (ZUMOFF, 1973), whereas the Unionidae has been reported to be generally comprised of dioecious species (VAN DER SCHALIE, 1969). Some members of the Margaritiferidae have been reported to be dioecious, with occasional hermaphroditic specimens being recorded (HENDELBERG, 1960; HEARD, 1970; VAN DER SCHALIE, 1970).

The life histories of numerous unionacean species have shown marked differences. These differences include the relative life-span of the species, the size and number of

broods produced each year, the season in which gametogenesis is most active, and the period and number of spawnings within a year. Freshwater mussels from Chile are representative of the Hyriidae, a family that has received little attention concerning its life history. The present study was undertaken to elucidate the annual reproductive cycle of *Diplodon chilensis chilensis*, a hyriid abundant in lakes and rivers of Chile. This species may prove useful as an indicator of environmental changes due to freshwater pollution considering the value of freshwater mussels as qualitative indicators of pesticides, radionuclides, and other substances as has been reported for several Unionidae (NELSON, 1962; MILLER *et al.*, 1956; LEE & WILSON, 1969; BEDFORD *et al.*, 1968) and Margaritiferidae (HENDELBERG, 1960; BJORK, 1962; McMILLAN, 1966).

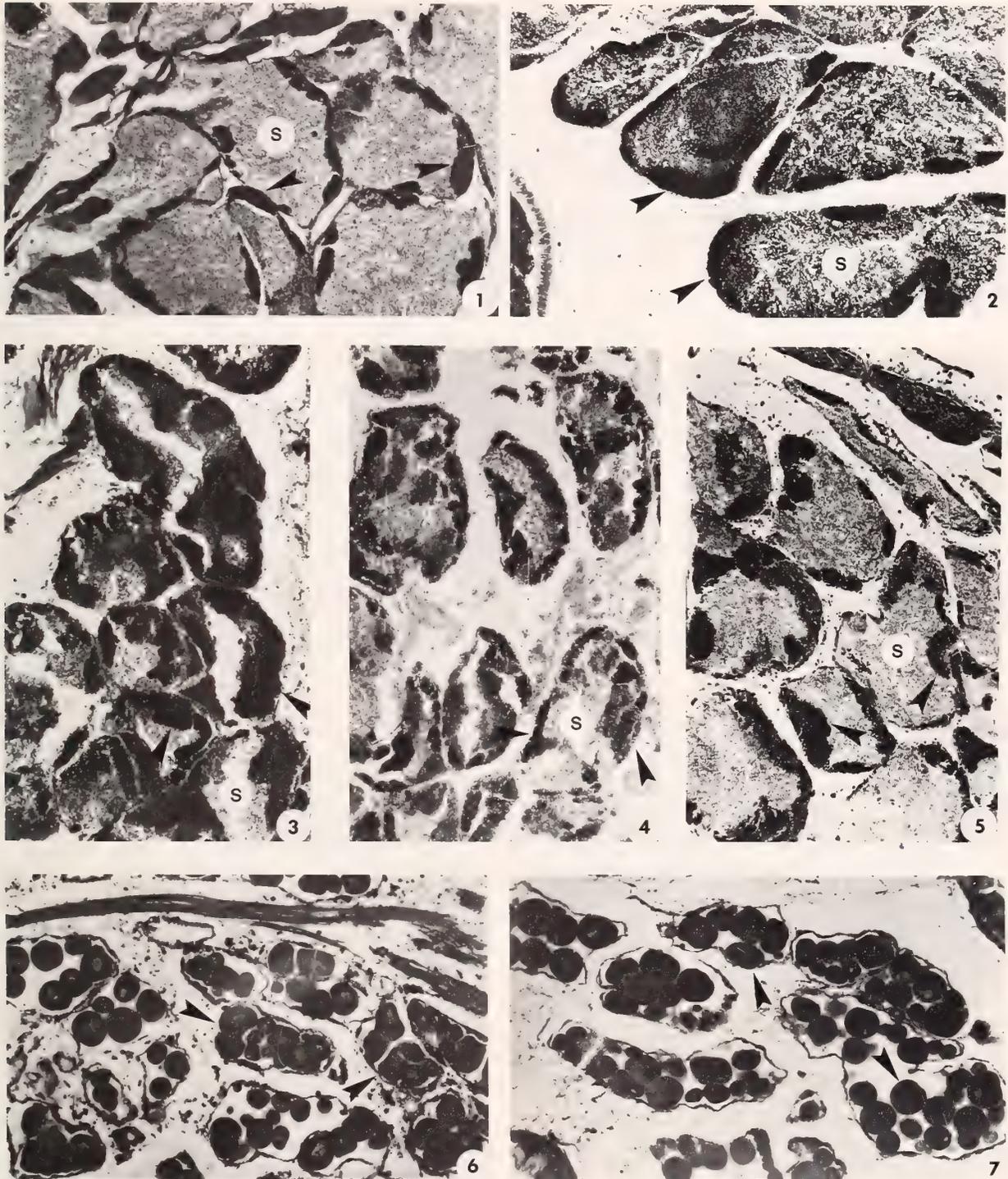
Explanation of Figures 1 to 7

Figure 1. Male gonad of *Diplodon chilensis chilensis* at the beginning of the fall-winter period (April). Gonadal follicles have abundant spermatozoa (S) in the lumen and immature gametes located at the periphery of the follicles (arrow heads). $\times 20$.

Figure 2. Male gonad of *Diplodon ch. chilensis* at the end of the winter (August). Spermatozoa (S) fill all the intrafollicular spaces,

and immature gametes are confined to the periphery of the follicles (arrow heads). $\times 20$.

Figures 3 and 4. Male gonads of *Diplodon ch. chilensis* in the spring-summer period (September and December, respectively). Spermatozoa (S) are less abundant than in preceding months



(Figures 1 and 2) and immature gametes occupy larger areas within the follicles (arrow heads) which are partially full at this time (spawning period). $\times 20$.

Figure 5. At the end of the spring–summer period (March) male follicles are partially full, with sperm located at the center of the

follicles (S) and immature gametes to the periphery close to the follicle walls (IG). $\times 20$.

Figures 6 and 7. Female gonad of *Diplodon ch. chilensis* in the fall–winter period (April and June, respectively). Female follicles contain abundant oocytes (arrow heads). $\times 20$.

MATERIALS AND METHODS

In March 1982, specimens of *Diplodon chilensis chilensis* were randomly collected from shallow waters (20–60 cm depth) of Lake Villarrica (39°17'S, 72°13'W). The individuals (564 in total) were placed in eight size classes (5-mm intervals) ranging from 16 to 65 mm in total length. The individuals of each size class were placed in wire cages (25 × 25 × 25 cm, 5-mm mesh). The cages were kept in a stream flowing from the Cautin River in the trout hatchery of Lautaro (39°17'S, 72°30'W).

Five individuals representing each size class were randomly selected each month from March 1982 to April 1983. The viscera were fixed in aqueous Bouin's fixative. After embedding in paraffin, 7- μ m serial sections were cut and stained with hematoxylin and eosin. Ten to 15 sections through different regions of the gonads of each specimen were examined under the light microscope to determine the type and abundance of germinal cells present in the gonads during the study period.

Chi-square (χ^2) analysis was used for sex-ratio determinations and Student's *t*-tests were employed to determine eventual differences in follicular areas occupied by spermatozoa and by clusters of immature germ cells throughout the year. The water temperature was recorded daily and the monthly mean temperature was calculated.

RESULTS

Diplodon chilensis chilensis is dioecious and its gonads are ramified organs bearing numerous follicles closely packed among the intestinal coils (PEREDO & PARADA, 1984).

Males

Inspections of gonadal sections revealed the presence of abundant gametes at various stages of maturation and abundant spermatozoa. These cells could be recognized by the morphological features described by PEREDO & PARADA (1984) in a study of gametogenesis in *Diplodon chilensis chilensis*. There were no major changes throughout the year either in the type or in the abundance of germinal cells present in the gonadal follicles.

In April, the gonadal follicles contained abundant spermatozoa in the lumen, and clusters of germinal cells at various stages of maturation were located at the periphery of the follicles (Figure 1). The same features were apparent in gonadal sections during the fall–winter months (April–August). At the end of winter (August) there was a slight increase in the number of spermatozoa, which by then almost filled all of the intrafollicular spaces; the cell clusters of immature gametes were confined to the periphery of the follicles (Figure 2).

From September to February there was a decrease in the number of spermatozoa and, conversely, an increase in the size of the cell clusters within the follicles. These changes were especially evident during September and November (Figures 3, 4). At the end of the spring–sum-

Table 1

Diplodon chilensis chilensis: follicular areas occupied by spermatozoa and immature germ cell clusters.

Month (1982–1983)	Percentage of area occupied by spermatozoa	Percentage of area occupied by immature germ cell clusters
March	61.69	32.67
April	67.72	26.52
May	70.10	20.52
June	61.96	32.55
July	58.99	27.33
August	60.87	33.44
Fall–winter mean area (\bar{X})	63.53	28.83
September	37.57	57.92
October	42.66	49.82
November	23.85	68.08
December	42.15	55.81
January	37.78	52.53
February	52.30	43.21
Spring–summer mean area (\bar{X})	39.38	54.56

mer months (February–mid-March) the follicles were partially full, with sperm located at the center of the follicles and with the cell clusters at the periphery, close to the follicular walls (Figure 5).

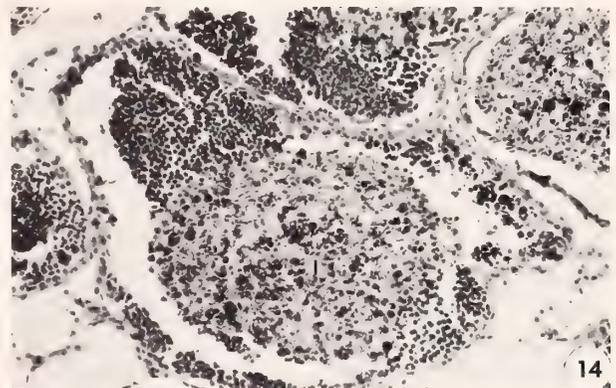
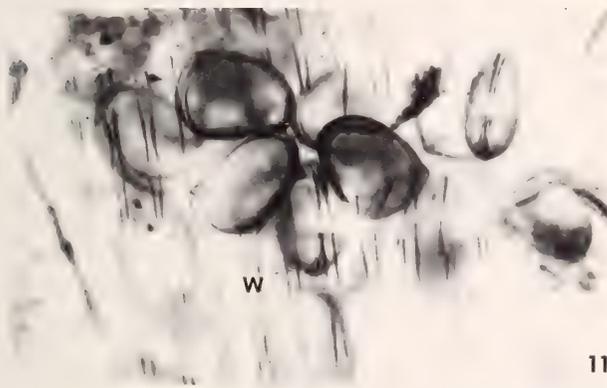
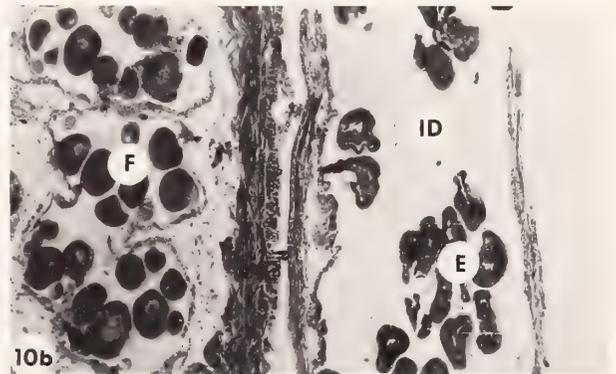
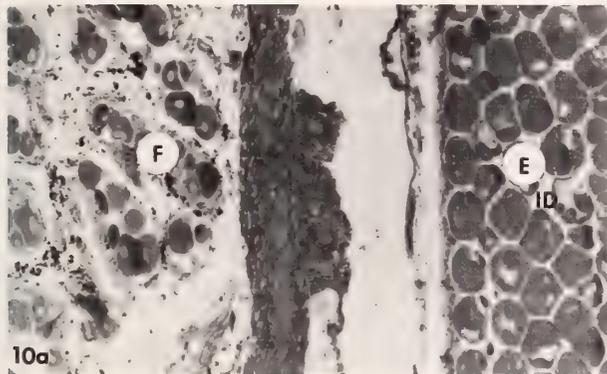
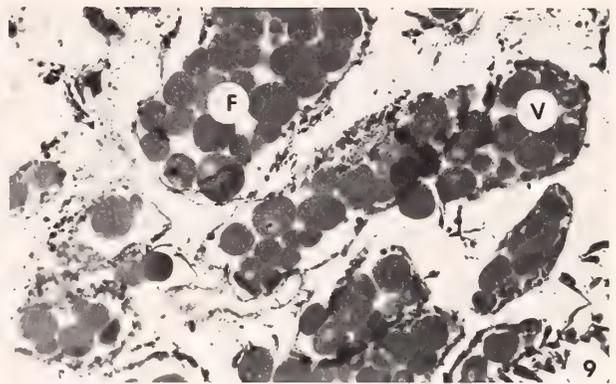
The cell population dynamics within the follicles, measured as the area of the follicle occupied by the spermatozoa versus that occupied by immature germinal cell clusters, showed that from March through August, the follicular area occupied by spermatozoa was larger than the area occupied by the cell clusters. From September until February, the converse was observed: the immature cell clusters occupied a larger intrafollicular area than did sperm (Table 1). Student's *t*-tests showed that the differences observed in the areas occupied by spermatozoa and by cell clusters in the different months throughout the year are statistically significant ($P \leq 0.05$).

The interstitial tissue did not show differences in the number or type of cells present throughout the year. Cells similar to the amoebocytes described by TRANTER (1958) were abundant in the tissue surrounding the follicles, especially in the areas close to the walls. These amoebocyte-like cells were not seen except occasionally within the follicles, either free or in close contact to germinal cells.

No differences in the histological features of the gonads throughout the year were found in the specimens of the different size classes studied, except, as expected, in the size and number of follicles.

Females

Gonadal follicles in the females showed few changes in the germ cell populations related to the types and numbers



Explanation of Figures 8 to 11, 14

Figure 8. Female follicle in the fall-winter period, with oogonia embedded in the walls and previtellogenic (PV), vitellogenic (V), and full-grown oocytes (F). $\times 50$.

Figure 9. At the end of the fall-winter period (August) increases in vitellogenic (V) and full-grown (F) oocytes are seen in the female follicles. $\times 20$.

Figure 10a. Gravid female in November with developing embryos (E) (blastulae) in the inner demibranchs (ID). Numerous oocytes can be seen in the gonadal follicles (F) at this time. $\times 20$.

Figure 10b. Gravid female in the same month (November) with more advanced embryos (E) in the inner demibranch (ID). Gonadal follicles (F) contain oocytes. $\times 20$.

Figure 11. Glochidia in the inner demibranch of a gravid female in November. Water tubes (W) of the gill can be seen. $\times 20$.

Figure 14. Male gonadal follicle showing tissue degeneration. Interstitial cells (I) can be seen within the follicle in contact with gametes. $\times 50$.

Table 2

Diplodon chilensis chilensis: monthly mean temperature, percentage of gravid females, and total females examined.

Month (1982-1983)	Monthly mean temperature	Percentage of gravid females	Total females examined
March	15.19	—	46
April	12.85	—	48
May	10.14	—	59
June	7.32	—	55
July	7.96	—	56
August	8.12	—	36
September	9.86	12	25
October	9.94	68	22
November	11.9	60	52
December	16.05	64	33
January	16.89	36	28
February	15.69	4	45
March	14.28	29	14

of oogonia and oocytes in the sections examined throughout the year.

During the fall-winter period, the female follicles contained abundant oocytes (Figures 6, 7) which, according to their morphology, correspond to previtellogenic, vitellogenic, and even vitelline (full-grown) oocytes (Figure 8). Embedded in the follicle walls were oogonia (Figure 8). During August increases in vitellogenic and vitelline oocytes were seen (Figure 9).

During the spring-summer period (September through February) similar characteristics were seen in the sections, with gonadal follicles containing various types of oocytes. No empty follicles were observed throughout the year. During the spring-summer season a slight decrease was observed in the number of oocytes within the follicles. Gravid females containing embryos in the inner demibranchs were observed from September until March. This condition was also verified by examination of gonad smears. October, November, and December were the months with the highest percentages of gravid females, with 68, 64, and 60% respectively (Table 2). In the same months, embryos in various developmental stages were present, including glochidia (Figures 10a, b, 11). The demibranchs of both sides of a gravid female contained embryos, which were all at the same stage of development; that is, the embryos housed in the inner demibranchs of a female were either zygotes, blastulae, gastrulae, or glochidia.

As in males, no empty follicles were observed in the sections examined throughout the year, including the period in which gravid females were present.

No differences in the histological characteristics of the gonads were observed throughout the year in females of the different size classes studied.

DISCUSSION

Examination of the gonadal sections of *Diplodon chilensis chilensis* reveals that in this species the gonad is continuously active throughout the year. All types of gametogenic cells, including mature gametes, can be seen in the gonadal follicles at the same time throughout most of the year. However, slight variations in the relative quantity of gametes within the follicles observed during the seasons of the year suggest the existence, in males and in females, of a continuous single reproductive cycle. In this cycle of *Diplodon ch. chilensis* a proliferation and maturation phase can be recognized that occurs throughout the year, but more intensively during the fall-winter months, and is characterized by an intensive maturation process; at the end of the winter (August) the follicles are packed with mature gametes. The spawning phase occurs only during the spring-summer months and is characterized by a partial evacuation of mature gametes; the gonadal sections indicated that the gonadal tissue was active, with the follicles producing early stages of gametogenesis.

Continuous gametogenic activity reported in the present paper has been described in the reproductive cycle of several freshwater bivalves, both dioecious (VAN DER SCHALIE & VAN DER SCHALIE, 1963; GHOSH & GHOSE, 1972; SMITH, 1979) and hermaphroditic (HEARD, 1965, 1975; ZUMOFF, 1973), although there are variations in the different species studied.

The proliferation and maturation phase observed in *Diplodon ch. chilensis* is more evident in males than in females, probably due to the accumulation of food reserves in the oocytes; consequently, this phase of the reproductive cycle is less noticeable. The proliferation and maturation of gametes in males is distinguishable from spawning by means of differences in the intrafollicular areas occupied by mature gametes (spermatozoa) versus immature gametes (cell clusters) during the seasons in which these processes occur. Thus, during the fall-winter season the area occupied by spermatozoa is larger than that occupied by cell clusters in the follicles. This difference becomes greater at the end of the winter (August) as a result of the intensive maturation of gametes at this time (Table 1). Conversely, during the spring-summer seasons the intrafollicular area occupied by immature gametes (cell clusters) is larger than that occupied by spermatozoa, and larger than that occupied by the cell clusters during the previous season, thus indicating evacuation of mature gametes and proliferation of immature gametes (Table 1, Figure 12).

Spawning is characterized as partial because during this period (September-March) the gonadal follicles of males and females are not depleted of gametes. On the contrary, they are partially full with growing and mature gametes (Figures 3-5, 10, 11). Spawning is also asynchronous in the individuals of the population studied, as shown by the occurrence of embryos at different stages of

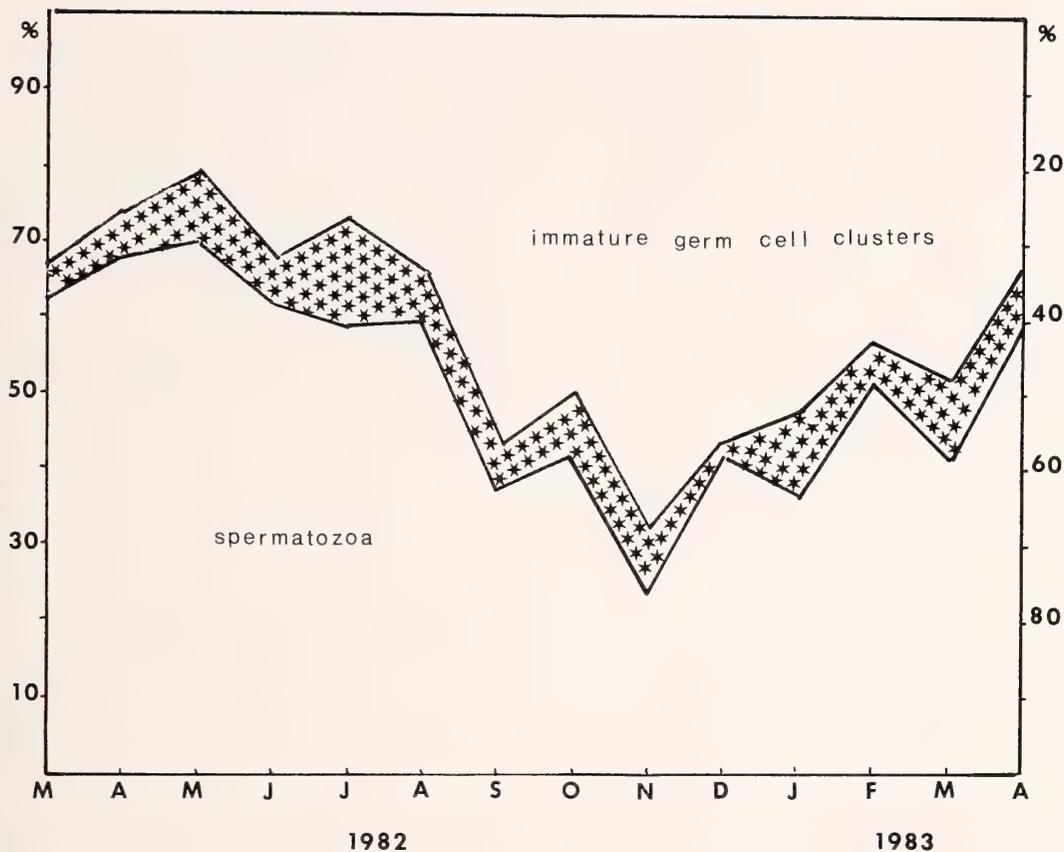


Figure 12

Follicular areas (in %) occupied by spermatozoa and cell clusters (immature gametes) in the reproductive cycle of *Diplodon chilensis chilensis* during the study period (t -test, $P \leq 0.05$).

development housed in the inner demibranchs of the females examined in the same month. This partial and asynchronous spawning explains the prolonged spawning period, extending from September until March, observed in *Diplodon ch. chilensis*. The continuous gonadal activity and the almost year-round occurrence of mature gametes in the gonads of *Diplodon ch. chilensis* could indicate the existence of two or more spawning periods within the year in this species as described for several freshwater bivalves (ZUMOFF, 1973; HEARD, 1975; CHUNG, 1980; KENMUIR, 1981). However, this situation seems to be unlikely in *Diplodon ch. chilensis* because gravid females were not present in the fall-winter months (April–August) (Table 2). Based on these observations it can be concluded that *Diplodon ch. chilensis* is a spring–summer breeder, unless gametes released during the fall-winter months for some reason were not fertile, an unlikely situation from the point of view of the reproductive effectiveness of this species.

As with other reports on the reproductive cycles of several mollusks, the spawning period observed in *Diplodon*

ch. chilensis coincided with increasing water temperatures in the study area (Figure 13). The role of temperature in the reproductive cycle of mollusks has been reviewed by several authors (GIESE, 1959; FRETTER & GRAHAM, 1964; GIESE & PEARSE, 1974; SASTRY, 1977), and water temperature could be the factor that induces spawning in *Diplodon ch. chilensis*. Specifically, it would be triggered when the water temperature reached values equal to or higher than those registered from September on. Lower temperatures would in turn determine the interruption of gamete emission during the fall-winter months, despite the presence of mature gametes (at least morphologically) in the gonadal follicles of males and females. Consequently, in *Diplodon ch. chilensis* abundant mature gametes are kept for months in the gonads before their release, a situation also reported by HEARD (1970) in the freshwater mussel *Margaritifera falcata*.

According to the results obtained in the present study, *Diplodon ch. chilensis* is a seasonal breeder with continuous gonadal activity, being coincident in this respect with other freshwater mussels. HEARD (1965) observed mature

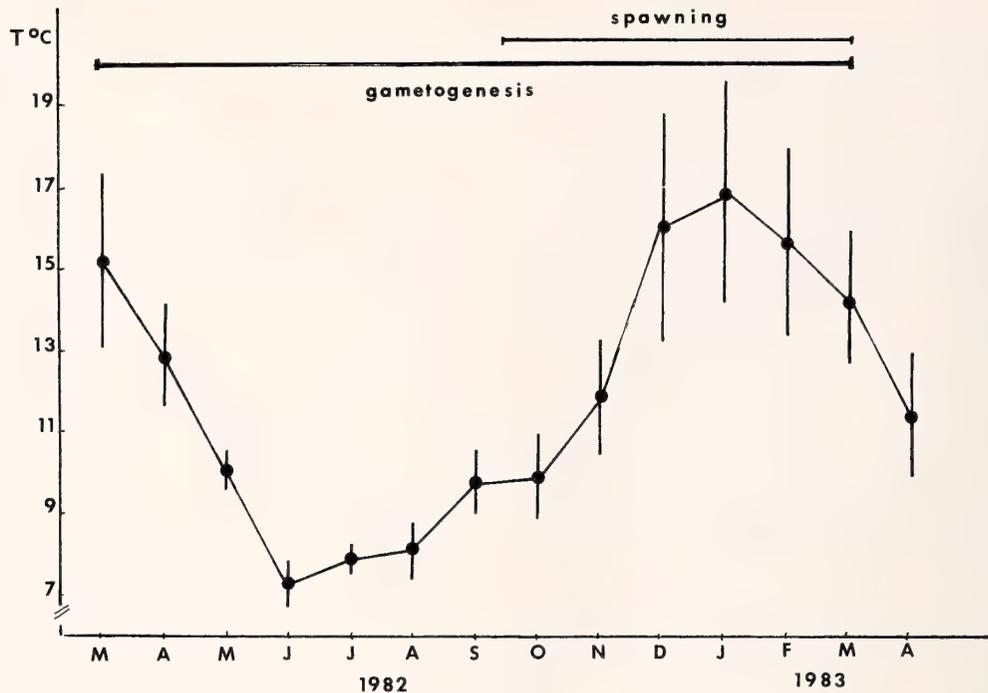


Figure 13

Monthly means and average ranges of water temperature of the stream flow in the trout hatchery of Lautaro during the study period.

gametes throughout the year in populations of *Anodonta imbecilis* and *Anodonta peggyae*. GHOSH & GHOSE (1972) reported a similar situation in the spermatogenesis of *Lamellidens marginalis*, and NAGABHUSHANAM & LOHGAONKER (1978) reported continuous gonadal activity and seasonal breeding in *Lamellidens corrianus*. *Diplodon ch. chilensis* also coincides in this aspect of reproduction with freshwater clams. WOODS (1931) observed mature gametes throughout the year in *Sphaerium striatum*, as did ZUMOFF (1973) in *Sphaerium simile*, a freshwater clam of the Northern Hemisphere. In the latter species fertilization occurs throughout the year, resulting in embryos housed in the brood sacs year round and differing from *Diplodon ch. chilensis* in which gravid females are found in the spring-summer months only.

The reproductive cycle of *Diplodon ch. chilensis* also shows differences from those reported for other freshwater bivalves. For instance within the Sphaeriidae, *Musculium securis* is a hermaphroditic species in which the gonads are spent during the winter months; it has been reported as having one fertilization period during its life-span, which is only one year (MACKIE *et al.*, 1976). *Lamellidens corrianus* is a functional hermaphrodite that has a gonadal cycle that includes spent and recovery stages in addition to growing, maturing, and spawning stages (NAGABHUSHANAM & LOHGAONKER, 1978). Spent and recovery stages were not observed in the present study. Within the Margaritiferidae, SMITH (1978) reported two gametogen-

ic cycles per year with only one spawning period in a population of *Margaritifera margaritifera* from northeastern North America. In New England *Margaritifera margaritifera* has been reported as dioecious, with a gametogenic period from mid-May to mid-August (spring-summer), mature gametes in the gonadal follicles in July, and spawning in August. Following evacuation of mature gametes a few remain in the gonads, being resorbed after a few weeks (SMITH, 1979).

Cells of the interstitial tissue have been reported to have an active role in the gonadal cycle of several bivalves, phagocytizing residual gametes or providing nutrients to developing gametes. In such cases, amoebocytes or phagocytes have been observed within gonadal follicles in close relation to gametes. In the present study, such a situation was not observed. Interstitial tissue cells similar to those described by TRANTER (1958) were always seen in the interstitial spaces or close to the follicle walls. In only one or two of the specimens examined, interstitial cells of the type mentioned above were observed within the gonadal follicles, providing an anomalous situation of gonadal tissue degeneration of unknown origin (Figure 14). This evidence suggests that interstitial cells do not have an active role in the normal gonadal cycle in *Diplodon ch. chilensis*.

The differences observed in the reproductive cycle of *Diplodon ch. chilensis* compared with other freshwater mussels point out the notable variations existing among

freshwater mollusks with respect to various reproductive aspects including life-span, sexuality, gonadal activity, number of spawning and breeding periods, and number of births in the year. HEARD (1965) points out that these differences are present in the various species of a genus and occasionally in different populations of a species that inhabit different latitudes (intraspecific variations). These considerations should be kept in mind to temper generalizations or extrapolations of results obtained in the study of the reproductive behavior of one species to another species or related groups. These considerations should also be kept in mind in the study of reproduction in populations of the same species occupying distant geographical subranges or markedly different environmental conditions.

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LITERATURE CITED

- BEDFORD, J. W., E. W. ROELEFS & W. J. ZABIK. 1968. The freshwater mussel as a biological monitor of pesticide concentrations in a lotic environment. *Limnol. Oceanogr.* 13: 118-126.
- BJORK, S. 1962. Investigations on *Margaritifera margaritifera* and *Unio crassus*. *Acta Limnol.* 4:1-109.
- CHUNG, E. Y. 1980. Reproductive cycle and breeding season of the freshwater clam, *Anodonta (Sinanodonta) woodiana* (Lea). *Bull. Korean Fish Soc.* 13(4):135-144.
- FRETTER, V. & A. GRAHAM. 1964. Reproduction. Pp. 127-163. In: K. M. Wilbur and C. M. Yonge (eds.), *Physiology of Mollusca*. Academic Press: New York.
- GHOSH, C. & K. C. GHOSE. 1972. Reproductive system and gonadal activities in *Lamellidens marginalis* (Simpson, 1900). *Veliger* 14(3):283-288.
- GIESE, A. C. 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. *Ann. Rev. Phys.* 21: 547-576.
- GIESE, A. C. & J. S. PEARSE. 1974. General principles. Pp. 1-49. In: A. C. Giese and J. S. Pearse (eds.), *Reproduction of marine invertebrates*. Vol 1. Academic Press: New York.
- HEARD, W. H. 1965. Comparative life histories of North American pill clams (Sphaeriidae: *Pisidium*). *Malacologia* 2:381-411.
- HEARD, W. H. 1970. Hermaphroditism in *Margaritifera falcata* (Gould) (Pelecypoda: Margaritiferiidae). *Nautilus* 83:113-114.
- HEARD, W. H. 1975. Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia* 15:81-103.
- HENDELBERG, J. 1960. The freshwater pearl mussel: *Margaritifera margaritifera* (L.). *Rep. Inst. Freshw. Res. Dottningh.* No. 41:149-171.
- KENMUIR, D. H. S. 1981. Repetitive spawning behaviour in two species of freshwater mussels (Lamellibranchiata: Unionacea) in Lake Kariba. *Trans. Zimbabwe Sci. Assoc.* 60(8):49-56.
- LEE, G. F. & W. WILSON. 1969. Use of chemical composition of freshwater clam shells as indicators of paleohydrologic conditions. *Ecology* 50:990-997.
- MACKIE, G. L., S. U. QADRI & A. H. CLARKE. 1976. Development of brood sacs in *Musculium securis*. Bivalvia: Sphaeriidae. *Nautilus* 88(4):109-111.
- MCMILLAN, N. F. 1966. *Margaritifera margaritifera* (L.) in hard water in Scotland. *J. Conchol.* 26:69-70.
- MILLER, C. W., B. M. ZUCKERMAN & A. J. CHARIG. 1966. Water translocation of diazinom-C¹⁴ and parathion-S³⁵ off a model cranberry bog and subsequent occurrence in fish and mussels. *Trans. Amer. Fish. Soc.* 95:345-349.
- NAGABHUSHANAM, R. & A. L. LOHGAONKER. 1978. Seasonal reproductive cycle in the mussel, *Lamellidens corrianus*. *Hydrobiologia* 61:9-14.
- NELSON, D. J. 1962. Clams as indicators of Strontium 90. *Science* 137:38-39.
- PEREDO, S. & E. PARADA. 1984. Gonadal organization and gametogenesis in the freshwater mussel *Diplodon chilensis chilensis* (Mollusca: Bivalvia). *Veliger* 27(2):127-134.
- SASTRY, A. N. 1977. Reproduction of pelecypods and lesser classes. Pp. 137-151. In: A. C. Giese and J. S. Pearse (eds.), *Reproduction of marine invertebrates*. Academic Press: New York.
- SMITH, D. G. 1978. Biannual gametogenesis in *Margaritifera margaritifera* in northeastern North America. *American Malacological Union* (1978):49-53.
- SMITH, D. G. 1979. Sexual characteristics of *Margaritifera margaritifera* (Linnaeus) populations in central New England. *Veliger* 21(3):381-383.
- TRANter, D. J. 1958. Reproduction in Australian pearl oysters (Lamellibranchia). II. *Pinctada albina* (Lamark): gametogenesis. *Aust. J. Freshw. Res.* 9:144-158.
- VAN DER SCHALIE, H. 1969. Two unusual unionid hermaphrodites. *Science* 163:1333-1334.
- VAN DER SCHALIE, H. 1970. Hermaphroditism among North American freshwater mussels. *Malacologia* 10(1):93-112.
- VAN DER SCHALIE, H. & A. VAN DER SCHALIE. 1963. The distribution, ecology and life history of the mussel, *Actinonaias ellipsiformis* (Conrad), in Michigan. *Occ. Pap. Mus. Zool. Univ. Mich.* 633:1-17.
- WOODS, F. 1931. The history of the germ cells in *Sphaerium striatum*. *J. Morphol.* 51:545-595.
- ZUMOFF, C. H. 1973. The reproductive cycle of *Sphaerium simile*. *Biol. Bull.* 144:212-228.

Egg Capsule and Young of the Gastropod *Beringius (Neoberingius) frielei* (Dall) (Neptuneidae)

by

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Abstract. The egg capsule and capsule young of the gastropod *Beringius frielei* are described for the first time. Two egg capsules, one containing two young, were collected in the eastern Bering Sea. The young closely resembled adults of the species, and the capsules were similar to those of other eastern Bering Sea members of the genus *Beringius*.

Beringius (Neoberingius) frielei Dall, 1895, occurs in the eastern Bering Sea (Dall, 1895), off the east coast of Sakhalin Island and in the northern part of the Okhotsk Sea (HABE & ITO, 1972) and off Hokkaido Island (Pilsbry, 1907). The nominate race, *B. (Neoberingius) frielei frielei*, is found in the eastern Bering Sea from Unimak Pass to the Pribilof Islands at depths of 121 to 350 m (DALL, 1895; author's unpublished data).

Although *Beringius frielei* is common in the eastern Bering Sea, the egg capsule and young have not been described. On 11 July 1977, several specimens and two egg capsules of *B. frielei* were collected from a trawl haul made at a depth of 300 m north of Unimak Pass (55°24'N, 168°08'W). The adult snails (Figure 1) were cleaned and stored dry. The egg capsules, which were attached to an empty shell of *Fusitriton oregonensis* (Redfield, 1848), were preserved in alcohol. Although one capsule was empty and open along its distal perimeter, the other contained two well developed young that were easily recognized as *B. frielei* (Figure 2).

Each capsule was pouchlike with a single internal chamber. The two capsules were 18 and 21 mm high. Both were 27 mm wide and 7 mm thick. Their width decreased to 16 mm above the point of attachment. They were firmly cemented to the *Fusitriton oregonensis* shell by a flat expanded base measuring 18 × 25 mm. The common base shared by both capsules (Figure 3) indicates that they were laid by a single female.

As in other members of the genus, the capsule of *Beringius frielei* was a complete envelope within an envelope (COWAN, 1964; MACINTOSH, 1979) (Figure 4). Outer and inner layers were 0.15 and 0.10 mm thick, respectively. The outer surface of each capsule was pale yellow, smooth, and rubberlike, while the interior surface of the outer envelope was covered with numerous fine lamellae running approximately parallel to the capsule base. These lamellae were 0.1–0.2 mm high and numbered 4–6 per mm. The outer surface of the inner envelope was circumscribed with similar fine lamellae. The lining of the brood chamber was smooth and without macroscopic structural

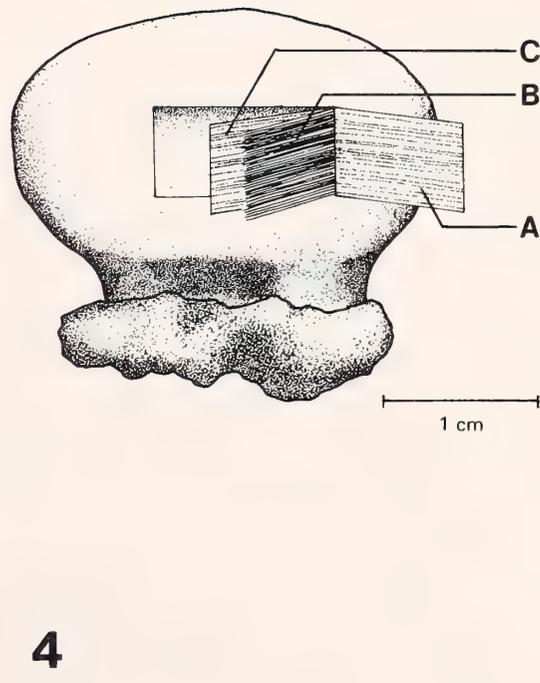
Explanation of Figures 1 to 4

Figure 1. Adult *Beringius frielei* taken at 300 m on the eastern Bering Sea shelf in same trawl haul with egg capsules.

Figure 2. Well developed young of *Beringius frielei* taken from an egg capsule.

Figure 3. Two egg capsules of *Beringius frielei* on empty shell of *Fusitriton oregonensis*.

Figure 4. Diagram showing capsule wall of *Beringius frielei* egg capsule. A, outer layer showing fine lamellae on inner surface; B, layer of slender yellow fibers; C, inner layer showing fine lamellae on outer surface.



detail. Between the two envelopes was a layer of slender 20–25 mm long yellow fibers parallel to the lamellae. They were mostly unattached and loosely packed, allowing easy separation of inner and outer layers. Some fibers were partially attached to the inner wall of the outer envelope.

The two capsule young were 16.2 and 15.0 mm in length (Figure 2). One shell was broken near the anterior canal while the other was whole. The shells were elongate, acute, and consisted of $4\frac{1}{4}$ well-rounded whorls with a deep suture. The three unsculptured nuclear whorls were pink, whereas the post-nuclear whorls were white. The first nuclear whorl was covered by a thin, parchmentlike film that made a shriveled apical cap. MacIntosh (1979) found similar caps on capsule young of *Beringius beringii* (Middendorff, 1849). The conspicuous sculpturing of the anterior quarter of the body whorl faded gradually towards the nuclear whorls. Spiral sculpture consisted of 34 evenly spaced, flattened close-set cords and an axial sculpture of fine but distinct incremental lines. Adults from the same area had this pattern in early whorls, but in the second to fourth post-nuclear whorls, the spiral cords became medially grooved or paired. The overall shape of the capsule young was similar to that of adults.

The egg capsules of *Beringius* (*Neoberingius*) *frielei* bear a striking resemblance to those of *B. (Neoberingius) turtoni* (Bean, 1834) from the North Sea and Skagerrak and *B. (Neoberingius) oassianus* from Norway (THORSON, 1940). Even the capsules of the more distantly related *B. eyerdami* Smith, 1959, and *B. beringii* are essentially identical in gross form and structure to those of *B. frielei* (COWAN,

1964; MACINTOSH, 1979), suggesting a greater degree of affinity among these species than might be presumed from studies of comparative shell morphology.

ACKNOWLEDGMENTS

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LITERATURE CITED

- COWAN, I. M. 1964. The egg capsule and young of *Beringius eyerdami* Smith. (Neptuneidae). *Veliger* 7(1):43–44, pl. 7.
- DALL, W. H. 1895. Scientific results of explorations by the U. S. Fish Commission steamer Albatross. No. XXXIV.—Report on Mollusca Brachiopoda dredged in deep water, chiefly near the Hawaiian Islands, with illustrations of hitherto unfigured species from northwest America. *Proc. U.S. Natl. Mus.* 17:675–733, pl. 23–32.
- HABE, T. & K. ITO. 1972. A new subspecies of *Beringius (Neoberingius) frielei* (Dall) from Okhotsk Sea. *Venus* 31(3): 113–114.
- MACINTOSH, R. A. 1979. Egg capsule and young of the gastropod *Beringius beringii* (Middendorff) (Neptuneidae). *Veliger* 21(4):439–441, 1 pl.
- PILSBRY, H. A. 1907. New and little-known whelks from northern Japan and the Kuril Islands. *Proc. Acad. Natl. Sci. Phila.* (1907):243–246, pls. 19, 20.
- THORSON, G. 1940. Notes on the egg-capsules of some North-Atlantic prosobranchs of the genus *Troschelia*, *Chrysodomus*, *Volutopsis*, *Sipho*, and *Trophon*. *Vidensk. Medd. Dan. Naturhist. Foren.* 104:251–266.

The Systematic Position of *Royella sinon* (Bayle) (Prosobranchia: Cerithiidae)

by

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Abstract. *Royella sinon* (Bayle), a marine prosobranch representing a monotypic genus, is herein assigned to the family Cerithiidae Fleming on the basis of characters derived from the shell, soft anatomy, operculum, and radula. A white shell sculptured with two nodular spiral cords per whorl, a short shallow anterior siphon, and the concave base of the body whorl are distinctive. The corneous operculum is circular-ovate, having few spirals and a central nucleus. The taenioglossate radula is typically cerithioid. Digitate papillae fringe the mantle edge, and within the mantle cavity a long monopectinate osphradium, a ctenidium comprised of long triangular filaments, and a thick, wide, open pallial oviduct with a large albumen gland are notable features. A pair of salivary glands that pass through the nerve ring, a midesophageal gland, and a large stomach with a short style sac, large cuticularized gastric shield, and complex sorting area indicate herbivory. The habitat is subtidal rubble bottoms. Development is inferred to be planktotrophic on the basis of the sculptured protoconch and distinct sinusigera notch.

INTRODUCTION

Royella sinon (Bayle) is an uncommon marine cerithiacean prosobranch of uncertain familial assignment that has a white shell about 20 mm long with rugose cancellate sculpture. It has an extremely wide geographic distribution throughout the Indo-Pacific region. Its exact affinity to other cerithiacean groups has long been unknown due to lack of information about the soft parts and radula.

Royella is a monotypic genus that has been assigned to the Potamididae H. and A. Adams, 1854, due to shell characters shared in common with some potamidid species such as *Pirenella conica* (Blainville), but this allocation is unsatisfactory. To resolve this problem I examined virtually all specimens of *Royella* in major national and international institutions and museums, but not a single preserved animal or shell with a dried animal was found. In addition, requests in *The Hawaiian Shell News* (HOUBRICK, 1984:12) for live-collected, preserved specimens were not successful, although some new locality records were obtained. Recently, Mr. Gustav Paulay collected *Royella sinon* alive in the Cook Islands and, through the kindness of Dr. Anders Warén, I was able to obtain the preserved specimen and study the soft anatomy and radula. The results are presented below and include a historical account, synonymy, description of the shell, animal, and radula, and the new family allocation for this taxon.

MATERIALS AND METHODS

Specimens of this uncommon snail were examined from major museums and from private collections throughout the world for shell measurements. Variables included total shell length and width, aperture length and width, and length of the penultimate whorl. The single available preserved specimen, a female, was dissected using methylene blue solution under a Wild M-5 dissecting microscope. The radula was removed, measured, and prepared for scanning electron microscope (SEM) study. Superficial and internal anatomy were studied, but swelling of the albumen gland due to the aqueous dissecting solution unfortunately obscured and partially destroyed details of the pallial oviduct. Scanning electron micrographs of the radula and operculum were made on a Cambridge 250 Mark II Stereoscan microscope.

The following abbreviations have been used in this paper: AMNH—American Museum of Natural History; AMS—Australian Museum, Sydney; ANSP—Academy of Natural Sciences, Philadelphia; BMNH—British Museum (Natural History); CAS—California Academy of Sciences; DMNH—Delaware Museum of Natural History; HUI—Hebrew University of Jerusalem; LACM—Los Angeles County Museum of Natural History; MNHNP—Museum National d'Histoire Naturelle, Paris; NMNZ—National Museum of New Zealand;

NMV—National Museum, Victoria; USNM—National Museum of Natural History; WAM—Western Australian Museum.

Material examined and literature records

RED SEA: Aqaba, Jordan (HUIJ 21.311/9); Elat, Israel (HUIJ 21.312/8). INDIAN OCEAN ISLANDS: Anse Boileau, Mahe, Seychelles (BMNH); Mauritius (BMNH). AUSTRALIA: North Australia (BMNH); outer reef, West Gun Id., Abrolhos Islands, Western Australia (WAM); Lodestone Reef, N of Townsville, Queensland (AMS); S Side Beach, York Id., Torres Strait, Queensland (AMS); Four Mile Beach, Port Douglas, Queensland (AMS); Saxon Reef, off Cairns, Queensland (Thora Whitehead coll.); Norfolk Id. (AMS); 44 m off Lord Howe Id., 31°38'25"S, 159°03'W (AMS); Lord Howe Id. (AMS, NMV). KERMADEC ISLANDS: Raoul (Sunday Id.) (AMS, NMNZ MF 141616, USNM 214757); 29°17.2'S, 177°57.2'W, 27–29 m, E end of Denham Bay, Raoul Id. (NMNZ MF26957); 29°15'S, 177°50.9'W, 31–45 m between Dayrell and Chanter Is., Herald Islets (NMNZ MF27068). JAPAN: Nada, Kii, Honshu (ANSP 224908); Shionomizaki, Kii, Honshu (ANSP 224769); Hachijojima Izu (ANSP 86166). RYUKYU ISLANDS: Ryukyus (ANSP 243288, DMNH 80887, USNM 666629); Kikai, Osumi (MNHNP, USNM 273329, 175588, CAS, AMS); Osuma, Osumi (USNM 343916, MNHNP). PHILIPPINES: Baclayon Id., Bohol (A. Adams, 1855); Cebu (LACM 25166, MNHNP). TAIWAN: (Kuroda, 1941). PALAU: SW tip, Ngatpaet Passage, E Babelthuap (ANSP 202742). MARSHALL ISLANDS: Taka Atoll (USNM 615494); Bock Id., Rongerik Atoll (USNM 594667); Majuro Id., Majuro Atoll (Bob Purtymun coll.); lagoon side, Edgigen Id., Kwajalein (DMNH 93854); Enewetak Atoll (LACM 70-72, USNM 821778). NEW CALEDONIA: (MNHNP). LOYATY ISLANDS: (BMNH); Lifu (ANSP 132658, 196063, ANS, AMNH, MNHNP). SAMOA ISLANDS: Pologa Bay, Tutuila (Bob Purtymun coll.). COOK ISLANDS: (MNHNP); off Kimiangatau, Mauke Id. (USNM 842296); RAPA: mouth of Ahurei Bay (USNM 725617); E side of Tematapu Point (USNM 725691). SOCIETY ISLANDS: Papeete, Tahiti (Trondle Coll.); Papara, Tahiti (Trondle coll.). PITCAIRN ISLAND: off NW corner, Pitcairn (USNM 789325). HENDERSON ISLAND: (BMNH 1913.7.28.85.6).

DESCRIPTION

Family CERITHIIDAE Fleming, 1822

Royella Iredale, 1912

Royella IREDALE, 1912:219. Type-species, by monotypy: *Cerithium clathratum* Sowerby, 1855; WENZ, 1940:739, fig. 2140; THIELE, 1931:205.

Diagnosis: Shell elongate, turreted, multi-whorled, having angulate whorls sculptured with two nodulose spiral cords and weaker axial riblets. Sculptured protoconch with sinusigera notch; early whorls cancellate; suture deeply impressed. Aperture circular, with short shallow anterior canal. Operculum corneous, circular, moderately spiral, with central nucleus. Radula taenioglossate (2+1+1+1+2). Mantle edge fringed, osphradium monopectinate. Pallial gonoduct open. Paired salivary glands, esophageal gland, and large stomach with style sac, sorting area, and gastric shield present.

Remarks: This monotypic genus is not well known in the literature. It was allocated to the Potamididae H. and A. Adams, 1854, by THIELE (1929:205) and WENZ (1940:739) on the basis of shell sculpture, but as this family comprises an intertidal estuarine group, it seems unlikely that *Royella* belongs here. The type-species was first assigned to *Cerithium* Bruguière, 1789, by SOWERBY (1855:883) and later allocated to *Pirenella* Gray, 1847, by KOBELT (1895:173) and TRYON (1887:165) and to *Cerithiopsis* Forbes & Hanley, 1850, by MELVILL & STANDEN (1895:116). IREDALE (1911:320) pointed out its distinctness from these genera and proposed *Royella* to accommodate it. IREDALE (1912:219) suggested that he had seen “. . . other forms which appear to be congeneric . . .” and figured an undescribed species (pl. 9, fig. 3), but his illustration is poor and does not allow critical comparison with *Royella* *sinon*. The figured shell does not appear congeneric.

Royella is herein assigned to the Cerithiidae on the basis of the radular and anatomical characters described in more detail below and in the discussion.

Royella *sinon* (Bayle, 1880)

Figures 1a–i, 2a, b

Cerithium clathratum A. Adams (*Cerithiopsis*) in SOWERBY, 1855:883, pl. 185, fig. 258 (Holotype: BMNH; Type-locality: Baclayon Id., Bohol, Philippines; not Deshayes, 1833 nor Menke, 1828, nor Grateloup, 1832, nor Roemer, 1841.) SOWERBY, 1865:pl. 20, fig. 147.

Cerithium (*Pirenella*) *clathratum* A. Adams: Kobelt in MARTINI-CHEMNITZ, 1895:173–174, pl. 32, fig. 13.

Cerithium *sinon* BAYLE, 1880:245 (new name for *clathratum* A. Adams, 1880); IREDALE, 1911:320.

Cerithiopsis *sinon* (Bayle): MELVILL & STANDEN, 1895:116, pl. 1, fig. 3.

Royella *sinon* (Bayle): IREDALE, 1912:219; HIRASE, 1936:54, pl. 84, fig. 18; KIRA, 1962:26, pl. 13, fig. 13.

Description: Shell (Figure 1a–h; Table 1). Shell elongate, turreted, reaching 29 mm in length and consisting of angulate whorls sculptured with two strong spiral, nodulose cords crossed by weak axial riblets. Numerous microscopic incised spiral lines give silky appearance to shell. Wide anterior and posterior sutural ramps present on each whorl due to deeply impressed suture. Nodules formed where axial riblets cross spiral cords and tend to be pointed; 23 axial riblets on penultimate whorl. Axial ribs more defined on early whorls, which have cancellate, pitted appearance where axial and spiral elements cross. Protoconch pink, with sinusigeral notch (Figure 1b). Body whorl sculptured with two major nodulose, spiral cords in middle and with two, closely spaced, smooth, spiral cords above siphonal constriction. Base of body whorl concave. Anterior siphonal canal short, shallow, and slightly reflected upwards and to the left. Outer lip thin, nearly straight, but wavy where spiral cords end. Shell color white, but light tan maculations may be present on spiral cords between nodules. Operculum corneous, thin, circular–ovate, with few spirals and central nucleus.

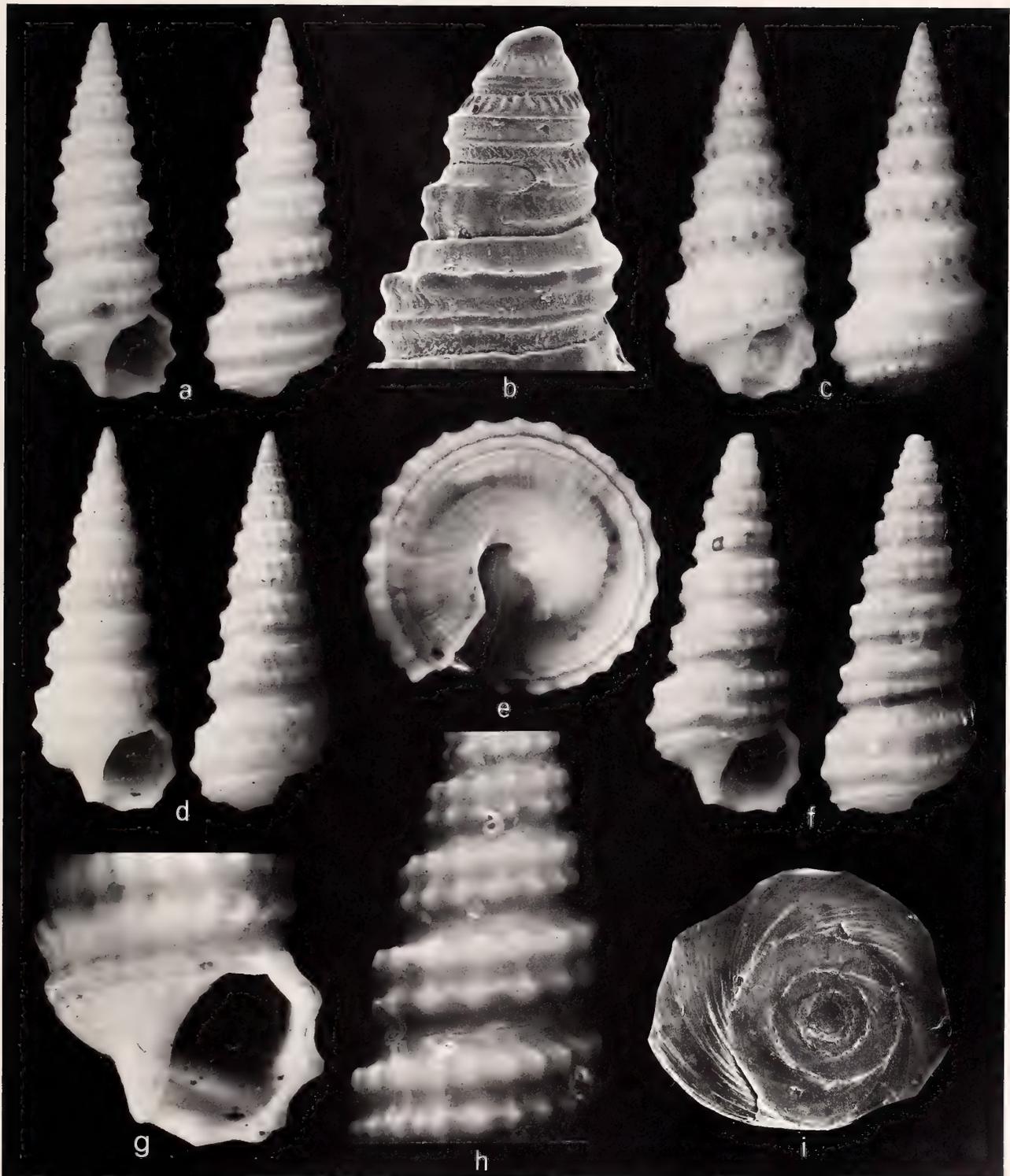


Figure 1

Shell and operculum of *Royella sinon*. a, Kikai, Osumi, Japan, 19.4 mm long (USNM 175588). b, protoconch showing larval sculpture and sinusigeral notch; 29°15'S, 177°50.9'N between Dayrell and Chanter Ids., Herald Islets, Kermadecs, New Zealand (NMNZ MF27068). c, Enewetak Atoll, Marshall Islands, 14.3 mm long (USNM 821778). d, Kikai, Osumi, Japan, 16.9 mm long. e, enlarged view of base of shell. f, Kikai, Osumi, Japan, 17 mm long (USNM 273329). g, enlargement of aperture. h, detail of sculpture on middle whorls. i, operculum, Mauke Id., Cook Ids., 1.8 mm diameter (USNM 842296).

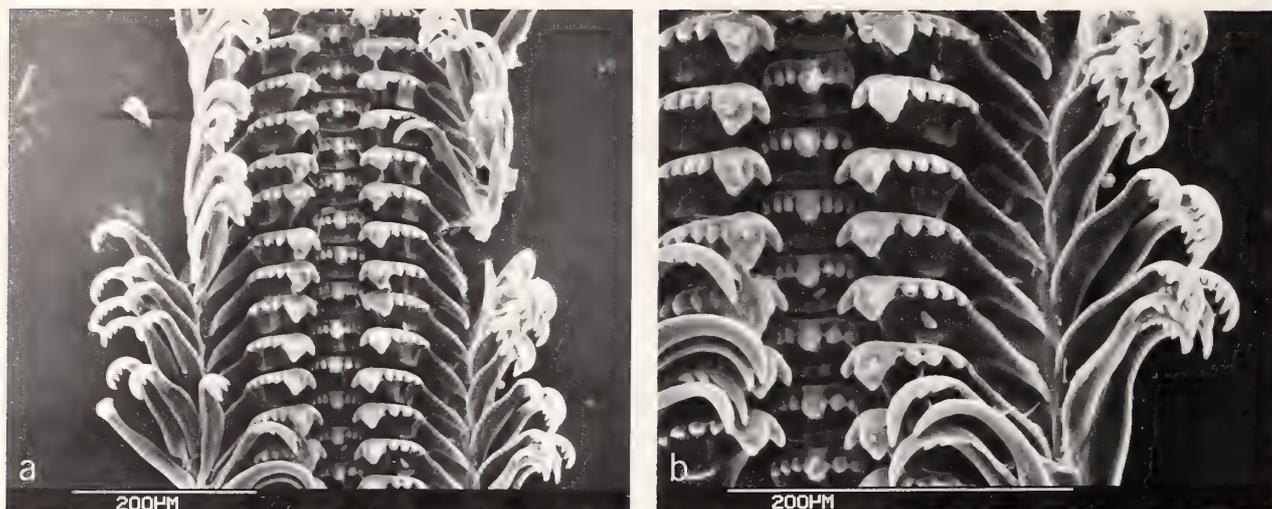


Figure 2

Radula from *Royella sinon*, Mauke Id., Cook Ids. (USNM 842296). a, general view of radula. b, half row showing details of central, lateral, and marginal teeth.

Radula (Figure 2a–b). Radula typically cerithioid. Central tooth ovate, wider than tall, having a short, pointed central cusp flanked on each side by 3, sometimes 2, small denticles. Lateral tooth trapezoid with long lateral extension and buttressed central plate with short ventral extension. Marginals long, moderately curved at tips. Central pointed cusp of inner marginal flanked with 5 short, pointed inner denticles and 2 or 3 outer denticles. Outer marginal same, only smooth on outer surface.

Animal. (This description is based on a single preserved animal from Mauke Id., Cook Ids., collected under a rock on a rubble bottom in 20–24 m depth. Removed from the shell, the body comprised about 5.5 whorls.) The animal is cream colored with darker gray lines on the head-snout. The head is broad and has a short wide snout with a bilobed tip. The cephalic tentacles are thick, each with a small dark eye at the outer base of the peduncular stalk. The left tentacle is shorter than the right. The foot is long and narrow and has a deep crescent-shaped propodial groove (gland). Behind the anterior pedal gland the sole of the foot stains heavily with methylene blue indicating a mucus-secreting area. The end of the foot is pointed. The dorsal edge of the mantle is fringed with many digitate papillae, but is smooth ventrally. There is no obvious siphonal fold or indentation. The mantle cavity is deep, extending about 2.5 whorls. Within the mantle cavity, a long, dark brown, monopectinate osphradium extends the length of the ctenidium. Individual osphradial

filaments are rectangular. The ctenidium is white, about 1.5 mm wide and extends the length of the mantle cavity. It is composed of long triangular filaments. The pallial oviduct is open, but was largely destroyed in the preserved specimen due to swelling of the albumen gland by water absorption. The buccal mass is elongate and relatively large and there is a pair of small jaws just inside the oral cavity. A short, wide, robust radular ribbon, 2.5 mm long and 0.5 mm wide, had 63 rows of teeth and was over one-seventh of the shell length (18.7 mm). A pair of large white, loosely coiled, salivary glands is present behind the nerve ring, and partially extends through it. The mid-esophagus is wide and has a large brown glandular area on its dorsal surface, which is the esophageal gland. The stomach is very large, about 2.5 whorls in length and comprises an extensive complex sorting area, a large cu-

Table 1

Summary of shell measurements of *Royella sinon* (in mm).

Statistic	n	Range	\bar{X}	SD
Length	45	11.1–28.6	17.91	4.44
Width	45	3.2–9.7	6.59	1.50
Aperture length	36	1.3–6.2	3.59	0.97
Aperture width	36	1.1–4.8	2.46	0.78
Body whorl length	25	3.5–10.4	6.86	1.50

Figure 3

Geographic distribution of *Royella sinon* (Bayle).

tical gastric shield and a short style sac. The intestine and rectum are large and contain transversely oriented, ovate fecal pellets. The nervous system is epiathroid and typically cerithioid in layout.

DISCUSSION

Although *Royella sinon* has a wide geographic distribution it is not a common species in museum collections and has not been well known to malacologists or conchologists. Most specimens are empty shells when collected, but living animals may be common in the proper habitat. The few records that cite details about collecting sites mention offshore, subtidal, coral-rubble habitats. The live-collected specimen described herein was taken in a similar habitat by SCUBA.

On the basis of the new data supplied by characters derived from analysis of the preserved specimen, I consider *Royella* to be a distinctive monotypic genus and assign it to the family Cerithiidae Fleming, 1822. The protoconch and shell sculpture resemble those of some members of the genus *Cerithium* Bruguière, 1798, but most *Cerithium* species are sculptured with three spiral cords per whorl and have an operculum with an eccentric nucleus; moreover, the short, shallow, anterior siphonal canal is atypical of cerithiids. The circular, spiral, corneous operculum with a central nucleus is much like those of some cerithiid genera such as *Argyropeza* Melvill & Standen, 1901, *Bittium* Gray, 1847, and *Varicopeza* Grundel, 1976, whereas the wide short snout, fringed mantle edge, and radula of *Royella* most closely resemble those of *Cerithium* species. The monopectinate osphradium differs from the bipectinate condition in *Cerithium* species and is a unique, distinctive anatomical character of *Royella*. The radular morphology, stomach contents, fecal pellet composition, and the elaborate stomach all indicate herbivory. A few sponge spicules were found in the stomach, but these are to be expected in any algal-detritus feeding cerithiid. The subtidal habitat on rubble is similar to that of many cerithiids.

Royella has been placed in the Potamididae, but there are no compelling reasons for this assignment. The fringed, digitate mantle edge is unlike that of potamidids, which is smooth, and most potamidids have long tapering tentacles and relatively extensible snouts; moreover, the osphradium in all potamidids is a simple ridge. The radula of *Royella* is very unlike that of any potamidid species I have seen: members of the Batillariinae have distinctive cusps on the basal plate of the central tooth while the Potamidinae usually have narrow central teeth with long ventral extensions and marginal teeth with spatulate serrated tips and lateral flanges. They also have long style sacs and well developed crystalline styles. Nothing like these features are found in *Royella sinon*. The subtidal, purely marine habitat of *Royella* is also distinctly different from that of any potamidid.

I had initially suspected that *Royella* might be a very large cerithiopsid and a sponge feeder, but it does not have

an acrembolic proboscis, and is clearly a herbivore. The radula and protoconch are totally unlike those of cerithiopsid species (see MARSHALL, 1978). The shell of *Royella sinon* superficially resembles some triphorid shells such as *Metaxia* Monterosato, 1884, especially in the concavity of the base of the body whorl. *Royella*, however, has a much larger, bulkier shell than any cerithiopsid or triphorid species, attaining a length of 26 mm and a width of 9.4 mm.

The uniquely sculptured shell does not resemble that of any other cerithiacean snail with the exception of *Cerithium excavatum* Sowerby, 1865, a species known only from SOWERBY's figures (1865, 1866). I have not been able to find the holotype of *C. excavatum*, nor have I seen any specimens so labeled. The pictures in SOWERBY (1865, 1866) show that *C. excavatum* does not have the two spiral nodulose cords. It is thus best to regard *C. excavatum* as a *nomen dubium*.

The two nodulose spiral cords per whorl, deeply impressed sutural area, short shallow anterior siphon, and the strong, keel-like spiral cord on the body whorl anterior to the siphonal constriction are the main distinguishing characters of this species. The range of variation in shell characters, such as the extent of pigmentation and node development on the spiral cords, as seen in Figure 1, is not great. Some specimens have distinct spots (Figure 1c) which others lack (Figure 1a, f). A specimen in the collection of J. Trondle, Papeete, Tahiti, had thin, brown spiral lines between the nodes. The largest specimens I have examined are from Norfolk Id. and Lord Howe Id., off the east coast of New South Wales, Australia, and from the Ryukyu Islands of Japan.

IREDALE (1911:320) mentioned juveniles from dredgings as having a minute sinusigeral protoconch, and I have confirmed this by SEM studies of the protoconch. As may be seen in Figure 1b, the protoconch comprises 3.5 whorls and has a distinct, deep sinusigera notch. Thus, on the basis of protoconch morphology and the extensive geographic range (JABLONSKI & LUTZ, 1980; JABLONSKI, 1982) it is reasonable to infer that *Royella* has a moderate to long planktotrophic larval stage.

Geographic distribution (Figure 3). *Royella sinon* has a wide Indo-Pacific distribution ranging from the Red Sea and western Indian Ocean eastward to Pitcairn Island. Within the Pacific, it occurs from Japan south to Lord Howe Id., the Kermadecs, and Rapa. It probably occurs elsewhere throughout the Indo-Pacific in suitable habitats.

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LITERATURE CITED

- ADAMS, H. & A. ADAMS. 1813-1878. The genera of Recent Mollusca. 3 volumes, London. 389 pp., 138 pls.
- AZUMA, M. 1960. A catalogue of the shell-bearing Mollusca of Okinoshima, Kashiwajima, and the adjacent area (Tosa Province) Shikoku, Japan. 102 pp., 5 pls.
- BAYLE, E. 1880. Liste rectificative de quelques noms de genres et d'espèces. *J. Conchyl.* 28(3):240-251.
- BRUGUIÈRE, J. G. 1789-1792. *Encyclopédie méthodique, histoire naturelle des vers*. Paris. 1(1):1-344 (1889), 2(1):345-757 (1792).
- DESHAYES, G. P. 1824-1837. *Description des coquilles des environs de Paris*. 2 volumes + Atlas. 814 pp., 55 pls. (volume 1); 106 pls. (volume 2).
- FLEMING, J. 1822. The philosophy of zoology or a general view of the structures, functions and classifications of animals, etc. Edinburgh. 2 volumes.
- FORBES, E. & S. HANLEY. 1850-1851. A history of British Mollusca and their shells. Volume 3. Van Voorst: London. 133 pls.
- GRATELOUP, J. P. S. 1832. Tableau (suite de) des coquilles fossiles qu'on rencontré de Dax, département des Landes: par M. Grateloup, membre honoraire, 5eme Article. *Actes Société Linnéenne de Bordeaux* 5(29):263-282.
- GRAY, J. E. 1847a. The classification of the British Mollusca by N. E. Leach, M.D. *Ann. Mag. Natur. Hist.* 20:267-273.
- GRAY, J. E. 1847b. A list of the genera of Recent Mollusca, their synonyma and types. *Proc. Zool. Soc. Lond.* 15:129-219.
- GRÜNDEL, J. 1976. Zur Taxonomie und Phylogenie der *Bitium*-gruppe (Gastropoda, Cerithiacea). *Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden* 5(3):33-59, 2 pls., 17 figs.
- HIRASE, S. 1936. A collection of Japanese shells. 5th ed. Tokyo. 217 pp., 128 pls.
- HOUBRICK, R. S. 1984. Going collecting? Look for a live *Royella sinon*. *Hawaiian Shell News* 32(4):12.
- IREDALE, T. 1911. On the value of the gastropod apex in classification. *Proc. Malacol. Soc. Lond.* 9:319-323.
- IREDALE, T. 1912. New generic names and new species of marine mollusca. *Proc. Malacol. Soc. Lond.* 10:217-228, pl. 9.
- JABLONSKI, D. 1982. Evolutionary rates and modes in late Cretaceous gastropods: role of larval ecology. *Proc. Third North Amer. Paleontol. Conv.* 1:257-262.
- JABLONSKI, D. & R. A. LUTZ. 1980. Molluscan larval shell morphology. Ecological and paleontological applications. Pp. 323-377. *In: D. C. Rhoads & R. Lutz (eds.), Skeletal growth of aquatic organisms*. Plenum: New York.
- KIRA, T. 1962. Shells of the western Pacific in color. Osaka. 224 pp., 72 pls.
- KOBELT, W. 1888-1898. Die gattung *Cerithium*. 297 pp., 47 pls. *In: F. H. W. Martini & J. H. Chemnitz, Neues systematisches Conchylien-Cabinet . . .* 1(26). Nürnberg.
- KURODA, T. 1941. A catalogue of molluscan shells from Taiwan (Formosa), with descriptions of new species. *Mem. Fac. Sci. Agri., Taihoku Imperial Univ.* 22(4):Geology no. 17:65-216, pls. 8-14.
- KURODA, T. 1960. A catalogue of molluscan fauna of the Okinawa Islands. 106 pp., 3 pls.
- MARSHALL, B. A. 1978. Cerithiopsidae (Mollusca: Gastropoda) of New Zealand, and a provisional classification of the family. *New Zealand J. Zool.* 5:47-120.
- MELVILL, J. & M. STANDEN. 1895. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs. Hadfield, with list of species. *J. Conchol.* 8:84-132.
- MELVILL, J. & M. STANDEN. 1901. The Mollusca of the Persian Gulf, Gulf of Oman and Arabian Sea, as evidenced mainly through the collections of Mr. F. W. Townsend, 1893-1900, with descriptions of new species. *Proc. Zool. Soc. Lond.* 2:327-400, pls. 21-24.
- MENKE, C. T. 1828. *Synopsis Methodica Molluscorum Generum Omnium et Specerum earum . . .* Pyrmont. Pp. i-xii, 1-91.
- MONTEROSATO, T. A., DI. 1884. *Nomenclatura Generica e Specifica di Alcune Conchiglie Mediterranee*. Palermo. 152 pp.
- ROEMER, F. A. 1840-1841. *Versteinerungen des norddeutschen Kreidegebirges*. Hannover. Pp. i-iv, 1-145, 16 pls.
- SOWERBY, G. B. 1855. Monograph of the genus *Cerithium*, Adanson. *Thesaurus Conchyliorum* 2:847-899, pls. 176-290.
- SOWERBY, G. B. 1865. Monograph of the genus *Cerithium*. *Conchologia Iconica* 15:20 pls.
- SOWERBY, G. B. 1866. (Supplementary plate) *Thesaurus Conchyliorum*. Volume 3(24-25); pl. 290 [pl. 12].
- THIELE, J. 1929-1931. *Handbuch der systematischen Weichtierkunde* 1:1-376 (1929), 377-778 (1931). Berlin.
- TRYON, G. W. 1887. *Manual of conchology; structural and systematic; with illustrations of the species. First series*; 9: *Cerithium*. Pp. 127-149, pls. 20-29. Philadelphia.
- WENZ, W. 1938-1944. *Gastropoda Allgemeiner Teil und Prosobranchia*. *Handbuch der Paläozoologie* 6(1):1-1639, 4211 figs.

New Philippine Cancellariidae (Gastropoda: Cancellariacea), with Notes on the Fine Structure and Function of the Nematoglossan Radula

by

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Abstract. Three new species of Cancellariidae, *Cancellaria boucheti*, *C. atopodonta*, and *C. aqualica*, are described, all from deep water off the western Philippines. The radula of two of these, *C. boucheti* and *C. atopodonta*, are figured, and a mechanism by which the cusps are interlocked is described. On the basis of mechanical considerations, we suggest that the function of the nematoglossan radula is limited to the penetration of tissues of prey organisms, in order to reach the internal fluids on which the cancellariids then feed suctorially.

INTRODUCTION

THE THREE SPECIES of *Cancellaria* described herein were brought to our attention by Dr. Philippe Bouchet, Curator of Marine Mollusca, Muséum National d'Histoire Naturelle, Paris. Specimens were collected during the MUSORSTOM-2 cruise in 1980, aboard the R/V *Coriolis*, with Dr. Bouchet as expedition malacologist. Additional specimens of one species were located in the collections of the National Museum of Natural History, Smithsonian Institution. That three rather large, undescribed species could be collected near the Philippines is indicative of our incomplete knowledge of the deeper water faunas.

In keeping with our recent work, both published and unpublished, on cancellariid anatomy, we have here adopted a conservative stand by placing these new species in the genus *Cancellaria*, even though they represent rather distinct morphological forms previously placed in different genera or subgenera. Placement of these species into more appropriate genera must await our proposed revision of cancellariid supraspecific taxa after additional study of soft parts is possible.

Abbreviations for museum collections cited are: MNHN, Muséum National d'Histoire Naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Genus *Cancellaria* Lamarck, 1799

Cancellaria boucheti

Petit & Harasewych, spec. nov.

(Figures 1-4, 9-14; Table 1)

Description: Shell large, reaching 47 mm, moderately thin, elongate-oval, with conical spire and rounded anterior. Protoconch of about $1\frac{1}{2}$ inflated, glassy, amber-colored whorls, deviated from shell axis by 10-15°. Transition to teleoconch marked by rapid development of spiral sculpture (Figure 3). Teleoconch with up to $6\frac{2}{3}$ strongly convex whorls. Suture deeply impressed. Surface sculpture of both spiral and axial elements, axial dominant in majority of specimens examined. Axial sculpture of 12-14 prosocline ribs on early whorls, 16-18 on body whorl of larger specimens. Ribs strong, evenly spaced, with narrow areas of weak, numerous ribs every $\frac{1}{2}$ to $\frac{1}{3}$ whorl indicating position of internal varices. Spiral sculpture of 15-18 major cords on body whorl, 7-8 on penultimate whorl, with 3-4 fine threads between adjacent cords. Aperture large, hemi-elliptical, deflected from coiling axis by 13-18°. Outer lip with shallow indentation at juncture of body whorl and short siphonal canal, containing 19-22

weak, recessed lirae that extend backward for several millimeters. Inner lip adpressed posteriorly, with two simple columellar folds and siphonal fold. Base color white, often with ginger along crests of axial and spiral sculpture. Some young specimens with broad patches of light ginger interrupted by white spiral bands along periphery and siphonal juncture. Aperture white. No specimens fractured or sectioned, as presence of internal varices (HARASEWYCH & PETIT, 1982) at intervals of 120–180° apparent in intact shells. Critical-point dried jaw (Figure 9) 2.5 mm long (4.8% shell length), furrowed along dorsal midline. Left and right margins overlapping ventrally along anterior portion of jaw (Figure 10), forming tube (about 75 μ m in diameter) leading from oral tube to buccal mass. Posterior portion of jaw broad, covering the buccal mass dorsally and laterally. Radular teeth long, ribbonlike, tricusped. Central cusp simple, smooth, with ventrally recurved rim (Figures 11–13) and laterally expanded basal areas (Figure 14). Lateral cusps each with 4 complex, anteriorly directed secondary cusps (Figures 11–14).

Holotype: MNHN, 569–595 m, SE of Batangas, Luzon, Philippines (13°31'N, 121°24'E), Musorstom-2 sta. CP 36, L = 46.3 mm.

18 Paratypes: MNHN, 299–320 m, S of Batangas, Luzon, Philippines (13°49'N, 120°50'E), Musorstom-2 sta. CP 26, L = 34.4 mm; MNHN, 416–425 m, NW of Boac, Marinduque, Philippines (13°38'N, 121°43'E), Musorstom-2 sta. CP 49, L = 24.7 mm; MNHN, 300–330 m,

off northwestern Mindoro, Philippines (13°51'N, 120°30'E), Musorstom-2 sta. CP 75, L = 26.5 mm, 36.6 mm, 39.2 mm; USNM 237060, 357 m, Tayabas Bay, off San Andreas, Philippines, U.S.B. Fish. sta. 5222, L = 37.7 mm; USNM 237580, 314 m, Batangas Bay, Luzon, Philippines U.S.B. Fish. sta. 5289, L = 32.0 mm; USNM 238191, 247 m, off Destacado Island, Philippines, U.S.B. Fish. sta. 5392, L = 46.0 mm; USNM 238675, off Opol, Mindanao, Philippines, U.S.B. Fish. sta. 5505, L = 29.1 mm; USNM 238902, 567 m, SE of Pt. Tanon, Cebu, Philippines, U.S.B. Fish. sta. 5535, L = 45.2 mm; USNM 242321, 247 m, off Destacado Island, Philippines, U.S.B. Fish. sta. 5392, L = 20.0 mm, 34.6 mm, 37.8 mm; USNM 242323, 247 mm, off Destacado Island, Philippines, U.S.B. Fish. sta. 5392, L = 19.5 mm; USNM 278521, 311 m, off Matocot Pt., W. Luzon, Philippines, U.S.B. Fish. sta. 5268, L = 22.4 mm; USNM 281805, 247 m, off Adyagan Island, E. Masbate, Philippines, Bur. Fish. sta. 5392, L = 20.2 mm, 28.5 mm, 30.4 mm.

Comparisons: *Cancellaria boucheti* lacks the angled, no-dose shoulder of *C. spengleriana* Deshayes, 1830, to which it is most closely related. *Cancellaria jonkeri* Koperberg, 1931, from the Tertiary of Timor, is also similar to this Recent species, but has much finer spiral and axial sculpture that does not form nodules at intersections.

Remarks: Cancellariid radular teeth become highly coiled during critical-point drying, the radular ribbon taking on the appearance of a plate of spaghetti. This process aids

Explanation of Figures 1 to 8

Figure 1. *Cancellaria boucheti* spec. nov., holotype, MNHN, taken in 569–595 m, SE of Batangas, Luzon, Philippines (13°31'N, 121°24'E) Musorstom-2 sta. CP 36. 1.5 \times .

Figure 2. *Cancellaria boucheti* spec. nov., paratype, MNHN, taken in 299–320 m, S of Batangas, Luzon, Philippines (13°49'N, 120°50'E) Musorstom-2 sta. CP 26. 1.5 \times .

Figure 3. *Cancellaria boucheti* spec. nov., protoconch of paratype, USNM 242323, taken in 247 m, SW of Destacado Island, Philippines. U.S.B. Fish. sta. 5392. 70 \times .

Figure 4. *Cancellaria boucheti* spec. nov., paratype, USNM 238902, taken in 567 m, SE of Pt. Tanon, Cebu, Philippines. U.S.B. Fish. sta. 5535. 1.5 \times .

Figure 5. *Cancellaria atopodonta* spec. nov., holotype, MNHN, taken in 441–510 m, SSW of Batangas, Luzon, Philippines (13°49'N, 120°28'E) Musorstom-2 sta. CP 78. 2.5 \times .

Figure 6. *Cancellaria atopodonta* spec. nov., paratype, MNHN, taken in 300–330 m, off northwestern Mindoro, Philippines (13°51'N, 120°30'E) Musorstom-2 sta. CP 75. 2.5 \times .

Figure 7. *Cancellaria aqualica* spec. nov., holotype, MNHN, taken in 299–320 m, S of Batangas, Luzon, Philippines (13°49'N, 120°50'E) Musorstom-2 sta. CP 26. 1.5 \times .

Figure 8. *Cancellaria aqualica* spec. nov., paratype, MNHN, taken in 170–187 m, off the northwestern tip of Mindoro, Philippines (14°00'N, 120°17'E) Musorstom-2 sta. CP 51. 2.0 \times .

Explanation of Figures 9 to 14

Radula and jaw of *Cancellaria boucheti* spec. nov., taken from the specimen in Figure 2.

Figure 9. Lateral view of critical-point dried jaw. Scale bar = 500 μ m.

Figure 10. View of distal end of jaw. Scale bar = 25 μ m.

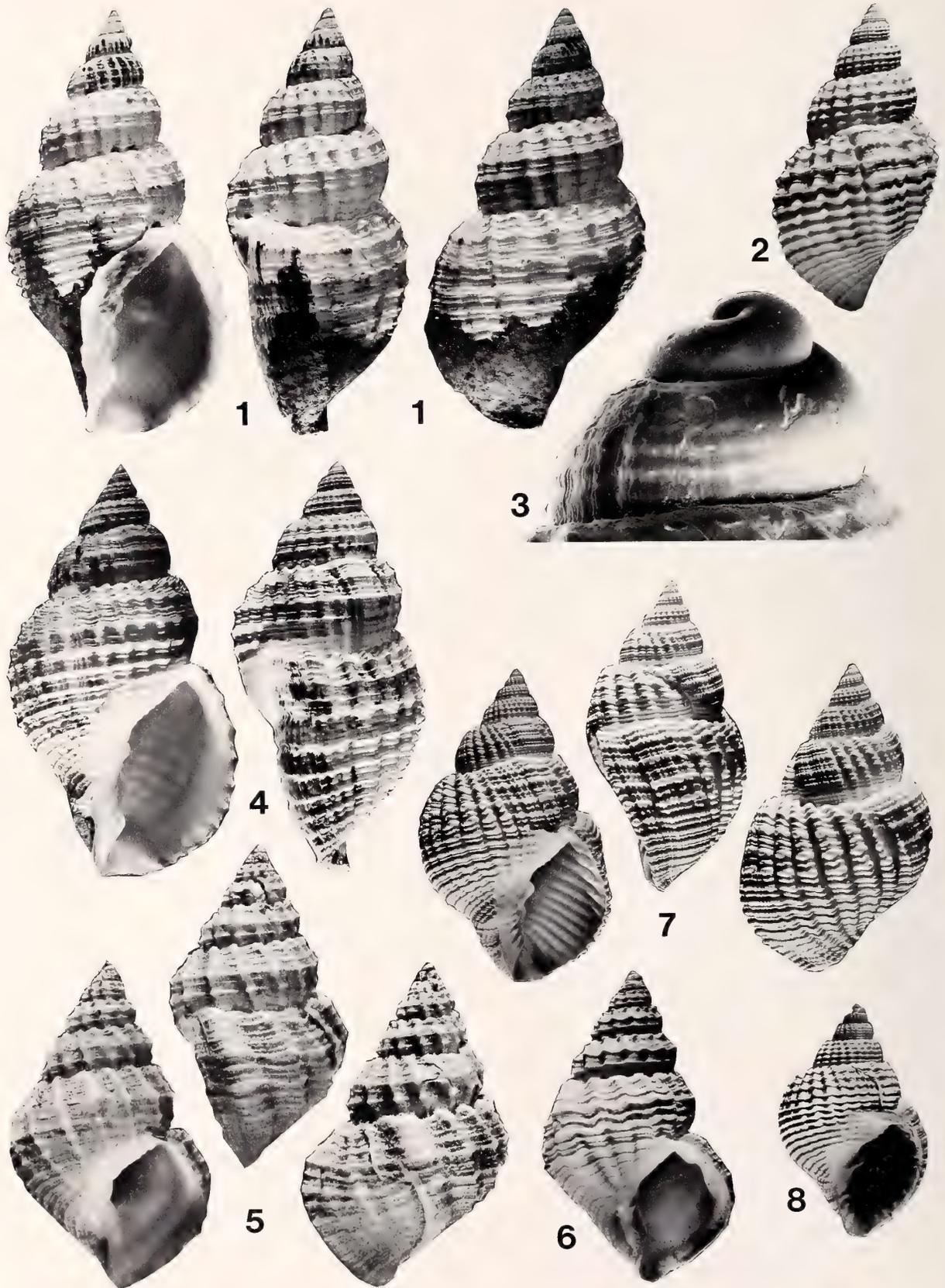
Figure 11. Axial view of distal ends of radular teeth. Dorsal tooth with cusps in expanded position. Scale bar = 1 μ m.

Figure 12. Detail of distal end of tooth. Stereo pair. The free

end of the cusp on the left is locked under the rim of the central cusp. The cusp on the right is free. Scale bar = 1 μ m.

Figure 13. Axial view of laterally expanded tooth. Both outer cusps are free. Scale bar = 1 μ m.

Figure 14. Lateral view of teeth in Figures 11 and 12. The outer cusps of the ventral tooth are in the interlocked position. The visible cusp on the dorsal tooth is in the expanded position. Scale bar = 5 μ m.



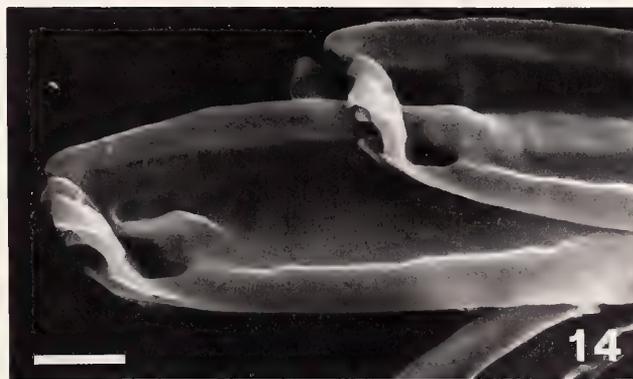


Table 1

Cancellaria boucheti spec. nov. Measurements of shell characters. Linear measurements in mm. n = 10.

Character	Mean	Standard deviation	Range
Shell length	35.6	10.2	19.5–46.5
Shell width	19.6	4.9	10.8–24.5
Aperture length	20.7	6.2	11.2–29.3
Aperture length Shell length	0.579	0.026	0.548–0.640
No. whorls, protoconch	1.53	0.24	1.33–2.00
No. whorls, teleoconch	5.53	0.65	4.67–6.67
Spire angle	53.0°	3.1°	48.5–59.0°

in the examination of the distal ends of the teeth, but makes accurate measurement of tooth length very difficult. Previous work has shown that the length of the tubular portion of the jaw approximates tooth length (OLSSON, 1970; HARASEWYCH & PETIT, 1982, 1984). Both tooth length (about 1.1 mm) and tooth width (about 16 μ m) are in the range reported for other cancellariids.

Etymology: This species honors Dr. Philippe Bouchet, of the Department of Malacology, Muséum National d'histoire Naturelle, Paris, who brought this material to our attention.

Cancellaria atopodonta

Petit & Harasewych, spec. nov.

(Figures 5, 6, 15, 16; Table 2)

Description: Shell small, reaching 22 mm, heavy, conispiral, with rounded anterior. Protoconch of 1¼ glossy, pitted whorls, slightly deflected from coiling axis. Transition to teleoconch marked by appearance first of spiral then axial sculpture. Teleoconch with up to 5½ convex whorls. Suture impressed. Axial ribs major sculptural feature, numbering 13–16 on body whorl, 10–13 on early whorls. Internal varices, first detected on outer surface of shell between 3rd and 4th postnuclear whorls, occur every 120° thereafter. Spiral sculpture of 10–13 major cords on body whorl, 3–4 on penultimate whorl, with 3–5 fine spiral threads between adjacent cords. Aperture ovate, deflected from coiling axis by 20–25°. Lack of shallow indentation marking juncture of siphonal canal on outer lip may be artifact, as all specimens heavily scarred by predators. Inner surface of outer lip with 9 or 10 strong, short lirae lining last internal varix. Inner lip adpressed posteriorly, with 2 simple columellar folds and siphonal fold. Shell white within and without. Internal structure not studied. Periostracum thin, yellow, finely lamellose, forming fine hairs along spiral threads. Intact jaw not recovered. Radular teeth long, ribbonlike. Central cusp with ventrally recurved rim and 2 dorsal, posteriorly recurved barbs (Figure 16). Thickening of basal areas (Figure 16) less

pronounced than in preceding species. Lateral cusps distally expanded, each with 4 secondary, anteriorly directed cusps (Figures 15, 16).

Holotype: MNHN, 441–510 m, SSW of Batangas, Luzon, Philippines (13°49'N, 120°28'E) Musorstom-2 sta. CP 78, L = 21.5 mm.

2 Paratypes: MNHN, 300–330 m, off northwestern Mindoro, Philippines (13°51'N, 120°30'E) Musorstom-2 sta. CP 75, L = 20.6 mm, 20.8 mm.

Comparisons: This species differs so markedly from other described taxa that it is difficult to make comparisons. Its columellar structure is similar to that of *Cancellaria garardi* (PETIT, 1974), but the latter species has more rounded whorls and lacks a deep suture and a distinct shoulder. *Cancellaria atopodonta* most closely resembles the Japanese Pliocene shell figured as "*Cancellaria (Merica) reevei laticostata* (Löbbecke)" by SHUTO (1962:72, pl. 13, fig. 12), which also has rounded whorls and lacks a pronounced shoulder. The names "*reevei*" and "*laticostata*" are incorrect spellings of *reeveana* Crosse, 1861, and *laticosta* Löbbecke, 1881, respectively, although neither of these names can, in our opinion, be correctly applied to the shell figured by Shuto. We have been unable to find an available name for this Japanese fossil.

Remarks: The presence of recurved barbs on the central cusps of the radula of *Cancellaria atopodonta*, a feature previously reported only from radulate species of Admetinae, suggests that such barbs are a primitive character, and were present in the common ancestor of all cancellariids. Such an interpretation implies that *C. atopodonta* is a primitive member of the lineage giving rise to the Cancellariinae and the Trigonostominae, as these barbs are absent in most species of these two "subfamilies."

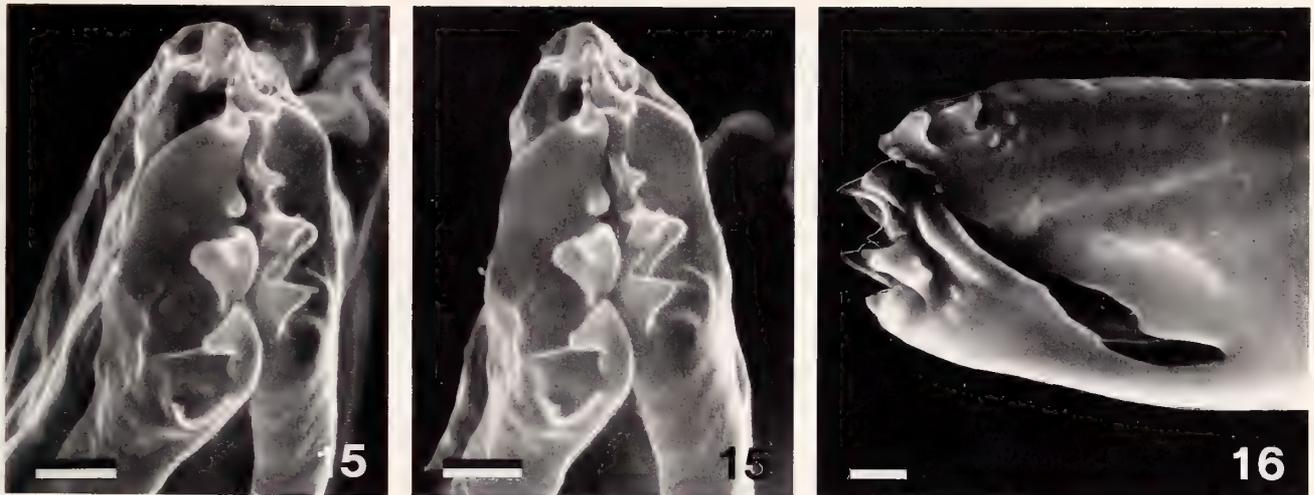
Etymology: The specific name is derived from the Greek *atopos*, meaning anomalous or out of place, and the Greek *odontos*, meaning tooth, and refers to the unusual structure of the radular teeth.

Cancellaria aqualica

Petit & Harasewych, spec. nov.

(Figures 7, 8; Table 3)

Description: Shell of moderate size, reaching 39 mm, heavy, biconic, pseudoumbilicate. Protoconch of 1 to 1½ whorls, smooth, glassy, slightly bulbous, deviated from shell axis by 10–15°. Transition to teleoconch evidenced by onset of spiral sculpture, followed within ¼ whorl by first appearance of axial ribs. Teleoconch with up to 6 strongly convex, highly sculptured whorls. Suture deeply impressed. Shell surface strongly cancellated by intersecting axial ribs and spiral cords. Axial sculpture of 14–16 prosocline ribs on early whorls, up to 19 on body whorl. Ribs strong, evenly spaced, becoming weak and more nu-



Explanation of Figures 15 and 16

Radula of *Cancellaria atopodonta* spec. nov., taken from the holotype.

Figure 15. Detail of distal end of tooth. Stereo pair. The free ends of both outer cusps are locked under the rim of the central cusp. Scale bar = 1 μ m.

Figure 16. Lateral view of the same tooth as in Figure 15. The outer cusps are distally expanded. The central cusp has 2 dorsal barbs. Scale bar = 1 μ m.

merous every 120°, giving appearance of single, broad rib marking location of broad internal varices. Spiral sculpture of 13–17 major cords on body whorl, 6–8 on penultimate whorl, with 1–3 fine threads between neighboring cords. Aperture large, hemi-elliptical, deflected from coiling axis by 18–25°. Outer lip with very shallow indentation posterior to siphonal canal and 11–13 strong, slightly recessed lirae extending ¼ whorl into aperture. Inner lip adpressed posteriorly, with 2 columellar and 1 siphonal fold. Folds simple, exhibiting periodic variation in size, reaching maximum extension into aperture in opposition to apertural lirae. Siphonal canal very short. Base color white, with light brown to ginger markings as in *Cancellaria reticulata* (see HARASEWYCH & PETIT, 1982). Aperture white. Soft parts and periostracum unknown.

Holotype: MNHN, 299–320 m, S of Batangas, Luzon, Philippines (13°49'N, 120°50'E) Musorstom-2 sta. CP 26, L = 34.0 mm.

3 Paratypes: MNHN, 326–330 m, WSW of Batangas, Luzon, Philippines (13°55'N, 120°29'E) Musorstom-2 sta. CP 15, L = 38.3 mm; MNHN, 170–187 m, off the northwestern tip of Mindoro, Philippines (14°00'N, 120°17'E) Musorstom-2 sta. CP 51, L = 15.7 mm, 19.5 mm.

Comparisons: *Cancellaria aqualica* most closely resembles *C. elegans* Sowerby, 1822, as figured by GARRARD (1975: fig. 1[1]), from which it may be distinguished by its stronger axial and spiral sculpture, its lack of color bands, and by having a more swollen body whorl.

Table 2

Cancellaria atopodonta spec. nov. Measurements of shell characters. Linear measurements in mm. n = 3.

Character	Mean	Standard deviation	Range
Shell length	21.0	0.6	20.4–21.6
Shell width	13.2	0.3	12.8–13.5
Aperture length	10.4	0.2	10.1–10.5
Aperture length / Shell length	0.494	0.016	0.485–0.512
No. whorls, protoconch	1.22	0.19	1.00–1.33
No. whorls, teleoconch	5.33	0.34	5.00–5.67
Spire angle	54.2°	0.8°	53.5–55.0°

Table 3

Cancellaria aqualica spec. nov. Measurements of shell characters. Linear measurements in mm. n = 4.

Character	Mean	Standard deviation	Range
Shell length	26.9	11.0	15.7–38.2
Shell width	16.8	6.3	10.0–23.1
Aperture length	14.8	5.6	9.2–20.4
Aperture length / Shell length	0.557	0.022	0.535–0.587
No. whorls, protoconch	1.16	0.19	1.00–1.33
No. whorls, teleoconch	5.08	0.92	4.00–6.00
Spire angle	62.0°	1.4°	60.0–63.0°

Remarks: Our concept of *Cancellaria elegans* does not agree with Garrard's interpretation. As mentioned by GARRARD (1975:4), the type lot (British Museum [Natural History] 1968387) contains 3 specimens. This lot is labelled "*C. elegans* Baclayon, Bohol. Id., Philippines" on the back of an old board. It is possible that two specimens with locality data were added later, as only one specimen has an old label with the number "4," the same sort as used by Sowerby, glued inside the aperture. In any event, the specimens in this lot are brown, with a brown protoconch, lack the white band present in many related species, and agree in all respects with the type figure. These specimens and the type figure have a finely cancellate sculpture that is quite distinct from the Australian species.

Although a color photograph of the holotype of *Cancellaria asprella* Lamarck, 1822, is available to us, we are unable to determine if *C. asprella* and *C. elegans* are conspecific, and this determination must await the opportunity to physically examine Lamarck's type. In any event, the specimens that we consider to represent *C. elegans* as well as the holotype of *C. asprella* have apertures that are $\frac{2}{3}$ the total length of the shell, while *C. aqualica* has an aperture that is only $\frac{1}{2}$ as long as the shell.

Etymology: From the Latin *aqualicus*, meaning belly or paunch, referring to the swollen body whorl of this species.

FUNCTIONAL MORPHOLOGY OF THE NEMATOGLOSSAN RADULA

Other than one anecdotal report of *Cancellaria crawfordiana* feeding on pieces of fish and egg capsules of squid and whelks (TALMADGE, 1972), there have been no published reports on the food or feeding of any cancellariid. Although examinations of the gut contents of a number of species have failed to uncover any identifiable traces of solid food (GRAHAM, 1966; HARASEWYCH & PETIT, 1982, 1984), several speculations as to the diet of cancellariids have been based on the unusual morphology of the anterior alimentary system, especially the radula (GRAHAM, 1966; OLSSON, 1970; OLIVER, 1982; HARASEWYCH & PETIT, 1982, 1984). Data presented in this paper on the morphology of the jaws and radulae of *Cancellaria bouchetti* and *C. atopodonta*, as well as figures of these organs of other cancellariids (OLSSON, 1970; OLIVER, 1982; HARASEWYCH & PETIT, 1982, 1984), permit the following observations and inferences regarding their functional morphology.

Although the length of the teeth is extreme, the cancellariid radula is formed and functions as a normal radular ribbon, with teeth produced posteriorly and migrating anteriorly, contrary to OLSSON's (1970:21) suggestion that teeth are either added from the center of the ribbon and directed anteriorly or posteriorly, or are no longer added once the radula is fully formed. HARASEWYCH & PETIT (1982) observed several teeth in the process of being redirected from posterior to anterior. GRAHAM (1966) sug-

gested that such redirection is accomplished by a change in the thickness and tension of the subradular membrane.

The majority of the cusps, both primary and secondary, on each tooth are directed anteriorly, parallel to the line of motion of the tooth rather than perpendicular to it, indicating a piercing or grappling rather than a rasping function for the radula. The extreme flexibility of the radular teeth limits their ability to transmit force. Like ribbons, they only transmit tensile and not compressive force.

Figure 12 reveals a mechanism by which the distal ends of the lateral cusps interlock under the recurved rim of the central cusp. The left cusp is shown in a locked position, the right cusp is free. Thickened areas on either side of the central cusp may serve to buttress the lateral cusps when they are in a locked position. When the radula is protruded, the distal-most tooth is in the compact, interlocked form. During the rasping motion, as each tooth slides posteriorly over the tooth ventral to it, its lateral cusps are pushed into the unlocked, laterally expanded position (Figures 11, 14) by the distal end of the tooth below. In the reverse action, the free distal end of each tooth passes under the next dorsal tooth, and the cusps are again compressed into an interlocked position. We suggest that this interlocking mechanism functions in the following manner. Each radular tooth is applied to the prey tissue in the compact, interlocked position, the anteriorly directed cusps impaling or entangling the tissue. The tissue is spread laterally when the cusps are pushed into the unlocked position by the next tooth, which repeats the action, penetrating deeper into the tissue. The length of the teeth and the tubular nature of the jaw make it unlikely that the cusped distal ends of the teeth can be retracted sufficiently to convey food to the esophageal opening, but instead suggest that their function is limited to the penetration of the tissues of prey organisms, or as suggested by TALMADGE (1972), of the walls of molluscan oothecae, in order to reach the internal fluids, on which the cancellariids then feed suctorially.

ACKNOWLEDGMENTS

We are indebted to Dr. Philippe Bouchet, Muséum National d'Histoire Naturelle, Paris, for making available most of the material on which this paper is based. We also wish to recognize the work of CENTOB (Centre National de Tri d'Océanographie Biologique) Brest, in sorting the material collected by MUSORSTOM-2.

W. O. Cernohorsky, Auckland Institute and Museum, furnished us with a color photograph of the type of *Cancellaria asprella* Lamarck.

LITERATURE CITED

- CROSSE, J. C. H. 1861. Étude sur le genre cancellaire, suivie du catalogue des espèces vivantes et fossiles actuellement connues. J. Conchyl. 9:220-256.

- DESHAYES, G. P. 1830. Encyclopédie méthodique (Vers.) 2(1): 1-256. Paris.
- GARRARD, T. A. 1975. A revision of the Australian Cancellariidae (Gastropoda: Mollusca). Rec. Aust. Mus. 30(1):1-62.
- GRAHAM, A. 1966. Fore-gut of marginellid and cancellariid prosobranchs. Stud. Trop. Oceanogr. Miami 4(1):134-151.
- HARASEWYCH, M. G. & R. E. PETIT. 1982. Notes on the morphology of *Cancellaria reticulata* (Gastropoda: Cancellariidae). Nautilus 96(3):104-113.
- HARASEWYCH, M. G. & R. E. PETIT. 1984. Notes on the morphology of *Olssonella smithii* (Gastropoda: Cancellariidae). Nautilus 98(1):37-44.
- KOPERBERG, E. J. 1931. Jungtertiäre und quartäre Mollusken von Timor. Jaarb. Mijnwezen Ned.-Indie. Verh. I, 1-165, pls. 1-3.
- LAMARCK, J. B. P. A. 1822. Histoire naturelle des animaux sans vertèbres. Vol. 7. Paris.
- LÖBBECKE, T. 1881-87. Das Genus *Cancellaria*. Syst. Conch. Cab. 4:1-96, pls. 1-23.
- OLIVER, P. G. 1982. A new species of cancellariid gastropod from Antarctica with a description of the radula. Brit. Antarct. Surv. Bull. 57:15-20.
- OLSSON, A. A. 1970. The cancellariid radula and its interpretation. Palaeontogr. Amer. 7(43):19-27.
- PETIT, R. E. 1974. Notes on Japanese Cancellariidae. Venus 33(3):109-115.
- SHUTO, T. 1962. Buccinacean and volutacean gastropods from the Miyazaki Group. Mem. Fac. Sci. Kyushu Univ., Ser. D, Geol. 12(1):27-85, pls. 6-13.
- SOWERBY, G. B. 1821-1825. The genera of Recent and fossil shells. Vol. 1: pls. 1-126 and text (pages not numbered). London.
- TALMADGE, R. 1972. "Pinky." Of Sea and Shore 3(4):189, 200.

A New Species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Cuyamaca Mountains of Southern California

by

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Abstract. A new species of land snail, *Helminthoglypta milleri* Reeder, is described from the Cuyamaca Mountains of San Diego County, California, and its relationships are discussed.

IN THE LATE 1800's, Henry Hemphill collected snails from the Cuyamaca Mountains, in San Diego County, which he labeled *Epiphragmophora traskii* v. *cuyamacensis*. He sent specimens to H. A. Pilsbry at the Academy of Natural Sciences of Philadelphia as well as to Paul Bartsch at the U.S. National Museum. However, he separated the shells from the preserved bodies, sending the shells to Bartsch in 1890 and the preserved bodies to Pilsbry in 1893, thereby raising an element of doubt that the bodies may not have come from the same population as the shells.

PILSBRY duly figured the reproductive system in the *Manual of Conchology* (1895:pl. 59, fig. 87) and cited it as *Epiphragmophora (Helminthoglypta) traskii* v. *cuyamacensis* Hemph. He later stated (PILSBRY, 1939:145) that he withheld description of the shells because he did not wish to trespass on Hemphill's field. He also stated: "with the locality, which I gave in 1897, there would be little doubt of what was intended." This reference (PILSBRY, 1897), however, merely repeated, with correct spelling: "*Epiphragmophora traskii cuyamacensis* Hemph. Cuyamaca Mt., San Diego Co."

Two decades later, P. BARTSCH (1916) published a description of the shell as *Epiphragmophora cuyamacensis cuyamacensis* Bartsch, 1916, and considered Pilsbry's earlier name to be a *nomen nudum*.

In 1933, Pilsbry, accompanied by Joshua L. Bailey, went to the Cuyamaca Mountains and collected snails at a locality "¾ of a mile above Cuyamaca Lake, ½ mile south of road at the 'beef pasture' under heaps of rotten wood in mixed evergreen and deciduous woods." There was no doubt in his mind that he had obtained *H. cuyamacensis cuyamacensis* and he figured the reproductive anatomy of this snail as fig. 71B (PILSBRY, 1939), labeled *H. cuyamacensis*, Cuyamaca Mountains. This anatomy,

however, was considerably different from the one published in the *Manual of Conchology* in 1895 and because he was uncertain about the origin of the bodies sent by Hemphill in 1893, he again figured an anatomy of the 1893 shipment as fig. 73 (PILSBRY, 1939), labeling it "Genitalia of a *Helminthoglypta* of uncertain status." It can now be ascertained, from fig. 73 (PILSBRY, 1939), that the genitalia are typical of the subgenus *Rothelix* Miller, 1985, and therefore are probably those of *H. c. cuyamacensis* Bartsch, 1916 (MILLER, 1985). On the other hand, the genitalia of fig. 71B (PILSBRY, 1939) are typical of the nominate subgenus; they appear to be referable to those of *H. thermimontis* Berry, 1953, but a firm identification will require a precise pinpointing of Pilsbry's exact locality and its population and a careful, detailed, microscopic examination of the reproductive anatomy.

During the 1960's, W. O. Gregg and W. B. Miller collected extensively at several localities in the Cuyamaca Mountains. They found populations of snails along the main highway in the Cuyamacas that correspond precisely with size, sculpture, description, and illustration of Bartsch's specimens as well as PILSBRY's original figure of the genitalia (1895:pl. 59, fig. 87; 1939:fig. 73). This locality can now be more precisely identified as "Cuyamaca Mountains, along Cold Stream in the vicinity of Cold Spring, 32°56.5'N, 116°33.8'W, elev. 4400 ft. (1350 m), in rotting logs." It can now be considered the more detailed type locality of *H. cuyamacensis cuyamacensis* Bartsch, 1916.

In the process of exploring the Cuyamaca Mountains, several populations of other species of *Helminthoglypta* were also discovered. Most of these populations live in rotting logs, as does *H. c. cuyamacensis*. One population, however, differs from all the others in that it is a rock

dweller, located in a large rock pile just below the summit of Cuyamaca Peak. Furthermore, this population does not belong in the subgenus *Rothelix* Miller, 1985, as does *H. c. cuyamacensis*, but rather in the nominate subgenus. Its anatomy clearly indicates that it is a new species, described below.

Helminthoglypta (Helminthoglypta) milleri

R. L. Reeder, spec. nov.

(Figures 1-4)

Diagnosis: A large sized, depressed *Helminthoglypta* with radial growth wrinkles and moderately papillose sculpture.

Description of shell of holotype: Shell (Figures 2-4) large, depressed, with conic spire, helicoid, umbilicate, the umbilicus contained about 7 times in the diameter of the shell. Color light brown, glossy, with a darker reddish-brown band on the round shoulder. Aperture broad, nearly round, with peristome moderately reflected, expanded slightly more at columellar junction. Embryonic shell of $1\frac{3}{4}$ whorls with faint radial wrinkles and minute papillae. Post-embryonic whorls with increasingly coarse radial growth wrinkles, superimposed with moderately dense papillae. Papillae weaker on base of shell, becoming prominent again within the umbilicus. Spiral sculpture wanting. Diameter 26.6 mm, height 12.3 mm, diameter of umbilicus 3.8 mm, number of whorls $5\frac{1}{4}$.

Reproductive anatomy of holotype: The reproductive system (Figure 1) is typical of the genus, having a large atrial sac with a dart sac at its proximal end. There are two mucus glands with mucus bulbs, the ducts of which form a common duct before entering the upper portion of the atrial sac. The spherical spermatheca is large with a long duct bearing a spermathecal diverticulum about midway along its length. The penis and epiphallus form a continuous duct with the epiphallus bearing a relatively long epiphallic caecum at its proximal end. The penis is divided into a short lower penis and a long upper penis, the latter being a double-walled tube. The upper penis is a cylindrical duct of nearly uniform diameter. The lower penis is initially as wide as the upper penis at their junction, then tapering into a venturi-like constriction, the throat of which is moderately narrow. There is no verge. 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	17.7 mm
Epiphallus	27.4 mm
Epiphallic caecum	17.1 mm
Spermathecal duct	33.7 mm
Spermathecal diverticulum	23.1 mm

Variations in paratypes: A total of 10 adult and 3 immature shells was examined. The largest adult paratype

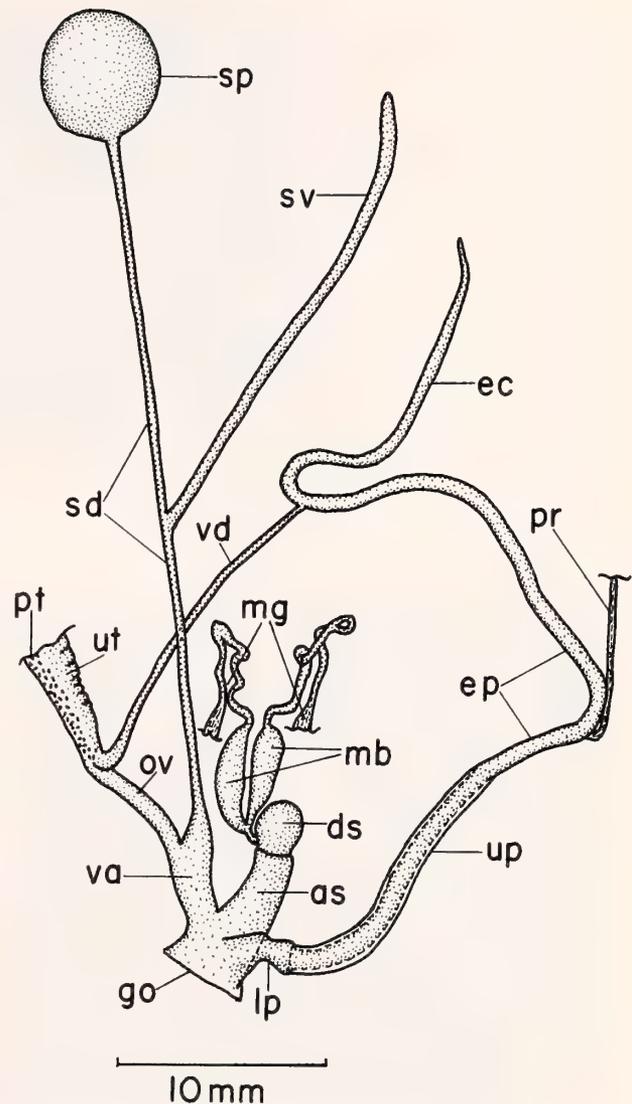
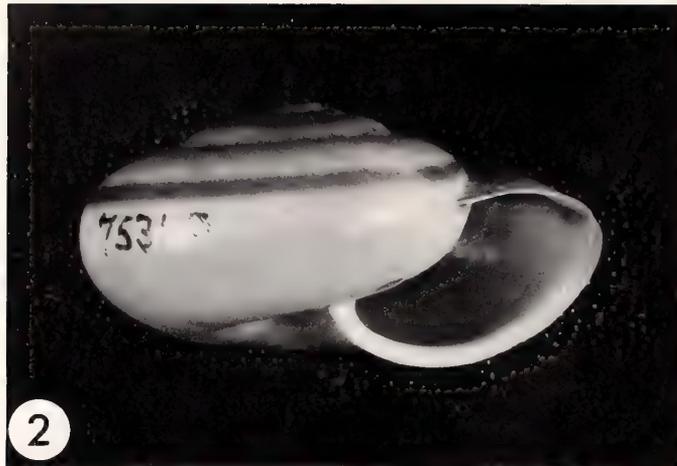


Figure 1

Portion of reproductive system of *Helminthoglypta milleri* Reeder, spec. nov., prepared from projection of stained whole mount of holotype; as, atrial sac; ds, dart sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; lp, lower part of penis; mb, mucus gland bulbs; mg, mucus 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.

measures 26.7 mm in diameter and 15.2 mm in height, and the smallest measures 22.2 mm and 12.8 mm respectively. All of the specimens demonstrate the radial wrinkles and papillae as described and two of the adult shells show a few faint spiral incised lines above the shoulder on the body whorl just behind the aperture.

Disposition of types: **Holotype:** Santa Barbara Museum of Natural History, No. 33915. **Paratypes:** The Academy



Explanation of Figures 2 to 4

Helminthoglypta milleri Reeder, spec. nov. Shell of holotype, SBMNH No. 33915; diameter 26.6 mm.

Figure 2. Aperture view.

Figure 3. Apical view.

Figure 4. Umbilical view.

of Natural Sciences of Philadelphia, No. 359212; U.S. National Museum, No. 842307; W. B. Miller collection, No. 2596, 7118, and 7440; R. L. Reeder collection, No. 574.

Type locality: San Diego County, California; Cuyamaca Peak, Cuyamaca Mountains; in rocks at junction of Burnt Pine Fire Road and Cuyamaca Peak Road; 32°56.9'N, 116°36.3'W; elevation 1900 m (6200 ft.).

Discussion: The long, cylindrical, double-tubed portion of the penis, and the short, thin, saccular, lower part of the penis clearly establish that *Helminthoglypta milleri*

belongs in the nominate subgenus. In that subgenus, its nearest geographical relatives are *H. tudiculata* (Binney, 1843) and *H. waltoni* Gregg & Miller, 1976. *Helminthoglypta milleri* can be separated from *H. tudiculata* and its subspecies have a strongly malleated shell while *H. milleri* has a papillose shell. From *H. waltoni* it can be separated by its reproductive anatomy in that *H. milleri* has a long, stout, cylindrical upper part of the penis while *H. waltoni* has a decidedly club-shaped upper part of the penis. Farther to the north, in the Hot Springs Mountains, another species of *Helminthoglypta* with papillose shells, *H. thermimontis*

Berry, 1953, appears to be related to *H. milleri*, but it can be separated by its reproductive anatomy in that *H. thermimontis* has an upper penis whose diameter decreases markedly before it joins the narrower lower penis; in turn the venturi-shaped lower penis has a very constricted throat, whereas that of *H. milleri* is only moderately constricted. Moreover, the shell of *H. thermimontis* is considerably more papillose than that of *H. milleri*. It is probable that *H. milleri*, *H. waltoni*, and *H. thermimontis* evolved from a common papillose ancestor. *Helminthoglypta thermimontis* speciated and adapted to an environment of fallen logs and humus in the Hot Springs Mountains, *H. waltoni* to a rock-dwelling existence in the Laguna Mountains, and *H. milleri* to its isolated rock pile on top of Cuyamaca Peak.

Distribution and habitat: *Helminthoglypta milleri* is currently known only from the type locality on Cuyamaca Peak. Vegetation at this locality consists principally of *Quercus kelloggi*, *Quercus chrysolepis*, *Pinus lambertiana*, *Abies concolor*, *Libocedrus decurrens*, and *Arctostaphylos* sp.

Etymology: This species is named for Walter B. Miller, friend and mentor, who has provided me the opportunity to study the *Helminthoglypta* of southern California.

ACKNOWLEDGMENTS

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manuscript and to my long-standing colleague and teacher, Walter B. Miller, for material and critical information. Thanks also to my colleagues Noorullah Babrakzai for help in collecting material and Susan J. McKee for photographs of the holotype. Thanks also to the University of Tulsa for kindly providing funds for field work and to the University of Arizona for providing laboratory facilities.

LITERATURE CITED

- BARTSCH, P. 1916. The Californian land shells of the *Epiphragmophora traskii* group. Proc. U.S. Natl. Mus. 51 (2170): 609-619.
- MILLER, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). Veliger 28(1):94-98.
- PILSBRY, H. A. 1895. Guide to the study of helices. Manual of Conchology, Series 2, 9:i-xlvi + 1-366 pp.; 71 plates.
- PILSBRY, H. A. 1897. A classified catalogue of American land snails, with localities. Nautilus 11(5):59-60.
- PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). Acad. Natur. Sci. Phila. Monogr. (3)I(1):i-xviii + 1-573 + i-ix; figs. A, B, 1-377.

A New Species of *Ischnochiton* (Mollusca: Polyplacophora) from the Tropical Eastern Pacific

by

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Abstract. *Ischnochiton skoglundii* Ferreira, spec. nov., dredged from 8-15 m, Nayarit, Mexico, differs from other species of the genus in the area by its very small size (less than 5 mm long), broad, ovate body, sculptureless tegmentum, and girdle scales with spherules on the upper surface, riblets on the sides, and a round concavity on the insertion face. A brief historical account of the genus *Ischnochiton* Gray, 1847, is given.

EXAMINATION OF A lot consisting of very small chitons, dredged off Nayarit, Mexico, revealed 13 minute specimens less than 5 mm long, which were dry and well preserved. Of these, eight were firmly attached to fragments of old shells, still maintaining a "living" position. The species, not hitherto recognized, is here allocated to the genus *Ischnochiton* Gray, 1847a.

Class Polyplacophora Gray, 1821

Order Neoloricata Bergenhayn, 1955

Suborder Ischnochitonina Bergenhayn, 1930

Family Ischnochitonidae Dall, 1889

Genus *Ischnochiton* Gray, 1847a

Type species: *Chiton textilis* Gray, 1828, by subsequent designation (GRAY, 1847b).

Remarks: Interpretations of the genus *Ischnochiton* are still in a state of flux. Although a full discussion of *Ischnochiton* is beyond the scope of this paper, some historical observations may better explain the allocation of *skoglundii* to the genus.

Ischnochiton was established by GRAY (1847a:126-127) for species characterized by "Valves thin; posterior valve entire; the plates of insertion very thin, smooth-edged, of the central valves each with a single notch [slit]; margin [girdle] covered with very small imbricated scales."

The large number of species in *Ischnochiton* and their diverse characteristics led Carpenter (*in* DALL, 1879) to partition it into eight subgenera. Similarly, PILSBRY (1892a) divided *Ischnochiton* into seven subgenera, some further split into "sections." Although several subgenera were eventually removed from *Ischnochiton*, either elevated to genera or synonymized, its number soon grew to 18 in the conservative view of SMITH (1960).

This unsatisfactory arrangement was further complicated by the finding (ASHBY, 1931:36; Allyn G. Smith *in* KAAS, 1974) that the intermediary valves of *Chiton textilis*, type species of *Ischnochiton*, are two-slitted and not one-slitted as assumed by GRAY (1847a) and PILSBRY (1892b: 99). Because this finding made it appear that *Ischnochiton* was without a type, VAN BELLE (1974) erected *Simplischnochiton* (type species, *Ischnochiton maorianus* Iredale, 1914, new name for *Chiton longicymba* Quoy & Gaimard, 1835, not Blainville, 1825) for the one-slitted species, retaining *Ischnochiton* for two-slitted species. KAAS (1974), instead, proposed *Chiton crispus* Reeve, 1847, as a new type for *Ischnochiton*, a proposal that did not conform with Article 61 of the International Code of Zoological Nomenclature (1964). Later, KAAS (1979:856) suggested that GRAY's (1847a) notion of a single slit in *Ischnochiton* be modified to encompass species with one or two slits, a concept long in use by PILSBRY (1892a:53-54) and SMITH (1960:55).

Thus, KAAS & VAN BELLE (1980) returned to the traditional interpretation of *Ischnochiton*, this time divided into seven subgenera, with *Simplischnochiton* suppressed. But, in the most recent systematic classification of the

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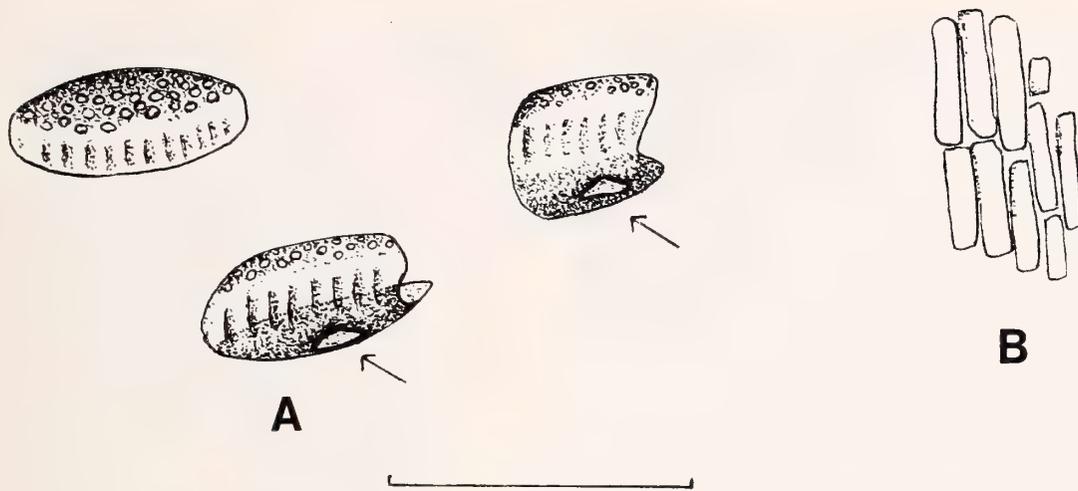


Figure 1

Ischnochiton skoglundi Ferreira, spec. nov.: Holotype (CAS 059841), girdle elements. A, dorsal surface scales, different views (arrow points to concavity on scale base); B, undersurface scales. Scale bar, 100 μ m.

chitons, VAN BELLE (1983), dividing *Ischnochiton* into eight subgenera, brought back *Simplischnochiton* for “*Ischnochitons* with no more than one slit . . . in the intermediary valves,” and *Ischnochiton* s.s. for species with “two or more slits.”

In my view of the systematics of Polyplacophora, subgeneric categories are neither necessary nor desirable. So, here as elsewhere (FERREIRA, 1983:311), *Ischnochiton*, a rather heterogeneous assemblage of species, is interpreted in accordance with the general characteristics outlined by SMITH (1960), i.e., accepting both one- and two-slitted species; and, as evidence may suggest, its well characterized “subgenera” are elevated to generic status (FERREIRA, 1981, 1985). *Simplischnochiton* is suppressed as a synonym.

Ischnochiton skoglundi Ferreira, spec. nov.

(Figures 1–5)

Diagnosis: Very small (up to 4.8 mm long), yellowish white chitons; shell wide, ovate; valves not beaked, carinate; tegmentum dull, sculptureless; lateral areas weakly elevated, hardly defined; mucro anterior. Slit formula 8-1-9. Girdle with imbricate, very small scales, with round spherules on upper surface, riblets on sides. Radula with unicuspid major lateral teeth.

Type material: Holotype (CAS 059841) and paratypes (CAS 059842; CAS 060251; LACM 2119; USNM 859001; ANSP 360105; SDNH 87085; Skoglund Colln.; Ferreira Colln.).

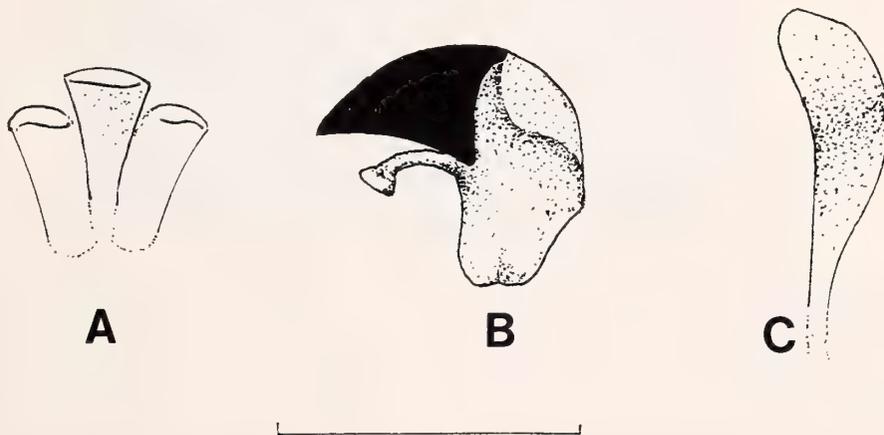
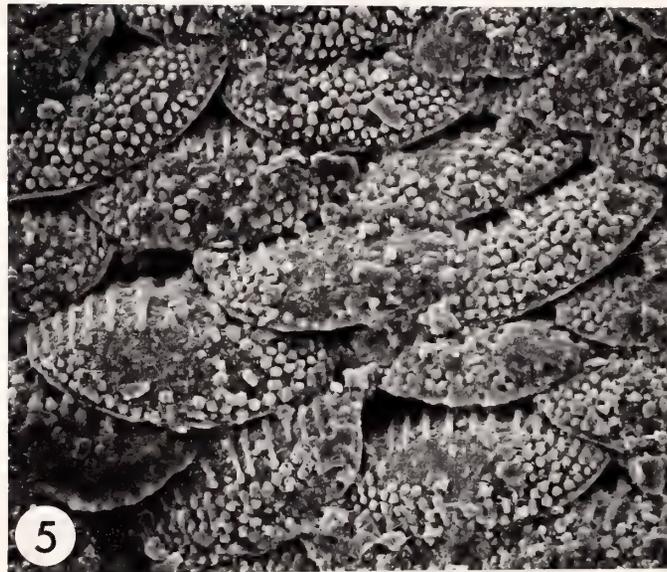


Figure 2

Ischnochiton skoglundi Ferreira, spec. nov.: Holotype (CAS 059841), radula. A, median and first lateral teeth; B, head of major lateral tooth; C, anterior end of spatulate tooth. Scale bar, 100 μ m.



Explanation of Figures 3 to 5

Figure 3. *Ischnochiton skoglundi* Ferreira, spec. nov.: Paratype, 2.4 mm long (CAS 060251), dorsal surface. SEM micrograph.

Figure 4. *Ischnochiton skoglundi* Ferreira, spec. nov.: Paratype (CAS 059842) on dead shell.

Figure 5. *Ischnochiton skoglundi* Ferreira, spec. nov.: Same paratype as in Figure 3, girdle upper surface scales. SEM micrograph.

Type locality: Off Playa Novillero, Nayarit, Mexico (22°23'N, 105°45'W), dredged at 8–15 m (*leg.* Sally & Peter Bennett, Dec. 1975).

Description: Holotype (CAS 059841), dry preserved,

creamy white, about 4.8 mm long (largest specimen in lot), ovate, widest (2.3 mm) at valve *v*; valves thin, carinate, not beaked, posterior edges straight. Tegmentum dull, with no noticeable sculpture; lateral areas hardly

defined, very slightly elevated, with faintly distinguishable concentric rugosities; mucro anterior. Gills holobranchial (?). Articulamentum white; sutural laminae short, subrectangular; sinus shallow; width of valve i/width of valve viii, 1.1; on valve viii, width of sinus/width of sutural laminae, 0.5. Insertion teeth small, sharp; slit formula 8-1-9. Girdle dorsal surface black (an artifact) with translucent, imbricated scales (Figure 1-A); scales up to 80 μm long, upper surface covered with minute, round spherules, lateral surface with some 12 riblets, base with roughly round, sharply defined concavity, about 15 μm in diameter (feature never noticed in any other species); girdle ventral surface paved with transparent, rectangular scales (Figure 1-B) 40 \times 12 μm , arranged in columns. Radula 1.2 mm long, comprising 28 rows of mature teeth; median teeth (Figure 2-A) about 50 μm long, 25 μm wide at anterior blade, narrowing sharply posteriorly; first lateral teeth 50 μm long, 15 μm wide at anterior blade; major lateral teeth with large, unicuspid head, with thin, long tubercle beneath (Figure 2-B); spatulate teeth 22 μm wide anteriorly (Figure 2-C); outer marginal teeth 40 \times 25 μm (length/width, 1.6).

Paratypes (Figures 3, 4) very similar to holotype, 2.0–4.1 mm long, width/length mean 0.76 ($n = 10$; $SD = 0.04$; range 0.71–0.85); ovate (mean width of valves v + vi consistently greater than mean width of valves iii + iv); curvature index (width of widest valve/average width of end valves) 1.28 ($n = 5$, including holotype). Girdle black in most specimens due to extraneous fuliginous material; SEM micrograph of girdle scales (Figure 5) shows the same ornamentation of round spherules and riblets.

Distribution: *Ischnochiton skoglundi* is known only from the type lot.

Remarks: Specimens of *Ischnochiton skoglundi* are of unusually small size, but they differ clearly from juveniles of any other known species in the eastern Pacific. It is quite distinct from any other *Ischnochiton* species in the area—*I. muscarius* (Reeve, 1847), *I. rugulatus* (Sowerby, 1832), and *I. eucosmius* Dall, 1919—in its ovate body-shape, carinate valves, sculptureless tegmentum, and in the girdle scales. The “ornamentation” seen on the girdle scales of *I. skoglundi*, consisting of minute spherules on the scale’s upper surface and riblets on the sides, has been seen and illustrated in three other species—*Lepidozona allynsmithi* Ferreira, 1974 (see FERREIRA, 1974: figs. 23 and 24), *Callistochiton portobelensis* Ferreira, 1976 (see FERREIRA, 1976: figs. 3–5), and *C. periconis* Dall, 1908 (see FERREIRA, 1979: figs. 22 and 23)—but not in *Ischnochiton*. The sharply delineated concavity observed at the base (insertion surface) of the scales of *I. skoglundi* seems to be a unique feature inasmuch as it has not been reported or here noted in any other species.

The species is named after Carol and Paul Skoglund, Phoenix, Arizona, who have generously provided these and many other specimens for study.

ABBREVIATIONS USED IN THE TEXT

- ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania.
 CAS—California Academy of Sciences, San Francisco, California.
 Colln.—Private collection.
 LACM—Los Angeles County Museum of Natural History, Los Angeles, California.
 SDNM—San Diego Museum of Natural History, San Diego, California.
 USNM—U.S. National Museum of Natural History, Washington, D.C.

ACKNOWLEDGMENTS

I thank Carol and Paul Skoglund, Phoenix, Arizona, who entrusted these specimens to my care and study, and Terrence M. Gosliner, Department of Invertebrate Zoology, California Academy of Sciences, for the SEM micrographs.

LITERATURE CITED

- ASHBY, E. 1931. Monograph of the South African Polyplacophora (Chitons). *Ann. S. Africa Mus.* 30(1):1–59, 2 text figs., 7 pls.
 BERGENHAYN, J. R. M. 1930. Kurze bemerkungen zur kenntnis der schalenstruktur und systematik der Loricaten. *Kungl. Svenska Vetensk. Handl.* (3)9(3):3–54, 5 text figs., 10 pls. Uppsala.
 BERGENHAYN, J. R. M. 1955. Die fossilen schwedischen Loricaten nebst einer vorlaufigen Revision des systems der ganzen Klasse Loricata. *Lunds Univ. Årsskrift. (Adv.2, N.S.)* 51(8):1–43, 2 pls. *Kungl. Fysiogr. Sallsk. Handl., N.F.*, 66 (8):3–42, 2 tables.
 BLAINVILLE, H. D. DE. 1825. *Oscabrion, Chiton*. In: *Dictionnaire des Sciences Naturelles*, Paris 36:519–555.
 DALL, W. H. 1879. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. *Proc. U.S. Natl. Mus.* 1(for 1878):281–344, 5 pls.
 DALL, W. H. 1889. Preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern Coast of the United States, with illustrations of many of the species. *Bull. U.S. Natl. Mus.* 37:3–221, 74 pls.
 DALL, W. H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission steamer “Albatross” during 1891, Lieut. Commander Z. L. Tanner, U. S. N., Commanding. XXXVIII. Reports on the scientific results of the expedition to the eastern tropical Pacific in charge of Alexander Agassiz, by the U. S. Fish Commission steamer “Albatross,” from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U. S. N., Commanding. XIV. Reports on the Mollusca and Brachiopoda. *Bull. Mus. Comp. Zool.* 43(6):205–487, pls. 1–22.
 DALL, W. H. 1919. Descriptions of new species of chitons from the Pacific coast of America. *Proc. U.S. Natl. Mus.* 55(2283):499–516.
 FERREIRA, A. J. 1974. The genus *Lepidozona* in the Panamic Province, with the description of two new species (Mollusca: Polyplacophora). *Veliger* 17(2):162–180, 6 pls.

- FERREIRA, A. J. 1976. A new species of *Callistochiton* in the Caribbean. *Nautilus* 90(1):46-49, 5 figs.
- FERREIRA, A. J. 1979. The genus *Callistochiton* Dall, 1879 (Mollusca: Polyplacophora) in the eastern Pacific, with the description of a new species. *Veliger* 21(4):444-466, 9 text figs., 3 pls.
- FERREIRA, A. J. 1981. A new species of *Stenosemus* Middendorff, 1847 (Mollusca: Polyplacophora) in the abyssal northeastern Pacific. *Veliger* 23(4):325-328, 5 text figs., 1 pl.
- FERREIRA, A. J. 1983. The chiton fauna of the Revillagigedo Archipelago, Mexico. *Veliger* 25(4):307-322, 10 text figs., 2 pls.
- FERREIRA, A. J. 1985. Chiton (Mollusca: Polyplacophora) fauna of Barbados, West Indies, with the description of a new species. *Bull. Marine Sci.* 36(1):189-219.
- GRAY, J. E. 1821. A natural arrangement of Mollusca, according to their internal structure. *London Medic. Repos.* 15:229-239.
- GRAY, J. E. 1828. *Spicilegia Zoologica; or Original figures and short systematic descriptions of new and unfigured animals. Part 1*, 8 pp., 6 pls. British Museum.
- GRAY, J. E. 1847a. Additional observations on Chitones. *Proc. Zool. Soc. Lond.* 15(178):126-127.
- GRAY, J. E. 1847b. A list of the genera of recent Mollusca, their synonyma and types. *Proc. Zool. Soc. Lond.* 15(178):129-219.
- IREDALE, T. 1914. The chiton fauna of the Kermadec Islands. *Proc. Malacol. Soc. Lond.* 11(1):25-51, pls. 1, 2.
- KAAS, P. 1974. Notes on Loricata. 7. On the type of the genus *Ischnochiton* Gray, 1847. *Basteria* 38:95-97.
- KAAS, P. 1979. The chitons (Mollusca: Polyplacophora) of Mozambique. *Ann. Natal Mus.* 23(3):855-879.
- KAAS, P. & R. A. VAN BELLE. 1980. Catalogue of living chitons. Dr. W. Backhuys, Publisher: Rotterdam. 144 pp.
- INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE, adopted by the XV International Congress of Zoology, 1964. London. xix + 176 pp.
- PILSBRY, H. A. 1892a. Polyplacophora. *In*: G. W. Tryon, Jr., *Manual of conchology*, 14:1-64, pls. 1-15.
- PILSBRY, H. A. 1892b. Polyplacophora. *In*: G. W. Tryon, Jr., *Manual of conchology*, 14:65-128, pls. 16-30.
- QUOY, J. R. C. & J. P. GAIMARD. 1835. Voyage de découvertes de l'*Astrolabe*, exécuté par ordre du Roi, pendant les années 1826-1827-1828-1829, sous le commandement de M. J. Dumont D'Urville. *Zoologies. Paris.* 3:369-411.
- REEVE, L. A. 1847-1848. Monograph of the genus *Chiton*. *In*: *Conchologia iconica, or Illustrations of the shells and molluscos animals.* London. 4:28 pls., 194 figs.
- SMITH, A. G. 1960. Amphineura. *In*: R. C. Moore (ed.), *Treatise on invertebrate paleontology, Part I, Mollusca* 1, pp. 41-76, figs. 31-45.
- SOWERBY, G. B. 1832. *In*: A. J. Broderip & G. B. Sowerby, *Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming.* *Proc. Zool. Soc. Lond.* 1832:50-61.
- VAN BELLE, R. A. 1974. À propos du genre *Ischnochiton* Gray, 1847 (Polyplacophora). *Informations Soc. Belge Malacol.* 3(2):27-29.
- VAN BELLE, R. A. 1983. The systematic classification of the chitons (Mollusca: Polyplacophora). *Informations Soc. Belge Malacol.* 11(1-3):1-178, 13 pls.

Three Temperate-Water Species of South African Gastropods Recorded for the First Time in Southwestern Australia

by

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Abstract. Three temperate South African species of gastropods (*Nassarius kraussianus*, *Bullia annulata*, and *Cymatium cutaceum africanum*) are recorded for the first time in southwestern Australia. Possible mechanisms by which these species were able to transmigrate the Indian Ocean are discussed.

INTRODUCTION

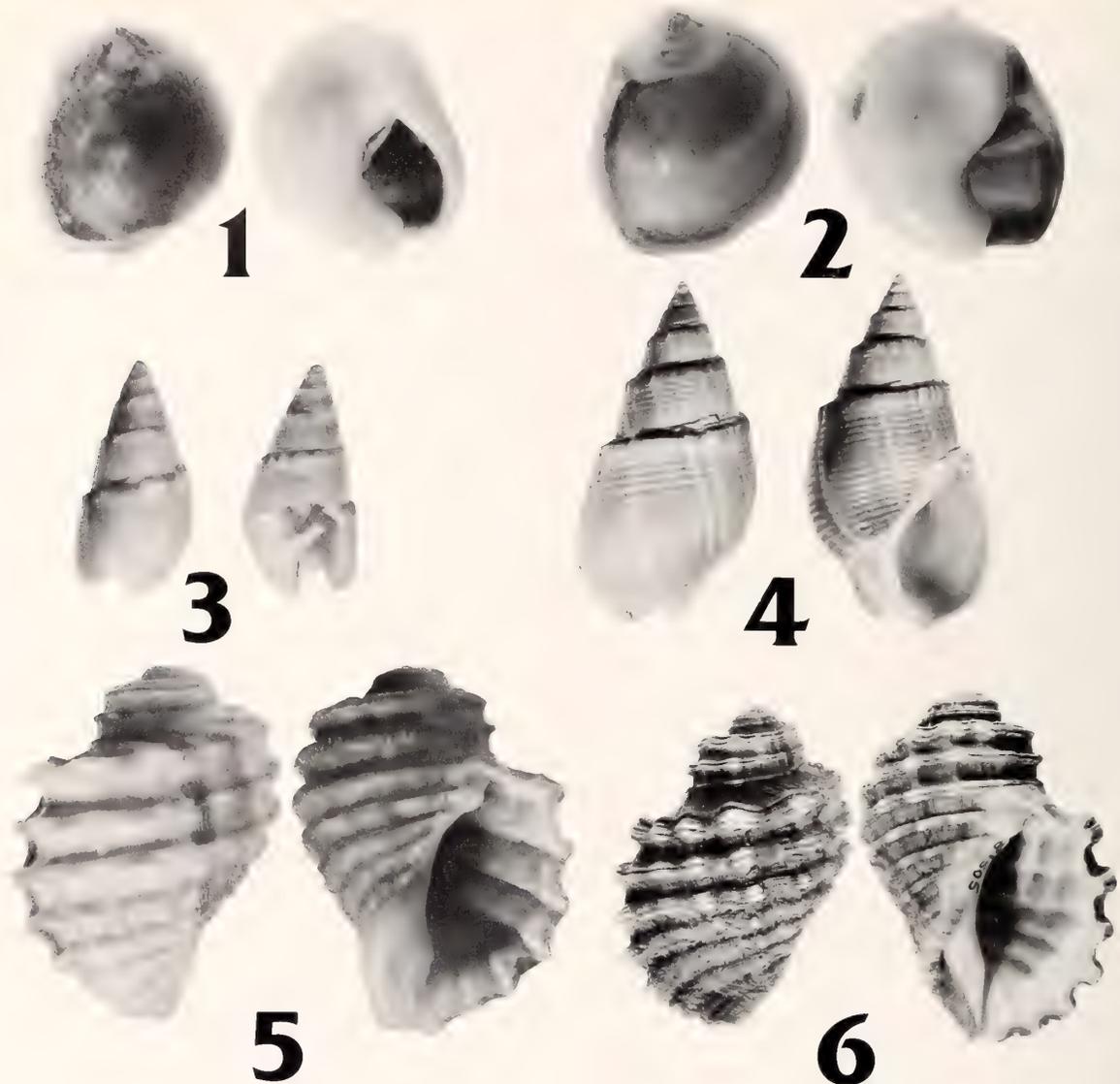
THE TEMPERATE waters of southern Africa and southern Australia are in distinct biogeographic regions (BRIGGS, 1975). Aside from a few circumtemperate species there are few mollusk species in common between southern Africa and southern Australia, as a comparison of species included in WILSON & GILLETT (1979) and KILBURN & RIPPEY (1982) shows. A number of mollusk species have been shown to have crossed the Pacific (EMERSON, 1967; VON COSEL, 1977) and Atlantic (SCHELTEMA, 1971) oceans. Only two temperate species of mollusks are known to have crossed the southern Indian Ocean. The southern African abalone *Haliotis spadicea* Donovan, 1808 (= *H. sanguinea* Hanley, 1840) has been collected in southern Western Australia at Cowaramup Bay, south of Cape Naturaliste (MACPHERSON, 1953). The southern Australian muricid *Bedevea paivae* (Crosse, 1864) has recently established itself in East London Harbour (KILBURN & RIPPEY, 1982) and also in the Canary Islands (GOMEZ, 1984). Three additional southern African temperate species have now been recorded in southern Western Australia and are reported here.

SOUTH AFRICAN SPECIES

Nassarius kraussianus (Dunker, 1846) has been recorded as two lots. WAM 51-82 (Figure 1) is an adult shell 7.7

mm long, which was collected dead at Augusta, W.A., by W. Anson in January 1974. The shell has the thick, glossy callus that overlaps the sides and reaches the apex, as described by KILBURN & RIPPEY (1982). The shell is smooth dorsally, has three grayish-brown spiral bands on the body whorl separated by whitish bands. A thin brown line occurs along the suture. The outer shell color shows through the aperture. The callus is white, with a thin brown line going posteriorly from the posterior edge of the aperture. Two specimens, one an adult 7.8 mm long and the other a juvenile of 5.4 mm, were collected dead by G. Hansen at Flinder's Bay, Augusta, W.A., on 2 July 1972 (WAM 2670-83). These shells closely resemble the specimen described above, except that the juvenile shell lacks the callus. A specimen of *N. kraussianus* from Durban, South Africa, is shown (Figure 2) for comparison.

A single beachworn specimen of *Bullia annulata* (Lamarck, 1816) was collected dead by W. Anson at Flinder's Bay, Augusta, W.A., on an unknown date, about the same time as the *Nassarius kraussianus* was collected. This specimen (WAM 52-82) is a juvenile shell that is 23.8 mm long, but the lower aperture is broken off (Figure 3). Despite being broken this specimen closely matches specimens from the Cape (NM and WAM collections; Figure 4). The Western Australian shell is not as heavy as the South African one but has the same stepped whorls, shallow spiral grooves, and faint growth lines. The shell is



Explanation of Figures 1 to 6

Figure 1. *Nassarius kraussianus* (Dunker, 1846) from Augusta, W.A. WAM 51-82.

Figure 2. *Nassarius kraussianus* (Dunker, 1846) from Durban, South Africa. WAM 50-82.

Figure 3. *Bullia annulata* (Lamarck, 1816) from Flinder's Bay, Augusta, W.A. WAM 52-82.

Figure 4. *Bullia annulata* (Lamarck, 1816) from False Bay, Mui-zenberg, South Africa. WAM 2672-83.

Figure 5. *Cymatium cutaceum africanum* (A. Adams, 1854) from Augusta, W.A. WAM 54-82.

Figure 6. *Cymatium cutaceum africanum* (A. Adams, 1854) from Nthlonyane, Transkei, South Africa. WAM 2671-83.

buff colored, with distinct brown splotches just below the suture. The aperture is white.

A single juvenile individual 19.7 mm long of *Cymatium cutaceum africanum* (A. Adams, 1854) was collected dead at Augusta, W.A., by W. Anson on 27 or 28 January 1979 (WAM 54-82). This species is discussed in detail by KILBURN & RIPPEY (1982) and is quite variable in South Africa, but the Western Australian specimen fits

easily into the range of variation observed in the species (Figures 5, 6). The Western Australian shell has a low spire, narrow umbilicus, and strong spiral cords—seven on the body whorl and two on the upper whorl. The spiral cords are crossed by several indistinct ribs and numerous fine growth lines. The spiral cords appear on the inside of the aperture as channels that extend onto the lip. The shell is a light brown and the aperture is whitish.

DISCUSSION

There are several points of similarity between the coastal environments of eastern South Africa and Western Australia. Both coasts show a parallel transition between a temperate-water fauna in the south and a tropical fauna of predominantly Indo-West Pacific incursions in the north (WELLS, 1980; KILBURN & RIPPEY, 1982). Although many such tropical species are common to both sides of the Indian Ocean, the respective temperate-water molluscan faunas are very different, apart from certain tonnacian gastropods with teleplanic larvae (see BEU, 1976) which have been dispersed at various times since the Oligocene by the Westwind Drift, and circumtemperate species. Environmental factors of temperature, salinity, and topography are not dissimilar. For example, mean summer temperatures along most of the southern Cape coast (the center of distribution of all four species) are 19–20°C (CHRISTENSEN, 1980), which agrees with those of southern Western Australia (HODGKIN & PHILLIPS, 1969). Physical factors may thus support the colonization of the region by South African migrants.

However, no direct evidence yet exists for the presence of established, viable populations of *Nassarius kraussianus*, *Bullia annulata* or *Cymatium c. africanum* in southern Western Australia. *Nassarius kraussianus* inhabits estuaries and salt marshes in South Africa (KILBURN & RIPPEY, 1982). The site at Augusta, W.A., where the species was found is near the mouth of the Blackwood River, but two surveys of the estuary (WALLACE, 1975; WELLS & THRELFALL, 1981) did not record the species. *Bullia annulata* in South Africa is washed up in sheltered bays and lives in sand at low tide, but is most abundant subtidally at depths of up to 100 m, and *C. c. africanum* lives among solitary ascidians offshore, under rocks at low tide or on sand near ascidians (KILBURN & RIPPEY, 1982). *Haliotis spadicea* was recorded by MACPHERSON (1953) as occurring alive near Cape Naturaliste in Western Australia. The Western Australian Museum conducted fieldwork in the Augusta to Cape Naturaliste area in January 1978 and April 1985 and failed to find living colonies of any of the South African species. Nor have local shell collectors reported additional finds of South African species, alive or dead, in Western Australia. Thus, the four species known to have crossed the southern Indian Ocean from South Africa to Western Australia appear to have arrived in small numbers and have not become established.

The mechanism by which these species reached Western Australia is not known, but the literature suggests several possibilities: dispersal by pelagic larvae (SCHELTEMA, 1971), rafting on algae on the sides or in the ballast water of ships or on floating logs (SMITH, 1890; CLENCH, 1947), on the feet of birds (KEW, 1893), or in the gut of fishes. Although the reproductive mechanism of *C. c. africanum* is not known, other cymatiids have long distance planktonic larvae that are able to cross open oceanic areas (SCHELTEMA, 1971). *Nassarius kraussianus* is ovovivipa-

rous with a planktonic veliger stage of a week or less (KILBURN & RIPPEY, 1982). Species of *Bullia* in which reproduction has been studied have either direct development (BROWN, 1982) or ovoviviparity (KILBURN, 1978). *Haliotis* have a planktonic stage of about one to two weeks (INO, 1952; LEIGHTON, 1972). Thus, none of these three species is likely to have arrived in southern Western Australia by means of a planktonic larval stage, but just how they arrived has not yet been determined.

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LITERATURE CITED

- BEU, A. G. 1976. Arrival of *Semicassis pyrum* (Lamarck) and other tonnacian gastropods in the southern ocean during Pleistocene time. *J. Roy. Soc. N.Z.* 6:413–432.
- BIGGS, J. C. 1975. Marine zoogeography. McGraw-Hill: New York.
- BROWN, A. C. 1982. The biology of sandy-beach whelks of the genus *Bullia* (Nassariidae). *Oceanogr. Mar. Biol. Ann. Rev.* 20:309–361.
- CHRISTENSEN, M. S. 1980. Sea-surface temperature charts for Southern Africa, south of 26°S. *S. Afr. J. Sci.* 76:541–546.
- CLENCH, W. J. 1947. The genera *Purpura* and *Thais* in the western Atlantic. *Johnsonia* 2:61–91.
- COSEL, R. VON. 1977. First record of *Mitra mitra* (Linnaeus, 1758) (Gastropoda: Prosobranchia) on the Pacific coast of Colombia, South America. *Veliger* 19:422–424.
- EMERSON, W. K. 1967. Indo-Pacific faunal elements in the tropical eastern Pacific, with special reference to the mollusks. *Venus* 25:85–93.
- GOMEZ, R. 1984. Primera cita para el Atlantico (Islas Canarias) de *Bedevea paivae* (Crosse, 1864). *Bull. Malacologico* 19: 249–252.
- HODGKIN, E. P. & B. F. PHILLIPS. 1969. Sea temperatures on the coast of southwestern Australia. *J. Proc. Roy. Soc. West. Austral.* 53:59–62.
- INO, T. 1952. Biological studies on the propagation of Japanese abalone (genus *Haliotis*). *Bull. Tokai Reg. Fish. Res. Lab.* 5:1–102.
- KEW, H. W. 1893. The dispersal of shells. Paul, Trench, Trubner & Co.: London.
- KILBURN, R. N. 1978. Four new *Bullia* species (Mollusca: Gastropoda: Nassariidae) from Kenya and Mozambique. *Ann. Natal Mus.* 23:297–303.
- KILBURN, R. N. & E. RIPPEY. 1982. Sea shells of southern Africa. Macmillan South Africa: Johannesburg.
- LEIGHTON, D. L. 1972. Laboratory observations on the early growth of the abalone *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. *Fish. Bull., Fish. Wildl. Serv. U.S.* 70:7–19.
- MACPHERSON, J. H. 1953. Record of a South African mollusc from Australia (*Haliotis sanguinea* Hanley). *Mem. Nat. Mus. Vic.* 18:169.
- SCHELTEMA, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biol. Bull.* 140: 284–322.

- SMITH, E. A. 1890. Report on the marine molluscan fauna of St. Helena. Proc. Zool. Soc. Lond. 1890:247-317.
- WALLACE, J. 1975. The macroinvertebrate fauna of the Blackwood River estuary. West. Aust. Dept. Cons. Environ., Tech. Rept. 4.
- WELLS, F. E. 1980. The distribution of shallow-water marine prosobranch gastropod molluscs along the coastline of Western Australia. *Veliger* 22:232-247.
- WELLS, F. E. & T. J. THRELFALL. 1981. Molluscs of the Peel-Harvey estuarine system, with a comparison with other south-western Australian estuaries. *J. Malacol. Soc. Aust.* 5:101-111.
- WILSON, B. R. & K. GILLETT. 1979. A field guide to Australian shells. Reed: Sydney.

Indomya, a New Subgenus of *Pholadomya* from the Middle Jurassic of Kachchh, Western India (Bivalvia: Pholadomyidae)

by

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Abstract. A new subgenus of *Pholadomya*, *Indomya*, type *Pholadomya (Indomya) rajnathi* Jaitly, spec. nov., is described on the basis of four specimens from the Middle Bathonian (Middle Jurassic) of Kala Dongar, Pachchham Island, District Kachchh (Gujarat), Western India. *Indomya* differs from other members of *Pholadomya* by its faint vertical umbonal-ventral sulcus, an oblique posterior ridge, and surface ornamentation that consists of both concentric and radial ribs or threads.

INTRODUCTION

THE FAMILY Pholadomyidae Gray is represented in Kala Dongar by five genera: *Pholadomya* G. B. Sowerby, *Homomya* Agassiz, *Oestomya* Moesch, *Pachymya* J. Sowerby, and *Agrawalimya* Singh, Jaitly & Pandey. *Agrawalimya* was created for specimens having a sulcus with asymmetrically inclined walls and extending from the umbo to just anterior to the middle of the ventral margin. The genus was tentatively referred to the Pholadomyidae because a sulcus was not previously considered to be of generic or subgeneric importance. However, this feature is frequently observed in many Middle Jurassic species of *Pholadomya*, and MOESCH (1878:58) and FURSICH (1982:96) even mentioned the presence of a shallow sulcus between the second and third anterior ribs in *Pholadomya (Pholadomya) hemicardia* Roemer. Subsequently, additional specimens have been collected that have an outline similar to that of *Pholadomya* and *Homomya*, but which also possess a faint sulcus in the anterior third of the shell. To receive them, a new subgenus is created and tentatively assigned to the genus *Pholadomya*.

A new subgenus, *Indomya*, with *Pholadomya (Indomya) rajnathi* Jaitly, spec. nov. as type, is described from Middle Bathonian rocks of Kala Dongar, Pachchham Island, Kachchh, India. The geology and stratigraphy of the area is described by JAITLEY (1985); for location see JAITLEY & SINGH (1983).

SYSTEMATIC PALEONTOLOGY

Class Bivalvia

Order Pholadomyoidea

Suborder Pholadomyacea
Family Pholadomyidae

Pholadomya Sowerby, 1823

Type: *Pholadomya candida* G. B. Sowerby, 1823, by subsequent designation of Gray, 1847.

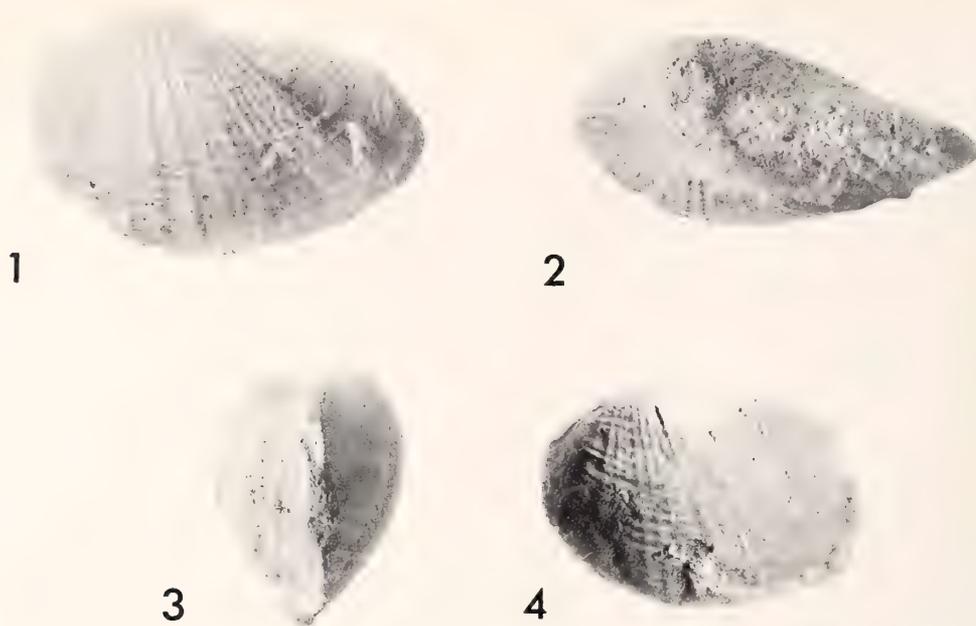
(*Indomya*) Jaitly, subgen. nov.

Etymology: Named after India.

Type: *Pholadomya (Indomya) rajnathi* Jaitly, spec. nov., Middle Bathonian (Jurassic), Kachchh, India.

Diagnosis: Shell sublunate with tapering posterior; surface with shallow, gradually downward widening sulcus extending vertically from anterior of umbo to ventral margin and oblique posterior ridge; ornamentation of both concentric and radial ribs or threads.

Remarks: In shape and size, *Indomya* is similar to *Pholadomya* s.s. and *Homomya*. The surface ornamentation, which consists of prominent radials that extend to the ventral margin, more closely resembles that of *Pholadomya* s.s. In *Homomya*, radial ornamentation is generally absent and, if present, is restricted to the umbonal region. *Tetorimya* HAYAMI (1959:151), from the Upper Jurassic of Japan, resembles *Indomya* in size and position of posterior gape, but lacks the vertical sulcus in the anterior region and differs in surface ornamentation. *Agrawalimya* differs in nature and position of its sulcus and the lack of radial ribs, which are prominent in *Indomya*.



Explanation of Figures 1 to 4

Pholadomya (Indomya) rajnathi Jaitly, subgen. et spec. nov.

Figure 1. Holotype PK/139/3; Middle Bathonian, Kala Dongar, Kachchh, India; exterior view of left valve.

Figure 2. Holotype, dorsal view.

Figure 3. Holotype, anterior view.

Figure 4. Paratype PK/145/5; Middle Bathonian, Kala Dongar, Kachchh, India; exterior view of left valve.

Pholadomya (Indomya) rajnathi Jaitly, spec. nov.

(Figures 1-4)

Etymology: Named for the late Prof. Rajnath, an expert on the Kachchh Jura.

Diagnosis: As for the genus.

Types: Four paired specimens: **holotype**, PK/139/3, and three **paratypes**, PK/145/5, PK/145/3, and PK/141/11, deposited in the Invertebrate Paleontology Laboratory, Department of Geology, Banaras Hindu University, Varanasi 221 005, India.

Type locality: Middle Bathonian of Pachhmaipir, Kala Dongar (23°48'39"N, 69°50'E), Pachchham Island, Kachchh, India.

Description: Shell medium sized (to 5 cm in length), highly inequilateral, moderately inflated and sublunate with tapering posterior end. Maximum inflation lies below umbones, about one-third of distance to ventral margin. Umbones orthogyrous, incurved, contiguous, and situated 6 to 8 mm from the anterior end. Lunule poorly defined, broadly ovate and small; escutcheon indistinct. Anterior margin broadly rounded, posterior margin acutely convex; ventral margin asymmetrically and gently convex, merging with anterior and posterior in smooth curves. An obtusely rounded ridge, defined by the abruptly steeper slope

of the surface posterior to it, extends obliquely from the umbo to the ventral margin slightly anterior to the postero-ventral end of shell. A shallow, broadly rounded sulcus extends vertically from the umbo downwards, gradually becoming shallower and wider.

Surface sculpture consists of both concentric and radial ribs and (or) threads. The area anterior to the sulcus has only a few weak radial threads, but the area between the sulcus and the oblique ridge has narrow, widely spaced radial ribs. The area just posterior to the sulcus has four prominent ribs with a secondary riblet in each interspace. The secondaries gradually become stronger posteriorly and primaries become weaker, so that both are of equal strength and arranged in pairs. The area posterior to the oblique ridge is devoid of radial ornamentation and possesses only concentric ribs. Internal characters are unknown.

Dimensions (mm):

Specimen no.	Length	Height	Inflation
PK/139/3 (holotype)	49.5	33.5	24.5
PK/145/5 (paratype)	48.5	33	24
PK/141/11 (paratype)	54	38.5	31
PK/145/3 (paratype)	59	39	29

Remarks: The present specimens show some similarities in general outline and surface ornamentation to *Pholadomya inaequiplicata* Stanton (IMLAY, 1964:C-36, pl. 4, figs.

37-38) and *Pholadomya ovalum* Agassiz (LYCETT, 1863: 84, pl. 35, figs. 18, 18a). However, both *P. inaequiplicata* and *P. ovalum* lack the anterior sulcus and the posterior ridge.

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LITERATURE CITED

- FURSICH, F. T. 1982. Upper Jurassic bivalves from Milne Land, East Greenland. *Greenland Geologiske Undersee-gelse Bull.* 144:1-126.
- HAYAMI, I. 1959. Late Jurassic isodont and myacid pelecypods from Makito, central Japan. *Jap. J. Geol. Geogr.* 30:151-167.
- IMLAY, R. W. 1964. Marine Jurassic pelecypods from central and southern Utah. *J. S. Geol. Surv. Prof. Paper* 483-C:1-42.
- JAITLY, A. K. 1985. Note on the Middle Jurassic rocks of Kala Dongar, Pachchham Island, Diast. Kachchh, Gujarat. *Proc. IV Indian Geol. Congr., Varanasi*:55-62.
- JAITLY, A. K. & C. S. P. SINGH. 1983. Stratigraphy of the Bajocian sediments of Kachchh, Gujarat (W. India). *Proc. Ind. Natl. Sci. Acad.* 49(A):503-508.
- LYCETT, J. 1863. Supplementary monograph on the Mollusca from Stonesfield Slate, Great Oolite, Forest Marble and Cornbrash. *Paleo. Soc. London.* 129 pp.
- MOESCH, C. 1878. *Monographie der Pholadomyen.* *Ach. Schweiz. Paläont. Ges.* 1:135 pp.

NOTES, INFORMATION & NEWS

Retention of *Nassarius corpulentus* (C. B. Adams, 1852) in West American Nassariid Nomenclature

by
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PETIT (1984) drew attention to the existence of the taxon *Cancellaria nassiformis* Lesson, 1842, as being an earlier name for *Nassarius corpulentus* (C. B. Adams, 1852) from the west coast of America. He advocated either the acceptance of *Cancellaria nassiformis* Lesson, which on examination of the type specimens proved to be conspecific with *Nassarius corpulentus* (C. B. Adams), or a rejection of Lesson's name by action of the International Commission on Zoological Nomenclature. The publication of Declaration 43 (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1970) has established binding rules for the treatment of unused names in zoology. Under these emended rules of Article 23(b), paragraph 2(b)(ii), a senior synonym is considered to be a *nomen oblitum* if during the immediately preceding 50 years (*i.e.*, 1934-1984) it has not once been applied to a particular taxon as its presumably valid name. Declaration 43 makes it clear that a *nomen oblitum* shall not replace a name that has been in current use for at least 50 years, and "current usage" has been defined as the usage of the name during the last 50 years by at least five different authors in 10 different publications.

Search through malacological literature has revealed a published usage between 1934-1984 of the name *Nassarius corpulentus* by nine different authors in 12 different publications as follows:

Nassarius corpulenta: BALES, 1938:45.

Nassarius corpulentus: DEMOND, 1951:16, 1952:314, pl. 1, fig. 6; KEEN, 1958:409, fig. 571; McLEAN, 1970:129; KEEN, 1971:606, fig. 1295; CERNOHORSKY, 1975:168, fig. 93, 1982:17-209; KAICHER, 1982: card 3148; ABBOTT & DANCE, 1982:179, fig. bottom row center.

Nassa corpulenta: TURNER, 1956:44, pl. 5, fig. 3.

Nassa corpulentus: OLIVEIRA *et al.*, 1981:209.

I am certain that more time and effort would have probably unearthed even a wider usage of *Nassarius corpulentus*, but this would have been purely of statistical interest. Unless a usage of the taxon *Cancellaria nassiformis* Lesson is found between 1934-1960, in which instance the name has been applied to a valid taxon (mention in synonymy, listing in an Index, or list of names does not qualify), the epithet *Nassarius corpulentus* (C. B. Adams) must be retained in nassariid nomenclature.

LITERATURE CITED

- ABBOTT, R. T. & S. P. DANCE. 1982. Compendium of sea-shells. A color guide to more than 4,200 of the world's marine shells. E. P. Dutton Inc.: New York. 411 pp.
- BALES, B. R. 1938. Marine collecting on the west coast of Mexico. *Nautilus* 52(2):41-46.
- CERNOHORSKY, W. O. 1975. The taxonomy of some west American and Atlantic Nassariidae based on their type-specimens. *Rec. Auckland Inst. Mus.* 12:121-173, figs. 1-93.
- CERNOHORSKY, W. O. 1982. Family Nassariidae Iredale, 1916. *Suppl.* 2:17-201-17-243. *In*: R. J. L. Wagner & R. T. Abbott, Standard catalogue of shells. 3rd ed. American Malacologists Inc.: Greenville, Delaware.
- DEMOND, J. 1951. Key to the Nassariidae of the west coast of North America. *Nautilus* 65(1):15-17.
- DEMOND, J. 1952. The Nassariidae of the west coast of North America between Cape San Lucas, Lower California, and Cape Flattery, Washington. *Pacific Sci.* 6(4):300-317, pls. 1, 2.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1970. Declaration 43. Repeal of Article 23(b). *Bull. Zool. Nomencl.* 27(3/4):135-162.
- KAICHER, S. D. 1982. Card catalogue of world-wide shells. Pack No. 31. Nassariidae. Part 1. S. D. Kaicher: St. Petersburg, Florida. 105 cards.
- KEEN, A. M. 1958. Sea shells of tropical west America. Marine mollusks from Lower California to Colombia. Stanford Univ. Press: Stanford, Calif. 626 pp.
- KEEN, A. M. 1971. Sea shells of tropical west America. Marine mollusks from Baja California to Peru. 2nd ed. Stanford Univ. Press: Stanford, Calif. 1064 pp.
- McLEAN, J. H. 1970. New species of tropical eastern Pacific Gastropoda. *Malacol. Review* 2:115-130, figs. 1-41.
- OLIVEIRA, M. P. DE, G. DE J. R. REZENDE & G. A. DE CASTRO. 1981. Catálogo dos Moluscos da Universidade Federal de Juiz de Fora. Sinonímia de Família, Gênero e Espécie. Minist. Educ. & Cultura: Juiz de Fora, Brasil. 520 pp.
- PETIT, R. E. 1984. An earlier name of *Nassarius corpulentus* (C. B. Adams, 1852). *Veliger* 26(4):330.
- TURNER, R. D. 1956. The eastern Pacific marine mollusks described by C. B. Adams. *Occas. Pap. Mollusks, Mus. Comp. Zool. Harvard* 2(20):21-136, pls. 5-21.

Observation of Predation on a Pleuronectid Fish by *Navanax inermis*

(Opisthobranchia: Cephalaspidea)

by

Stephen A. Karl

1260 Oliver Ave.,

San Diego, California 92109, U.S.A.

Navanax inermis (Cooper, 1862), which ranges from Monterey Bay, California, to the Gulf of California, Mexico, is an active and voracious predator reported to

eat gastropods, annelids, arthropods, and fish (PAINE, 1963, table 1; BLAIR & SEAPY, 1972).

On 23 July 1981, a 40-mm long (2.0 g wet weight, displacing 0.9 mL seawater) *Navanax inermis* was observed off Naples Reef, Naples, California, with a 25-mm total length (19 mm standard) live spotted turbot (*Pleuronichthys ritteri*) in its pharynx. The animal was discovered and collected on a sand-rock interface in 13.7 m of water. When it was found, approximately one quarter (6.5 mm) of the turbot's anterior region was inside the opisthobranch's buccal mass. The turbot was still alive, as the tail was moving quickly from side to side.

Although *Navanax inermis* has been previously reported to eat fish, these reports have been mainly of *Porichthys myriaster* (PAINE, 1963). These fish seasonally migrate inshore to mate and deposit their eggs on the underside of rocks. The male guards the eggs which remain attached to the rocks until the yolk sac is completely absorbed (BREDER & ROSEN, 1966). Because they are not able to swim the larvae are vulnerable to attack by *N. inermis* and this may account for PAINE's (1963) observation of large numbers of 20–30-mm fish in the fecal remains from *N. inermis*. Whether or not *N. inermis* was actively pursuing the turbot or if mucus secreted by the fish was involved in its detection and eventual capture is difficult to determine; the *Navanax* may have encountered the turbot only by chance.

LITERATURE CITED

- BLAIR, G. M. & R. R. SEAPY. 1972. Selective predation and prey location in the sea slug *Navanax inermis*. *Veliger* 15(2): 119–124.
- BREDER, C. M., JR. & D. E. ROSEN. 1966. Modes of reproduction in fishes. Natural History Press: Garden City, New York. 598 pp.
- PAINE, R. T. 1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). *Veliger* 6(1):1–9.

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 42, part 3, on 30 September 1985:

- Opinion No. 1331 (p. 230). Sphaeriidae Jeffreys, 1862 (1820) (Mollusca, Bivalvia): placed on the Official list.
- Opinion No. 1350 (p. 283). *Conus antiquus* Lamarck, 1810 (Mollusca, Gastropoda): neotype suppressed.

Erratum: Volume 28, Number 3 (2 January 1986)

A typographical error has unfortunately escaped our attention in the article by Steven M. Chambers, "Two new bulimulid land snail species from Isla Santa Cruz,

Galápagos Islands," which appeared in Volume 28, Number 3 (2 January 1986). In Table 2 the value given for the "No. whorls, other" of the holotype should be 5.25, not 4.25 as printed.

California Malacozoological Society

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed 6 January 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger*. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); or Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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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.

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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 Veli-*

ger. 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.

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 be US\$25.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will be US\$50.00, also now with postage to domestic addresses included. An additional US\$3.50 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. There is a one-time membership fee of US\$2.00, after payment of

which, membership is maintained in good standing by the timely renewal of the subscription.

Send all business correspondence, including subscription orders, membership applications, payments for them, and changes of address to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

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All back volumes still in print, both paper-covered and cloth-bound, are available only through "The Shell Cabinet," 12991 Bristow Road, Nokesville, VA 22123. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Morgan Breeden at the above address.

Volumes 1 through 13, 24, 26, and 27 are out of print.

Supplements still available are: part 1 and part 2, supplement to Volume 3, and supplements to Volumes 7, 11, 14, 15, and 16; these can be purchased from "The Shell Cabinet" only. Copies of the supplement to Volume 17 ("Growth rates, depth preference and ecological succession of some sessile marine invertebrates in Monterey Harbor" by E. C. Haderlie) may be obtained by applying to Dr. E. C. Haderlie, U.S. Naval Post-Graduate School, Monterey, CA 93940; the supplement to Volume 18 ("Chitons") is available from "The Secretary," Hopkins Marine Station, Pacific Grove, CA 93950.

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:

Volumes 1–6: \$9.95 each.

Volumes 7–12: \$12.95 each.

Supplement to Volume 6: \$3.95; to Volume 18, \$6.95. Send orders to Mr. Steven J. Long, Shells and Sea Life, 1701 Hyland, Bayside, CA 95524.

A. Myra Keen
(1905–1986)

Malacologists everywhere have lost a friend and colleague, A. Myra Keen (23 May 1905–4 January 1986). She contributed frequently to the *Veliger* as author, reviewer, and member of the Editorial Board, her kindness and care in reading manuscripts endearing her to Founding Editor Rudolf Stohler and to all whose papers passed her desk. A formal memorial is in preparation, but we acknowledge here our affection for the First Lady of Malacology and our appreciation of her as a teacher, author, nomenclatural expert, curator, and advisor. In one or more of these roles she affected the work of most malacologists during the last quarter of a century.

Dr. Keen was associated from 1934 to 1970 with the Department of Geology, Stanford University. A psychology major (A.B., Colorado College; M.Sc., Stanford University; Ph.D., University of California, Berkeley), she graduated during the depression when there were no jobs and directed her diagnostic skills and scientific background to an interest in shells, eventually becoming an international authority in malacology and professor of paleontology. She taught advanced paleontology, biological oceanography, and curatorial methods, and concurrently wrote more than 75 scholarly papers and nine books.

Thoroughly knowledgeable on taxonomic procedure, she chaired the nomenclatural committee of the Society of Systematic Zoology and was directly involved in refining the rules by which all new animal taxa are named. As curator of the Stanford University research collections, Dr. Keen was proud of the fact that the Tertiary and Recent specimens were not only well arranged but also identified. She acquired shells from all over the world in return for identifying duplicate lots, and maintained a type collection that exceeded 6,400 lots before it was transferred to the California Academy of Sciences.

Visitors who climbed to her third-floor office recall the exhibits, as pleasing as they were informative, and the bookshelves lined with reprint boxes and journals. There Dr. Keen painstakingly unscrambled "thorny problems," as she called the more complicated nomenclatural puzzles, and administered the French exam required of many graduate students. She advised more than a dozen advanced degree candidates in geology and biology (several now head the molluscan sections of some of the nation's

most important institutions for malacological research). She had many foreign visitors, the most publicized being Emperor Hirohito of Japan, and carried out an immense correspondence, some of it scholarly and some leaving her chuckling over yet another request for "everything you know about shells."

Dr. Keen was able to envision projects of enormous scope and break them into increments she could accomplish between lecture preparations, oral exams, classes, and caring for her invalid mother. Long before the word processor, she worked at an old manual typewriter, putting masses of information into a book that provoked a surge of research on eastern Pacific mollusks. Recognizing the gaps in our knowledge of west coast taxa described by early foreign workers, she obtained a prestigious John Simon Guggenheim Fellowship to visit European museums and photograph the type specimens. Her greatest work, "Sea Shells of Tropical West America" (1971. 2nd ed. Stanford University Press: Stanford, Calif. 1064 pp.), is the standard reference for eastern Pacific mollusks.

In private life, Dr. Keen was a member of the Religious Society of Friends, a quiet pacifist, and an ardent feminist. Shy, but sure of her convictions, she firmly opposed smoking and frequently wrote letters in support of wildlife and conservation. She enjoyed classical music, especially Brahms, poetry referring to the sea, and keeping in touch with students and close friends. Her thorough, meticulous research and thoughtful ways will continue to inspire all who share her interests and build on her work.

Judith Terry Smith

Donald Putnam Abbott
(1920-1986)

Stanford University Professor Emeritus Professor Donald P. Abbott died at his home in Honolulu, Hawaii, on 18 January 1986. He was 65 years old. Dr. Abbott is survived by his wife, University of Hawaii Botany Professor Isabella A. Abbott and daughter Ann K. Abbott of Honolulu. Don Abbott will be greatly missed by not only his family but also his numerous colleagues, former graduate students, and the hundreds of other students who had the opportunity to take the courses he taught between 1950 and 1982 on the Stanford campus and at the Hopkins Marine Station in Pacific Grove, California.

Donald Abbott was born in Chicago, Illinois, on 14 October 1920, and there received his primary and secondary education. He enrolled as a freshman at the University of Hawaii in 1937, at the age of 16, and was awarded a bachelor's degree in Zoology in 1941. His master's degree program at the University of Hawaii was interrupted by the attack on Pearl Harbor, and he turned to instructing in Zoology at the University of Hawaii until enlisting in the U.S. Army in 1943. Donald Abbott married his undergraduate classmate, Isabella Aiona, in 1943, and they remained in Hawaii throughout the war years. In

1946, after his discharge from the Army, Abbott enrolled in the graduate program in Zoology at the University of California at Berkeley, receiving a master's degree in 1948 and a Ph.D. in 1950.

Stanford University hired Dr. Abbott to its faculty at the Hopkins Marine Station in 1950, and he remained there until his retirement in 1982. His summer invertebrates course at Hopkins became one of the best known in the world and was an introduction to marine animals that launched many students on their lives' work. A consummate teacher, Don Abbott provided a model that a generation of graduate students still seeks to emulate in style and substance. Abbott was a major force in the establishment of a Hopkins Marine Station "spring course" that eventually attracted national attention for its success in involving undergraduate students and faculty in joint, original research in marine biology. Donald Abbott was major advisor to 26 doctoral and 10 master's degree students, and an *ex officio* mentor to many more. In recognition of his superior teaching accomplishments, Abbott received a number of prestigious teaching awards from Stanford University.

Professor Abbott's major research interests were in the biology and taxonomy of tunicates and in animal phylogeny. He was the author of numerous research papers and co-author of two books: "Coral island: Portrait of an atoll" (1958, with Marston Bates) and "Intertidal Invertebrates of California" (1980, with R. H. Morris & E. C. Hadlerlie). A book of Dr. Abbott's drawings of invertebrate animals is currently being prepared for publication in the careful editorial hands of his former student Galen H. Hilgard. Another of Abbott's former students, Prof. A. T. Newberry of U.C. Santa Cruz is completing a summary of the Hawaiian tunicate fauna on which Abbott had been working at the time of his death.

The international community of invertebrate zoologists has lost one of its finest colleagues, best teachers, and most creative thinkers. Don Abbott will be sorely missed.

Michael G. Hadfield

American Malacological Union, Meeting

The 52nd annual meeting of the American Malacological Union will be held in historic Monterey, California, from 1-6 July 1986, at the new Sheraton Hotel. The new Sheraton is adjacent to Fisherman's Wharf, within a few blocks of Steinbeck's Cannery Row, and is surrounded by many historic sites.

An international symposium on opisthobranch mollusks in honor of Dr. Eveline Marcus is being planned and organized by Dr. Terrence Gosliner and Dr. Michael Ghiselin. A second international symposium on molluscan morphological analysis is being planned by Drs. Carole Hickman and David Lindberg. There will be contributed papers and a poster display. A special cephalopod session honoring Dr. S. S. Berry is being organized by Dr. Roger

Hanlon (you can watch the boats fish for squid from the hotel).

A workshop on photography is planned as well as the traditional auction. Tentative field trips will include tours of the California Granite Canyon Shellfish Culture Laboratory, the Moss Landing Marine Laboratories, the rich molluscan intertidal areas of the Monterey Peninsula, and some special fossil-rich cliffs. A dredging trip on the research vessel "Cayuse" is also planned. The meeting will be highlighted by a special afternoon affair at the all new

Monterey Bay Aquarium, with its spectacular kelp tank and associated displays, and a banquet featuring MacArthur Fellow Dr. Michael Ghiselin as the speaker.

The Western Society of Malacologists will meet jointly with the AMU for this meeting, ensuring that this will be an outstanding meeting.

For further information contact: Dr. James Nybakken, AMU President, Moss Landing Marine Laboratories, Box 223, Moss Landing, CA 95039.

EDITOR'S NOTE: The Tables of Contents and Author Index for papers that appeared in Volume 28 will be printed in the first issue of Volume 29.

BOOKS, PERIODICALS & PAMPHLETS

A Guide to the Common Molluscs of South-western Australian Estuaries

by FRED E. WELLS, with photography by Clayton W. Bryce. 1984. Western Australian Museum: Francis Street, Perth 6000, Australia. 112 pp.; 41 pls. Paperback, \$3.50 Australian, plus postage.

This compact book, intended as an easy identification guide for professional scientists, students, and interested amateurs, illustrates 82 of the common and widespread macromollusks occurring in estuaries of southwestern Australia, from Esperance to the Moore River (75 km north of Perth). Included are 50 gastropods, 31 bivalves, and 1 chiton. Although all are to be found in the estuaries covered, the species' salinity tolerances and distributions vary considerably in specifics: some are characteristic of purely freshwater habitats, whereas others show distinctly marine affinities. For each species, a black-and-white half-tone plate is provided, along with other basic information: family, common name, scientific name, a description of the shell or animal, habitat and geographical range, and notes. In addition to these 82 descriptions, the book contains a glossary, many useful references, and an appendix listing species known to occur in estuaries of the region but not presented in detail.

D. W. Phillips

Archaeogastropod Biology and the Systematics of the Genus *Tricolia* (Trochacea: Tricoliidae) in the Indo-West-Pacific

by ROBERT ROBERTSON. 1985. Monographs of Marine Mollusca, Number 3. American Malacologists, Inc.: P.O. Box 2255, Melbourne, FL 32902. 104 pp.; 96 pls. Stapled, \$13.50.

In Number 3 of "Monographs of Marine Mollusca," Robertson has provided a useful biological and systematic treatment of the genus *Tricolia* in the Indo-West Pacific, in which nine species are accepted and treated. The title's prominent reference to coverage of "archaeogastropod biology" is perhaps a bit misleading, as only a few pages deal with the biology of species other than *Tricolia* and these with only selective aspects. Also, the rather muddy printing of the many half-tone illustrations has not done justice to the author's undoubtedly fine original photographs. However, the work as a whole is a scholarly monograph of the Indo-West Pacific representatives of a world-wide, temperate and tropical genus, placed in a context of relevant work on other archaeogastropods; as

such it should be of interest to general students of mollusks as well as specialists on archaeogastropod systematics.

D. W. Phillips

Larval Forms and Other Zoological Verses

by WALTER GARSTANG. Reprinted 1985. University of Chicago Press: 5801 S. Ellis Ave., Chicago, IL 60637. 98 pp. Paperback, \$5.95.

Garstang, a Professor of Zoology at Leeds and a Fellow of Lincoln College at Oxford University, first published a collection of his verses about ontogeny and phylogeny in 1951. These delightful, witty verses express, in a whimsical way, Garstang's fascination with larval forms but also capture the more serious essence of several scientific debates on evolutionary biology, past and present. Certainly one of the more famous verses, "The Ballad of the Veliger, or How the Gastropod got its Twist," is a marvelous presentation of Garstang's notion of the adaptive advantage of gastropod torsion. In addition to the original 26 verses, this 1985 edition also includes Garstang's Presidential Address to the British Association for the Advancement of Science (entitled "The Origin and Evolution of Larval Forms") and a new Foreword, by Michael LaBarbera, that provides explanatory notes for many of the verses and relates Garstang's work to the evolutionary thinking of his time. This book is sure to be enjoyed by students, teachers, and professional scientists alike, indeed by anyone who shares Garstang's fascination with the lives of larvae and the relationships between ontogeny and phylogeny.

D. W. Phillips

The Printer's Catch An Artist's Guide to Pacific Coast Edible Marine Animals

by CHRISTOPHER M. DEWEES. 1984. Sea Challengers: 4 Sommerset Rise, Monterey, CA 93940. 112 pp.; 63 color pls. Hardcover, \$26.95.

Although the pages of the "Books, Periodicals & Pamphlets" section are usually reserved for publications having a formally scientific and distinctly molluscan focus, occasionally there appears a book that presents the beauty of nature in such a way that our readers may wish to know about it. Such a book is "The Printer's Catch." Constructed around 63 color plates of original fish rubbings (*gyotaku*) made by naturalist, fisheries biologist, and artist Christopher Dewees, the book combines art and

nature in an unusual and pleasing way. Each print, beautifully reproduced (as seems to be standard for Sea Challengers publications) is accompanied by the common and scientific names of the subject and by pertinent life history, fisheries, and consumer information. Also provided are methods and materials for *gyotaku*, which some see as a unique form of scientific illustration and documentation as well as art. Although most of the prints are of marine fish, covering the majority of Pacific coast fish families, eight species of mollusks are included in the prints. Enjoy.

D. W. Phillips

The Distributions of the Native Land Mollusks of the Eastern United States

by LESLIE HUBRICHT. 1985. Fieldiana, Zoology, New Series, No. 24. 191 pp., 523 distribution maps. \$23.00.

Terrestrial malacologists have waited a long time for the publication of Mr. Leslie Hubricht's distribution maps of eastern United States land mollusks. This book contains maps and habitat notes for the 523 species and subspecies of native land mollusks of the eastern United States (east of the western boundaries of North and South Dakota, Nebraska, Kansas, Oklahoma, and Texas east of the Pecos River) recognized by Hubricht. The maps summarize data from 55 years of collecting by Mr. Hubricht (about 43,000 lots), his identifications of material for other workers, 20 years of examining material in major eastern United States museums, and data from PILSBRY'S (1939-1948) monograph. An important feature of the book in addition to the distribution maps is the inclusion of nomenclatural and systematic changes since publication of Pilsbry's monograph. Because this book is not intended as an identification guide, it contains no descriptions of taxa.

The five sections of the book are (1) a short introduction, (2) an annotated systematic list, (3) a list of references from which distribution records were taken, (4) the distribution maps, and (5) an index to taxa.

The index is alphabetical for all levels of taxa from subclass to subspecies, and includes synonyms of taxa from genus to subspecies. For example, *Glyphyalinia rhoadsi austrina*, formerly known as *Retinella rhoadsi austrina*, can be found in the index under six permutations of the trinomials.

The distribution maps make up the bulk of the book. They are drawn on base maps showing the counties of the United States. The maps are of good quality and are easily readable. Nowhere are states or counties on the maps identified. A separate map is used for each taxon. County records are shown with different symbols used to indicate living individuals, Pleistocene fossil occurrences, and occurrences known only from river drift. This is the first time that many of the distribution records have been published.

This book can be compared to British mapping of non-

marine Mollusca by vice-counties which began in 1876 (KERNEY, 1982). More recently, the Conchological Society of Great Britain and Ireland has mapped detailed distributions of British species of terrestrial molluscs on a grid system of 10 × 10 km squares (KERNEY, 1976). Hubricht's distribution maps are based on counties (mean 1746 km² per county, my calculation) and are comparable to the British mapping by vice-counties. Finer scale mapping and more intensive surveys of United States land Mollusca will undoubtedly follow.

Not only should distribution maps show where individuals of a species occur, maps should also show enough detail to reveal possible correlations between the geographic range of a species and various environmental factors such as geology, vegetation, and climate, and maps should be able to show temporal changes in the distribution of a species (KERNEY, 1967). Hubricht's distribution maps provide sufficient detail for environmental comparison, although no maps of environmental factors are included. Unfortunately, Hubricht's maps give only a partial indication of temporal changes. Map symbols showing Pleistocene occurrences indicate reductions but not expansions in range, and range changes in historical times are not shown. Furthermore, as the title indicates, introduced species are not included in this book, although their distributions would be interesting from a perspective of historical distribution change.

In the systematic list Hubricht gives, for each taxon, a list of references (exclusive of titles) published since Pilsbry's monograph that affect the systematics or nomenclature of the taxon, and brief notes on habitat. Remarks or notes on variation are included for about one-tenth of the taxa.

Systematists may be frustrated that Hubricht introduced in this book a systematic revision of taxa for which some of the changes in rank or status have not been justified in print. Hubricht promises that justification for these changes will be published elsewhere. The new classification is similar to previous arrangements of other authors, but reflects Hubricht's opinions on the status of some taxa. For example, Hubricht uses the suborders Aulacopoda and Holopodopes, but he did not use the long recognized suborder Holopoda.

One might expect Hubricht's list of references affecting the status of taxa, or naming new taxa, to replace the paper by MILLER *et al.* (1984) because Hubricht covers all native United States terrestrial Mollusca in contrast to the work of Miller *et al.* which updated only volume 1 (Helicacea and Polygyracea) of PILSBRY (1939-1948). However, each work has a few unique references for the taxa they have in common, so the two works complement each other.

The distribution maps, updated systematic list, and references make this a necessary book for terrestrial malacologists, and the maps are of value to biogeographers. Ecologists will find it useful in seeking correlations of molluscan distributions with environmental parameters.

Quaternary paleontologists will find the fossil and Recent distribution records useful for documenting temporal changes in species ranges. The references are valuable to people tracing the nomenclatural history of a species. Environmental consultants will find this a helpful book as well.

Houbrecht points out that this is a working document. It is a starting point for future, more intensive mapping of faunal distributions. At the same time it is a useful and significant step toward documenting and understanding the distributions of United States native Mollusca.

Literature Cited

- KERNEY, M. P. 1967. Distribution mapping of land and freshwater Mollusca in the British Isles: a brief history and future prospects. *J. Conch.* 26:152-160.
- KERNEY, M. P. 1976. Atlas of the non-marine Mollusca of the British Isles. Institute of Terrestrial Ecology, Cambridge. 199 pp.
- KERNEY, M. P. 1982. Vice-comital census of the non-marine Mollusca of the British Isles (8th edition). *J. Conch.* 31(1): 63-71.
- MILLER, W. B., R. L. REEDER, N. BABRAKZAI & H. L. FAIRBANKS. 1984. List of new and revised Recent taxa in the North American terrestrial Mollusca (north of Mexico) published since 19 March 1948, part 1. *Tryonia* 11:1-14.
- PILSBRY, H. A. 1939-1948. Land Mollusca of North America (north of Mexico). *Acad. Natur. Sci. Phila.*, Monograph No. 3, 2 volumes in 4 parts: 2007 pp.

Timothy A. Pearce

Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia)

by RICHARD S. HOUBRICK. 1985. Smithsonian Contributions to Zoology, no. 403. 131 pp., 62 figs., 33 tbls.

A recurring problem arising in literature pertaining to the ecology, physiology, or natural history of mollusks is doubt about the actual identity of species studied. This problem is more acute with certain groups of mollusks than with others and blame cannot rest entirely with the nonsystematist(s) whose results are in question. It is not their fault that the systematics of abundant and ecologically important or otherwise interesting species are poorly understood. A case in point is the cerithiid genus *Clypeomorus*, species of which commonly occur in high density populations on tropical intertidal shores where they constitute an ecologically important group of microphagous herbivores. The tortuous nomenclatural history of many of the species, and the high degree of interspecific similarity and intraspecific variability, have led to uncertainty of identification in the literature on the ecology and reproduction of members of the genus. These problems in nomenclature and variation, and the identities of the species studied in the nonsystematic literature if that can be determined, have been admirably sorted out by Houbrick.

Richard Houbrick has brought many forms of evidence to bear on the systematics of this very confusing group. In addition to nomenclatural history and detailed study of shells, radulae, and soft parts, he includes data on biogeography, the fossil record, habitat, ecology, and reproduction, in assessing the status of 15 Recent and fossil *Clypeomorus* species. His conclusions are based upon extensive field research, study of thousands of specimens from major museum collections worldwide, and examination of relevant type material. These data are summarized and presented in parallel fashion under subject headings, in tables, and with clearly reproduced photographs for each species treated. This consistent arrangement makes it particularly easy to compare data among species. The extensive lists of material examined would have been less obtrusive if placed in an appendix, but this hardly detracts from the usefulness of the work. Houbrick also calls attention to gaps in our knowledge of *Clypeomorus* where future research opportunities lie. Of special interest to evolutionary biologists are possible examples of sibling species and candidates for incipient speciation.

A refreshing trend in several recent molluscan monographs including this one is the inference of species phylogeny by cladistic methods. In such attempts it often becomes clear that even the most basic information is missing for some species and unresolved polychotomies may result; but even so, hypotheses of relationships are rigorously formulated and presented in a manner conducive to further testing. Unfortunately, typographical errors (otherwise rare in this work) necessitate caution in the interpretation of the cladogram supplied. For example, *Clypeomorus adunca* is scored as beaded in Table 5 (characters 1 and 7) although the description and illustrations indicate it has smooth sculpture. Similarly, *C. subbrevicula* is scored as unbeaded at character 1, but is beaded according to the description and illustrations. On the cladogram (Figure 1) *C. subbrevicula* is indicated as having state 2 of character 1 (beaded sculpture) although states 0 (present) and 1 (absent) are the only possibilities presented in Table 5. Seven character changes are indicated for *C. adunca*, but there are actually 9 if the scores for characters 1 and 7 are corrected. None of these apparent errors change the topology of the resulting cladogram, however, and the thoroughness and clarity used in presenting characters and methods make the errors easy to spot.

The publication of this monograph should make future nonsystematic work on *Clypeomorus* more useful by facilitating the proper identification of this interesting group. Systematic monographs have extra value when they treat organisms that are difficult to identify and are used in nonsystematic work. Good systematics, as exemplified in this monograph, not only inform, but also provide direction for nonsystematic studies.

Michael G. Kellogg

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, not justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the tables.

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.

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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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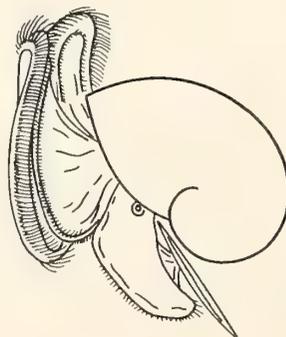
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