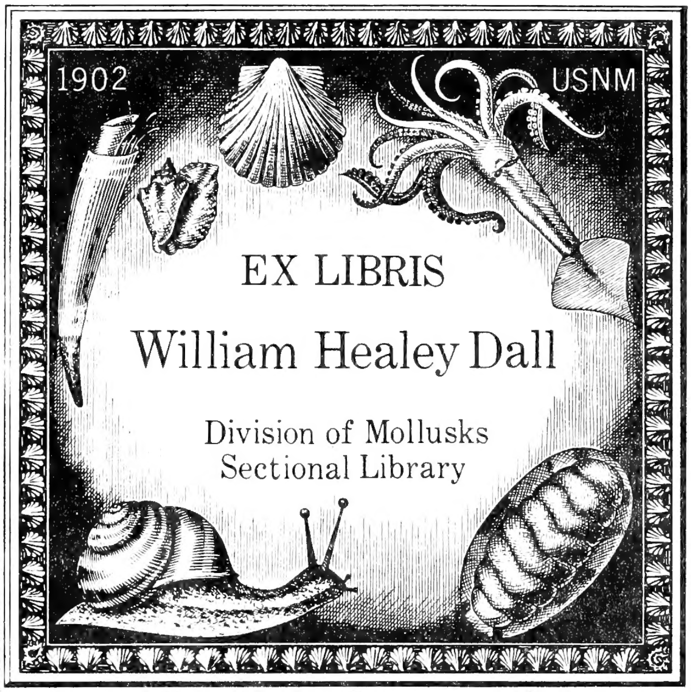

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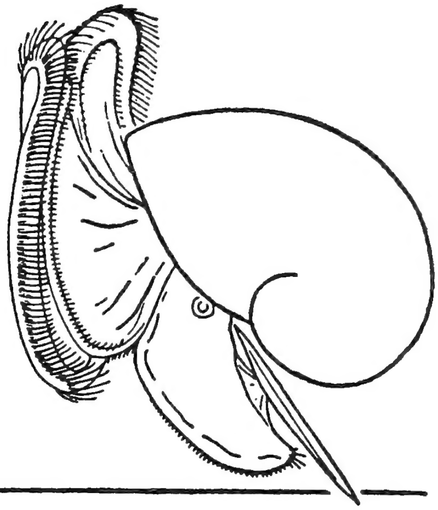

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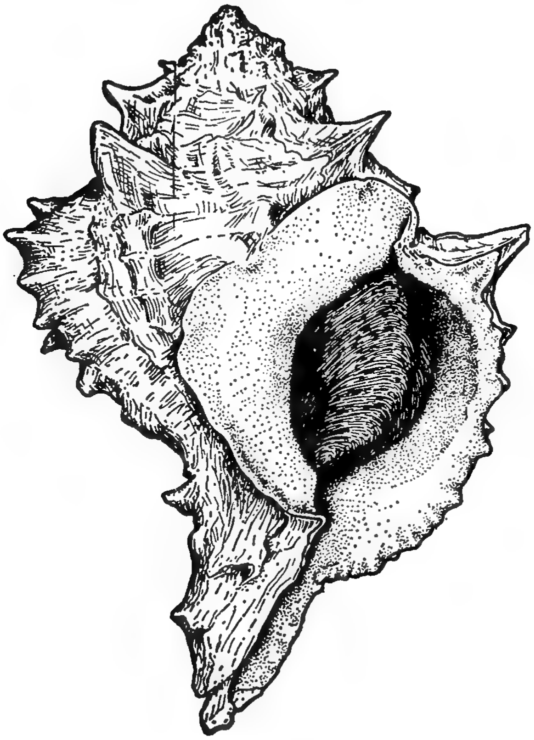

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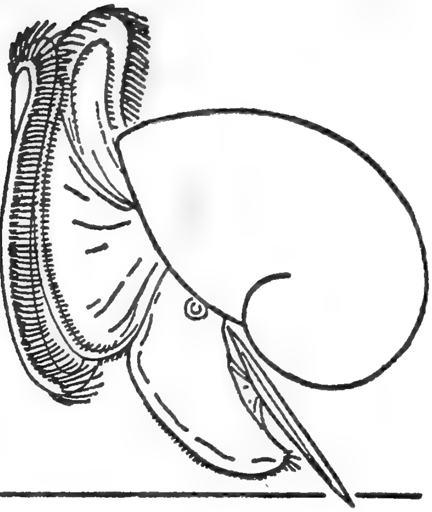

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, *(Subgenus)*
New Taxa

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Integration of Electron Scan and Light Imagery in Study of Molluscan Radulae

BY

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(1 Plate; 4 Text figures)

INTRODUCTION

Our perception of the natural world is strongly molded both by the nature of our sensory apparatus and the characteristics of the investigative tools we employ, to an extent that is seldom explicitly discussed in science. Too often we assume that intellectual objectivity is the only cornerstone of good science. In particular, we place a great deal of faith in our instrumentation.

Optical microscopy (OM), typically utilizing absorption contrast imagery, has long been the standard method of studying the molluscan radula, and most illustrations in the literature consist of camera lucida drawings, composite drawings, or reconstructions based on optical examination. Advances in photomicrography make it possible to produce relatively good photographs containing information not conveyed in artistic renditions, although few workers have used this tool in publication. The advantages of scanning electron microscopy (SEM) have been amply demonstrated in the literature, and Solem (1972) has predicted that these advantages "will combine to make optical examination of radular structure obsolete."

Having experimented with all of the above methods of observation and communication, it is clear to me that, while SEM is the most powerful tool in radular study, (1) different tools of observation (*i. e.*, different imaging processes) show us substantially different things, and (2) no single graphic method of communication can transmit all that our instruments show us.

This paper demonstrates the manner in which data from light and electron scan images can be integrated to provide maximum information about radular form and function. First, I review the uses, advantages, and disadvantages of each method. Second, I present specific examples of alternative views of radulae from the phasianellid *Tricolia pullus* (Linnaeus, 1758) and the trochid *Solariella nuda* Dall, 1896.

Effective basic techniques for mounting radulae for OM and SEM examination are readily available in the literature (see especially Meeuse, 1950; Solem, 1972) and are not reviewed herein. Black-and-white photomicrographs in this paper were taken with an American Optical Series 10 Microstar trinocular microscope with Spencer Model 600 Ortho-Illuminator, AO Photostar Exposure Meter and 35 mm camera back. Scanning electron micrographs were taken with the Cambridge Mark II-A and S4-10 instruments at the U. S. National Museum of Natural History with a Tectronix oscilloscope camera Model C-27.

The following discussion and illustrations are based on morphological and evolutionary studies of radulae of rhipidoglossate marine archaeogastropods (Hickman, 1976, and in preparation). Optical microscopy and scanning electron microscopy are combined to document convergent radular configurations that include: (1) complex within- and between-row basal overlap and interlock systems; (2) within-row shaft interlock and cusp interlock systems; (3) a variety of modifications to simultaneously accomplish close packing of teeth when the radula is collapsed and maximum reach when it is in use; (4) disproportional development of the outermost lateral tooth cusp, in extreme cases with compensatory development of radular asymmetry; (5) systems of pivotal or articulatory plates in the hinge regions between the portions of the radula functioning along different major axes; (6) modifications and specializations of marginal teeth suggestive of as yet undocumented selective deposit-feeding strategies.

Some of the above patterns are similar to those documented in other groups of mollusks. The original studies of adaptive convergence were conducted by Solem (1971, 1972, 1973, 1974) on the radulae of land snails. His research elegantly established the utility of SEM in radular studies. Similar surveys are now available for cephalopods (Solem & Richardson, 1975; Solem & Roper, 1975) and nudibranchs (Bertsch *et al.*, 1973; Bertsch & Ferreira, 1974; Ferreira & Bertsch, 1975). Preliminary work on the rhipidoglossate radula has revealed a much more complex set of patterns. This is, in part, because the rhipidoglossate radula is mechanically and morphologically the most complex type of molluscan radula.

The typical rhipidoglossate radula is unique in possessing a large number of long slender marginal teeth, arrayed symmetrically on either side of the flat central portion of the ribbon. The marginal "books" of teeth are erected by outfolding of the ribbon and subsequently collapsed over the central part of the ribbon during the feeding stroke, as the ribbon passes over the tip of the odontophorial cartilage (Ankel, 1938; Eigenbrodt, 1941; Fretter, 1965; Fretter & Graham, 1962; Nisbet, 1973; Graham, 1973). The central part of the ribbon is specialized primarily for various kinds of food preparation and acts along an axis parallel to the length of the ribbon, while the marginals engage primarily in food gathering and act through a broad arc perpendicular to the length of the ribbon.

For both OM and SEM examination it is necessary to perform delicate manipulations on the radula (*e. g.*, folding out or removing parts of the marginal books, separating longitudinal and transverse rows) in order to minimize overlap of teeth and observe individual tooth morphologies and interrelationships. Because SEM viewing requires dry specimens coated with a conductive metal while optical mounts are made in a fluid medium, different configurations inevitably result from the two basic kinds of preparation.

The most important single complementary difference between SEM and OM viewing of the rhipidoglossate radula is related to the transparent but differentially mineralized and tanned nature of the chitinous teeth and ribbon to which they are attached. Because SEM viewing is restricted to surface features, it is possible to eliminate the confusion of multiple overlapping that occurs in standard OM preparations. On the other hand, OM permits study of completely obscured teeth and parts of teeth that would never appear in SEM preparations as well as enabling observation of internal structure patterns related to readily visible differential mineralization and differential tanning revealed through staining.

LIGHT MICROSCOPY

The decrease in depth of field and resolving power that accompany increased magnification in optical systems are among the most serious problems in the traditional method of studying and illustrating radulae, although these are spectacularly minimized in the finest modern laboratory microscopes. Ease of varying illumination parameters, and, in particular, the use of color filters to bring out detail and contrast (Figure 8b), enhance the data gathering potential of such instruments and play a key role in black-and-white photomicrography. Problems of photomicrography related to adaptation of camera optics (Solem, 1970) are eliminated in trinocular systems utilizing built in photographic objectives and rapid means of establishing parafocality between visual image and film plane.

An additional, often cited, disadvantage of light microscopy lies in the fact that the radula must be mounted ("squashed," in the words of the most severe critics) between 2 pieces of glass and viewed from a single position. Limited angle of observation may be compensated by dissecting portions of the radula so that individual teeth are mounted in a variety of positions as well as by use of depression slides or coverslip supports so that the radula retains three-dimensionality within the medium.

As suggested in the introduction, the optical properties of radulae present both advantages and disadvantages. In the complex rhipidoglossate radula in particular, there is a great deal of overlapping of elements, making it time consuming and difficult to sort out the morphology and interrelationship of individual teeth. In careful optical preparations, however, it is possible to determine relationships by focusing at different levels within groups of teeth and individual teeth in a way that is not possible in SEM viewing, which is restricted to surface features. OM is of great importance in detecting structures that can be subsequently explored more effectively with SEM, but which do not appear in preliminary SEM preparations.

One of the most important advantages of OM study of the rhipidoglossate radula is the potential amount of preparation time available for mounting in a fluid medium. Using a relatively low-viscosity water-soluble medium (*e. g.*,Turtox CMCP-10), one can spend an hour or more dissecting and arranging the radula before adding the cover slip. Even some of the more viscous media allow more preparation time than is available while drying a radula for SEM viewing. The more viscous the medium, the more likely that an arrangement will be preserved when the cover slip is added, although interesting and fortuitous configurations and structures may be revealed by turning and rotating of elements that may result. Distortions resulting from shrinkage of the radular membrane during drying for SEM viewing may likewise be either detrimental or fortuitous, the important point being that the two methods of preparation inevitably provide different configurations offering different kinds of information.

Differences in the flexibility and hardness of different parts of a radula or of individual teeth must evolve in close relationship to the mechanical constraints on radular functioning and the feeding habits and substrates of individual species. Thus OM observations of mineralization and staining patterns are of importance in radular studies. Documentation of mineralization in radular teeth is primarily restricted to the more spectacular instances of polyplacophorans and docoglossate archaeogastropods in which salts of iron and silicon increase tooth hardness (Jones *et al.*, 1935; Carefoot, 1965; Towe & Lowenstam, 1967; Runham *et al.*, 1969), although various minerals may be added during the transformation of the soft first-formed radula into the toughened and hardened active portion of the radula (Gabe & Prenant, 1957, 1958). Differential tanning, or formation of protein cross-linkages within the primary chitin structure, is indicated by differential staining patterns. For example, tooth bases are often heavily stained, while the slender flexible shafts of long marginal teeth often do not stain at all.

There are three major graphic methods of presenting OM observations of radulae: the camera lucida drawing, the composite drawing or reconstruction, and the photomicrograph. Camera lucida drawings provide faithful outline reproductions of tooth proportions and are a simple rapid means of illustrating a single half-row of teeth for comparative taxonomic purposes. Such drawings do not incorporate variations within an individual or population, and, as line drawings of complex objects, they often contain a great deal of subjectivity or ambiguity, or both. They are most useful for showing cusps and seldom show details of tooth bases. Camera lucida drawings that attempt to show three-dimensional structure and overlapping are often difficult to interpret.

Composite line drawings and reconstructions also contain a strong subjective element, but if camera lucida is used to establish proportions, such drawings may be extremely useful as summaries of observations at a variety of magnifications, of different portions of a single radula, or of different radulae. Such reconstructions can incorporate data from electron scan images as well as light images.

Photomicrography is most useful for producing a "true" image of the radula. Light micrographs are not particularly informative, however, if there is too much loss of resolution and depth of field in the image. Few authors have published light micrographs of radulae, but see McLean, 1971, for a series of informative light micrographs of turrid radulae. Micrographs at lower magnifications are particularly efficient for documenting basic taxonomic characters (number of longitudinal rows of teeth, numbers and kinds of transverse elements, gross morphology, etc.). Micrographs are also an important means of documenting more detailed information and discoveries, and it should not matter that part of an image is blurred if the structure of specific interest is clearly resolved. Indications of differential strength and hardness in teeth resulting from tanning and mineralization are best recorded through light microscopy.

Alternative optical methods to standard absorption contrast may also be useful in radular study. Maes (oral communication, 1977) has experimented with low angle incident illumination to produce some remarkably three-dimensional photomicrographs of glycerine jelly mounts of rachiglossate radulae (see Orr, 1956; Maes, 1967). Phase contrast microscopy is extremely useful for producing in-focus contrast in unstained preparations (as opposed to the phase contrast that can be achieved in ordinary light microscopy by defocusing). Mills (1977) has published some excellent phase contrast photomicrographs of toxoglossate radulae. Nomarski optics may also prove useful for examining some aspects of surface contour and should be explored as Nomarski systems become more widely available in this country.

SCANNING ELECTRON MICROSCOPY

Scanning electron microscopy has largely replaced light microscopy as the preferred tool for radula study during the past decade. Its most important advantages lie in broadening the potential scope of investigations, particularly at magnifications beyond the resolving power of light microscope optics.

In functional morphological studies, SEM has become an indispensible tool, not only in its ability to explore microtopography from various angles, but also in the inherent ability of the incident electron probe to penetrate and explore narrow fissures and deep cavities that cannot be exposed by light.

Research on functional morphology of the molluscan radula has focused on the obvious food-preparing and food-gathering operations of the teeth and their relationship to design. These aspects are ideally examined from different angles with SEM and require some knowledge of the radula in functioning position. Less attention has been paid to the more routinely mechanical economics of occupying space. Solem (1971, 1974) and Solem & Roper (1975) have recognized the need to fold teeth together efficiently to prevent interference with food passage and have identified several adaptations in land snails and cephalopods (grooving, curved fit surfaces) that function in tooth compaction. In the complex rhipidoglossate radula, occupation of space might be more profitably explored in terms of designs that simultaneously satisfy maximum coverage of space by erected marginal teeth (as a function of tooth lengths and degrees of arc covered) during sweeping activities and minimum occupation of space when collapsed. Interlocking and complex lock-and-key fits between tooth bases, shafts and cusps, viewed heretofore only as functioning in stress support, also appear to play an important role in the economics of space occupation, particularly in the complex rhipidoglossate radula of marine archaeogastropods. These relationships are most effectively investigated by contrasting SEM data from preparations with marginal teeth erected with OM data from preparations with teeth in overlapping and tightly folded position.

Although the great depth of field and high resolution of the electron scan image are impressive, aesthetically satisfying, and "state-of-the-art" in appearance, SEM images do not automatically contribute anything useful to comparative taxonomic research and can be detrimental and confusing if they have been produced from different viewing angles and cannot be compared. Mounting between 2 pieces of glass for optical microscopy produces one of the most standard methods for comparing radulae of closely related congeners or for studies of variation patterns within populations, species, or along the length of a single radula. If SEM is used in illustrating strictly taxonomic studies, comparability of images should be maintained by standardizing the viewing angle and mounting the radula flat.

Electron micrographs serve as the primary method of recording data during SEM viewing and are the usual means of illustrating published studies. Composite drawings based on a series of SEM images could be used to greater effect. Stereoscopic paired micrographs are invaluable in interpreting SEM imagery. Low magnification stereoscopic pairs of entire preparations are particularly helpful for planning efficient viewing strategies.

THE RADULA OF *Tricolia pullus*

The major features of the radula of the phasianellid *Tricolia pullus* are illustrated in Figures *1* to *4*, 11, and 12.

I have chosen this radula for illustration for two reasons: (1) it has been known for nearly a century and has been figured by previous authors (Troschel, 1878: plt. 18, fig. 10; Pilsbry, 1888: plt. 61, fig. 2; Robertson, 1958: plt. 138, fig. 3) and (2) it contains several features that are difficult to interpret but potentially important in understanding basic functioning patterns of the rhipidoglossate radula.

Drawings of the *Tricolia pullus* radula based on light microscope examination (Figure 10) establish the basic pattern of dentition and overlap of an oval rachidian flanked on either side by 5 strongly cusped, progressively narrower laterals with expanded overlapping bases and series of numerous marginals. The inner marginals have

Explanation of Figures *1* to *9*

Tricolia pullus (Linnaeus, 1758). USNM 179033

Figure *1*: Central portion of whole mount. OM × 100

Figure *2*: Central and inner lateral teeth, illustrating transverse basal overlap system. SEM × 570

Figure *3*: Detail of inner marginal cusp and rectangular "lateromarginal plate" with adjacent marginal teeth removed. OM × 300

Figure *4*: Isolated inner marginal tooth, demonstrating that "lateromarginal plate" is the tooth base. Note that cusp was broken during manipulation. OM × 300

Solariella nuda Dall, 1896. USNM 209300

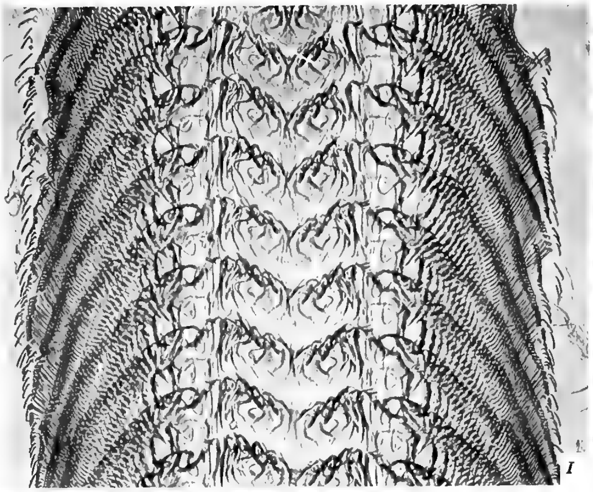
Figure *5*: Detail of first lateral tooth from which cusp is broken, revealing basal interlock with central tooth (lower right) and basal interlock with second lateral tooth (upper left). SEM × 760

Figure *6*: Detail of lateromarginal plates where marginal teeth have been removed. OM × 160

Figure *7*: Detail of lateromarginal plates with first marginal teeth folded out, other marginals removed. OM × 160

Figure *8*: Central portion of folded whole mount with a. normal illumination and b. red filter to enhance contrast. OM × 115

Figure *9*: Low angle side view showing a. erected marginal teeth; b. lateromarginal plate with thin membranous rudimentary cusp; c. cuspless lateromarginal plate; d. grooves and ridges on heavy outer lateral tooth; e. depression on rachidian accommodating cusp of following rachidian. SEM × 225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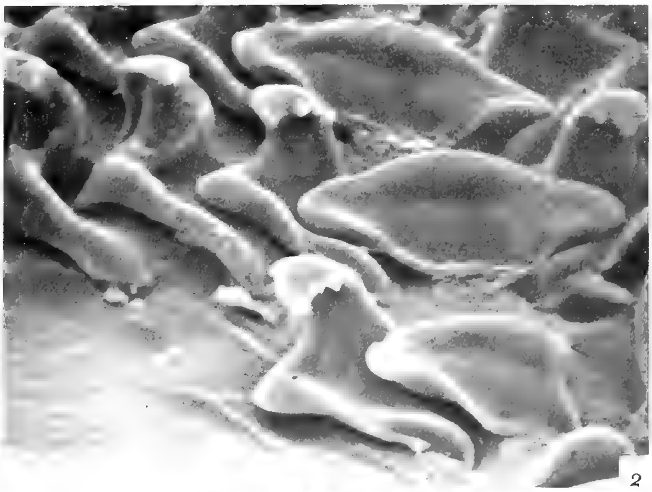
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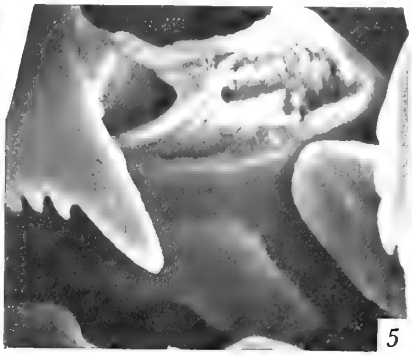
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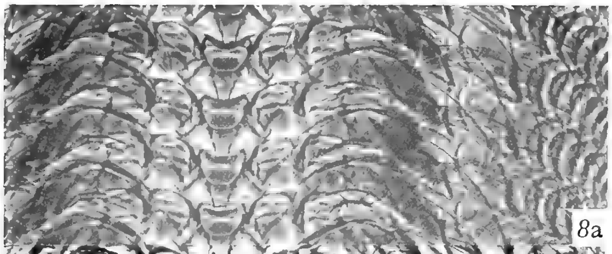
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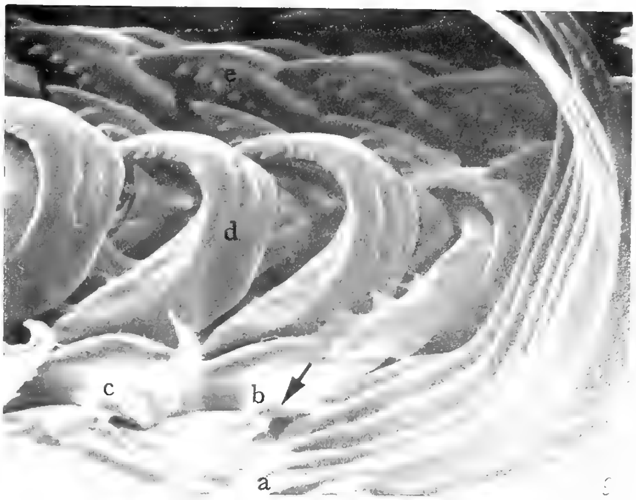

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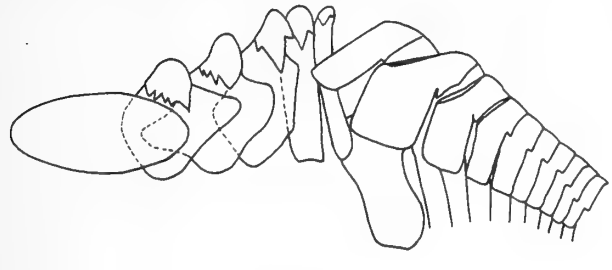

Figure 10

Line drawing of a part of a half-row of the radula of *Tricolia pullus*, based on light microscopy, after Robertson (1955).

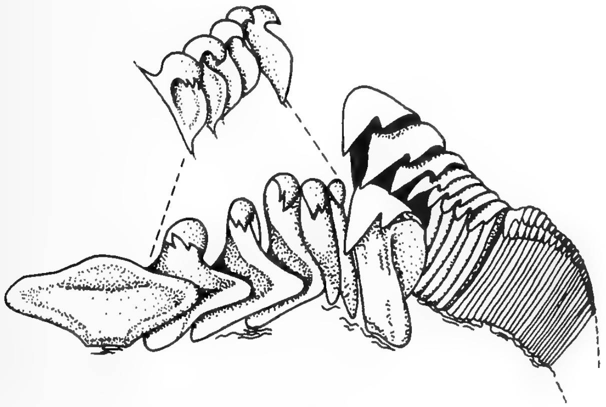

Figure 11

Reconstruction of part of a half-row of the radula of *Tricolia pullus*, from light and scanning electron microscope imagery. Inset of lateral teeth shows semi-profile view of cusps.

a strong primary cusp and a short secondary cusp along the outer margin. The outer marginals have a single, narrow, serrate cusp. For comparative taxonomic purposes, drawings of this kind provide excellent documentation from a standard vantage point of characteristic configurations or patterns (Robertson, 1958: plt. 138, figs. 3 - 6). Although cusp details are depicted, the drawings are basically two-dimensional outlines that do not attempt interpretation of the thickness of teeth or parts of teeth, the manner in which teeth are attached to the radular ribbon, or the significance of overlapping elements.

A photomicrograph of the radula of *Tricolia pullus* (Figure *1*) illustrates the kind of image upon which the line drawing of Figure 10 was based. The photomicrograph contains a great deal more complexity and additional kinds of information, the most obvious of which are the patterns of multiple overlap of transverse rows and the variation in optical properties of different radular elements. Micrographs such as this and the comparable one for *Solariella nuda* (Figure *8*) provide a rapid means of documenting sources of variation within longitudinal rows, including (1) random variation in actual morphology, as in the number of cusps, resulting from developmental differences, (2)random variation in apparent morphology resulting from viewing a tooth from a slightly different angle, and (3) systematic variation along the length of the ribbon resulting from tooth wear.

It is also evident that parts of the absorption contrast image are subject to more than one interpretation. A particularly interesting case of interpretational ambiguity arises from a prominent series of dark-staining rectangular structures between the outer lateral and inner marginal teeth in a whole mount of the *Tricolia* radula. Robertson (1958) interpreted the structure as a cuspless tooth and proposed the name "lateromarginal plate" for it. Marcus & Marcus (1960) rejected Robertson's interpretation and suggested that the plate is the base of the innermost marginal tooth. Dissection of the radula to isolate individual teeth confirms the latter view, and photomicrographs of the first lateral tooth with its enlarged rectangular base appear in Figures *3* and *4*.

Examination of large numbers of rhipidoglossate radulae, however, does reveal the presence of a cuspless structure between the lateral and marginal teeth in many archaeogastropods (Hickman, unpubl.), and the name lateromarginal plate is perfectly applicable. It is also interesting to note that there are a number of overlooked illustrations of and independent allusions to these cuspless structures in earlier literature (*e. g.*, Sars, 1878, *Margarites*; Pilsbry, 1889, *Trochus*, *Clanculus*; Troschel & Thiele, 1891, *Moelleria, Puncturella*; Schepman, 1908, *Solariella;* Torr, 1914, *Emarginula, Lucapinella, Megatebennus*).

In many cases the plate is clearly a pivotal or articulatory structure, either supporting or holding the bases of the marginal books of teeth as they are erected and collapsed during feeding. In several trochid genera (*e. g.*, *Margarites, Calliotropis, Bathybembix*) rudimentary cusps are associated with the plate, suggesting its independent derivation through progressive enlargement of the base and reduction and loss of the cusp (Hickman, in preparation).

SEM examination adds significantly to our understanding of the *Tricolia* radula, particularly in interpretation of overlapping structures. Figure *2* reveals a complex and relatively heavy basal stress support system whereby the stress applied to any one tooth may be spread outward to other teeth within the same transverse row. In addition to the basal overlap features, Figure *2* also reveals interlock features higher on the teeth that are more likely to function in compaction of the radula when it is not in use. Note the potential fit of the thickened convex ridge on the shaft of the third lateral into the corresponding pocket beneath the cusp of the second lateral in Figure 2.

A reconstruction of the *Tricolia* radula (Figure 11), based on a series of 7 SEM images from a variety of angles and magnifications, including 2 stereo pairs, also shows a complex system of interlocking of the inner marginal cusps in which the secondary outer cusp fits into a groove on the flattened top of the neighboring primary cusp.

THE RADULA OF *Solariella nuda*

The radula of *Solariella nuda* has not been figured previously. Radulae have been illustrated by line drawings for at least 15 species of *Solariella*, however (SARS, 1878; TROSCHEL, 1878; MARTENS & THIELE, 1903; SCHEPMAN, 1908; ODHNER, 1912; POWELL, 1951; GALKIN, 1955; MCLEAN, 1964), and some of the major features of the solarielline radula, as heretofore understood, are illustrated in a line drawing of *Solariella delicata* Dall (Figure 12).

Recurrent characteristic features of the line drawings in the literature and features cited in accompanying texts, all based on optical examination, include (1) the shortness of the radula, which is sometimes less than twice as long as it is wide; (2) the small number of marginal teeth (approximately 10 per half-row); (3) the prominent dip at the center of each transverse row; (4) the prominent, coarsely serrated cusp of the rachidian; and (5) the apparent restriction of serrations to the outer margins of the first and second lateral teeth.

Other features are ambiguous or variably interpreted from one drawing to another, particularly with respect to basal overlapping and the shapes of the third, fourth, and fifth lateral teeth, if these are recognized as being present.

The reason for the ambiguity lies in the fact that the marginal teeth in the folded solarielline radula multiply overlap and obscure all but the rachidian and inner 2 lateral teeth in an unmanipulated preparation. This is illustrated by a photomicrograph of the folded radula of *Solariella nuda* (Figure 8).

When the marginal books of teeth are folded out or carefully removed, a broad-based third lateral tooth with a serrate, long, medially-directed cusp is revealed, as well as a narrow but heavily based and extraordinarily long, cusped fourth lateral tooth. In addition there is a longitudinal series of rectangular lateromarginal plates (Figures 6, 7) against which the marginal books articulate. I have found similar series of lateromarginal plates in 7 other solarielline species, although SCHEPMAN (1908: plt. 9, figs. 8, 9) is the only author to have recorded them.

A SEM preparation in which the marginal teeth have been removed for viewing from the side (Figure 9) presents an alternative view of the lateromarginal plates of *Solariella nuda*. Note that, although the posterior 2 plates have a small hooked projection on their inner margins,

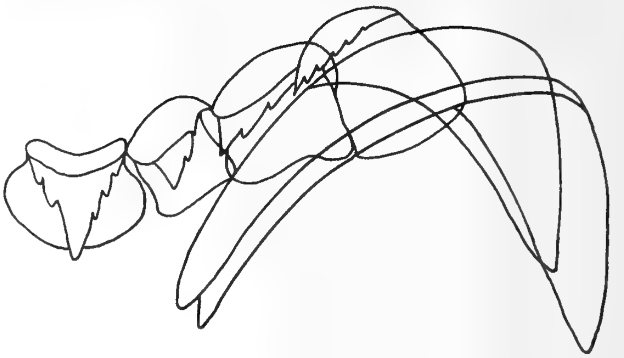

Figure 12

Line drawing of a half-row of teeth from the radula of *Solariella delicata*, redrawn from GALKIN (1955) and retaining ambiguity of line from his drawing.

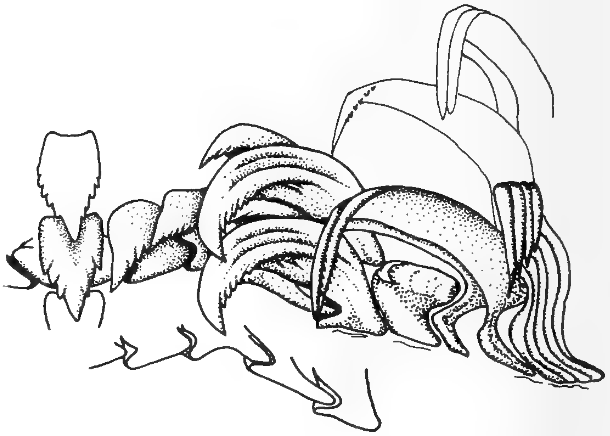

Figure 13

Reconstruction of the basic solarielline dentition pattern as exemplified by *Solariella nuda*, from light and scanning electron microscope imagery. A diagrammatic representation of the basal interlock system appears beneath the main part of the reconstruction.

they are uncusped; while the next anterior plate has a thin "cusp" that fits compactly beneath the folded, large, heavy blade of the fourth lateral tooth of the next-most anterior row.

By making an additional OM preparation of the radula of *Solariella nuda*, it became apparent that the "cusp," when present on the lateromarginal plate, is a flexible membranous structure that does not resist stress and can be bent easily through an arc of 180° without any movement of the fixed lateromarginal plate. Although the vestigial cusp looks "solid" in the SEM image, the wrinkling and filamentous projections from the trailing edge suggest its extreme thinness in contrast to the heavy outer lateral. From both SEM and OM as well as physical manipulation of the radula with minuten insect pins, it appears that the marginal books are supported, probably through fine muscular adjustments (Nisbet, 1973), in erect position against the thick outer edge of the lateromarginal plate as they nearly are at the arrow in Figure 9.

An interesting feature revealed by SEM that does not appear in OM preparations is the grooving in the upper surfaces of the fourth lateral teeth. In folded position these grooves accommodate closer, more economical packing of the marginal books. Each of the broad thin marginal tooth blades is convex on its inner surface and concave on its outer surface. This design simultaneously facilitates close packing of the collapsed marginal books of teeth into the folded lateral tooth complex and confers greater strength to each of the thin marginal blades than it would have if it were perfectly flat. Also note how the depression at the top of each rachidian accommodates the top of the cusp of the overlapping rachidian and base immediately posterior.

As in the *Tricolia* radula, there is a complex basal interaction system in the solarielline radula. Unlike the simple *Tricolia* overlap system, however, the solarielline system involves complex interlocking. It cannot be studied effectively using SEM because the broad cusps completely obscure the tooth bases from nearly all angles of viewing when the teeth are in interlocked position. Fortuitous breakage of an inner lateral cusp confirms the nature of the interlocks between the first lateral and the rachidian on one side and the second lateral on the other (Figure 5).

A reconstruction of the radula of *Solariella nuda* (Figure 13), based on a combination of light images and SEM images, including stereoscopic pairs, is offered to illustrate some of the major features of the solarielline radula.

SUMMARY

Although SEM provides many new possibilities for understanding morphology and function of the molluscan radula, it does not replace OM as a source of data. Differences in specimen preparation as well as differences in imaging processes lead to different kinds of data, so that it is particularly instructive to use both in radula studies. The resulting information, likewise, can be graphically transmitted most effectively by combining photomicrographs, scanning electron micrographs, camera lucida outline drawings, and composite diagrams and reconstructions.

Applied to the complex rhipidoglossate radula of marine archaeogastropods, exemplified herein by *Tricolia pullus* and *Solariella nuda*, these methods are elucidating a broader and more complex range of structural patterns than has been documented in other mollusk groups.

ACKNOWLEDGMENTS

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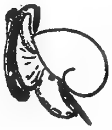

A New Species Tentatively Referred to *Antonietta*, *Antonietta janthina*, from Japan

(Nudibranchia : Eolidoidea : Facelinidae)

BY

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(4 Text figures)

THE FIRST SPECIMEN of the species which forms the subject of this paper was collected by Baba in March 1937, when he lived in the Amakusa Marine Biological Laboratory, Kyushu University. The animal, though seemingly distinctive in the vermilion rhinophores and purple branchiae, could not at that time be identified. In later years more specimens were collected from some other stations of Japan which enabled him to continue a taxonomical study of the species. Meanwhile, Hamatani who was the collector of one of these latter specimens came to join with Baba in order to conduct the study of internal organs of the species from serially sectioned material. A new taxon, *janthina*, was finally established by the two authors and it was tentatively referred to *Antonietta* Schmekel, 1966 from the Mediterranean Sea, mainly because of the patterns of liver branchings.

Antonietta janthina Baba & Hamatani, spec. nov.

(Japanese name: Murasaki-mino-umiushi)

(Figures 1 to 4)

Distribution: Pacific coast of middle and southern Japan: Hayama, Sagami Bay; Seto, Kii; and Tomioka, Amakusa. Japan Sea coast of middle Japan: Ushitsu, Toyama Bay.

Holotype: Collected by Hamatani from the shore of Yuzaki, vicinity of the Seto Marine Biological Laboratory, 15 August 1962. After taking a picture of the living animal by Baba, it was fixed and prepared in serial horizontal sections.

Additional data referred to are as follows: One specimen collected and figured by the Biological Laboratory, Imperial Household, from shallow water of Samejima near Hayama, Sagami Bay, 19 March 1948. This was used especially for demonstrating jaws and radula. One specimen collected and figured by Baba from the outer shore of Magarizaki, vicinity of the Amakusa Marine Biological Laboratory, 2 March 1937. The animal was found feeding on a light brown hydroid colony (cf. *Hydractinia epiconcha*) which covered the surface of a snail shell housing a hermit crab. Two specimens collected and figured by Mr. Abe and other members of the Takaoka Biological Club, from the shore of Hime, near Ushitsu, Toyama Bay, 10 August 1971.

DESCRIPTION

External Form: The holotype measures 10 mm in length. The general body form is fundamentally as usual in the family Facelinidae. That is, the body is slender, the oral tentacles are elongated, the rhinophores are shorter,

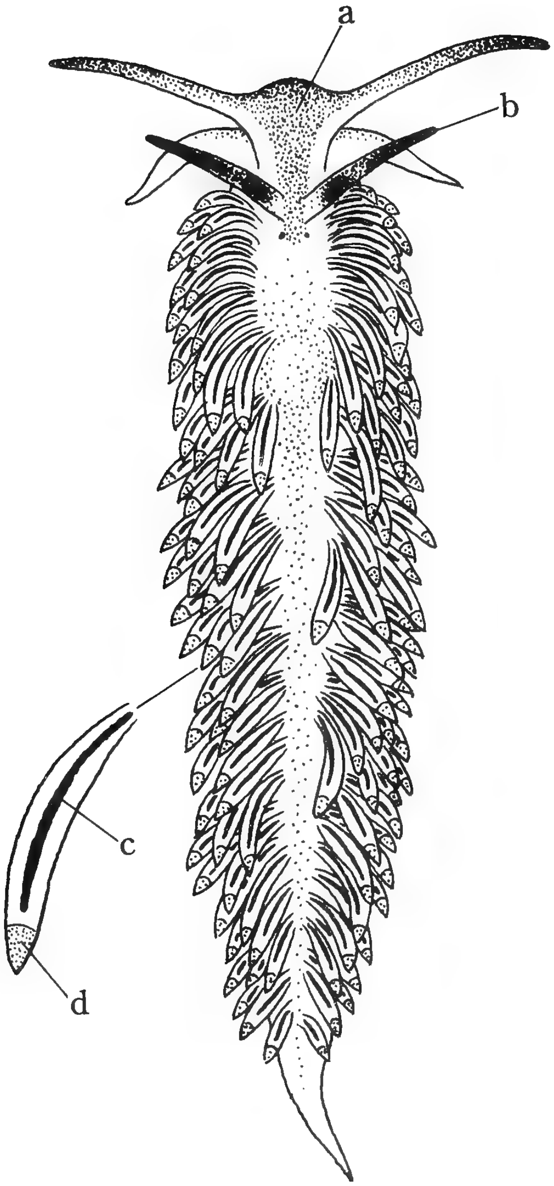

Figure 1

Antonietta janthina Baba & Hamatani, spec. nov.
from Seto, Kii, Japan

Living animal from dorsal side, length (Ac) 10 mm

a – orange yellow head
b – vermilion rhinophore
c – purple diverticulum
d – pale yellow cap

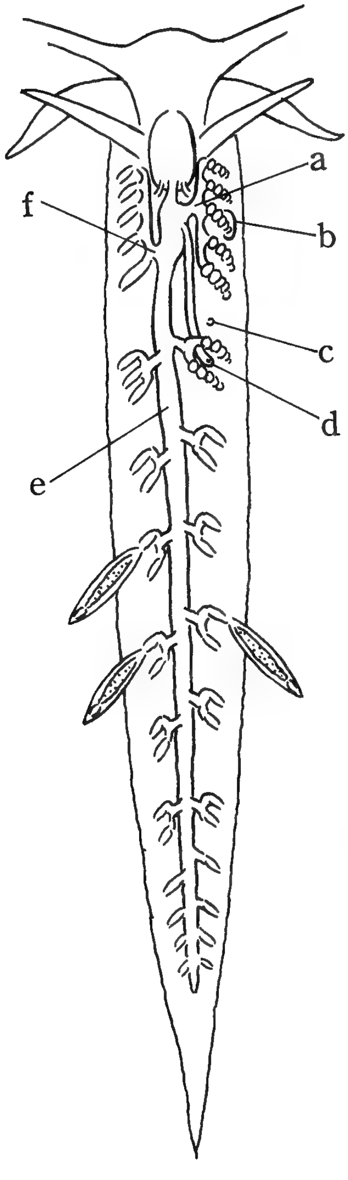

Figure 2

Antonietta janthina Baba & Hamatani, spec. nov.
from Seto, Kii, Japan

Digestive system; salivary glands not shown

a – right liver
b – genital orifices
c – nephroproct
d – anus
e – left posterior liver
f – left anterior liver

and the foot forms tentaculiform corners anteriorly. The rhinophores themselves are smooth on the surface. The tail is short and tapering behind.

The liver system is more similar in constitution to *Antonietta* (see SCHMEKEL, 1966), and *Palisa* (see EDMUNDS, 1964) than to *Learchis* (see BABA, 1969) which is synonymized by BURN & NARAYANAN (1970) with *Caloria*. The right liver (and the partner on the left side) is formed of 5 simple oblique branches, and the arrangement of branchial papillae on them is shown as 3, 5, 5, 6, and 8, successively. The left posterior liver is differentiated on each side into 6 horseshoes followed by 4 short oblique rows. The cleioproctic anus lies in the middle of the 1st right horseshoe which contains 5 papillae in each of two legs. The papillae decrease in number in the succeeding horseshoes. They are simply elongated fusiform. The nephroproct is interhepatic. The genital orifices are found below the middle of the right liver branches.

Coloration: The median part of the head is tinged with orange yellow. The oral tentacles are also orange yellow though this color is more or less accentuated towards the tip. The rhinophores are prominently vermilion-tinted except at their midlength where this color tends to disappear. The vein (= liver diverticulum) of the papillae is purple throughout its length, and not marked

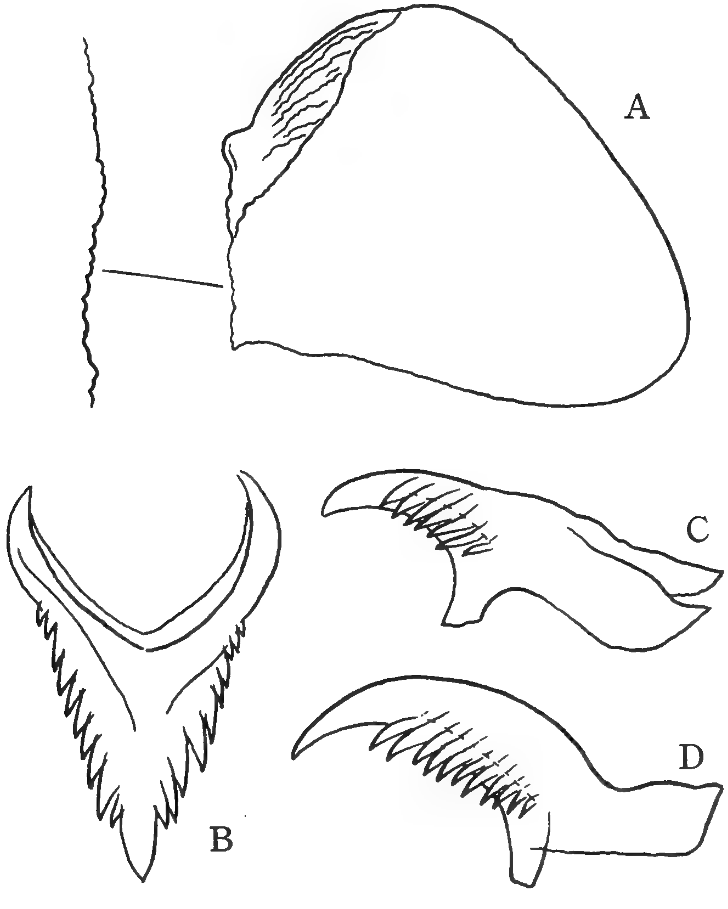

Figure 3

Antonietta janthina Baba & Hamatani, spec. nov.
from Hayama, Sagami Bay, Japan

A: Right jaw with the jagged edge enlarged (× 60) B - D: Teeth in different views (× 520)

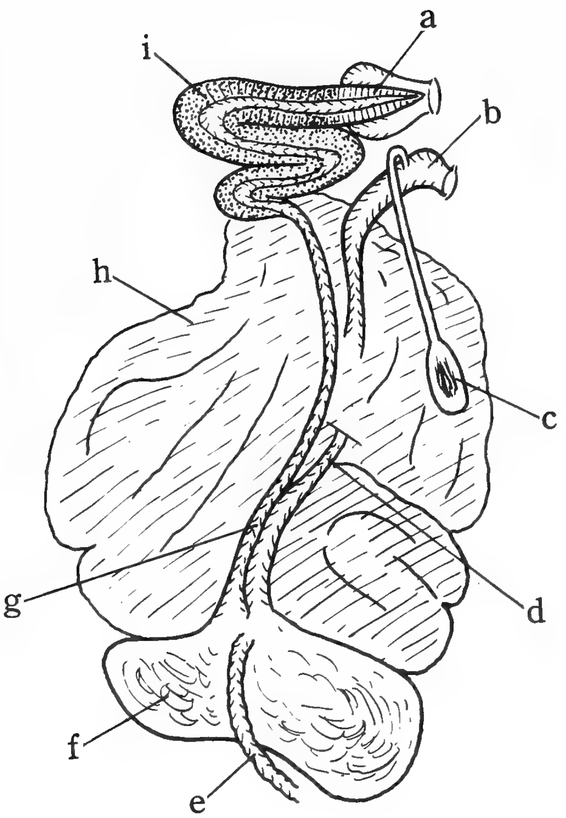

Figure 4

Antonietta janthina Baba & Hamatani, spec. nov.
from Seto, Kii, Japan

Genital system from dorsal side (× 40)

a – penis b – outer oviduct c – spermatocyst
d – inner oviduct (distal part not defined)
e – hermaphrodite duct f – ampulla
g – muscular part of vas deferens
h – accessory female gland mass i – prostatic part of vas deferens

distally with a melanin black spot as shown in *Caloria* (see Haefelfinger, 1960) and *Learchis* (see Baba, 1969). The cap of the papillae is tinted pale yellow. The ground color of the integument (back, sides and sole) is fleshy white. The pericardial prominence is opaque white. Also there are irregular mottlings of opaque white on the median line of the dorsum. The anterior margin of the foot is slightly orange yellow. The tail is colorless.

Internal Anatomy: The mouth parts were studied on a specimen from Sagami Bay. As in *Learchis* and *Antonietta*, the jaws have no dorsal indentation (in *Caloria* these are indented dorsally). The jaw edge is jagged now, but details of denticulation could not be defined exactly (in *Antonietta* the jaw edge is said to be smooth). The radular formula is 35 × 0 · 1 · 0. The central tooth is typically cuspidate as in that of *Antonietta*, and bears 8-11 denticles on either side of the highly produced median cusp. As in *Learchis* and *Antonietta*, the penis of the holotype is conical, unarmed, and without an accessory penial gland. The distal portion of the vas deferens forms a prostate. In the holotype there occurs a single bursa (=spermatocyst) attached to the outer oviduct (in *Learchis* there is a single bursa, and in *Antonietta* it is shown that there are 2 bursae on the female duct; see also Miller, 1974).

DISCUSSION

It seems still difficult to identify the genera (and species) of the family Facelinidae satisfactorily (see Edmunds, 1970 and Miller, 1974). Here the new species ***janthina*** was referred to *Antonietta* Schmekel, 1966 (Type: *A. luteorufa* from Naples) merely for the horseshoe-shaped composition of the left posterior liver branches, for the non-indented jaws, and for the unarmed penis not accompanied by an accessory gland. Actually there may be seen some minor differences existing between the genital systems of the 2 species, *A. luteorufa* and ***A. janthina***.

According to Burn & Narayanan (1970) the southwest Pacific species *Learchis indica* Bergh, 1896 (see Baba, 1969) is synonymous with the Indian form *Eolis militaris* Alder & Hancock, 1864 (see also Miller, 1974); furthermore, the genus *Learchis* Bergh, 1896 constitutes a junior synonym of *Caloria* Trinchese, 1888 known from the Mediterranean Sea (Type: *C. maculata*; see Haefelfinger, 1960). Then, *Caloria* (= *Learchis*) is distinguished from *Antonietta* by the left posterior liver which is formed of clusters (not horseshoes) of branches.

The species *Learchis poica* Marcus & Marcus, 1960 (from Miami) and *Palisa papillata* Edmunds, 1964 (from Jamaica and Miami) are similar to *Antonietta* in the type of the liver system, but they are distinguished from the latter, respectively, as follows: *Learchis poica* is provided with an accessory gland to the penis, and *Palisa papillata* has the rhinophores covered with small papillae on their posterior surface.

A thorough re-examination of the interrelationship between the above-mentioned genera (and species) is, therefore, to be expected in the future.

SUMMARY

1. A new species, *Antonietta janthina*, is suggested from Japan.

2. Externally this new species is especially distinctive in the vermilion rhinophores and purple diverticula of the branchial papillae.

3. Anatomical accounts regarding the jaws, radula, liver system and genitalia of this new species are given, together with some taxonomical comments.

4. This new species is assigned to the Mediterranean genus mainly for the horseshoe-shaped composition of the left posterior liver branches. The penis is unarmed, and there is no accessory gland to this organ.

ACKNOWLEDGMENTS

One of the authors (Baba) wishes to express his appreciation to the Chief of the Biological Laboratory, Imperial Household, and to Mr. Takeo Abe of the Takaoka Biological Club, for giving him the opportunity of identifying specimens collected by them.

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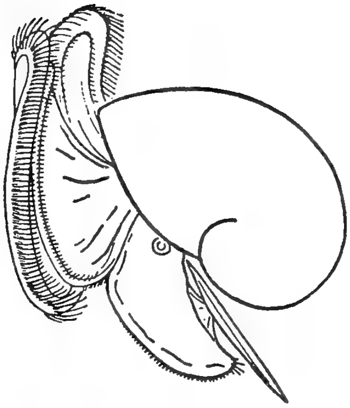

A Sand-Dwelling *Elysia* from Guam

(Opisthobranchia : Sacoglossa)

BY

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(5 Text figures)

IN OCTOBER, 1971, the authors were searching for opisthobranchs in a large bed of the green alga *Caulerpa racemosa* (Førskal) J. Agardh when 2 specimens of a new species of *Elysia* were found. Since that time, 27 additional specimens have been collected in the same area inside Cocos Lagoon, Merizo, Guam, Mariana Islands.

Elysia arena Carlson & Hoff, spec. nov.

Description: The animals are from 5.0 to 32.0mm long. A 23.0mm animal was 5.0mm wide at the widest point with parapodia erect. With parapodia completely opened, a 16.0mm preserved animal is 14.0mm wide; almost as wide as it is long and it is rectangular rather than triangular.

The animal (Figure 1) is very heavy bodied, covered with conical projections on the head, rhinophores, and parapodia. The largest projections are about midway down the parapodia. The parapodia are high, irregular in height, undulating on edges, held fairly close but not tight and at times have several openings – frequently with an opening at the highest point. There is no division between the sole and the parapodia, but there is a slight ventral transverse furrow where the head joins the foot. The angles of the foot are prominent.

The head is very high, almost square from a dorsal view, sometimes appearing bilobed anteriorly. The rhinophores are set close together and are heavy, blunt, and auriculate. The eye spots (Figure 1) are clearly visible.

The pericardial prominence (Figure 2) is fairly small considering the size of the animal, and extends posteriorly in a large, long tube (Figure 2). There is a very thin tube (Figure 2) situated on top of the larger tube, and the renal pore (Figure 2) is easily visible on the right side of the pericardial prominence. There are numerous

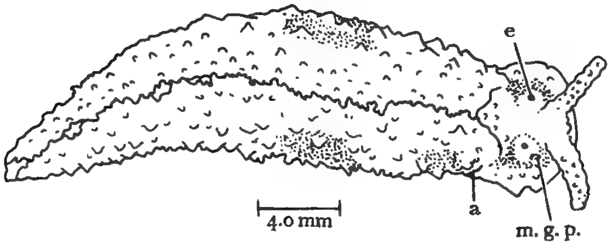

Figure 1

Elysia arena. Dorsal view of living animal

a – anal opening e – eye m. g. p. – male genital pore

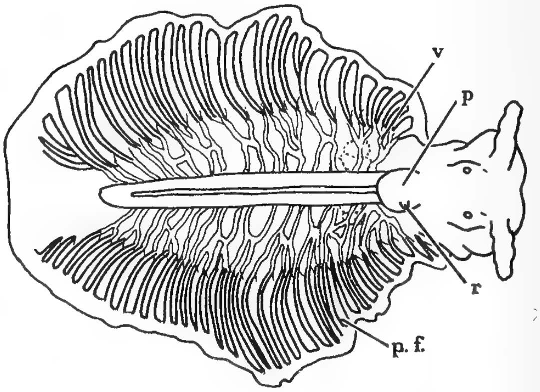

Figure 2

View of *Elysia arena* with parapodia open

p – pericardium p. f. – parapodial folds r – renal pore v – venous network

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[1] Contribution No. 99 from the University of Guam Marine Laboratory

veins (Figure 2) extending outward from the reno-pericardial complex which have some branching. This venous network is similar to that of other *Elysia* species on the internal dorsal area, but on the internal lateral surface of the parapodia the veins terminate in extremely large, heavy parapodial folds (Figures 2 and 3) extending almost to the edge of the parapodia. These large folds, reminiscent of lamellae, are the most distinctive aspect of the animal. On an animal that was 14.0 mm wide when preserved, the longest folds were 4.5 mm in length, thus equaling about one third of the animal's width with parapodia open. The anus and genital pore (Figure 1) are lateral, opening in a single aperture at the furrow just anterior to the right parapodium. The penial opening (Figure 1) is under the right rhinophore.

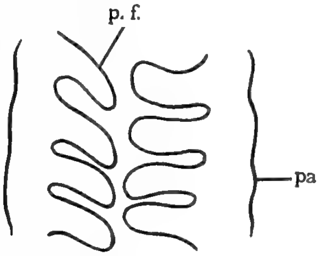

Figure 3

Horizontal section showing parapodial folds

Sectioned animal is 3.2 mm wide with parapodia erect

p. a. – outer wall of parapodia p. f. – parapodial folds

The mouth has a slight "T" shape. The pharynx (Figure 4) is extremely large with the dorsal part covered with heavy annular muscles. The radula is anterior and ends straight in the ascus (Figure 4) with no loose pile of discarded teeth. The radula in a 14.0 mm specimen had 17 teeth in the descending series and 7 in the ascending. That of a 23.8 mm specimen had 7 teeth ascending and 23 in the descending series. In the latter specimen the tooth in use was 0.31 mm in length, the newest tooth 0.35 mm, and the oldest 0.02 mm. The teeth (Figure 5) have very fine serrations on the cutting edge. Under a microscope the serrations are visible at 400 power but not at 100.

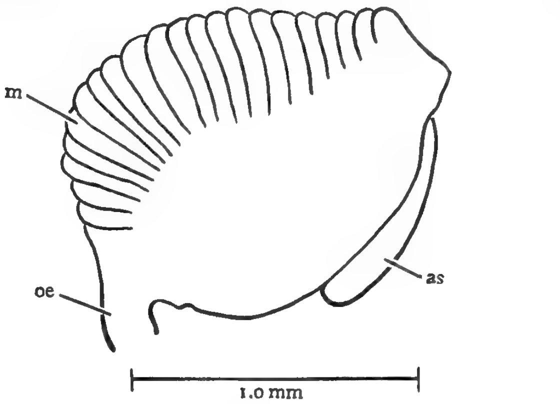

Figure 4

Pharynx of *Elysia arena*

as – ascus m – annular muscles oe – oesophagus

In the living animal the head is light green, or sometimes tan with a greenish tinge, and has widely scattered black dots and some creamish tan mottling. The projections are white. Minute dots of chocolate brown or black form a triangular pattern immediately anterior to the rhinophores. Very dark brown dots appear at the sides of the head below the eye spots and extend to the anterior edge of the parapodia. The rhinophores are tan with white projections and white spots, and have brown dots which are more predominant on outer edges toward the tip. The parapodia are tan, sometimes having an orangish tinge with scattered fine brown flecks and white projections. The brown flecks are denser at the anterior of the parapodia and toward the lower central part of the parapodia; some faint white patches are over the tan. The intensity of the brown pigmentation may vary from ani-

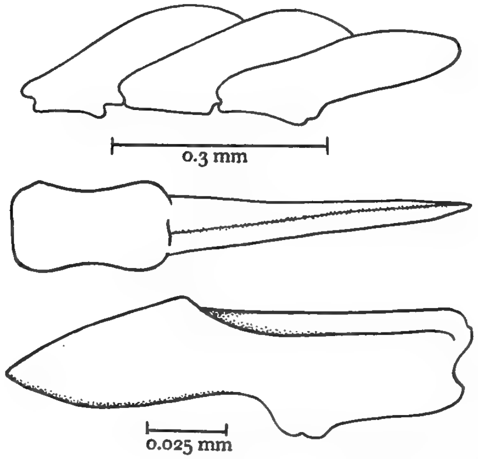

Figure 5

Teeth of *Elysia arena*

mal to animal with the exception of the area below the eye spots which so far has been consistently dark. The foot is yellowish green, with the posterior somewhat orange on a few animals, and has a faint white mottling. The large folds on the inner side of the parapodia are salmon to orangish tan. The internal dorsal surface is translucent pale green with cream colored ovotestes showing through on either side of the tube leading from the pericardial prominence.

Elysia arena lays an orange egg mass with the ribbon being about 1.6mm wide and each 0.25mm capsule containing a single egg.

Habitat: *Elysia arena* has only been found in one area of Cocos Lagoon in southern Guam west of a small sand island near Cocos Island. This area has a thick sand substrate with very little coral and a water depth of from 0.5 to 1.5m. The animal is directly associated with two species of *Caulerpa*: *C. racemosa* and *C. cupressoides*. *Elysia arena* differs in its habits from other caulerpan associated *Elysia* in that it is found just under the surface of the sand around the rhizoids of the algae rather than crawling on the thalli. As is true of many other sand dwelling opisthobranchs, *E. arena* surrounds itself with a layer of mucus when under the sand. The first animals were found by pulling up the algae and shaking them. Subsequently, animals have been found by searching a shallow area through the sand around the rhizoids of the algae. Occasionally an animal has been seen because of its habit of leaving a slight opening in the sand above the parapodia. *Elysia arena* has never been found in great numbers in the collecting area and since 1971, only 29 specimens have been examined: 12 in October, 1971; 1 in November, 1971; 5 in October, 1973; 1 in May, 1975; 4 in June, 1975; 3 in July, 1975; and 3 in November, 1975.

Remarks: *Elysia arena* differs from all previously described *Elysia* by the presence of the large parapodial folds. Comparison can be made with 2 *Elysia* that have previously been described as being heavily papillate with conical projections over most of the body – *Elysia cauze* Marcus, 1957, and *E. papillosa* Verrill, 1901 (MARCUS & MARCUS, 1967: 27 - 28; figs. 22 - 25), both from the West Atlantic.

Elysia cauze and *E. arena* are very similar. From both dissection and serial sections it appears that the genital system of both animals is practically identical. The size of the pharynx with the large annular muscles, the oesophagus (Figure 4) opening posteriorly from the pharynx, the radula extending straight into the ascus, and the shape and size of the teeth are all comparable. Besides the presence of the folds inside the parapodia, *E. arena* differs from *E. cauze* in the relative size of the parapodia. A 16.0mm preserved *E. arena* was 14.0mm wide with parapodia unfolded, and a 27.0mm preserved *E. cauze* was 14.0mm wide when unfolded. *Elysia papillosa* with a coarsely denticulate radula differs from the finely serrate radulae of both *E. cauze* and *E. arena*. The tube extending from the reno-pericardial complex is short in *E. papillosa* and extends most of the length of the animal in *E. cauze* and *E. arena*.

In the Indo-Pacific, a collection of 7 specimens from Hawaii has been described as *Elysia* aff. *cauze* (KAY, 1964: 195 - 196; plt. 9, fig. 3; fig. 2). This form is covered with fine papillae, has a smooth radula, and lacks a transverse furrow. It seems to have little similarity to *E. arena* and probably represents a distinct species.

The specific name is derived from *Elysia arena*'s habit of burying itself in the sand.

Type specimens are deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii.

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Some Aspects of Spatfall of the New Zealand Rock Oyster During 1974

BY

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(4 Text figures)

INTRODUCTION

Mahurangi estuary in New Zealand (Lat. 38°30′S; Long. 174°43′E) is an important spat source of the New Zealand rock oyster, *Saccostrea glomerata* (Gould, 1850) [= *Crassostrea glomerata* (Gould, 1850)], being the only area where commercial-scale spatfall had been consistently recorded. Commercial seed collection began in 1968, and Curtin (1971, 1973) has provided spat collection records from 1970 through 1972. Spatfall usually begins early in January and extends into April, with one or two peak settlements occurring around February. The larvae settle in the intertidal region through a 1 m vertical range about mean low water level (personal observation). Collectors are usually set out at MLWN about the end of December, and are removed to growing areas at the end of April.

The spatting area in Mahurangi is less than 5 ha and catches fluctuate. For these reasons methods of increasing production are being investigated: one method is to time the setting out of collectors and the handling so as to get abundant catches of spat and to avoid heavy settlement of fouling organisms that interfere with survival and growth of spat.

The summer of 1974 was a successful breeding season which made it possible to study the precise seasonal history of spatfall, patterns of settlement on collectors and other practical problems and procedures in seed collection that are not well understood. The results of these studies are presented and discussed in this paper.

MATERIALS AND METHODS

Commercial spat collectors were used for all observations for monitoring spat settlement. A standard collector (Figure 1) consists of 30 fibrolite (asbestos-cement) slats, each 120×5×0.6 cm, arranged in a bundle of 10 layers and 3 columns, with 5 cm between the columns; each layer is separated by 2 wooden spacers, about 12 mm thick. Collectors were set out in racks in Huawai Bay in the Mahurangi estuary in the middle of January, and every 4 weeks thereafter 1 collector was examined. A set of collectors was exposed to monitor spatfall between middle of December 1973 and mid-January 1974.

For analysis, 1 slat was taken from each layer (usually a slat from the middle column) and the total number of spat was counted on its upper and lower surface, and their sizes measured. The size of the spat refers to its greatest width (Thompson, 1968) measured in mm. Where spat density was very high, it was necessary to restrict counting and measuring to one-half of each slat, particularly of the lower surface. In some collectors, with uneven spat distribution, one more slat was examined from each layer to obtain a better estimate of the number of spat/slat. These collectors, examined at 4-weekly intervals gave cumulative spat counts (less mortality) for the period January through May 1974.

We also made tests to determine the effects of spat collector manipulations practised by some farmers. For example, it is well known that rock oyster settlement is heavier on lower than on upper horizontal surfaces of

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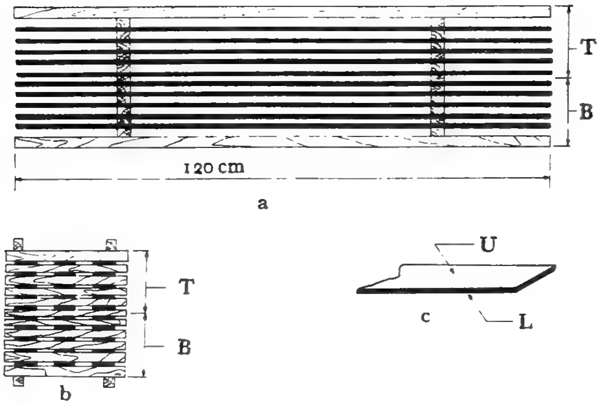

Figure 1

Arrangement of slats, (a) side view, (b) end view, in a commercial bundle of spat collector; T: top half and B: bottom half of bundle; (c) portion of slat, with U: upper, and L: lower surface

the slats, and some farmers overturn their collectors halfway through the spatfall season in the hope of securing an even distribution of spat on both sides of the slat. Our tests were made at the same site and began in February: every month one experimental collector was overturned and at the end of the spatfall season the spat distribution on these collectors was compared with normally handled collectors.

Some farmers raise the level of their collectors after the peak spatfall season hoping thereby to avoid settlement of competitive organisms like mussels and thus improve spat survival. We tested this by shifting one collector in February, March and April from the rack where it received its catch of spat to another rack at the same site that was 30 cm higher. At the end of the season spat counts were made on test collectors and compared with counts on collectors that were normally handled.

The results observed have been presented in four ways: for each period of cultch exposure, 1) the total count of spat per each collector has been estimated, 2) size frequency distributions (in 5 mm groups) of spat within the collector have been analysed, 3) counts of spat settlement on upper and lower surfaces have been presented separately to show preferences, and 4) the slats in each collector have been grouped according to whether they came from the top or bottom 5 layers of the collector (see Figure 1). The terms "upper" and "lower" (within quotation marks) surfaces in the following description refer to new orientations, consequent on collectors being overturned through 180°, but which actually represent the original lower and upper surfaces respectively.

OBSERVATIONS

Monitoring collectors exposed from mid-December to mid-January (4 weeks) showed sparse settlement (approximately 3 spat/slat of sizes 1 to 1.5 mm), and it is therefore probable that no successful spawning or settlement occurred during this period. Most of the seasonal settlement took place after 15 January and Table 1 shows results of spat settlement on experimental collectors that were exposed for approximately 1, 2, 3 and 4 months from mid-January to mid-May 1974. Since collectors were examined only about the middle of each month, precise times of spatfall could not be determined simply from counts of spat. However when considered with size-frequency distribution (Figure 2), and what is known

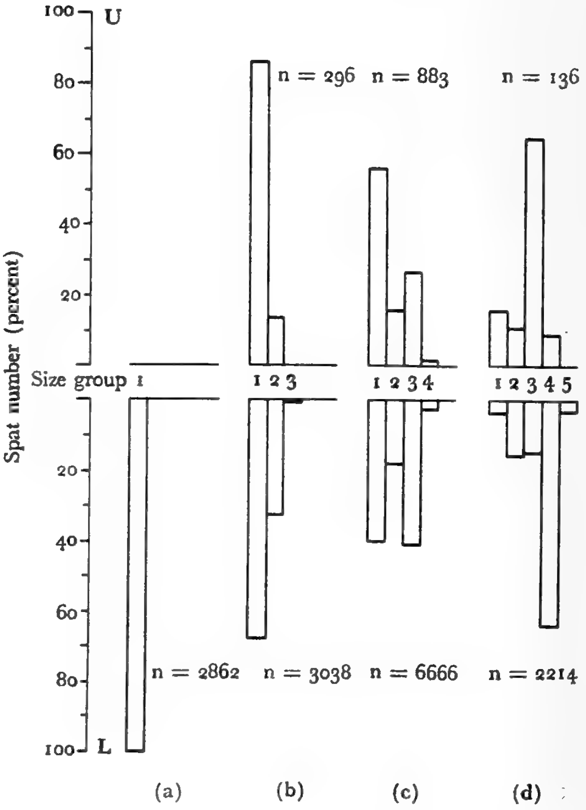

Figure 2

Size distribution and number of spat on collectors set at the normal level (MLWN) on 19 January 1974, and examined at monthly intervals in (a) February, (b) March, (c) April and (d) May. Spat settled on upper (U) and lower (L) surfaces are shown separately. Size groups: 1 = < 5 mm, 2 = 5 - 10 mm, 3 = 10 - 15 mm, 4 = 15 - 20 mm, 5 = > 20 mm about spat growth (normal growth rate is nearly 1 mm per week during the summer months – own unpublished data) it is obvious that settlement had been spread out through the 1974 season, with a fairly heavy set in February and again another set after the middle of March.

A mean settlement rate of 255 spat/slat was recorded on 19 February when the first collectors were examined (Table 1). The spat averaged 2 mm in width suggesting that the first commercial settlement probably began at the end of January/early February. Apparently no heavy spatfalls occurred between February and the middle of March, because collectors examined on 18 March indicate a reduction in number of spat from 255 to 238/slat (Table 1), perhaps from natural mortality, and only 12.9% of these were $<$ 2 mm wide (Figure 2). However, in the next period, from mid-March to mid-April, there is a marked increase to 417 spat/slat, and nearly 30% of these spat were $<$ 2 mm in size, obviously the result of a heavy spatfall during this period. During the second spatfall of the season, the settlement was also heavy in the top half of the collectors. This brought about an increase in the top/bottom ratio of spat from 0.67 for 18 March to 1.09 on 17 April (Table 1). This shows an increase from 37% to 57% of the total number of the spat settling on the top layers of the collector.

Table 1

Density of spat settlement on normal collectors examined at monthly intervals, January through May 1974. Each collector of 30 slats has been split into two halves, T: top and B: bottom, of 5 layers and 15 slats each. The number of spat on upper (U) and lower (L) surface of each slat has been shown separately.

Period and Date examined	Portion of Collector	Surface	No. of slats examined	No. of spat measured	Mean No. of spat/ surface	Spat Density (/cm^2)	Total No. of spat on surfaces	% of Total	Total No. spat/ collector	Mean No. of spat/ slat	Mean spat density/ slat (cm^2)
Jan-Feb											
19 Feb	T	L	7	1083	154.7	0.269	2321	30.3			
	T	U	7	0	0		0				
	B	L	5	1779	355.8	0.619	5337	69.7			
	B	U	5	0	0		0				
	[1]								7658	255.3	0.222
Jan-March											
18 March	T[2]	L	7	1248	178.3	0.310	2674	37.4			
	T	U	7	93	13.3	0.023	200	2.8			
	B	L	7	1790	255.7	0.445	3836	53.7			
	B	U	7	203	29.0	0.050	435	6.1			
									7145	238	0.207
Jan-April											
17 April	T	L	10	3902	390.2	0.679	5853	46.7			
	T[3]	U	10	457	45.7	0.079	685	5.5			
	B	L	8	2764	345.5	0.601	5182	41.4			
	B	U	8	426	53.2	0.092	798	6.4			
									12 519	417.3	0.363
Jan-May											
17 May	T	L	5	1258	251.6	0.437	3774	48.6			
	T	U	5	60	12	0.021	180	2.3			
	B[4]	L	4	956	239	0.416	3585	46.2			
	B	U	5	76	15.2	0.026	228	2.9			
									7767	258.9	0.225

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[1] First spatfall.

[2] No spatfall.

[3] Second spatfall.

[4] Bottom slats heavily fouled.

SETTLEMENT PATTERNS IN EXPERIMENTAL COLLECTORS

(a) Overturned Collectors

On 19 February no spat were found on the upper surfaces of slats in collectors that had been exposed at the normal level for 4 weeks from 19 January. Consequently, when these collectors were overturned on 19 February, what then became their lower surfaces had probably no spat in them. All the spat subsequently recorded on these "lower" surfaces must therefore have settled after 19 February (Table 2). This is borne out by the fact that 61.1% of the spat on the "lower" surface were <5 mm, and only 17% were >10 mm (Figure 3). In the controls that were examined at the same time (Figure 2), only 3.2% were <5 mm, and 81.1% were >10 mm. Correspondingly, in experimental collectors, spat counts on "upper" surfaces actually represent settlement that took place on lower surfaces before collectors were overturned.

By the middle of March, spat had begun to settle naturally on the upper surfaces of slats as well, reaching a density of 0.036 spat/cm² (sizes <5 mm) in normal collectors. The lower surfaces of these collectors showed a spat density of 0.377 spat/cm². Collectors that were overturned in March showed a higher spat density (0.136 spat/cm²) on "lower" surface but spat were mostly of sizes <5 mm. The "upper" surfaces of overturned collectors showed densities of 0.390 spat /cm², and spat were

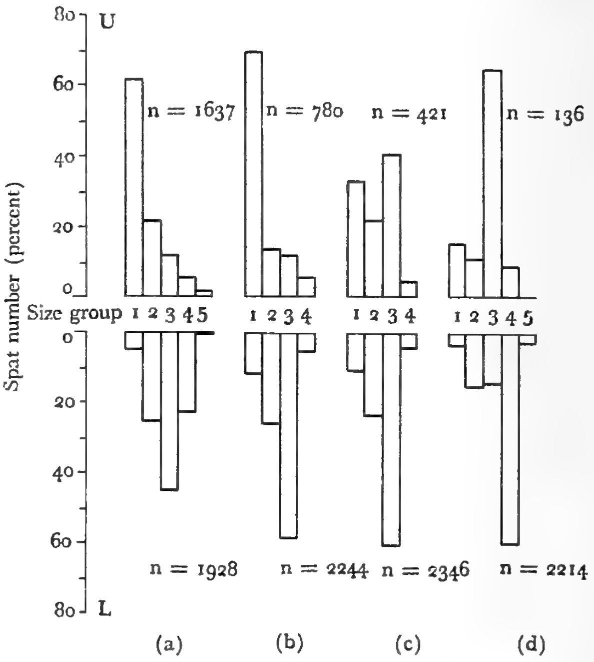

Figure 3

Size distribution and number of spat on upper and lower surfaces of experimental collectors which were overturned at monthly intervals in (a) February, (b) March and (c) April, compared with (d) a normal unturned bundle. All collector bundles removed from racks on 17 May 1974. Other legend as in Figure 1

Table 2

Density of spat settlement on experimental collectors that were overturned in February, March and April 1974. L˙ and U˙ refer to original lower and upper surfaces respectively, and therefore denote present U and L surfaces. Similarly T˙ and B˙ are original positions.

Date Re-oriented	Portion of Collector	Surface	No. of slats examined	No. of spat measured	Mean No. of spat/surface	Spat Density (/cm²)	Total No. of spat on surfaces	% of Total	Total No. spat/collector	Mean No. of spat/slat	Mean spat density/slat (cm²)
19 Feb	B˙	L˙	5	678	135.6	0.236	2034	19.0			
	B˙	U˙	5	729	145.8	0.254	2187	20.4			
	T˙	L˙	5	1250	250	0.435	3750	35.1			
	T˙	U˙	5	908	181.6	0.316	2724	25.5			
									10695	356.5	0.310
18 March	B˙	L˙	5	1196	239.2	0.416	3588	39.5			
	B˙	U˙	5	445	89	0.155	1335	14.7			
	T˙	L˙	5	1048	209.6	0.364	3144	34.6			
	T˙	U˙	5	335	67	0.116	1005	11.1			
									9072	302.4	0.263
17 April	B˙	L˙	5	1164	232.8	0.405	3492	42.1			
	B˙	U˙	5	158	31.6	0.055	474	5.7			
	T˙	L˙	5	1182	236.4	0.411	3546	42.7			
	T˙	U˙	5	263	52.6	0.091	789	9.5			
									8301	276.7	0.241

of larger size when compared to normal March collectors; however both spat modal size and densities (0.421 spat/cm^2) were lower than corresponding surfaces of normal collectors examined in May (Figure 3).

(b) Collectors Raised to Higher Levels

In collectors that were raised 30 cm on 19 February, the overall spat density was 0.221/cm^2 of available surface, with 0.368 spat/cm^2 on lower surface and 0.074 spat /cm^2 on upper surface (Table 3). The overall spat density was thus very similar to those of normal (control) collectors, which had 0.225 spat/cm^2, though the distribution of spat was denser on lower surfaces (0.426 spat/cm^2) and lighter on upper surfaces (0.023 spat/cm^2) of normal collectors. When compared to overturned collectors of February, the raised collectors had slightly higher spat densities (+0.033/cm^2) on lower surfaces but much lower densities (−0.211/cm^2) on upper surfaces (cf. Tables 2 and 3). However, size frequency distributions (Figure 4) show marked differences on sizes of spat, especially on upper surfaces.

Collectors that were raised 30 cm in March showed an overall density of 0.231 spat/cm^2, a slight increase over those raised in February. The spat were also denser on lower (0.404/cm^2) and lighter on upper (0.057/cm^2) surfaces, but were of smaller size. A similar difference was observed when these experimental collectors were compared with normal collectors which had also a larger modal size of spat.

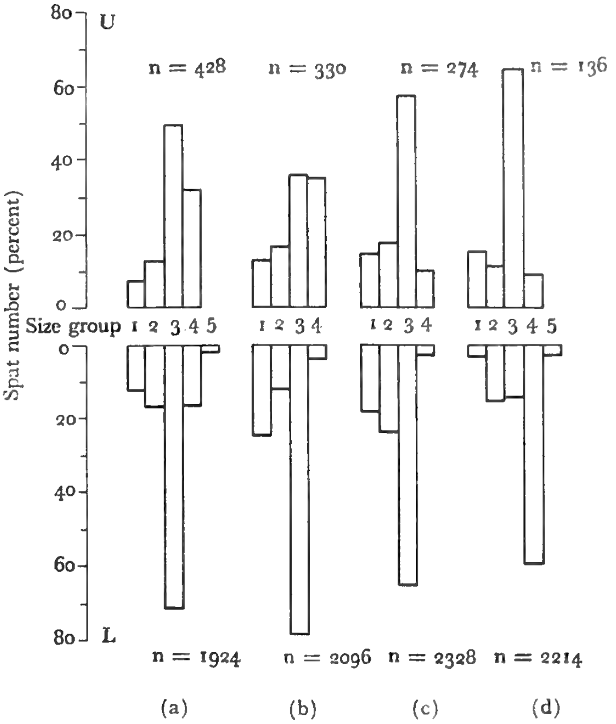

Figure 4

Size distribution and number of spat on upper and lower surfaces of experimental collectors which were raised 30 cm to a higher rack at monthly intervals in (a) February, (b) March and (c) April, compared with (d) a normal level bundle. All collector bundles removed from racks on 17 May 1974. Other legend as in Figure 1

Table 3

Density of spat settlement on experimental collectors that were raised 30 cm from normal level in February, March and April 1974. Legend as in Table 1.

Date Shifted	Portion of Collector	Surface	No. of slats examined	No. of spat measured	Mean No. of spat/ surface	Spat Density (/cm^2)	Total No. spat on surfaces	% of Total	Total No. spat/ collector	Mean No. of spat / slat	Mean spat density (/cm^2)
19 Feb	T	L	5	1144	228.8	0.398	3432	44.9			
	T	U	5	172	34.4	0.060	516	6.7			
	B[1]	L	4	780	195	0.339	2925	38.3			
	B	U	5	256	51.2	0.089	768	10.1			
									7641	254.7	0.221
18 March	T	L	5	1186	237.2	0.412	3558	44.7			
	T	U	5	130	26	0.045	390	4.9			
	B	L	4	910	227.5	0.396	3412	42.9			
	B	U	5	200	40	0.069	600	7.5			
									7960	265.3	0.231
17 April	T	L	5	1166	233.2	0.388	3498	44.3			
	T	U	5	158	31.6	0.055	474	6.0			
	B	L	5	1162	232.4	0.404	3486	44.2			
	B	U	4	116	29	0.050	435	5.5			
									7893	263.1	0.229

[1] Bottom slats heavily fouled.

Collectors that were raised 30 cm in April were nearly identical to those raised in March as regards overall spat density (0.229/cm^2), as well as distribution on lower (0.405/cm^2) and upper (0.052/cm^2) surfaces. They were also similar to experimental collectors overturned in April as regards spat density and modal size. When compared to normal collectors (controls) spat size differences were observed, with bigger size spat in larger numbers in the control collectors (cf. Figures 2 and 4).

SETTLEMENT ON UPPER vs. LOWER SURFACES

In normal collectors placed on the racks on 19 January and examined on 19 February, the entire spat settlement was on the lower surfaces of slats; but in normal collectors examined towards the end of the spatting season (17 May) 5.25% of spat had settled on upper surfaces of slats. However, collectors examined on 17 April showed a slightly higher rate of settlement (11.86%) on upper surfaces as a result of a second spatfall but these spat had probably failed to survive. This is indicated by the reduction of spat densities on upper surfaces of slats, from 0.085/cm^2 in April to 0.023/cm^2 in May (Figure 2 and Table 1). Analyses of size frequencies reveal that smaller sized spat ($\sim$5 mm) were greatly reduced in numbers between April and May.

Spat distribution was different in collectors that were experimentally treated: those overturned early in the spatting season (February) had somewhat similar spat densities on both surfaces, 0.335/cm^2 on lower and 0.285/cm^2 on upper surfaces, but their size composition showed marked differences (Figure 3); smaller sized spat were predominant on upper surfaces, those $<$ 5 mm constituting 61.1% of the spat on the upper surface against 5% on the lower surface. Thereafter, the numbers that settled on upper surfaces of overturned collectors gradually decreased (Table 2 and Figure 3), so that at the end of the spatting season spat densities were similar to corresponding surfaces of normal collectors. In collectors that were raised to higher levels, spat distribution and densities did not vary greatly from month to month, but those shifted in February had slightly fewer spat on their lower surface. This was probably due to the fact that raising the level of the collectors early in the season had caused interruption of spat settlement, and failure of the spat to settle or survive at the new levels. However, spat settlement on upper surfaces of all raised collectors was more than double the density of normal level collectors.

SETTLEMENT PATTERNS WITHIN THE COLLECTOR

Initial settlement was predominantly in the bottom half of the collectors (Table 1), accounting for 69.7% of the spat counted on normal collectors in February; however, as the season progressed, the relative number of spat settling in the top half increased, from 40.2% on 18 March to 52.2% on 17 April and, at the end of the spatting season, spat numbers were nearly evenly distributed with 50.9% at the top and 49.1% in the bottom half. As a result of differences in spatfall times on the two halves of the collectors, size differences were noticed: thus in the bottom half spat were predominantly ($>$77%) of larger size (15 mm and above) and there were no spat smaller than 5 mm; in the top half nearly 30% of the spat were $<$10 mm and only 53% were $>$15 mm.

In experimental collectors (Tables 2 and 3) the same trends were seen, the degree of difference being related to the time at which the collectors were re-oriented. Thus collectors overturned in February showed greater spat density and settlement on slats which were originally in the top half, but small sized spat ($<$5 mm) occurred in greater number in the original bottom half of the collector. However, collectors overturned in March showed lesser spat density and settlement in the original top half, while collectors overturned in April showed slightly higher numbers in the same half. The percentage of small sized spat in the original bottom half of the collector was somewhat higher than in the layers of the top half in both March and April collectors. In collectors that were shifted to higher level in different months, top halves of collectors showed on each occasion higher percentage of spat, which were made of small sized spat ($<$10 mm) particularly in those shifted in March and April.

SETTLEMENT OF COMPETITIVE ORGANISMS

(a) **Other Oysters**

Spat of two other oyster species are sometimes found on collectors laid out for rock oysters (DINAMANI, 1971). These were an unidentified flat oyster, *Ostrea* sp., and the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793), which are somewhat difficult to distinguish from one another at early spat stages. Flat oyster spat were rare in 1974, only 8 - 10 spat/bundle were noted on 19 February, and none were found during the three subsequent monthly samplings. However, Pacific oyster spatfall was heavier than in previous seasons (Dinamani, 1974b): Table 4 gives details of the Pacific oyster settlement on collector samples examined during the season. It may be observed that the Pacific oyster settled in densities of 96 spat/bundle of normally handled collectors, 70% of them being on the lower surfaces of slats. Maximum settlement (213 spat/bundle) was observed in collectors that were overturned on 19 February. The distribution of these spat indicates that most settled on lower surfaces of slats between 19 February and 18 March, just before and soon after the collectors were overturned: this is revealed by the fact that the settlement of the Pacific oysters gradually decreased through March and April, and also because collectors overturned in March and April caught more Pacific oyster spat than the normally handled collectors and by the fact that numbers of spat on upper and lower surfaces of overturned collectors in April were almost equal.

Table 4

Pacific oyster spat recorded on collectors examined on 17 May 1974.

Type of collector	No. of spat upper surface	lower surface	Total spat /collector
1. Normal collector	27	69	96
2. Overturned collectors:			
Reoriented Feb.	74[1]	159[1]	213
Reoriented Mar.	36[1]	130[1]	166
Reoriented Apr.	66[1]	67[1]	133
3. Collectors raised 30 cm:			
Raised Feb.	42	55	97
Raised Mar.	24	50	74
Raised Apr.	28	36	64

[1] Refers to present upper and lower surface.

(b) Barnacles

Settlement of the barnacle, *Elminius modestus*, on spat collectors was light in 1974 compared with other years. Normally handled collectors exposed from mid-January to 19 February showed barnacle settlement densities between 0.15/cm^2 in the top half, to 0.75/cm^2 in the bottom half. Collectors exposed for longer periods showed moderate to heavy barnacle settlements (15 to 20/cm^2). Overturned collectors also showed moderate to heavy settlement, but collectors raised to higher level showed an even denser settlement rate; this was particularly true of collectors that were raised in March and April, which had a heavy settlement of > 25 barnacles/cm^2 as well as a dense deposit of silt on the upper surfaces of the slats. Greenway (1969) has recorded denser barnacle settlement at higher levels in Huawai Bay.

(c) Polyzoans

A cheilostomatous polyzoan, *Watersipora cucullata*, was found to settle in isolated small groups (1 to 4 polypides each) in all collectors examined from March onwards, and was most numerous on middle layer slats of collectors overturned in March. It normally appears on the shaded surfaces of slats and grows over settled spat in the form of a thick mat.

DISCUSSION

Seasonal differences in intensity of rock oyster settlement may be attributed to variable environmental factors such as water temperature which affects spawning, whereas patterns of settlement are usually thought of as dependent on behavioral characteristics of larval oysters. The first major settlement of rock oysters occurred about the end of January in 1974 but settlement has varied from year to year; our observations (unpublished data) show that it took place in middle and late February in 1973, and after the middle of January in 1972. A second settlement maximum usually occurs in February or March, depending upon the timing and duration of spawning (Dinamani, 1974a). However spatfalls have been observed as late as the end of April or early May in years when the first spawning has been delayed.

Observations on spawning, as indicated by plankton monitoring of oyster larvae, and on spatfalls, as recorded in commercial collectors, showed the following pattern: oyster larvae (80 - 150 μm in length) appeared in Huawai Bay during the 3rd week of December 1973, and were common up to the end of the month. Appreciable numbers (average 40 - 60 larvae/500*l* sample) were not found until after the middle of January. These observations checked well with spatfalls on trial collectors exposed from mid-December to mid-January, which showed only 3 spat/slat all < 1.5 mm in size. Late stage larvae were found from the last week of January, and the first spat on our monitoring collectors were observed about the middle of February. Thus the evidence points to a major spatfall (settlement rate of *ca.* 0.250 spat/slat) during the first week of February. The length of larval life has been reckoned to be about 18 to 24 days (Dinamani, 1973) at a temperature of 21 - 22° C.

From the end of February to the middle of March, no regular larval monitoring was possible in the Mahurangi area, but experimental collectors examined in the middle of March showed only a few spat of < 2 mm (about 12% of the total), and the mean number of spat/slat on these collectors was also lower than that of February. This probably meant that there were few larvae in the water and very little settlement occurred during that period. However, plankton samples taken from 18 March onwards revealed late-stage larvae, which suggested that a second peak in larval numbers probably occurred in March, and gave rise to a second spatfall. The large number of small spat observed in the collectors examined in April points to this.

Thus Mahurangi ordinarily has a long breeding season (Greenway, 1969), with probably two spatfall maxima from January to April. In the Australian rock oyster, Thompson (1950) recorded two maxima during the spring (November) and autumn (March). We have however no conclusive evidence of spring spawning in the New Zealand rock oyster (Dinamani, 1974a).

Saccostrea glomerata larvae like those of many other species of oyster settle more heavily on lower than upper surfaces of collectors (Nelson, 1927; Hopkins, 1935; Schaefer, 1937; Cole & Knight-Jones, 1939; Siebing, 1950; Thompson, 1950; Medcof, 1955). This characteristic is well demonstrated by our data for collectors that were experimentally overturned at various times in 1974 (Table 2, Figure 3), the subsequent settlement being largely confined to the 'new' lower surface. There was also a tendency at the beginning of the settlement season for the spat to settle in the bottom half of the collector bundle as demonstrated in data listed in Table 1. However towards the end of the settlement season, roughly equal numbers of spat are found in the top and bottom halves of the collector bundles. This was shown by the greater percentage of small-sized spat settling on the top half of the bundle after February. This may indicate a tendency, under natural conditions, for late-season settlement to occur higher in the intertidal zone than early season settlements.

There is also a tendency for the settlement to be almost exclusively on the lower surfaces early in the season, but to occur in small numbers (8 to 10% of the total) on the upper surfaces late in the season. This could be taken as evidence that oyster larvae avoid settling on lower surfaces that are already heavily populated by their own species. Knight-Jones & Stevenson (1951) and Wisely (1959) have observed that settling larvae tend to avoid surfaces where recently settled individuals of their own kind have attained a certain density. The term 'gregariousness' has been used to indicate the selection by settling larvae of surfaces associated with organisms of the same species, though, as pointed out by Bayne (1969), it also "implies a response by the larvae to the previously settled individuals of the same species." This response could therefore either favour aggregation, or result in an avoidance reaction, depending upon the density of the individuals on a surface at any time. In the rock oyster the results of settlement on commercial collectors indicate that larvae probably begin to settle on upper surfaces of slats when spat densities on lower surfaces become high. In this type of collector, as the distance between the lower surface of one slat and an adjoining upper surface of another is only 12 mm, gregarious response could be a factor. In a series of experiments on the settlement of *Crassostrea virginica* (Gmelin, 1791), Shaw (1967) reported that more larvae settled on upper surfaces when slats were about 25 mm apart, but only on lower surfaces when the slats were 100 mm apart.

Analyses using '*t*-test' values for differences in mean spat density between normal and experimental collectors show significant values only for collectors overturned in February ($t = 2.147$, $P = 0.05$) and March ($t = 2.290$, $P = 0.05$), compared to normal collectors exposed for the same period. No significant differences were observed in mean spat density between normal collectors and raised collectors. However, it is obvious that in spite of increases in spat density in collectors overturned earlier in the season, spat sizes in these are generally smaller than in normal collectors (cf. Figures 2 and 3). This is also true of collectors raised to higher level. Therefore, reorientation of cultch material, either by overturning or raising during the spatting season, most probably affects spat growth. It remains to be seen whether the more even dispersion of spat on both surfaces of slats (a feature of overturned collectors) may, in later seasons, have the advantages of lesser overcrowding and hence better growth. This has to be weighed against the higher settlement rate of competitive species such as the Pacific oyster in the same collectors.

No obvious benefits, *e. g.*, higher survival of spat or abatement of barnacle settlement, were seen in collectors shifted to higher level. On the other hand, there were signs of higher silt deposition, which normally smothers small sized spat. Spat which settle later in the season generally have a poorer survival rate, as is evidenced here by the considerable drop in percentage of small size spat between April and May in normal collectors, as also in those overturned in April (see also Greenway, 1969).

CONCLUSIONS

1. Rock oyster commercial seed operations should preferably be initiated to coincide with the period of the first major spawning. This would ensure clean cultch surfaces for maximal settlement, better growth and survival of spat, with minimal fouling by organisms such as *Elminius modestus*, which have several spawning peaks and could settle at the same level. The extended oyster breeding season from January to March and the occurrence of at least two spawning maxima provide some safety factor for farming operations.

2. Plankton monitoring programmes which provide information on spawning activity and larval abundance might be of use to the seed industry, to enable the growers to catch the first set and to help them plan ahead. As pointed out by LOOSANOFF & ENGLE (1940), information on spawning time, intensity of setting and the probable rate of survival of spat under different conditions, would lead to better planned oyster farming. A monitoring programme was in fact tested during the 1975 season, and with refinement it may permit forecasts of dates and sizes of spatfall.

3. The study has also indicated that spatfall on the present type of collectors follows a seasonal pattern: initially spat settle almost exclusively on lower surfaces of slats, in the lower halves of bundles that are positioned close to MLWN; as the season progresses, spat may settle on both upper and lower surfaces of collector slats, in both top and bottom halves of collector bundles, and at higher levels in the intertidal zone than at the beginning of the spatfall season. Thus, at the end of a good season all slats in the bundle have a somewhat even distribution of spat.

4. The study also reveals that spat which settle early in the season survive better and are larger at the end of the season than spat which settle later in the season. It may therefore be worthwhile to maintain a monitoring programme of planktonic populations of oyster larvae to forecast the first sets of the year.

5. The study shows that turning collectors up-side-down during the early part of the spatting season may increase their catch of spat: *e. g.*, collectors overturned in February took 37% more spat than normally handled (unturned) collectors, and collectors overturned in March took 17% more spat. In both cases, however, the increase counts were largely due to the greater number of small-sized late-settling spat. In contrast, the overturned collectors have fewer spat of sizes over 10mm compared to the normal collector.

6. Another factor is the possibility of settlement of other organisms such as the Pacific oyster on the 'new' surface; collectors overturned in February had more than double the number of Pacific oysters of normal collectors, and collectors overturned in March had more polypides of *Watersipora*. The incidence of other competitive species and the time of their settlement may have a marked effect on rock oyster spat, particularly their growth.

7. In good breeding seasons, with at least two spatfalls between January and March, normal settlement patterns provide adequate spat densities and growth in commercial type collectors. Whether there is need for special handling of collectors is an open question.

SUMMARY

Settlement of the New Zealand rock oyster, *Saccostrea glomerata* (Gould) [= *Crassostrea glomerata* (Gould)] on bundles of slat-type commercial collectors in the Mahurangi estuary in New Zealand, showed two peaks of spatfall between January and March 1974 in a definite pattern: the first sets were predominantly on the lower surface of slats and on the lower layers of slats in the bundles. As the season progressed sets were still largely on lower surfaces but spread more uniformly through the several layers of collector slats. By overturning the bundles at intervals during the season, significantly higher ($P = 0.05$) mean density of spat was obtained if carried out in the earlier part of the season, but brought about a reduction in maximum spat size, and also a greater settlementment of competitive species such as the Pacific oyster. Moving collectors at intervals to higher tidal level did not affect spatfall appreciably but increased silting on collector surfaces.

ACKNOWLEDGMENTS

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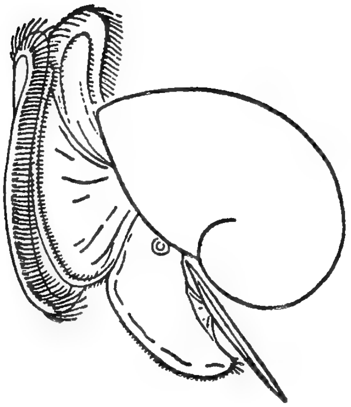

A New Species of Chiton from the Aleutian Islands

(Mollusca : Polyplacophora)

BY

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(1 Plate; 1 Text figure)

THE ALEUTIAN ISLANDS, extending westward some 2000 km from the Alaskan peninsula towards the peninsula ot Kamchatka, are an integral part of the Aleutian Province which, variously defined (SCHENCK & KEEN, 1936; EKMAN, 1953; BRIGGS, 1974), stands between the eastern Pacific Cold Temperate Region to the south, and the icy waters of the Arctic Region to the north. For mollusks in general, the endemism of the Aleutian Province has been estimated at 24% (VALENTINE, 1966). Still, its chiton fauna is poorly known. This paper reports on a new species of chiton which appears to be endemic to the Aleutian Islands.

POLYPLACOPHORA de Blainville, 1816

NEOLORICATA Bergenhayn, 1955

ISCHNOCHITONINAE Bergenhayn, 1930

ISCHNOCHITONIDAE Dall, 1889

Ischnochiton Gray, 1847

Ischnochiton allyni Ferreira, spec. nov.

(Figures *1* to *4* and 5)

Diagnosis: Chiton of moderate size, uniform rusty-brown color. End valves with 15 - 20 radial ribs, often bifurcated, crowned by minute tubercles, and separated by well defined sulci. Lateral areas with 3 - 4 similar ribs. Central areas uniformly pitted for a net-like effect. Girdle covered with imbricating, relatively large, mammilated, faintly striated scales. Articulamentum of intermediate valves with 2 - 3 slits per side.

Description - Holotype: Oval shaped with quasi parallel sides, circular in front and in back. Dried, but fully extended, it measures (including the girdle) 19 mm in length, 12 mm in width, and 4.5 mm in height. Width/length ratio = 0.63. Jugal angle about 103°. The tegmentum and girdle are a uniform rusty-brown color. The tegmentum is microgranulose throughout. The anterior valve displays some 22 radial ribs, most of which bifurcate resulting in about 36 ribs when counted at the valve's periphery. The radial ribs tend to have a distinct triangular outline in cross-section; they are crested by a row of minute tubercles (about 0.05 mm in diameter), often poorly defined, close together, sometimes fused. The radial ribs are neatly separated by a sulcus. The posterior valve has a well defined but not prominent mucro; the post mucro area is plane and shows about 16 radial ribs in every respect similar to those in the anterior valve. The central areas of the intermediate valves are grossly but uniformly pitted resulting in a net-like appearance. The lateral areas are well defined and moderately raised; they exhibit 3 - 4 radial ribs with the same characteristics of those in the end valves. Girdle not banded, about 2 mm in width, covered with loosely imbricated scales. The girdle scales (Figures *3*, *4*) are strongly convex, weakly striated, often reaching 250 μm in length; their dorsal edge tends to point inwardly, and is usually crowned by a striated mammillus. Towards the periphery, the girdle scales are much smaller, and columnar in shape.

The gills, about 28 on each side, extend from about 2 mm in front of the anus to about 3 mm behind the anterior edge of the foot. The articulamentum is white. Insertion teeth are sharp and straight edged. The slit formula is 16 - 2/3 - 14. Eaves are small and subspongeous. The sutural laminae are sharp and semi-oval continuing without notch or demarcation with a thin sinusal lamina which protrudes 0.1 - 0.2 mm in front of the anterior edge of the tegmentum. The sinus is well developed but moder-

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ate in size. The radula (Figure 5) is 9.5 mm long and contains about 45 rows of teeth. The uncinate plate (major lateral) is unicuspid.

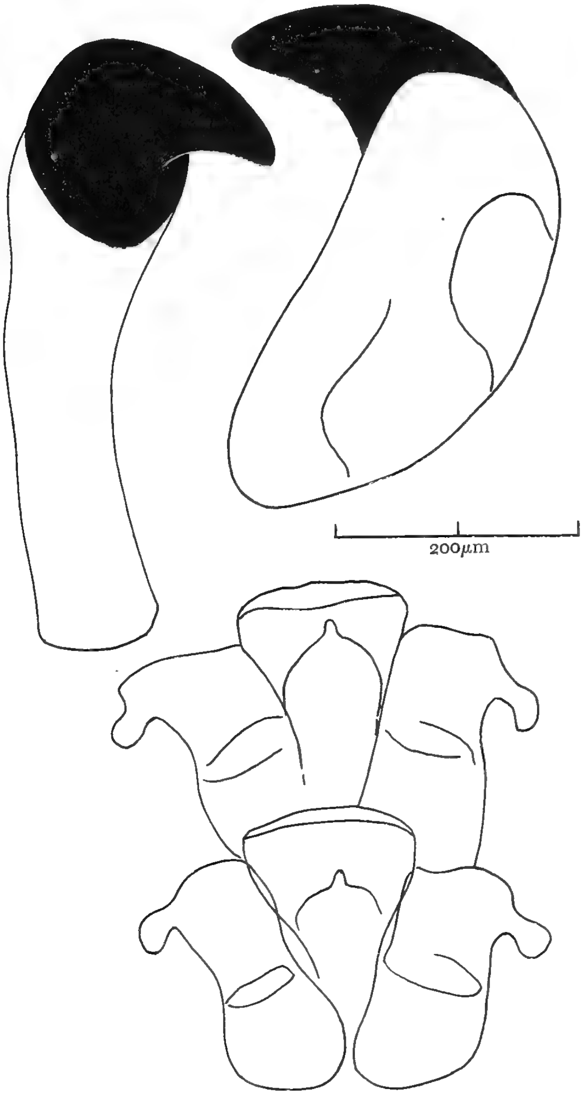

Figure 5

Ischnochiton allyni Ferreira, spec. nov.
Holotype – radular teeth [Camera lucida drawing]

Paratypes: 23 mm, and 36 mm in length; same color as holotype.

Type Locality: North side of Constantine Harbor, Amchitka Island (51°30′N; 179°00′W), Aleutian Islands, Alaska. The 3 specimens, here designated as holotypes and paratypes, were collected by L. Barr *et al.*, with SCUBA, on a rock substrate, in 17 - 27 m (50 - 80 feet) of water on June 12, 1973; they were made available through the generosity of J. M. Barnes, Brigham Young University, Provo, Utah.

Type Material: The holotype, partly disarticulated (CASIZ Type Series No. 683; Type Slide No. 496), and the two paratypes (CASIZ, Type Series Nos. 684 & 685), together with color slides of the specimens (CASIZ, Color Slides Series, Nos. 2949 - 2951) are deposited in the California Academy of Sciences, San Francisco.

Remarks: The question of a subgeneric assignment for *Ischnochiton allyni* cannot be readily decided at this time. Similarities in tegmental sculpture, girdle scales and articulamentum suggest that *I. allyni* may have a not too remote kinship with *I. trifidus* (Carpenter, 1864) from the adjacent eastern Pacific Cold Temperate Region, and for which Berry (1919) erected the monotypic subgenus *Tripoplax*. However, *I. allyni* with its *Lepidozona*-like features and radsioid valves seems to have an even greater affinity with a group of species described from the Sea of Okhotsk and the northern part of the Sea of Japan, in the genera *Gurjanovillia* and *Lepidozona*. The close examination of specimens graciously donated by Dr. B. Sirenko, University of Leningrad, U. S. S. R., suggests a phylogentic tie between *I. allyni* and *Gurjanovillia albrechti* (Schrenck, 1867), *G. lindberghi* Jakovleva, 1952, *L. multigranosa* Sirenko, 1975, *L. thielei* Sirenko, 1975, and *L. ima* Sirenko, 1975.

The synonymization of the genus *Gurjanovillia* Jakovleva, 1952 (Type species: *Chiton albrechti* Schrenck, 1867, by OD) under *Lepidozona* Pilsbry, 1892 (Type species: *Chiton mertensii* Millendorff, 1847, by OD), as previously proposed (Smith, 1960; Ferreira, 1974; Sirenko, 1975) is incorrect: The species listed by Jakovleva in the genus *Gurjanovillia* are radsioid, *i.e.*, 2-slitted, and therefore not members of the genus *Lepidozona*

Explanation of Figures *1* to *4*

Figure *1*: *Ischnochiton allyni* Ferreira, spec nov. Paratype; length 36 mm [Allyn G. Smith, photograph]

Figure *2*: *Ischnochiton allyni* Ferreira, spec. nov. Paratype, close-up of valves i and ii [Allyn G. Smith, photograph]

Figure *3*: *Ischnochiton allyni* Ferreira, spec. nov. Holotype – girdle scales [SEM micrograph by Hans Bertsch] approx. × 62

Figure *4*: *Ischnochiton allyni* Ferreira, spec. nov. Holotype – girdle scales [SEM micrograph by Hans Bertsch] approx. × 186

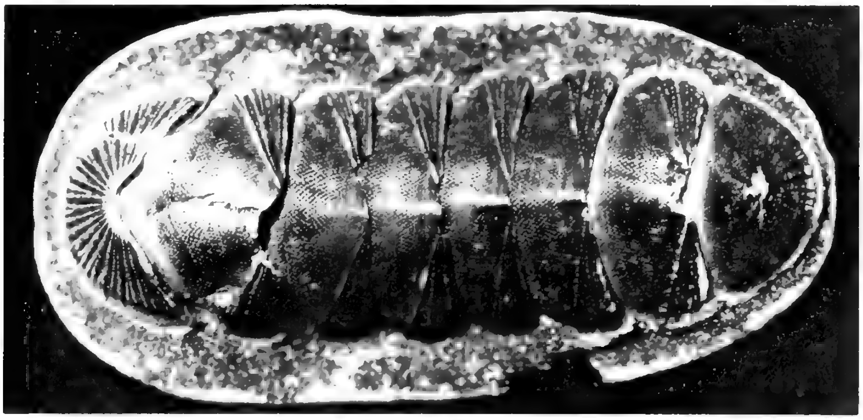

Figure *1*

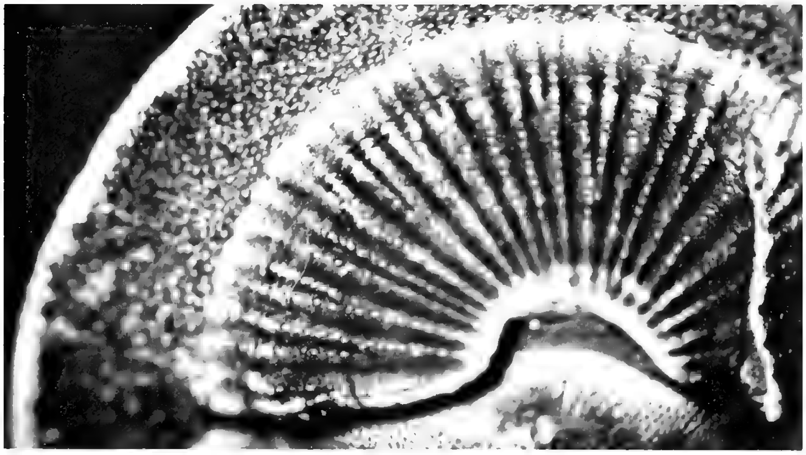

Figure *2*

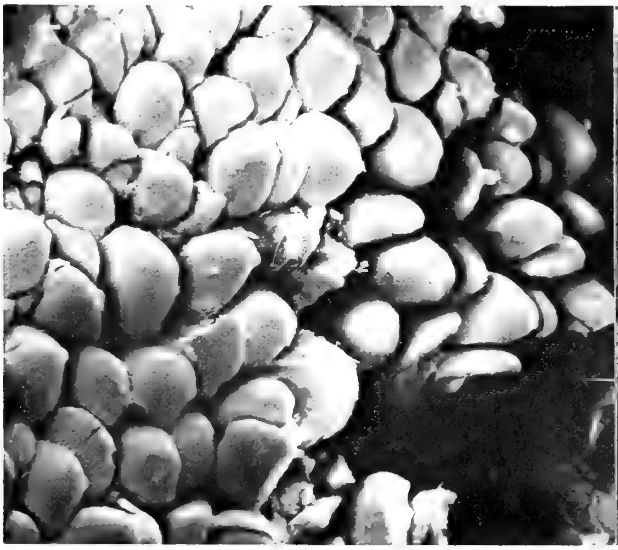

Figure *3*

Figure *4*

which (*sensu* FERREIRA, 1974) contains 1-slitted species exclusively. Thus, the taxon *Gurjanovillia* must be taken out of the synonymy of *Lepidozona* and considered anew.

The likely kinship between *Ischnochiton allyni* and the above mentioned northwestern Pacific species suggests the possibility of grouping them at the subgeneric or even generic level. However, the problem is complicated by the fact that the genus *Ischnochiton* Gray, 1847 (Type species: *Chiton crispus* Reeve, 1847, by SD, KAAS, 1974) is much in need of revision, and the definitions and differential diagnosis of its all too numerous subgenera remain unsettled. So, for the moment, whether *I. allyni* would be better assigned to the now available genus *Gurjanovillia*, or to one of the ill-defined subgenera of *Ischnochiton* must remain an open question pending further investigation. Under the circumstances, and until a clearer perspective of these taxa can be achieved, it seems appropriate to retain *I. allyni* in the genus *Ischnochiton* with no subgeneric assignment.

The apparent phylogenetic relationship between *Ischnochiton allyni*, seemingly endemic to the Aleutian Province, and the above mentioned group of species from the Sea of Okhotsk Province suggests that a common ancestor might have inhabited the northernmost part of the Pacific in a possibly continuous distribution between the two great coastal arches. Conceivably, *I. allyni* (and perhaps also *I. trifidus*) stemmed from the eastern part of that original stock, and unto the present has remained separated from counterparts in the northwestern Pacific by the deep waters of the North Aleutian Basin.

The species is here called ***allyni*** after a great man, Allyn Goodwin Smith, who guided my steps and inspired much of my work.

ACKNOWLEDGMENTS

Appreciation is here expressed to Lou Barr, Auke Bay Fisheries Laboratory, Alaska, who collected the specimens and provided some additional data; to Dr. James Barnes, Department of Zoology, Brigham Young University, Provo, Utah, who generously donated the specimens; to Dr. B. Sirenko, Academy of Sciences of USSR, Leningrad, USSR, and Dr. Iwao Taki, Hiroshima University, and Dr. Kohman K. Arakawa, Hiroshima Fisheries Experimental Station, Hiroshima, Japan, who have enriched our knowledge of the north western Pacific chiton fauna with the donation of many specimens; to Hans Bertsch, Donner Laboratory, University of California, Berkeley, for the SEM micrographs; and to Dustin Chivers and Dave R. Lindberg, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, for their critical reading of the manuscript and assistance in several other phases of this work.

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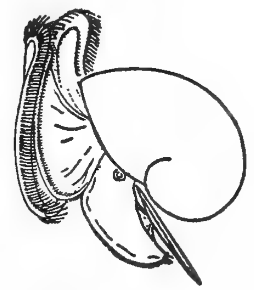

Homing in *Urosalpinx cinerea* in Response to Prey Effluent and Tidal Periodicity

BY

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(1 Text figure)

INTRODUCTION

At the University of Rhode Island's Narragansett Bay Campus, two parallel breakwaters extend at right angles from a sandy beach out into the bay, forming a basin for small boats. They are made of jumbled angular blocks of undressed stone up to 1 m^3, are heavily populated with *Balanus balanoides* (Linnaeus, 1758) and, from June to September with oyster drills, *Urosalpinx cinerea* (Say, 1822), feeding apparently exclusively on the barnacles. The floor of the basin is flat, its sediment a coarse sand. Oyster drills are never found on the sandy shoreline between the breakwaters, and during the summer the two snail populations are discrete. The situation raised the following questions: 1) if snails from the two populations were deposited at an intermediate point, would they tend to home to the breakwaters from which they were taken? and 2) how quickly would they return?

MATERIAL and METHODS

On July 8, 1975, 1625 oyster drills were taken from the inner side of the southern breakwater, which is 35 m long, and 1928 from the inner side of the northern breakwater, 41 m long. They were spray painted with fast drying enamels: the southern snails yellow, the northern snails white; and within 5 hours of capture all were returned to the middle of the boat basin where at Mean Low Water the water is 1.6 m deep and the breakwaters are 20 m apart at water level. The assistance of Brian Melzian in this day's task is gratefully acknowledged.

For the next 75 days the breakwaters were searched daily at or near low tide, allocating time and effort in approximate proportion to the length of each breakwater. Marked snails were collected and taken to a distant area for release.

RESULTS and DISCUSSION

The results are summarized in Table 1. The snails' tendency to return to the breakwater of their origin was quantified in a normal approximation to a test of proportions, which yielded the highly significant value of 5.235 ($t_{0.001,\infty} = 3.291$). The probability of no homing response, *i. e.* random dispersal, is therefore less than one in a thousand. What directional clue they used is not known.

Table 1

Number of oyster drills marked and recaptured

	North Breakwater	South Breakwater	Total
marked	1928	1625	3553
recaptured on breakwater of origin	350	234	584
recaptured on opposite breakwater	165	254	419
total recaptured	515	488	1003

Strong as this statistical result is, the homing response was complicated by an attraction to the north breakwater that affected not only the snails originating there (68% of recaptures) but also those from the south breakwater (52% of recaptures). This may be explained as follows.

Balanus balanoides exerts a powerful olfactory distant attraction for this oyster drill population (Pratt, 1974). There are more barnacles on the north breakwater, which is not only longer than the south breakwater but also is thickly populated with barnacles for more of its length. In addition, the tide along this shore ebbs southward with visible velocity but on the flood no northward current is perceptible. The presumed greater volume of barnacle effluent and rate of flow from the north may combine to explain why slightly more snails from the south breakwater were recaptured on the north breakwater than on the south.

The temporal pattern of the snails' return to the breakwaters can be seen in Figure 1, which shows the numbers of marked snails recaptured daily (all results combined). Thirteen days elapsed before the first returning snails accomplished the 10m trek along the bottom from the release point. Their return occurred in waves, of which at least 3 are clearly shown and a fourth is suggested. These waves came during periods of neap tides as can be seen in the correspondence of daily returns with the daily means of the predicted semidiurnal low tides. The lower edge of the band of barnacles is at about 5cm above Mean Low Water. During spring tides, these prey of the snails are exposed to air for varying periods twice a day. Only during neap tides are they continuously immersed and infusing the water with their chemical attractant. This may account for the biweekly pulsed return of the oyster drills to the breakwaters.

The oyster drill populations of the breakwaters, numbering several thousands in July and August, declined sharply in September. Water temperatures ranged between 20 and 23° C during July and August except for readings of 24 - 26° C for August 2 - 5; the September

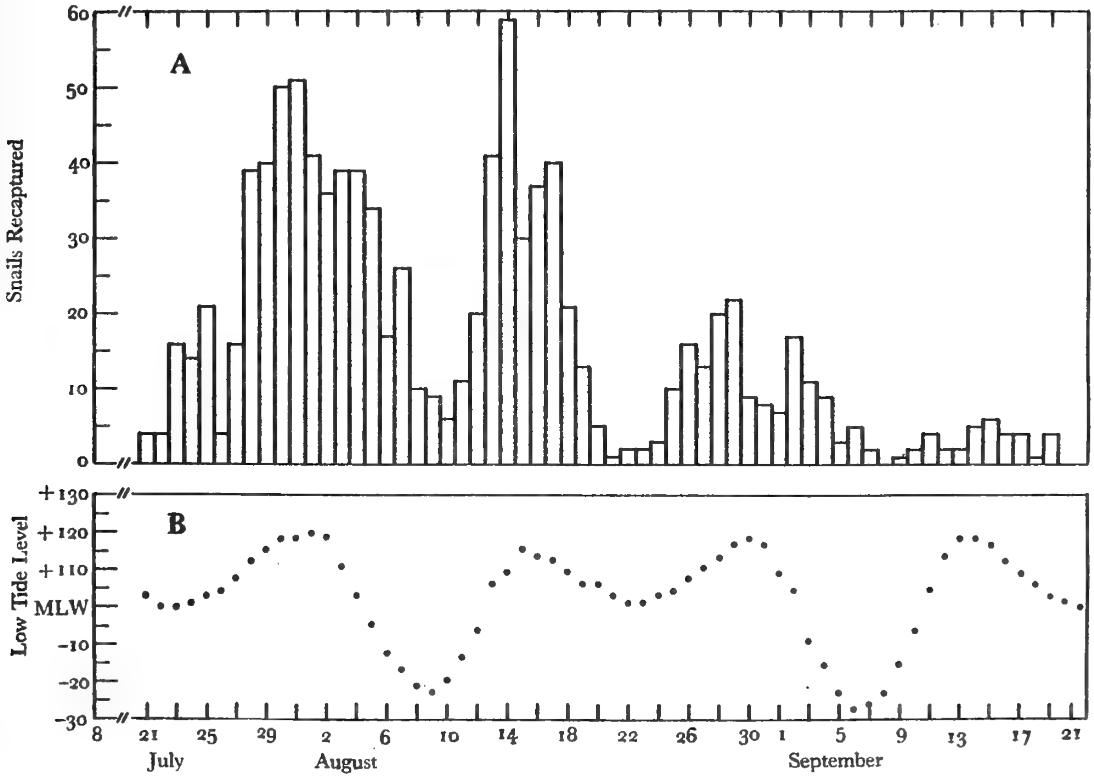

Figure 1

A. Daily recaptures of marked snails on the breakwaters
B. Daily averages of low tide levels (cm)

temperatures declined from 19.9 to 18.0° C. Oyster drills normally disappear from the breakwaters in October, presumably to overwinter on the bottom of the boat basin (Carriker, 1954, 1955). The return of marked snails to the breakwaters during the September neap tides was counter to, and largely obscured by, the seasonal downward mass movement.

Movements on the order of a meter and an hour or two, which return the animal to its approximate starting point, are known in a number of prosobranch and pulmonate snails, their precision and adaptive advantage varying with the species' way of life. Individual periwinkles, *Littorina littorea* (Linnaeus, 1758), make short feeding excursions during a tidal cycle in a U-shaped course that maintains their vertical position on the shoreline (Newell, 1958). Limpets, whose homing has been studied for nearly 150 years, home with great precision to their individual scars on the rock surface where they can withstand the molar action of waves (MacGinitie & MacGinitie, 1949). In spite of considerable experimentation (Cook, 1969; Cook *et al.*, 1969) their navigational systems remain obscure. Funke (1968) lists 34 species of marine gastropods (29 of them limpets) and 10 species of land snails but none from fresh water that are known to have homing abilities.

The homing tendency of *Urosalpinx cinerea* is on larger spatial and temporal scales than those described for other snails. Quantities and concentrations of prey adequate for the summer's foraging of a population of oyster drills are highly localized. The drill's habit of overwintering at some distance from its food supply, coupled with its limited powers of locomotion, would be a serious drawback in a random springtime search for a summer feeding ground. These disadvantages are overcome by any tendency to migrate in an appropriate direction. Upward movement from the deeper overwintering grounds will provide enough direction in some situations but in others will misguide the snail. Here the chances for success will be improved if the geotactic response is supplemented by some other clew that has previously rewarded the snail. The oyster drills' decided preference for the home breakwater suggests such an additional directional impulse.

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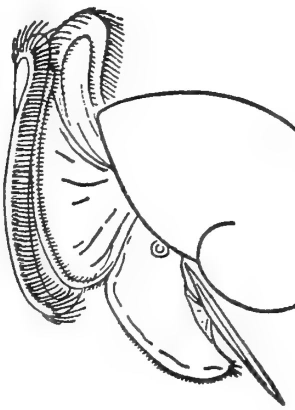

Notes on the Opisthobranch Fauna of South San Francisco Bay

BY

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AND

MERRITT TUEL

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(2 Text figures)

The reported occurrences of opisthobranch mollusks in San Francisco Bay have previously been restricted to the northern and central portions of the estuary (Aplin, 1967; Gosliner & Williams, 1970; Behrens, 1971a, 1971b; Holleman, 1972; Goddard, 1973). This report deals with the opisthobranch fauna of the southern reaches of the bay (Figure 1). Included are a range extension, two occurrences new to San Francisco Bay, one occurrence new to the Pacific coast, and description of an atypical color pattern.

Biological samples were taken periodically in South San Francisco Bay over a period of 2¾ years (February 1972 to October 1974). Collection was by means of an 18 foot (5.4m) otter trawl sampling at a depth of 3 - 5m from the R/V *Inland Seas* (operated by the education program of the Marine Ecological Institute, Redwood City).

Hand collected samples were also taken off the boat floats at marinas within the Port of Redwood City, Redwood City, California (Spring through Autumn 1974). Opisthobranchs were collected at Pete's Harbor at the foot of Whipple Avenue and at the Port of Redwood City, end of Harbor Boulevard.

DISTRIBUTION AND OCCURRENCE

SACOGLOSSA

1. *Elysia hedgpethi* Marcus, 1961

April, July, August 1972
    west of Redwood Creek, otter trawl, silty clay bottom; north of Dumbarton Bridge, otter trawl, silty clay bottom;
September 1974
    Port of Redwood City, intertidal, silty clay and riprap;

NUDIBRANCHIA

Doridacea

2. *Diaulula sandiegensis* (Cooper, 1862)

April 1972
    southwest of Bay Farm Island, otter trawl, bottom silty clay with shell material;

3. *Rostanga pulchra* MacFarland, 1905

April 1972
    southwest of Bay Farm Island, otter trawl, bottom silty clay with shell material;

Aeolidacea

4. *Eubranchus misakiensis* Baba, 1960

March 1974
    Redwood Creek, otter trawl, silty clay bottom;
October 1974
    Port of Redwood City, off boat floats;

5. *Hermissenda crassicornis* (Eschscholtz, 1831)

February - August 1972 - 1974
    throughout South San Francisco Bay, otter trawl, silty clay bottom;

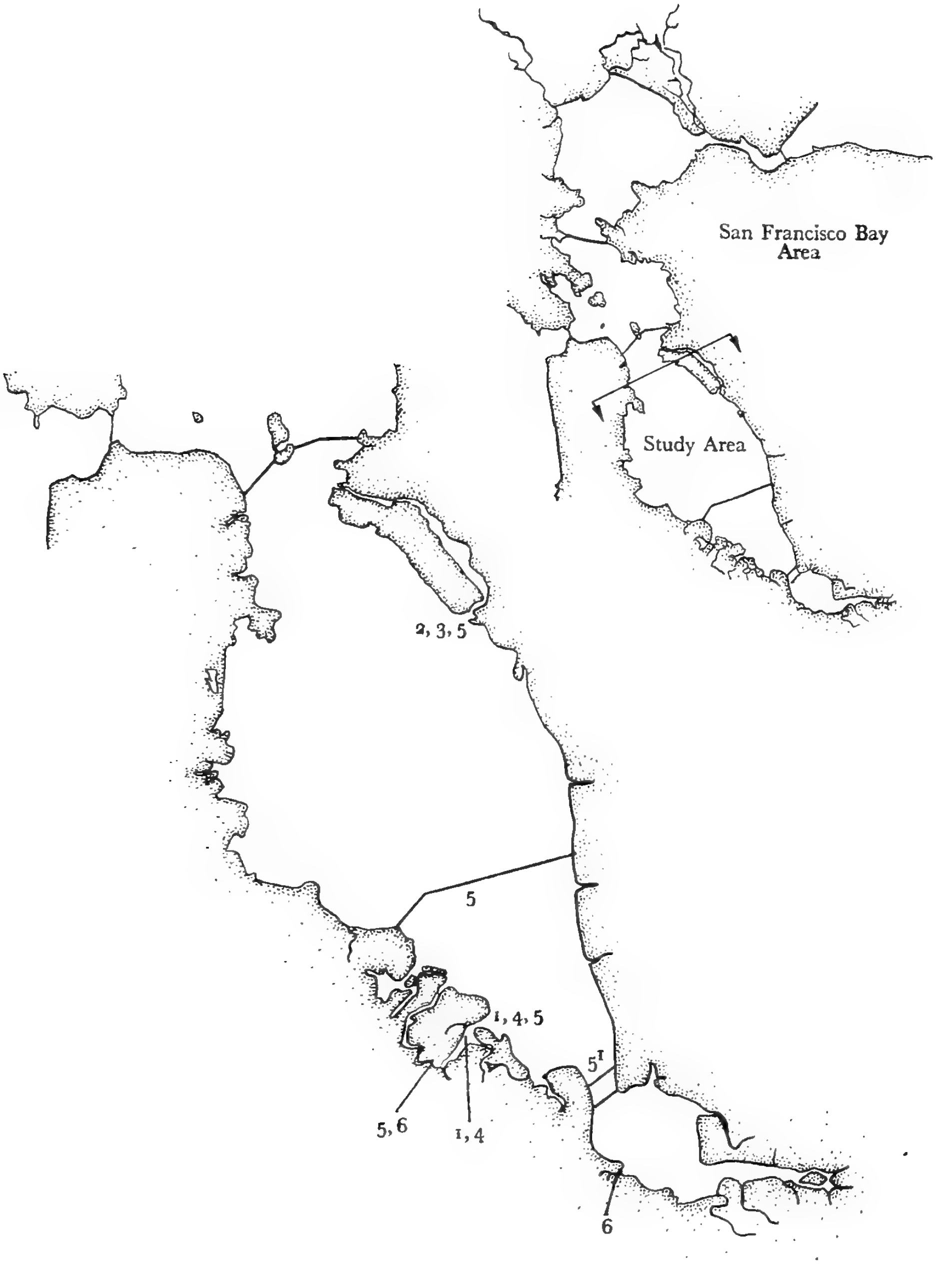

Figure 1

Map of South San Francisco Bay showing distribution of species

1. *Elysia hedgpethi*	4. *Eubranchus misakiensis*
2. *Diaulula sandiegensis*	5. *Hermissenda crassicornis*
3. *Rostanga pulchra*	6. *Trinchesia* sp.

October 1974
Pete's Harbor, off boat floats;

6. *Trinchesia* sp.

September - October 1974
Pete's Harbor, off boat floats;
September 1972
Palo Alto Yacht Club, off boat floats.

The only report of *Elysia hedgpethi* within San Francisco Bay was made by GODDARD (1973). Goddard collected 30 specimens from the Richardson Bay mudflat during the summer of 1972. On several occasions *Elysia* was encountered in trawl samples taken in the South Bay (see Figure 1). Trawls were at a depth of about 3 m. The *Elysia* were always in association with the algal species of *Bryopsis*, *Ulva* or *Gigartina*. Four specimens were collected on September 19, 1974 along the riprap shoreline of the industrial wharf at the Port of Redwood City. All specimens were in association with *Ulva* sp., and were collected at the minus 30 cm tide level. Fresh spiral egg masses were found near each specimen. This report accounts for the first occurrence of this species in the South Bay.

Diaulula sandiegensis was represented by a single specimen only. This specimen was trawled up offshore of Bay Farm Island. HOLLEMAN (1972) reported it from this same locality. Its occurrence in the North Bay was reported by GODDARD (1973).

To the authors' knowledge, *Rostanga pulchra* has never before been reported from within San Francisco Bay. On April 26, 1972, 2 specimens of *R. pulchra* were collected by trawl just southwest of Bay Farm Island. Regretfully, no additional observations or ecological comments can be added for this species at this time.

BEHRENS (1971b) first reported the occurrence of *Eubranchus misakiensis* in the eastern Pacific. That report, constituting a disjunct range extension from Japan, established the presence of this species at the San Francisco Municipal Marina. As noted in the original report, *E. misakiensis* from the boat floats occurred in association with campanularid hydroids. Egg masses were found on the hydroids.

Of particular interest is the atypical color pattern shown by the *Hermissenda crassicornis* collected in this area. Although BÜRGIN (1964) describes color variation in this species, none of the more than 50 specimens collected during this study exactly fits any of the previous descriptions.

In summarizing the color pattern of this highly variable species, Bürgin says, "The body pattern consists of blue lines running along the middle of the body and tail, forming two rhomboid patterns, one behind the rhinophores, a second outlining the pericardium. White or bluish lines also run along the sides of the body between the groups of cerata. They all converge on the tail. Within the first, and sometimes within the second of the rhomboid patterns, and on the side of the head there are very conspicuous orange markings."

In the animals we have collected the longitudinal lines on the body are always white, never blue.

Indeed, this lack of blue coloration is what called our attention to the apparent color difference.

The white lines along the cephalic tentacles and foot corners are as described by BÜRGIN (1964). However, just anterior to the rhinophores, where these lines normally converge and continue down the dorso-medial surface to the tail, the pattern deviates from the description. In the South Bay specimens the white lines become broken and irregular just before convergence dorso-medially. Posteriorly they form a single broken line which disappears in the region of the pericardium. Further posteriorly on the dorsal surface, particularly between the ceratal groups, is an assemblage of random white specks. The white stripe reforms in normal fashion once again at the last ceratal group, and continues as such to the tip of the tail (Figure 2). No rhomboid patterns typical of *Hermissenda* were observed. The only orange coloration on the body was restricted to the head region.

The cerata differed in color pattern from BÜRGIN's (1964) description only slightly, the most obvious difference being the lack of yellow, orange or blue exterior patches or bands. The cerata were seen to be transparent to yellowish-orange in ground color. They were tipped with the typical white or very light yellow cone. Below the cone the coloration deviated from the described color variations. Pigmentation in this region of the cerata consisted of white speckles and blotches arranged in a vertical line. The color and shape of the digestive diverticula extending up through the cerata conform with Bürgin's description.

Other than the described deviations in color pattern, the specimens were in full agreement with previous descriptions. A radular analysis was conducted to eliminate any questions of misidentification. The results of this analysis confirmed the identification as *Hermissenda*, and most probably *H. crassicornis*.

During September and October, 1974, a nudibranch referable to *Trinchesia* was found living in the South Bay.

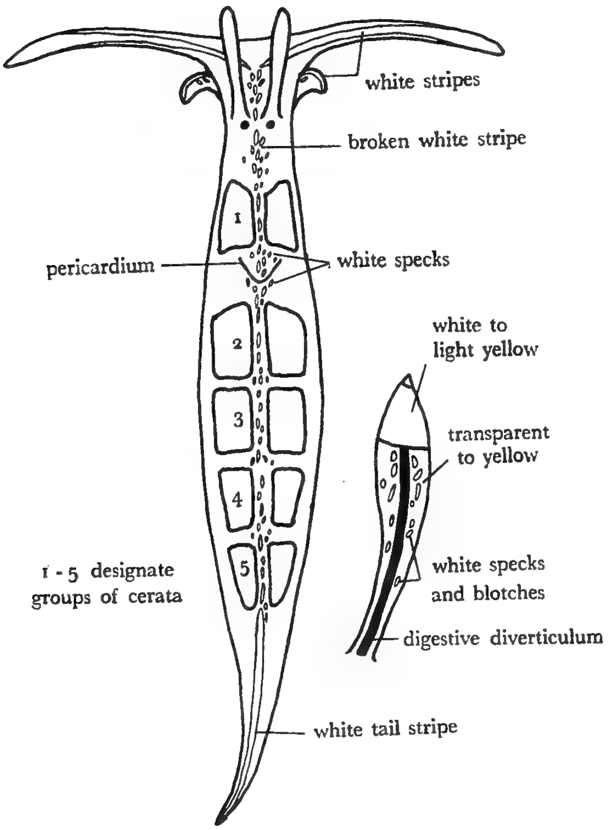

Figure 2

Drawing of *Hermissenda crassicornis*

left – body showing atypical white striping
right – cerata showing color pattern

Although this species does not appear to be one of the local coastal resident forms, we have not ascertained whether it is a foreign introduction or an undescribed species. Some 105 specimens were either collected or observed with egg masses on dense growths of the naked hydroid, *Tubularia crocea* (Agassiz, 1862) growing on the boat floats and boat bottoms at Pete's Harbor, Port of Redwood City, Redwood City, California. The specimens measured from 2 to 28mm in length and displayed a wide variation in ceratal color (from yellow to reddish-brown). Egg masses were numerous.

Gary McDonald of the Moss Landing Marine Laboratories (personal communication 27 November 1974) informed us that a similar eolid nudibranch was collected from the Palo Alto Yacht Club docks on 20 September 1972, by Mr. Mark Silberstein. On that occasion, 7 specimens measuring from 5 to 10mm in length were collected. All were found on the introduced anemone *Haliplanella luciae* (Verrill, 1898).

ACKNOWLEDGMENTS

The authors are extremely grateful for the cooperation and assistance of the staff at the Marine Ecological Institute, Redwood City, California, during this study. Thanks to Mark Kehoe for the estuarine sediment descriptions. Thanks are also due to Gary McDonald for his critical comments on the manuscript, and to Miss Joan E. Steinberg for her assistance in the analysis of the radulae of *Hermissenda* and confirmation of the identification of *Trinchesia*.

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Notes on a California Hybrid *Haliotis*

(Gastropoda : Haliotidae)

BY

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(1 Plate)

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SINCE THE 1950s, hybridization between species of *Haliotis* has been noted and recognized as such in California species of abalone. In 1971, OWEN, McLEAN & MEYER published a detailed paper on such hybridization. In addition to the descriptions and illustrations of the hybrid specimens, they included many of the collecting localities, most of which were either in southern California, U. S. A., or northern Baja California, Mexico. The northernmost station was Piedras Blancas in San Luis Obispo County, California (Lat. 35°40'N). Although no definite records were presented for a cross between *H. rufescens* Swainson, 1822, and *H. k. kamtschatkana* Jonas, 1842, it was stated that such a cross was possible in more northern waters, as both species occupied a similar range as far north as Cape Arago, Oregon (Lat. 43°18'30"N).

Recently such a cross was found and deposited in the Talmadge Collection, Eureka, California (No. 3357). The specimen was taken in a depth between 6 and 9m on a rocky wall of a surge channel at Point Cabrillo, Mendocino County, California (Lat. 39°21'N). The specimen measures: length, 114mm; width, 81mm; height of dorsal shell surface, 25mm; height of spire, 32mm. The general appearance of the shell is more elongate than the typical *Haliotis rufescens* of similar dimensions, more elevated than *H. rufescens*, but not as much as *H. kamtschatkana* (s. s.) in like-sized shells and with the sculpture of a relatively smooth *H. kamtschatkana*. In coloration the shell is a basic reddish, but close examination shows on the first 45mm the "Tapestry Pattern" of red with blue-green maculations is present.

The open pores are badly distorted. When the shell was 80mm in length, a major injury occurred along the siphonal angle, obviously damaging not only the shell but the mantle with the shell-secreting glands as well. The 2 open pores do not match either *Haliotis rufescens* or *H. kamtschatkana* (s. l.), while the closed pores are lower than normal in *H. kamtschatkana*, but with the shape and number of that species. The interior of the shell is as in *H. rufescens*.

Unfortunately I did not see the soft parts, but was told they were "different" from any of the associated specimens. This specimen was obtained from the exposed face of a nearly vertical wall which was covered with a low growth of coralline algae and in association with *Haliotis kamtschatkana* (s. s.). In the deep crevices at the base of the wall were found normal *H. rufescens*, and amid the brown algae growing near the surface were found specimens of *H. walallensis* Stearns, 1891.

ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. John De Martini and Mr. Donald Hethcock of Humboldt State University for making their field data available to me.

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Explanation of Figures *1* to *4*

Figure *1*: Left: *Haliotis rufescens* Swainson, 1822. Little River, Mendocino County, California
Middle: Hybrid of *Haliotis rufescens* × *Haliotis kamtschatkana*, Cabrillo Point, Mendocino County
Right: *Haliotis kamtschatkana* Jonas, 1899. Cabrillo Point, Mendocino County, California

Figures *2* - *4*: Hybrid of *Haliotis rufescens* × *H. kamtschatkana* Cabrillo Point, Mendocino County, California. Specimen 3357
Figure *2*: dorsal view; Figure *3*: ventral view
Figure *4*: lateral view
All figured specimens are in the Talmadge Collection

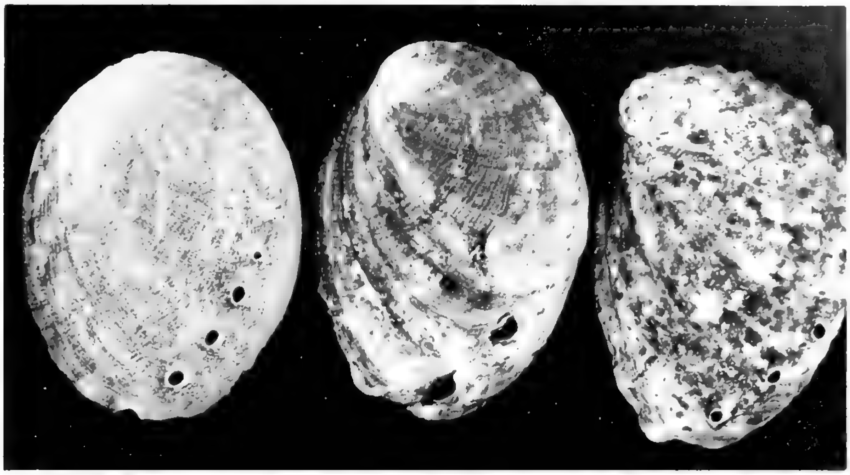

Figure 1

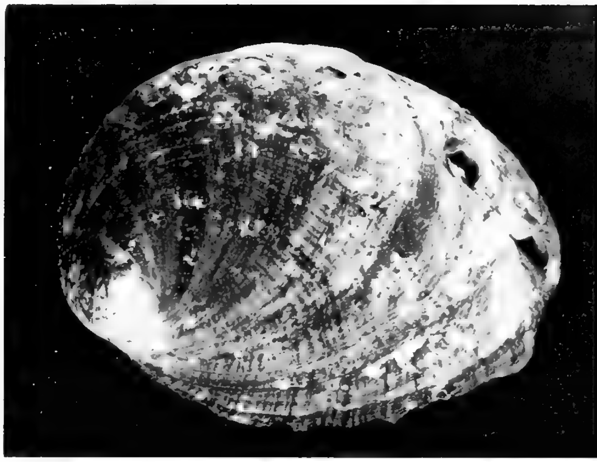

Figure 2

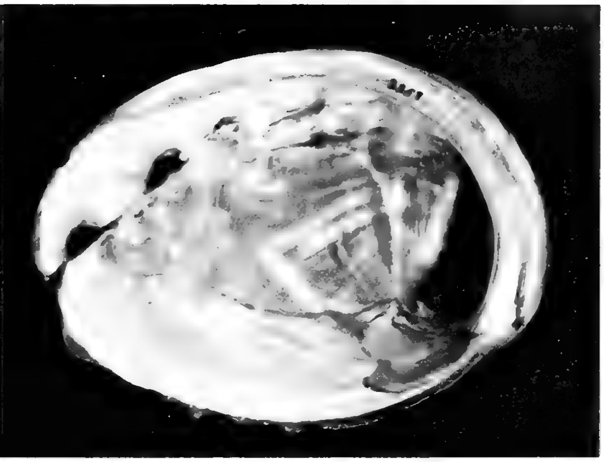

Figure 3

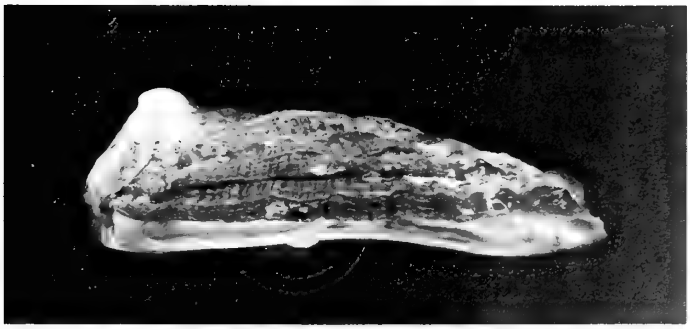

Figure 4

The Effect of Temperature on the Distribution and Biomass of *Mytilus edulis* in the Alamitos Bay Area

BY

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(1 Map)

INTRODUCTION

THE COSMOPOLITAN BIVALVE, *Mytilus edulis* Linnaeus, 1758 is abundant in bays and harbors in southern California. The purpose of the present study is to describe the distribution of this species with respect to water temperature in the Alamitos Bay area (Los Angeles County) where 4 large electrical power generating plants utilize bay water for cooling purposes and discharge the heated effluent into the lower San Gabriel River. The power plants increase sea water temperatures in the river up to 10° C above ambient, while other water quality parameters, such as salinity, pH, and dissolved oxygen concentration, appear not to be substantially changed.

Although *Mytilus edulis* is abundant in both Alamitos Bay and the lower San Gabriel River, its abundance appears to decrease in the warmer waters near the generating plants. The following study describes to what extent high water temperature affects the presence, size, and total biomass of *M. edulis* communities in the Alamitos Bay area.

MATERIALS AND METHODS

Alamitos Bay is a small boat harbor and marina used mainly for recreational puproses. *Mytilus edulis* forms a climax community on both floating boat docks and pilings throughout the Bay (REISH, 1964). Water is drawn from Alamitos Bay into electrical power generation plants for cooling purposes and then discharged into the adjacent San Gabriel River.

Sampling of *Mytilus edulis* took place at 3 stations within Alamitos Bay and 3 additional locations on the San Gabriel River. Samples were obtained by scraping all organisms from an area of concrete wall or piling from the high water mark vertically downward to the substratum using a putty knife 7.6cm in width attached to a 3m pole. The water depth at each station was 3m (at mean sea level). Each sample was placed into a large plastic bag and returned fresh to the laboratory. The number of mussels in each sample was counted, the mussels were measured to the nearest millimeter and the wet weight of the entire sample was determined. No attempt was made to remove barnacles from the samples, so their weight is included in the results.

To determine how much of each sample was shell as opposed to animal (tissue) material, a dry weight and ash free dry weight were determined. Dry weight was determined after 24 hours at 105° C and the ash weight was taken after placing the dried sample in a furnace for 20 minutes at 600° C. The ash free dry weight was calculated by subtracting the ash weight from the dry weight and used as biomass of animal material for comparative purposes. The above procedure was used because in a dense *Mytilus edulis* community numerous shells of dead mussels are included in a sample.

To determine if any weight loss occurred due to CO_2 evolution of shell $CaCO_3$ during the furnace combustion, a pre-weighed sample of $CaCO_3$ was placed in the furnace with the mussels, and its weight change was measured along with that of the sample.

Water quality for the 2 habitats was also analyzed using the following methods: dissolved oxygen concentration was measured using a polarographic oxygen analyzer (International Biophysics Co.), salinity was determined with an American Optical Refractometer (sea water model) as total dissolved salts in parts per thousand, and water clarity was measured with a standard Secchi disc.

Water temperature was measured with an electronic telethermometer (Hydrolab, Mark IV).

RESULTS AND DISCUSSION

Dissolved oxygen concentration ranged from 8.0 to 10.3 ppm for the warm and cool stations with no apparent correlation to temperature. As waters are discharged from the generators with force, considerable turbulence and aeration probably occur and hence the warmer San Gabriel River has as much and often more dissolved oxygen as does Alamitos Bay. Salinity ranged from 32.8 to 34.0 %, while water clarity varied from 2.0 to 2.9 m (Secchi disc), again with no consistent correlation for the 2 habitats.

In Alamitos Bay temperature measurements were taken at the collection sites and were 14.8° C on 18 February and 15.8° C on 1 April, 1971 when the study terminated.

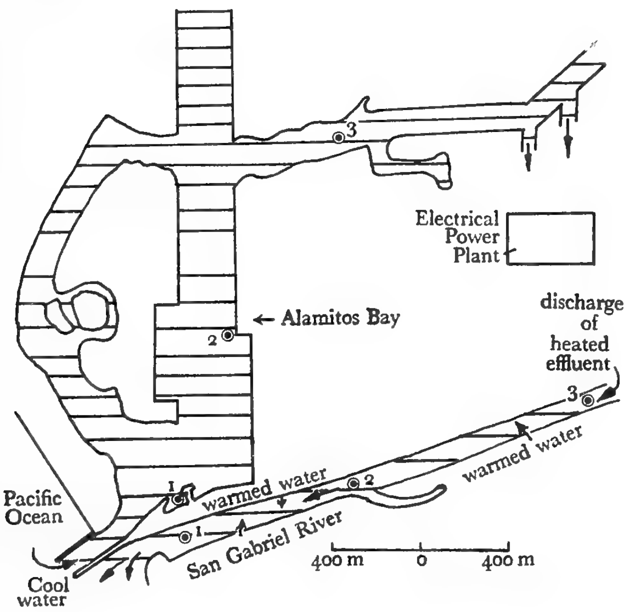

Figure 1

Alamitos Bay - San Gabriel River study site

Ambient temperature ocean water is drawn from Alamitos Bay and passed through four fossil fuel burning electrical power generating facilities and then discharged into the San Gabriel River. Three stations were located in the cooler waters of Alamitos Bay and three were located in the adjacent San Gabriel River

Water temperature in the San Gabriel River was considerably higher with a temperature gradient occurring between the generating plant outfall and the Pacific Ocean about 3.5 km to the west (Figure 1). Site 1 in the San Gabriel River was located nearest to the generating plant (ca. 2 km east of the ocean), with site 2 located about 1 km to the west and site 3 near the river's mouth. Temperatures taken near site 2 ranged from 22.7° C on 18 February to 25.0° C on 1 April, 1971. Undoubtedly, summer water temperatures are considerably higher than those measured in this study.

The warmer waters of the San Gabriel River appear to have a definite effect on the *Mytilus edulis* population size and biomass (Table 1).

The mean number of mussels collected in the colder Alamitos Bay waters was 321 per sample, while the mean for the San Gabriel River was 22 per sample. Shell length was not significantly different ($P < 0.05$) for the 2 habitats, but overall biomass was considerably greater in the colder habitat. The mean wet weight of Alamitos Bay samples was approximately 4 times greater than of those from the San Gabriel River, while the mean ash free weight (soft animal tissue only) was almost 10 times greater in Alamitos Bay samples (Table 1). There appeared to be no significant trend toward increased biomass of mussels in the cooler, down-stream stations.

Physical and biological environmental factors other than temperature may be responsible for the difference in numbers and biomass in these 2 habitats. However, standard water quality analyses for dissolved oxygen, salinity, and water clarity (Secchi disc) showed virtually no differences for the 2 habitats. **Landenberger** (1967) found that *Mytilus edulis* distribution was significantly limited by sea star predation at the lower end of their vertical distribution on a pier piling. However, no sea stars were observed at any of the collection sites in the San Gabriel River, yet these predators were quite numerous in Alamitos Bay.

Coe & Fox (1942) found that a related species, *Mytilus californianus* Conrad, 1837 which inhabits wave-exposed intertidal areas of southern California, showed a sharp decrease in growth in temperatures above 20° C. However, the mussels collected in this study were of similar size in both the warm and cool habitats, hence growth may not have been significantly affected by the warmed temperature of the San Gabriel River.

Perhaps the lower biomass of mussels in the San Gabriel River is due to the loss of both gametes and larvae by the sudden thermal shock upon transport through the power generation facilities. **Barnett** (1972) reports some

Table 1

Numbers, size and weights of mussels from Alamitos Bay and the San Gabriel River

Site	Total Number of Mussels	Mean Size (mm)	Wet weight (gm)	Dry weight (gm)	Ash free dry weight (gm)
ALAMITOS BAY					
Station					
1	543	26.2	1831.0	1184.0	
2	289	32.9	2252.2	1030.7	
3a	227	47.7	2310.0	817.6	130.7
3b	*225*	*26.4*	*2348.6*	*1152.1*	*323.1*
X =	321	33.3	2185.5	1046.1	226.9
S.D. =	150.9	17.5	238.4	166.0	136.1
S.E. =	75.45	8.8	119.2	83.0	96.2
SAN GABRIEL RIVER					
Station					
1a	5	38.2	352.4	214.0	9.2
1b	8	33.2	521.0	330.0	8.3
1c	*8*	*33.7*	*449.7*	*278.9*	*3.7*
X =	7	35.0	441.3	278.9	3.7
S.D. =	2.45	2.75	85.1	66.9	2.96
S.E. =	1.42	1.59	49.2	38.7	1.71
2a	28	13.4	520.4	318.6	23.2
2b	58	25.8	616.7	350.5	40.0
2c	64	35.0	439.3	551.5	2.5
mean	50	24.73	525.5	406.87	21.9
S.D.	19.28	10.84	88.81	126.26	26.56
S.E.	11.15	6.27	51.335	73.0	15.35
3a	2	24.5	724.2	444.1	33.7
3b	3	28.3	669.4	439.6	30.6
mean	2.5	26.4	696.8	441.85	32.15
S.D.	1.96	2.69	38.75	3.18	2.2
S.E.	1.13	1.55	22.4	1.84	1.27

mortality of bivalve larvae, and Carpenter *et al.* (1974) found mortality of copepods, upon passage through the cooling system of electrical power generation facilities. Since virtually all the water in the San Gabriel River (except during occasional heavy winter rains) passes through these power generation stations, and then flows back into the ocean there may be sufficient mortality to significantly lower the population size of *Mytilus edulis* in the San Gabriel River.

Reish (1964) found that larval settlement of *Mytilus edulis* in Alamitos Bay occurred in late winter and early spring when water temperatures would be coldest. Also, Moore & Reish (1969) observed that mature ova of *M. edulis* were present in Alamitos Bay only in late fall and winter when water temperatures were 13 to 15° C. The almost immediate thermal shock of 25° C water, as ova or larvae are passed through the generation plants, may cause sufficient mortality to explain the small numbers of mussels in the San Gabriel River.

ACKNOWLEDGMENTS

We wish to thank Pitzer College for providing research funds to carry out this project.

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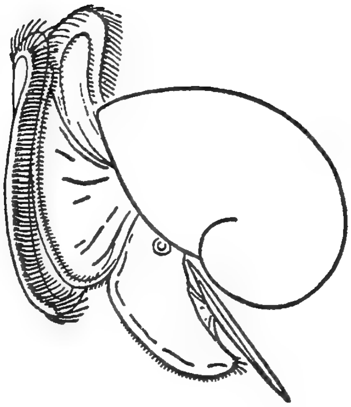

Substrate Angle, Movement and Orientation of Two Sympatric Species of Limpets, *Collisella digitalis* and *Collisella scabra*

BY

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(4 Text figures)

INTRODUCTION

Homing behavior in limpets has been widely discussed in the literature (Wells, 1917; Villee & Groody, 1940; Hewatt, 1940; Frank, 1964; Galbraith, 1965; Craig, 1968; Jessee, 1968; Eaton, 1968; Miller, 1968; Millard, 1968; Breen, 1971). Homing is generally defined as the consistent returning to exactly the same location with the same orientation (Eaton, Craig, Miller, Millard, Jessee, all *op. cit.*) Frank (*op. cit.*) makes a distinction between homing and a home range, or area to which limpets return.

The results of homing studies are varied. Breen (1971) states that discrepancies in observations on homing of *Collisella digitalis* (Rathke, 1833) in the literature (Frank, 1964; Galbraith, 1965; Miller, 1968; Millard, 1968) could be due to variations in the methods used to study homing. It is assumed in most studies that the effect of tagging (Frank, *op. cit.*), painting (Miller, *op. cit.*; Millard, *op. cit.*; Hewatt, 1940; Villee & Groody, 1940) or filing (Wells, 1917) or other methods of marking the experimental populations has a negligible effect on the animals. Variations in homing methods are not only of interest, but also such variables as length of animal (Jessee, 1968); time of tide (Dearnaley, Del Mar, Parr & Popham, 1969); duration of the experiment; tidal level (Jessee, *op. cit.*; White, 1968); population density (Breen, *op. cit.*); species; substrate type (Villee & Groody, *op. cit.*; Hewatt, *op. cit.*) and angle of slope of substrate (Eaton, 1968). Eaton (*op. cit.*) reports 12 of 13 *Acmaea limatula* (Carpenter, 1864) not homing on a vertical surface, while 9 of 15 homed on a horizontal surface. Homing in *C. digitalis* has been generally studied on vertical surfaces (Frank; Galbraith; Miller, all *op. cit.*). Villee & Groody (*op. cit.*) and Hewatt (*op. cit.*) studied homing in *C. scabra* (Gould, 1846) on horizontal surfaces. In this study I investigate the relationship between angle of substrate and movement of *C. digitalis* and *C. scabra*. Orientation of the 2 limpet species is also studied with respect to angle of substrate. The significance of all results is discussed with respect to allocation of space and food resources in competition between these 2 species of limpets.

METHODS AND MATERIALS

The relationship between the angle of slope of substrate, movement and orientation of *Collisella digitalis* and *C. scabra* was studied on 17 intertidal rock habitats in Zone 1 (Ricketts, Calvin & Hedgpeth, 1968) in a locality at Dillon Beach, California, U.S.A. during October 1974. Each rock was partitioned into quadrats using a 0.25 m^2 grid. Grid corners were marked with paint. The entire surface of each rock was covered with as many quadrats as would fit. The angle of each quadrat was measured to the nearest degree using a Brunton pocket transit attached to a board placed flat on each quadrat. Limpets were marked without removal from rocks since this seems to disrupt their behavior (Breen, 1971). A variation of the marking method of Frank (1965) was used. Adhesive tape tags, 5 × 3 mm in dimensions, numbered with India ink, were attached to limpets with Dekophane cement, and covered with 2 coats of glue to prevent abrasion of

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numbers. Limpets were tagged by either marking all snails that occurred in a quadrat or by selecting them at random on a rock surface. The size distribution of the limpets used was identical for each species. Limpets varied from 10.0 to 17.0 mm in length. The 0.25 m^2 quadrat grid was divided into 25 10 cm × 10 cm squares with nylon cord. The limpet's position in the grid was defined by a number and a letter. For each tagged limpet, the following information was obtained: position in the grid, orientation, and size. Orientation was analyzed by a variation of the method used by Miller (1968). In my experiments the orientation of a limpet on a rock surface was recorded in terms of an 8-hour clock toward which the head of the animal was pointing:
Animals with their heads straight up were in the 8 o'clock position; those with the heads straight down 4 o'clock, etc.

Observations in this study were made on consecutive days at day low tides when limpets were stationary. It was not possible to make observations at high tides, whether at night or during the day. It is not possible to detect those limpets which moved and came back to the same spot and those that did not move at all during the period of observation. Thus, a distinction could not be made between homing and non-homing limpets that move and limpets that do not move at all or very little.

RESULTS

Movement Experiment:

The analysis of the data followed that of Breen (1971). He believed that a significant deviation of observed migration frequencies from expected Poisson migration frequencies would be indicative of homing. The fit of data to a Poisson distribution indicates that the probability of movement is random, the limpets moving independently of each other in any time interval irrespective of whether they have moved previously or not. Data for *Collisella scabra* (Table 1) show that the observed migration frequencies do not deviate significantly from an expected Poisson distribution, yet there were many limpets found in the same spot. Since there is a probability of less than 1 of movement in any time interval, it is expected that some limpets do not move at all, some move once, some twice, etc., the frequency of the number of moves being a Poisson distribution. It is expected that many limpets do not move at all if the probability of movement is low, so that in a time interval many would not be observed moving. As the probability of moving in some time interval increases, the number of movements in a time interval will be greater and the frequency of zeros (the frequency of no movements) will decrease. I use the sample mean of observed migration frequencies as indicative of the amount of movement in a population. The larger the sample mean, the more limpets will not be observed in the same position on consecutive low tides (Table 2).

Table 1

Observed migration frequencies for *Collisella scabra* over time in days. The total number of limpets observed, sample mean of the observed migration frequencies and chi square is given.

Number of Migrations	Number of Days Observed 3	4	5	6	7
0	42	39	31	23	11
1	15	9	10	3	6
2	7	4	4	3	5
3		0	3	0	0
4			0	0	0
5				0	0
6					0
Sample mean (μ) =	0.45	0.33	0.56	0.31	0.73
Total number of limpets observed =	64	52	48	29	22
X^2 =	ns	ns	ns	ns	ns

ns = not significant

Table 2

Observed migration frequencies for *Collisella digitalis* over time in days. The total number of limpets observed, the sample mean of the observed migration frequencies and the chi square is given.

Number of Migrations	Number of Days Observed 3	4	5	6	7
0	34	29	20	10	2
1	36	19	11	15	9
2	17	32	16	15	3
3		11	24	8	8
4			5	6	6
5				8	6
6					2
Sample mean (μ) =	0.81	1.3	1.8	2.1	2.9
Total number of limpets observed =	87	91	76	62	36
X^2 =	ns	[3]	[4]	[3]	ns

ns = not significant

[3] = $0.025 > p > 0.01$, significant

[4] = $p < 0.005$, significant

The sample mean is graphed against time in Figure 1 for *Collisella digitalis* and *C. scabra*. The figure shows that at any time the sample mean of *C. digitalis* is greater than the sample mean of *C. scabra*. For *C. digitalis*, the sample mean increases linearly with time ($p < 0.001$).

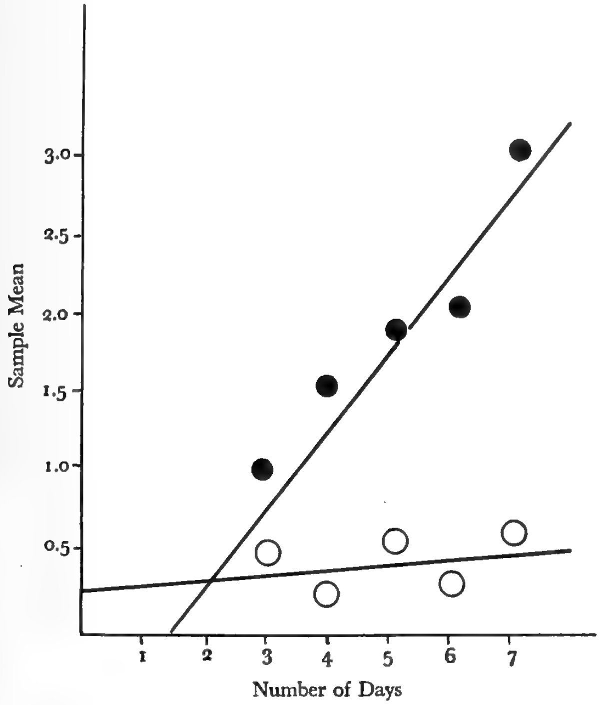

Figure 1

Sample means of observed migration frequency distributions plotted against the number of days observed

●: *Collisella digitalis* ○: *Collisella scabra*

The regression equation for *Collisella digitalis* is

$$Y = 0.50\,X - 0.71$$

where $r = 0.99$ and $p < 0.001$, $df = 3$

The regression equation for *Collisella scabra* is

$$Y = 0.05\,X + 0.21$$

where $r = 0.49$ and $0.2 < p < 0.4$, $df = 3$

For *C. scabra* there is no such trend ($0.2 < p < 0.4$) Regression analysis for *C. scabra* may detect more movement when an increase in sample size and time intervals is used. The sample means for each species are also plotted against time for 0 - 30°, 35 - 60°, and 65 - 90° angles (Figure 2). The sample mean of *C. digitalis* is less than that of *C. scabra* on 0 - 30° angles only. The observed migration frequency data are summarized with respect to 0 - 30°, 35 - 60° and 65 - 90° angles in Table 3 for *C. digitalis* and in Table 4 for *C. scabra*. The sample mean for *C. scabra* appears to decrease with increase in angle. The sample mean for *C. digitalis* appears to increase with increase in angle. Thus, movement decreases with increase in angle for *C. scabra* and movement increases with increase in angle for *C. digitalis*. In summary, the results indicate that *C. digitalis* moves more

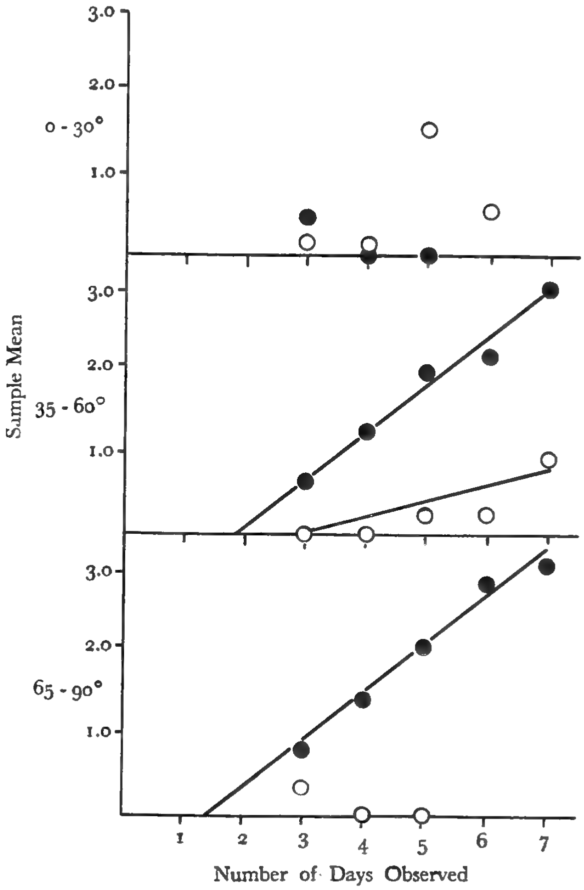

Figure 2

Sample means of observed migration frequency distributions plotted against the number of days observed for 0 - 30°, 35 - 60°, and 65 - 90° angles for *Collisella digitalis* and *Collisella scabra*

●: *Collisella digitalis* ○: *Collisella scabra*

The regression equation for *Collisella digitalis* at 35 - 60° is

$Y = 0.53\,X - 0.84$, where $r = 0.98$ and $p < 0.001$

at 65 - 90°

$Y = 0.60\,X - 0.89$, where $r = 0.99$ and $p < 0.001$

The regression equation for *Collisella scabra* at 35 - 60° is

$Y = 0.23\,X - 0.83$, where $r = 0.87$ and $0.05 > p > 0.01$

Table 3

Summary of total number of limpets observed, the sample mean, and chi square of observed migration frequency data over time in days for 0-30°, 35-60°, and 65-90° angles for *Collisella digitalis*.

	Number of Days Observed					
Angle	3	4	5	6	7	
0-30°	2	1	1	—	—	Number of limpets observed
35-60°	44	48	40	44	25	
65-90°	37	42	24	10	9	
0-30°	0.5	0	0	—	—	Sample mean
35-60°	0.73	1.3	2.0	2.1	3.0	
65-90°	0.89	1.5	2.1	2.9	3.2	
0-30°	ns	ns	ns	—	—	X^2
35-60°	ns	[1]	[2]	ns	ns	
65-90°	ns	[1]	[1]	ns	ns	

ns = not significant

[1] $0.05 > p > 0.025$ = significant

[2] $p < 0.005$ = significant

Table 4

Summary of total number of limpets observed, sample mean and chi square of observed migration frequencies over time in days for 0-30°, 35-60°, and 65-90° angles for *Collisella scabra*.

	Number of Days Observed					
Angle	3	4	5	6	7	
0-30°	50	35	13	20	—	Number of limpets observed
35-60°	10	12	12	11	3	
65-90°	5	5	1	—	—	
0-30°	0.30	0.06	1.6	0.60	—	Sample mean
35-60°	0	0	0.25	0.27	1.0	
65-90°	0.40	0	0	—	—	
0-30°	[5]	[6]	[6]	ns	—	X^2
35-60°	ns	ns	ns	ns	ns	
65-90°	ns	ns	ns	—	—	

ns = not significant

[5] $0.01 > p > 0.005$, significant

[6] = $p < 0.005$, significant

than *C. scabra* on 35-60° and 65-90° angles only. *Collisella scabra* is more stationary than *C. digitalis* at these angles because the chance that it moves in a time interval is very low in comparison to *C. digitalis*.

Orientation:

The results of the orientation data are shown in Figure 3 and the results for 0-30°, 35-60°, and 65-90°

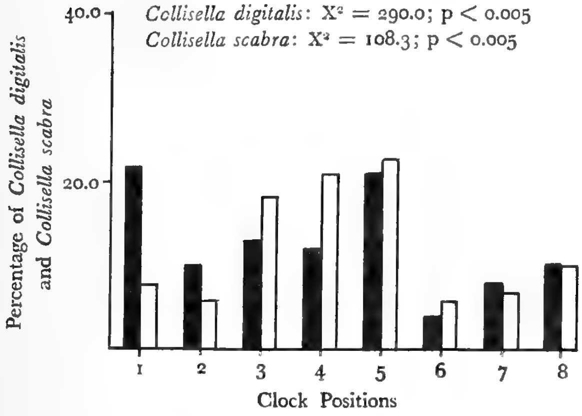

Figure 3

Percentage of *Collisella digitalis* and *Collisella scabra* in a particular clock position. Data are summed over 10 days of observation. The total number of *Collisella digitalis* observed is 801, that of *Collisella scabra* is 483. □ = *Collisella digitalis*, ■ = *Collisella scabra*

angles are shown in Figure 4. A chi square was calculated comparing observed limpet orientation and expected orientation assuming equal chance of moving in any direction. The results show that *Collisella scabra* and *C. digitalis* do not orient evenly in any direction on rocks at low tide. In Figure 3, *C. digitalis* is found in downward positions 3, 4, 5, and *C. scabra* in position 1 and 5. This confirms Miller's (1968) findings for *C. digitalis* on vertical rocks (Figure 4). *Collisella digitalis* does not appear to orient in this manner on 0 - 30° angles. *Collisella scabra* orients downward on 35 - 60° and 65 - 90° angles.

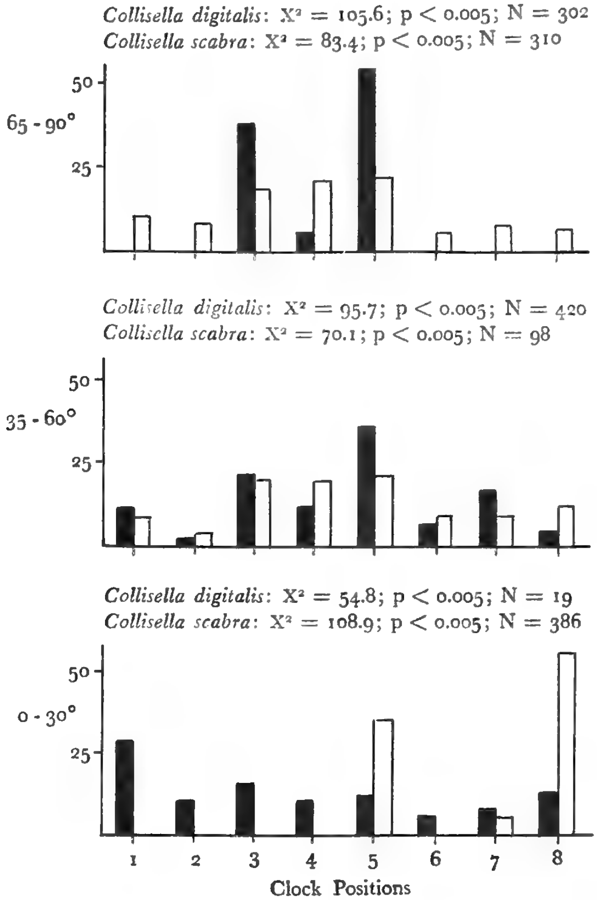

Figure 4

Percentage of *Collisella digitalis* and *Collisella scabra* in a particular clock position at 0 - 30°, 35 - 60°, and 65 - 90° angles. Data are summed over 10 days of observation. The total number of limpets and chi square is given for each species. □ = *Collisella digitalis*, ■ = *Collisella scabra*

DISCUSSION

Homing behavior in limpets is possibly an adaptation to reduce desiccation during periods of low tide (Haven, 1970; Breen, 1972) or prevent dislodgement of the animal during periods of wave splash (Test, 1945). However, there is no agreement among observers in regard to the time at which limpets move and actually home. Hewatt (1940) reported that specimens of *Collisella scabra* between 14.0 and 30.0mm move away from their homesites when covered by the tide. Specimens less than 14.0mm in length were observed moving during day low tides. White (1968) reported moving *C. scabra* when submerged or amidst heavy wave action. Villee & Groody (1940) observed no movements of *C. digitalis* and *C. scabra* at low tide, but small members of both species moving during day, high tides. Larger *C. scabra* tended to stay in one spot during low and high tides. Galbraith (1965) observed *Lottia gigantea* and *C. digitalis* to remain stationary when dry and exposed. Miller (1968) reported moving *C. digitalis* at day and night high tides. This contradicts Breen (1971) who reported *C. digitalis* to be in their shelter sites during the day, high tides. Miller (*op. cit.*) also observed *C. digitalis* to be stationary at day and night low tides. I have observed *C. digitalis* and *C. scabra* moving during night, low tides.

In this study, movement and orientation of *Collisella digitalis* and *C. scabra* were correlated with angle of substrate. There is evidence that the amount of movement of *C. scabra* decreases with increase in angle and the amount of movement of *C. digitalis* increases with increase in angle. *Collisella digitalis* moves more than *C. scabra* on 35 - 60° and 65 - 90° angles. Larger sample sizes are needed to prove this definitively. *Collisella scabra* and *C. digitalis* do not orient randomly on rocks at low tide. Although no differences in desiccation resistance could be detected between *C. digitalis* and *C. scabra* on 3 angles in laboratory experiments (Collins, 1976), desiccation resistance may play a part in accounting for differences in movement between the 2 species on various angles of substrate in the field. It is clear that other factors may also be important, such as food resources. Limpet size and abundance appear to be related to the availability of microalgae on a particular slope of substrate (MS in preparation). Differences in the amount of movement between the 2 species may be related to time and distance traveled when foraging for food. Stimson (1975) found that in laboratory tanks *C. digitalis* grazed for a greater percentage of time than *C. scabra* and that in field enclosures, *C. scabra* grazed less efficiently than *C. digitalis*, leaving more algae behind. White (1968) showed that *C. scabra* from +1.8m tidal levels have lower metabolic activity and larger glycogen stores than animals from +0.6m levels. *Collisella scabra* may be able to physiologically compensate for a lack of mobility which precludes frequent feeding.

The movement of limpets and its relation to angle of substrate needs to be studied from the viewpoint of food resource partitioning. Previous studies (Stimson, 1970; Haven, 1973; Lomnicki, 1969) have shown this to be the likely factor to pursue in more detail.

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Prey Preferences of Carnivorous Intertidal Snails in the Florida Keys

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INTRODUCTION

Six species of carnivorous gastropods are commonly found in the midtidal region (yellow zone, Stephenson & Stephenson, 1950) of the intertidal rocky platform in the Florida Keys. These snails occur primarily from the southeastern United States through the Caribbean. Their feeding habits are poorly known.

The prey preferences of these snails were studied as a first step toward a better understanding of the intertidal trophic relationships in this area and the effects of the predators on the distribution, zonation and diversity of their prey.

The relationships between preference and availability of food and the feeding methods and activity patterns were examined for the following species of carnivorous snails: *Thais haemastoma floridana* (Conrad, 1837), *Th. deltoidea* (Lamarck, 1822), *Th. rustica* (Lamarck, 1822), *Morula nodulosa* (Adams, 1845), *Pisania tincta* (Conrad, 1846) and *Leucozonia nassa* (Gmelin, 1791).

STUDY AREAS AND METHODS

Observations were made on sections of limestone beachrock parallel to the shore at sites located on Pigeon Key (24°42'N; 81°09'W) and on the south shore of Key Vaca (24°43'N; 81°05'W). The sections, centered at the midtidal level, varied in width from approximately 1.0m to 1.5m, depending upon the slope of the platform.

Feeding activity was observed at low tide when the platform surface was exposed. Snails were considered to be actively feeding if they proved difficult to remove when gently rolled onto their sides and if the proboscis was seen retracting from the prey. Removing the predator prevented duplicating the same observation and allowed the predator to select another prey before the next observation period. For each feeding observation the following were recorded: species and size of predator and prey; percent of snails feeding, and method of entry by snail. At each site the same strip of platform was examined during each observation period which lasted about 90 minutes and included over 100 observations of feeding. Population sizes of predators and prey were obtained from random square meter samples taken within the "yellow" zone.

RESULTS

Food Preferences

The relationships between preference for and abundance of food for the 5 species of carnivorous snails at Pigeon Key are shown in Table 1. The vermetid snail, *Spiroglyphus annulatus* (Daudin, 1800), was the most common prey (relative abundance 99.2%) and made up 83.9% (*Pisania tincta*) to 99.8% (*Morula nodulosa*) of the diets of the predators. The other species of prey: the tree oysters *Isognomon bicolor* (Adams, 1845) and *I. radiatus* (Anton, 1839), the mussel *Brachidontes exustus* (Linnaeus, 1758) and the barnacle *Tetraclita squamosa* (Lamarck, 1818) constituted no more than 8.1% of the diet of any predator. *Thais deltoidea* and *Th. rustica* had the most varied diets, feeding on all 4 of the common species of prey. Occasional prey of the Pigeon Key carnivores were the gastropod *Astraea tecta americana* (Gmelin, 1791), *Batillaria minima* (Gmelin, 1791), *Cerithium eburneum* (Bruguière, 1792) and *Columbella mercatoria* (Linnaeus, 1758). Cannibalism by *Thais deltoidea* was also observed.

On Key Vaca the 3 species of *Thais, Th. deltoidea, Th. haemastoma floridana* and *Th. rustica*, were the only predators found (Table 2). The commonest prey of the 3 predators combined was *Tetraclita* (46%), followed by *Isognomon* (37.2%) and *Brachidontes* (14.7%). *Spiroglyphus*, the most common prey on Pigeon Key, was not found on Key Vaca. Among the 3 thaids, *Th. rustica* preferred barnacles (60% of its diet) and *Th. haemastoma*

Table 1

Relationship of frequency of prey in the diets of carnivorous intertidal snails to the abundance of prey species at Pigeon Key, Florida

Prey	Relative abundance (%)	Frequency in diet — % of total prey					
		Thais deltoidea	*Thais rustica*	*Morula nodulosa*	*Leucozonia nassa*	*Pisania tincta*	Sum of all predators
Spiroglyphus annulatus	99.2	92.2	92.2	99.8	97.9	83.9	95.7
Isognomon bicolor and *I. radiatus*	0.5	5.5	6.0	0.2	0.7	8.1	2.8
Tetraclita squamosa	0.2	0.5	0.6	0	0	0	0.2
Brachidontes exustus	0.1	0.2	0.6	0	0	0	0.16
Other	—	1.6	0.6	0	1.4	8.0	1.14
% observed feeding		49.0	69.6	52.9	51.4	23.6	50.2
Total observations		784	240	946	554	263	2787
Total observed predations		384	167	500	285	62	1398

ate large numbers of mussels (30.8% of its diet). Only *Th. deltoidea* fed on species (*Batillaria minima* and *Th. rustica*) other than the 3 major prey.

Feeding Methods and Activity Patterns

Although all of the predators studied, except *Leucozonia nassa*, are functional drills, active drilling was confirmed in only 8 of the 1704 predations observed. Entry into the most common prey, *Spiroglyphus*, was obtained by inserting the proboscis into the tubular shell and forcing the operculum aside.

High wave action caused a pronounced reduction in feeding activity. In one case there was a 100% increase in the number of feedings observed immediately after 2 days of high winds.

Feeding activity of all of the predators was higher at night. The percentages of snails of the different species feeding at midday versus midnight at Pigeon Key were as follows: *Thais deltoidea* 37% and 65%; *Th. rustica* 38% and 48%; *Leucozonia nassa* 46.6% and 64.6% and *Morula nodulosa* 50.7% and 62.4%. *Pisania tincta* is almost completely nocturnal; only 5 of 263 (1.9%) individuals observed at Pigeon Key were feeding during daylight hours.

Specimens of *Thais* (7 *Th. rustica*, 6 *Th. haemastoma*, and 5 *Th. deltoidea*) were transplanted from Key Vaca, where no *Spiroglyphus* occurred, to Pigeon Key to determine their reaction to unfamiliar prey. During a 7 day observation period following transplantation 15 feeding snails were observed, all on *Spiroglyphus*.

Table 2

Relationship of frequency of prey in the diets of carnivorous intertidal snails to the abundance of prey species at Key Vaca, Florida

Prey	Relative abundance (%)	Frequency in diet — % of total prey			
		Thais deltoidea	*Thais haemastoma*	*Thais rustica*	Sum of all predators
Isognomon bicolor and *I. radiatus*	27.6	41.9	44.2	34.0	37.2
Tetraclita squamosa	71.1	35.5	25.0	60.0	46.0
Brachidontes exustus	1.3	16.1	30.8	6.0	14.7
Other	—	6.5	0	0	2.1
% observed feeding		28.8	38.3	45.6	40.2
Total observations		149	227	386	762
Total predations		43	87	176	306

CONCLUSIONS

Thais haemastoma has been reported to feed primarily on mussels, oysters, clams and barnacles (BUTLER, 1953, RADWIN, 1968) but there is no published quantitative information on the food preferences of *Th. deltoidea* or *Th. rustica*. Our observations show that the common thaids in the Florida Keys feed primarily on sessile vermetid snails, when they are available, but that in the absence of vermetids they feed on barnacles, oysters and mussels in direct relation to the relative abundance of the prey species.

Pacific coast relatives of *Morula nodulosa* and *Pisania tincta* are reported to feed almost exclusively on barnacles (PAINE, 1966a). In the Keys these 2 species occur low in the intertidal zone and thus their preference for *Spiroglyphus* as prey may be because they do not normally move up to the levels where barnacles or bivalves are common.

Leucozonia nassa (family Fasciolariidae) is not a drill but enters its prey by inserting the proboscis together with mild rasping of the radula and use of the shell margin. PAINE (1966b) reports that many small fasciolarids feed on tubicolous worms and WILLCOX (1895) observed *Fasciolaria hunteria* (G. Perry, 1811) eating the vermetid snail *Petaloconchus nigricans* (Dall, 1884). The feeding mechanism of *L. nassa* probably restricts its diet in the Keys primarily to vermetid snails and tubicolous polychaetes.

Preference of all of the predators for *Spiroglyphus* as food is most easily explained by the abundance and ease of entry to the prey. However, because of its small size (under 10 mm long by 2 mm wide) the consumption rate for this prey must be very high. Predators on this species, accordingly, would be expected to spend a greater amount of their time feeding. Indeed, the percent of *Thais deltoidea* and *Th. rustica* observed feeding on Pigeon Key was much higher than on Key Vaca, 49.0% versus 28.8% and 69.9% versus 45.6% respectively. Further, all of the predators on Pigeon Key, except *Pisania tincta*, fed both day and night.

Boring activity by the predators was rarely observed although most possess a drilling mechanism. There is probably little or no drilling involved in entering barnacles and vermetid snails which made up a large portion of the prey. CONNELL (1961) has observed that the thaids in California are barnacle specialists and seldom drill.

Only the 3 species of *Thais* were found where *Spiroglyphus* was absent. However, the exact relationships between predator and prey distribution, abundance and diversity in the Keys will require further study.

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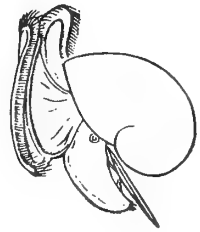

A New Species of *Subcancilla*

(Gastropoda : Mitridae)

from the Gulf of California

BY

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(1 Plate)

A SPECIES OF *Subcancilla* which has not been described previously was received from the Gulf of California. The specimens were obtained from local fishermen who had trawled them off the Sonoran coast of Mexico in 1974 near Punta Colorado. As is generally the case with specimens procured from fishermen, the data are quite general, although Punta Colorado is a well known landmark at the west end of Bacochibampo Bay. This bay lies north of the town of Guaymas, Sonora, Mexico. The area is noted for its fine shrimp, and much commercial trawling is done at a depth of 54 to 90m, so it may be assumed the specimens came from this depth.

Subcancilla welkerorum Whitney, spec. nov.

(Figures *1* to *4*)

Description: Size medium; biconic; color white with sculpture of raised reddish brown spiral ribs, narrower than interspaces; vague brown stains and blotches on shell; nucleus missing; first 5 postnuclear whorls with 4 spiral ribs per whorl; next 2 whorls with 4 spiral ribs per whorl; numerous small axial striae on shoulders of whorls and between spiral ribs, more prominent on posterior portion of whorl; sutural ramp angles at 50°; reddish brown axial lirae on 4 anterior whorls, unevenly spaced and more prominent on body whorl, giving cancellate appearance; aperture approximately ½ the length of the shell with outer lip slightly crenulate; ends of spiral ridges appear emarginate inside aperture on outer edge; columella straight with 3 plications, the anterior plication being quite weak; inside of aperture pale buff; fasciole with spiral ridges; anterior canal broad, slightly twisted; length 29.5mm; diameter 9.4mm; 8 whorls, nucleus truncated.

Holotype: Los Angeles County Museum of Natural History, Type Collection No. 1814.

Type Locality: The holotype and paratypes were collected during 1974 off Guaymas, Sonora, Mexico.

Paratypes: Paratypes are deposited in the following collections: R. A. Whitney collection, no. 48; length 32 mm; width 9.75mm; no. 49, length 28.6mm; width 9.2 mm; and the third paratype, length 25.3mm; width 8.1 mm is in the Douglas and Sherry Welker collection, no. 15, Decatur, Illinois.

Explanation of Figures *1* to *4*

Subcancilla welkerorum Whitney, spec. nov.

Figure *1*: Holotype. Los Angeles County Museum of Natural History, type no. 1814 × 2.7

Figure *2*: Paratypes; Whitney specimens on left; Welker specimen on right × 2.5

Figure *3*: Enlarged view of body whorl. Paratype in Whitney Collection × 7

Figure *4*: Enlarged view of aperture. Paratype in Whitney Collection × 7

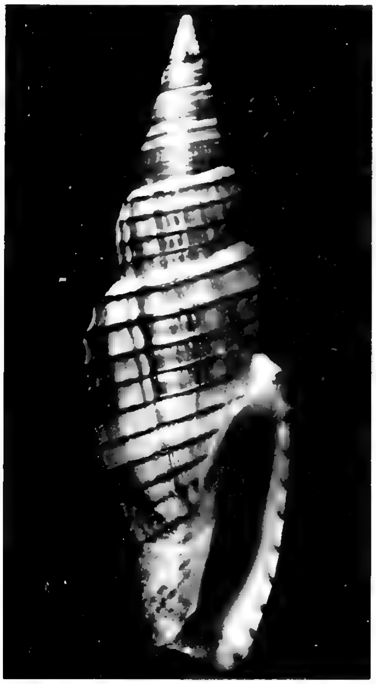

Figure *1*

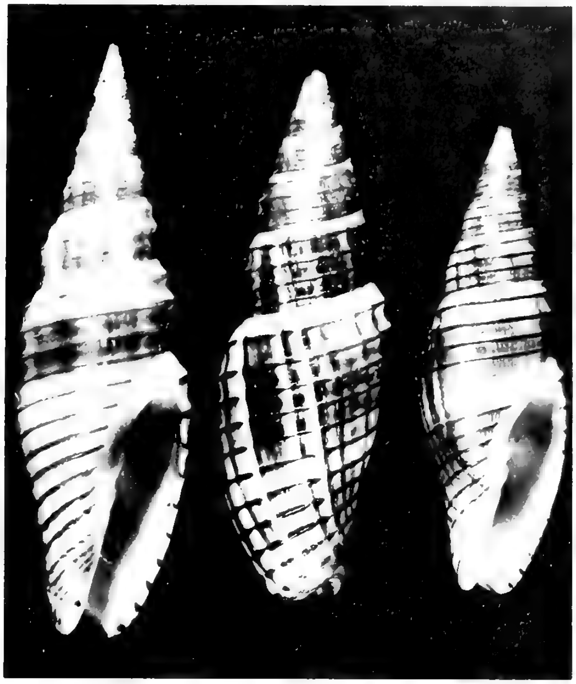

Figure *2*

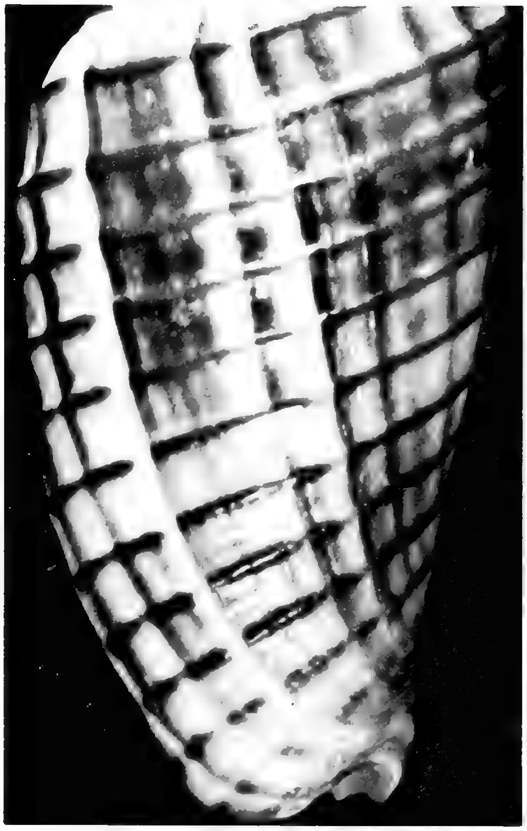

Figure *3*

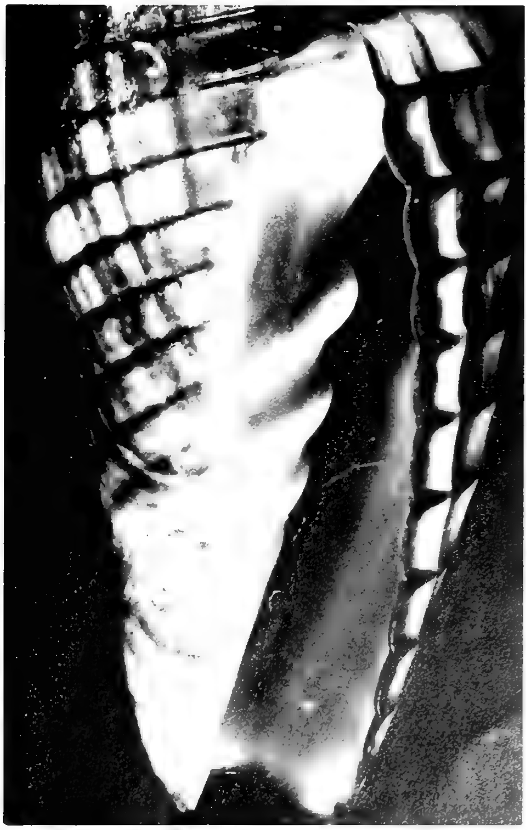

Figure *4*

Other Material Examined: In addition to the type lot, we have examined one other specimen, Los Angeles County Museum Type A. 9350.73 which was dredged near El Tobari, Sonora, Mexico.

Largest Specimen Examined: Whitney Paratype no. 48: length 32 mm, width 9.75 mm.

DISCUSSION

There is only minor variation among the specimens examined. The sculpture consists of 4 reddish brown spiral ribs per whorl on a white background. The anterior spiral rib of the body whorl is almost keel-like, accentuating the overall biconic appearance of the shell. The main difference is in the number of axial lirae, and the intensity of the color of the lirae. This is most prominent on the body whorl and causes some specimens to have a cancellate appearance. ***Subcancilla welkerorum*** superficially resembles several other species of the genus *Subcancilla*. In *S. erythrogramma* (Tomlin, 1931) the shell has 2 or 3 spiral ribs per whorl and the axial markings are vague streaks and blotches, whereas in *S.* ***welkerorum*** the axial markings are distinct lirae and give the shell a cancellate appearance; *S. attenuata* (Broderip, 1836) lacks the brown spiral ribs; *S. phorminx* (Berry, 1969) has a narrower aperture, the spiral ribs are yellowish brown and the shell lacks the brown blotches and axial markings characteristic of *S.* ***welkerorum***. There are 11 species of *Subcancilla* listed in Keen (1971) as being found in the Eastern Pacific. However, Sphon (1976) has transferred *S. sphoni* (Shasky & Campbell, 1964) from the subgenus *Strigatella* to the genus *Subcancilla*, and he also has named a new species, *S. edithrexae*. Thus, with the changes noted and the naming of the new species, *S.* ***welkerorum***, there are now 14 species of *Subcancilla* found in the Eastern Pacific.

The new species is named in honor of Douglas and Sherry Welker of Decatur, Illinois, in appreciation of their encouragement of the author's study of Mitridae. The Welkers have also accompanied the author on several shell collecting trips.

ACKNOWLEDGMENT

I am sincerely grateful for the generous cooperation given me over a period of many months by the individuals who have contributed so much of their time towards the completion of this paper. I wish to express my thanks to James H. McLean of the Los Angeles County Museum for his advice, and to Gale Sphon of the Los Angeles County Museum for arranging a loan of museum specimens for comparative studies.

I also wish to acknowledge with gratitude the excellent photographs of the holotype and paratypes by Bertram C. Draper, Museum Associate, Los Angeles County Museum of Natural History.

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Feeding in Gastropod Mollusks: Behavioral and Neurophysiological Substrates - A Symposium

INTRODUCTION

BY

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During the summer of 1975, a number of investigators at the Marine Biological Laboratory in Woods Hole, Massachusetts, were working on various aspects of feeding in gastropod mollusks. Investigators concerned with both behavioral and neurophysiological aspects of feeding in the 5 most widely used opisthobranchiate and pulmonate species were present at the laboratory. In order to facilitate comparisons between the bodies of data available for these various species and promote identification of the most insightful lines of further work, a one-day symposium on feeding in gastropod mollusks was organized. To broaden the coverage somewhat, three speakers were imported from New York and Princeton. The remaining seven speakers were investigators for the summer at the Marine Biological Laboratory. The presentations and discussion provided a unique opportunity to assess the relative progress being made in the several experimental programs, behavioral and neurophysiological. It was felt that a brief summary of the proceedings would be of general interest to students of molluscan behavior, evolution and neurobiology.

Thursday, August 14, 1975, Whitman Auditorium
Marine Biological Laboratory, Woods Hole, Mass.

Session I Feeding: Behavioral Analyses

1:20	Introduction	A. Gelperin
1:40	*Navanax*	M. Murray
2:00	*Pleurobranchaea*	J. Ram
2:20	*Aplysia*	A. Susswein
2:40	*Limax* and *Ariolimax*	D. Senseman
3:00	*Helisoma*	C. Kaneko
3:20	Summary	A. Gelperin
3:45	General Discussion	

Session II Feeding: Neurophysiological Analyses

7:20	Introduction	M. Bennett
7:40	*Navanax*	D. Spray
8:00	*Pleurobranchaea*	M. Siegler
8:20	*Aplysia*	C. Weiss
8:40	*Limax* and *Ariolimax*	D. Senseman
9:00	*Helisoma*	C. Kaneko
9:20	Summary	M. Bennett
9:45	General Discussion	

ABBREVIATIONS

EJP = excitatory junctional potential
EPSP = excitatory postsynaptic potential
IPSP = inhibitory postsynaptic potential

Predatory Behavior in *Navanax inermis*

BY

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Navanax inermis (Cooper, 1862) is carnivorous, and consumes chiefly other opisthobranchs (Paine, 1963). Predation in *Navanax* proceeds in three main stages: (1) following the mucous trail left by the prey; (2) recognition of the prey upon encounter, signalled by protraction of the pharynx; and (3) engulfing the prey by a sucking action of the pharynx (Paine, *op. cit.*; Murray, 1974; Spray, this issue, p. 59).

Trail following is mediated by two symmetrical sets of chemoreceptors located on either anterior fold (ALF) of the cephalic shield, and pharyngeal protraction is evoked by appropriate stimulation of similar receptors found on the tentacles (Murray, 1974). These two types of receptor, known as **phalliform organs**, are morphologically alike, consisting in unitary bundles of cilia mounted on and retractible into a basal tube. However, their physiologies presumably differ, since those on the ALFs are sensitive to trail mucus, while pharyngeal protraction is typically driven only by contact with the prey (Murray, *op. cit.*).

Navanax' trail following is imperfectly coordinated, and errors occur frequently which result in trail loss. Upon loss, the anterior parts of the body may be swept back and forth in a repeated broad pattern; this search mechanism frequently permits the predator to reestablish tracking. Nonetheless, since *Navanax* is likely to follow trails in the wrong direction (Paine, 1963) a certain non-zero error rate can be shown to minimize the time between meals, and so presumably possesses adaptive value.

On rare occasions, laboratory specimens will follow the trails of other *Navanax*, and copulate upon overtaking. This conspecific following behavior appears to proceed similarly to predatory tracking, and presumably involves the same sensory organs – but it is infrequent behavior and has not been studied in detail.

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Mechanisms Underlying "Singleness of Action" in the Feeding Behavior of *Pleurobranchaea californica* (MacFarland, 1966)

BY

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The simultaneous presentation of stimuli normally eliciting different behaviors usually results in "singleness of action" (Sherrington, 1948: 325); *i. e.*, the performing of one behavior to the partial or complete exclusion of other behaviors. This is seen in reference to the feeding behavior of *Pleurobranchaea californica* (MacFarland, 1966). Righting behavior, oral veil withdrawal, and mating are inhibited during feeding; whereas, animals are reluctant to feed during egg laying (Davis *et al.*, 1974a, 1974b).

To investigate the interaction of egg laying and feeding, a hormone which causes egg laying in *Pleurobranchaea* has been localized and partially purified. Injection of pedal ganglia extracts into large (greater than 450ml) recipient *Pleurobranchaea* caused egg laying in 14 out of 18 recipients. Other ganglia, if dissected from animals not actually in the act of laying eggs, never caused egg laying (cerebro-pleural ganglion, 0/4 recipients; buccal plus visceral ganglia, 0/2 recipients). Fractionation of the supernatant of the pedal ganglia on Sephadex G-50 yields hormone in fractions corresponding to a molecular weight of about 6000 daltons. Injection of this partially purified hormone into large recipients caused both egg laying and a greater than 100 fold increase in the threshold for eliciting feeding with a standard homogenate of squid mantles ($N = 3$). Controls ($N = 3$) receiving non-hormone containing fractions showed no significant change in feeding threshold. The working hypothesis, to be tested when the hormone has been further purified, is that feeding behavior is inhibited during egg laying by a direct inhibitory action of the egg-laying hormone on the neuronal circuitry underlying feeding.

To test whether righting and oral veil withdrawal were inhibited during feeding by the stimulus to feeding or the behavioral act of feeding itself, the effect of a feeding stimulus (squid mantle homogenate, SMH) on these behaviors was tested before and after satiation. Oral veil withdrawal was inhibited by SMH before satiation but was unaffected after satiation. In contrast, SMH inhibited righting behavior both before satiation, when animals exhibited feeding behavior in response to SMH, and after satiation, when most animals did not show feeding behavior. This suggests a model in which there is a direct inhibitory chemosensory pathway to the righting circuitry, whereas withdrawal circuitry is inhibited by output from the feeding circuitry which is present only during feeding.

David Dansky provided technical assistance in the localization of the egg-laying hormone. Feeding experiments were done in collaboration with J. M. Pinneo, and G. J. Mpitsos.

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Internal Variables Controlling Food Consumption in *Aplysia*

BY

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The consummatory phase of feeding in *Aplysia* consists of a fixed action pattern biting response whose intensity is affected in a graded manner by the intensity of the lip chemostimulus which elicits the response. Parametric features of the biting response which were found to be affected were the amplitude and latency of individual responses, and the interresponse interval of repetitive biting responses. These features are also affected in a graded manner as animals ingest a meal, so that as animals satiate the intensity of the biting response elicited by a given stimulus decreases. The effects of satiation on biting may be mimicked by injections of non-nutritive bulk into the anterior gut of animals. This indicates that the effects of satiation are due to mechano-stimuli in the gut. A second internal variable affecting the intensity of the biting response is arousal, *i. e.*, the potentiation of a biting response due to previous exposure to food. Arousal represents an internal process which, in food deprived animals, requires over 1 minute of constant food stimulation to build to a maximal level. When food stimuli are removed, arousal declines over a period of 30 minutes. Both the rise time and decay time of arousal are affected by satiation, so that in partially satiated animals the time needed to produce arousal is increased and arousal falls off more rapidly. These data are sufficient to account for a number of features of *Aplysia* feeding that have been observed in field studies.

Neurobehavioral Studies on Feeding in the Terrestrial Slug *Ariolimax californicus*

BY

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The consummatory feeding response of the terrestrial slug *Ariolimax californicus* Cooper has been investigated, using a combined behavioral and electrophysiological approach. Behavioral experiments have focused on the factors influencing food intake. It has been found that the hardness of the food determines the rate of ingestion. With increasing hardness there is a concomitant decrease in depth of radular penetration, and therefore in bite volume. Hardness was not found to have any significant effect on bite frequency or chemosensory quality.

Advantage was taken of the inverse relationship between hardness and consumption rate to manipulate meal size. Feeding slugs hard artificial diets significantly reduces the amount of food ingested during a feeding bout. Under such conditions the duration of the consummatory response is a direct function of the concentration of feeding stimulant contained in the diet. A regression analysis of these data leads to a simple linear equation that accurately predicts mean meal duration, given the concentration of feeding stimulant. This equation is mathematically equivalent to a decay process in which the efficacy of the

chemosensory input linearily declines as a function of time. It is postulated that the decline in chemosensory efficacy is the result of sensory adaptation.

Feeding slugs an artificial diet of similar chemosensory quality, but of various hardnesses, allows the effects of meal size on the consummatory response to be assessed. Decreasing food hardness results in an increase in consumption rate, and therefore an increase in meal size. Increasing the meal size results in a decrease in meal duration. The reduction in mean meal duration is significantly correlated with the increase in meal size. A simple linear equation derived from the regression analysis of these data allows the reduction in meal duration to be predicted given the amount of food consumed during the meal. It is postulated that bulk distention of the gut is the salient characteristic triggering the post-ingestional inhibitory input.

The linear equations describing the decline in chemosensory efficacy and the build-up of post-ingestional feedback can be combined into a "Feeding Equation." This "Feeding Equation" can predict mean meal duration and mean meal size to a high degree of accuracy given the hardness and chemical composition of the food. Present electrophysiological studies are designed to elucidate the physiological substrate embodied in the "Feeding Equation." To date, 3 symmetrical populations of primary effector neurons have been identified within the paired buccal ganglia. These effector neurons have been found to receive a number of inputs from pre-synaptic interneurons. Of particular interest is a large pair of interneurons within the buccal ganglia (*i. e.*, L 500 and R 500). These interneurons make widespread excitatory and inhibitory connections on primary effector neurons in the buccal ganglia and the metacerebral giant cells in the cerebral ganglia. The behavioral significance of these interneurons remains unknown.

Feeding in *Helisoma trivolvis*

BY

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THE BEHAVIORAL ANALYSES of feeding in the fresh-water pulmonate *Helisoma trivolvis* Say, 1816, can be conveniently summarized using an ethological framework. Little is known about the chemical composition of sufficient sign stimuli. It is known, however, that *Helisoma* is omnivorous, grazing on vegetation and carrion when available. The sign stimulus is perceived by receptors located on the anterior foot and tentacles. The ciliated tentacles channel food substances to the highly sensitive flap area located at the base of each tentacle. The response to the sign stimulus is a klinotaxis. When the concentration of the food substances is high enough anticipatory feeding commences. The behavior itself consists of 5 arbitrarily defined stages: 1. movement of the lips and mandibles which results in opening and closing the mouth; 2. movement of the odontophore back and forth; 3. movement of the radula on the odontophore; 4. movement of the buccal mass; and 5. activity of salivary glands. Since feeding behavior has been shown to be genetically programmed (below) and to be independent of external sensory input as a source of timing or ordering, the feeding behavior of *Helisoma* fits the definition of a fixed action pattern.

Preliminary experiments have used another approach to analyze the feeding behavior: behavioral genetics. The question is whether there are any naturally occurring gene differences which result in individual differences in feeding. The answer is yes. Various geographically isolated strains were brought into the laboratory and inbred over 8 to 10 generations to maintain gene frequencies at initial levels but to eliminate behavioral differences due to environmental factors. Consistent differences between 4 lines tested for rasping rate lead to the conclusion that the differences are due to gene differences. Heritability was calculated to be 0.41 ± 0.14. The interesting questions such as whether or not differences are due to differences in the nervous system and whether the differences reflect some sort of behavioral adaptation are yet to be approached.

The neurophysiological analysis of feeding in *Helisoma* has moved in a stepwise fashion from the effectors more centrally, that is from the muscles to the neural elements which control the muscles. Neuromuscular synapses in *Helisoma* are vertebrate-like. That is, there is little peripheral integration since the suprathreshold excitatory junction potentials give rise to overshooting action potentials and neither inhibitory junctional potentials nor polyneuronal innervation has been observed. Five symmetric pairs of protraction related motor neurons (PMns) and 8 pairs of retraction related motor neurons (RMns) have been identified and classified. Since there are 19 paired muscles which comprise the buccal mass (*i. e.*, the feeding musculature) and since each known motorneuron innervates only a single muscle, these figures represent a maximum of roughly $\frac{2}{3}$ of the motor neurons involved in moving the buccal mass. Proprioceptive feedback arises from stretch-activated receptors located in the buccal mass and feeds back positively to RMns and negatively to PMns with excitatory postsynaptic potentials (EPSPs) and inhibitory postsynaptic potentials (IPSPs). Feedback regulates the intensity of the power stroke (*i. e.*, retraction phase).

The motoneurons can be activated to give cyclically recurring feeding-like bursts of activity from any of a group of neurons which we have termed Cyberchron neurons (CNs). A particular CN is inhibitory to PMns and another is excitatory to RMns. CNs are electrically coupled via non-rectifying, attenuating, high-frequency filtering electrical junctions. The electrical coupling accounts for the ability to initiate feeding from any CN.

Our present hypothesis is that the electrical coupling between CNs is the control point of the behavior. Specifically: 1. the electrical coupling mediates the positive feedback between CNs which results in characteristic explosive massive activity which in turn results in the typical antiphase bursts of activity in Mns; 2. decreases in coupling between CNs appear to mediate termination of activity in CNs and thus terminate feeding. Evidence which is consistent with but does not prove the foregoing hypothesis is of 3 types: 1. Activity of CNs controls the timing of the feeding cycle and can be modulated by artificial polarization of CNs; 2. Scrutinization of activity recorded simultaneously in various CNs is consistent with the theory that positive feedback via electrical synapses is important for burst generation. 3. Burst termination is correlated with inhibition and decrease in coupling both during normal feeding and during termination of feeding as the result of the presentation of aversive stimuli.

Since blockage of input to CNs from the rest of the nervous system (via cerebrobuccal connectives) either reversibly with procaine or by section results in feeding, the CNs are apparently potentially autoactive and are normally turned off by inhibition. The mechanisms responsible for the spacing of bursts in CNs are, however, not clear.

Behavioral Studies of Gastropod Feeding

BY

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THERE ARE SEVERAL TYPES of information necessary to a complete understanding of an animal's feeding behavior. These include the following:

1) What cues and type of navigation system guide the animal to the food?
2) How do the mechanics of ingestion operate?
3) What factors determine meal length?
4) What factors determine intermeal spacing?
5) How large is the genetic component of food selection?
6) What aspects of food selection are learned?
7) What internal and external variables determine the switching probabilities between feeding and other behaviors?

The various gastropods currently being asked questions such as these exhibit a diversity of lifestyles and habitats. Behavioral questions have been motivated by the desire to physiologically dissect neuronal mechanisms; hence there is little overlap in the behavioral data currently available. The questions outlined above serve mainly to highlight the range of data available for a few species as a guide to further work.

One glimmering of mechanistic commonality is evident in that for several of these gastropods the critical internal variable determining meal size is bulk of food eaten, as monitored by presumed gut stretch receptors. Feeding experiments with *Limax maximus* support this hypothesis in the following way. When individual slugs are offered 2 agar diets simultaneously for 1 hour once each day, they sometimes eat some of each diet during the hour, although more often they eat only one diet or the other. The volume of food ingested during the feeding session is the same whether they eat one food or some of both foods, suggesting that feeding is suppressed when the gut contains some critical volume of food. As with insects, the screening of potential foods as to their nutritional value is done by external chemoreceptors which have tuned over evolutionary time to those chemical stimuli associated with nutritious prey. Once the food is ingested, no direct monitor of nutritional value is available.

The specificity of food selection varies from a few prey species (*Aplysia*, *Navanax*) to many dozen (*Limax*). Rapid food-avoidance learning has been demonstrated for *Limax* (GELPERIN, 1975) and it will be very interesting to see if other polyphagous herbivores exhibit this form of plasticity.

Literature Cited

GELPERIN, ALAN
1975. Rapid food-aversion learning by a terrestrial mollusk. Science 189: 567 - 570

Feeding in *Navanax inermis,* Neurophysiological Aspects

BY

D. C. SPRAY, M. E. SPIRA
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Navanax IS CARNIVOROUS. It lacks a radula and instead of rasping away bits of food, it engulfs its prey whole by rapid expansion of its pharynx. When prey is located and touched with tentacular receptors, the pharynx is protracted and the lips are exposed. Appropriate contact with lip mechanoreceptors elicits pharyngeal expansion. Peristaltic swallowing then moves the prey from pharynx to esophagus.

Protractor motoneurons, identified by antidromic stimulation and evoked EJPs in the muscle receive excitatory input from the cerebral ganglia and lip mechanoreceptors. Protractor sensory receptors respond to protractor stretch or compression and form excitatory synapses on the electrically coupled pharyngeal expansion motoneurons. The bilateral pair of largest expansion motoneurons each innervate the entire pharynx, while innervation by the remaining motoneurons is unilateral and partially overlapping in the antero-posterior axis so that the pharynx is divided into sequentially expandable regions. Pharyngeal mechanoreceptors possess small discrete receptive fields and have somata within the buccal ganglia. These stretch receptors form either excitatory or inhibitory synaptic contacts with expansion motoneurons, the latter both inhibit and decrease electrical coupling between motoneurons when activated. Lip mechanoreceptors also form excitatory or inhibitory connections with expansion motoneurons. Within each group of sensory receptors there appear to be mutually excitatory interactions. Several motoneurons innervating circumferential pharyngeal muscles have been identified; their activity is reciprocally related to that of expansion motoneurons. Expansion motoneurons inhibit circumferential motoneurons, but the converse does not occur. Our working hypothesis is as follows: Activation of (excitatory) lip mechanoreceptors causes activity within the pool, augmented by mutual excitation, that initiates pharyngeal expansion. Stimulation of pharyngeal mechanoreceptors by engulfed prey initiates prolonged activity of this sensory pool that causes swallowing. Thus pools of mutually excitatory sensory neurons act as command nuclei that remain active, well after the initial stimulus has been removed.

Neuronal Basis of *Pleurobranchaea* Feeding

BY

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FEEDING BEHAVIOR in *Pleurobranchaea californica,* a carnivorous marine gastropod, consists of rhythmic alternating eversion and withdrawal of a muscular proboscis and underlying buccal mass. Movements of the intrinsic buccal mass musculature are controlled by the bilaterally symmetrical fused buccal ganglia. The basic cyclic pattern underlying feeding is endogenous to the central nervous system and can be elicited by tonic stimulation to the paired stomatogastric nerves of the buccal ganglia (DAVIS, SIEGLER & MPITSOS, 1973: 258; SIEGLER, MPITSOS & DAVIS, 1974: 1173).

Coordination of Motor Neurons: Antagonists: Cyclic activity in antagonistic buccal ganglion motor neurons is driven by complementary, alternating barrages of IPSP's and EPSP's. These opposing synaptic inputs arise from coupled but apparently largely discrete populations of interneurons, as opposing events are only rarely observed to be 1:1. Synergists: The predominant means of coupling between synergistic motor neurons, however, is via alternating barrages of 1:1 EPSP's and IPSP's, apparently from common presynaptic sources.

Sensory Influences: During cyclic feeding sensory input from the buccal mass is phasic. Motor activity in the buccal mass-buccal ganglia preparation was compared with that in the buccal ganglia, in response to identical stomatogastric nerve stimulation. Upon deafferentation both the frequency of the feeding rhythm and the firing frequency of units within eversion and withdrawal bursts were significantly reduced. In addition the largest motor neurons were recruited less frequently.

Burst Modulator Cells: A population of neurons with central somata in the buccal ganglia, and axons in peripheral roots were identified as "burst modulators." In the isolated ganglia they show no cyclic synaptic inputs during rhythmic feeding output, and rarely fire. Intracellular stimulation to individual neurons can elicit or terminate eversion or withdrawal bursts, in some cases via 1:1 synaptic events in motor neurons. Burst modulator cells are likely identical with central sensory cells previously reported by SIEGLER, MPITSOS & DAVIS, 1974: 1173.

Literature Cited

DAVIS, WILLIAM J., MELODY V. S. SIEGLER & GEORGE J. MPTISOS
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SIEGLER, MELODY V. S., GEORGE J. MPITSOS & WILLIAM J. DAVIS
1974. Motor organization and generation of rhythmic feeding output in buccal ganglion of *Pleurobranchaea*. Journ. Neurophysiol. 37 (6): 1173 - 1196 (November 1974)

Cholinergic and Serotonergic Control of Buccal Muscle in *Aplysia*

BY

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AND IRVING KUPFERMANN

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WE HAVE BEEN ANALYZING feeding in *Aplysia* as a means of studying the neurophysiological bases of motivational controls of behavior. As a first step we investigated the motor control of the buccal mass – the muscular organ that executes the biting response. We recorded intracellularly from buccal motor neurons and muscle fibers. All muscles studied appeared to be polyneuronally innervated, receiving 2 to 5 distinct EJPs. It was possible to distinguish characteristic EJPs within identified muscles on the basis of size, and rate and extent of facilitation and post-tetanic potentiation. We have studied in detail the accessory radula closer muscle (ARC muscle). Motor neurons producing the 4 characteristic EJPs seen in the ARC muscle have been identified in the buccal ganglion. The EJPs in this muscle were chemically mediated, most likely by acetylcholine. They were increased in high (Ca^{++}) sea water and decreased in high (Mg^{++}) sea water. Bathing the muscle in acetylcholine caused it to contract; cholinergic blocking agents reduced both evoked contraction and EJP size. Action potentials were not observed during contraction of this muscle.

On the basis of lesion studies we hypothesized that the cerebral ganglion may be involved in some higher order modulation of feeding behavior, and we investigated the possible role of the metacerebral cells (MCCs), a pair of giant serotonergic cells located in the cerebral ganglia.

We found that the MCCs produce subthreshold synaptic potentials in buccal motor neurons. In addition, the MCCs had a peripheral action on buccal muscle. Stimulation of a MCC did not produce any EJPs, but resulted in a potentiation of muscle contraction elicited by a motor neuron or by acetylcholine applied to the muscle. The mechanism of MCC potentiation of muscle contraction was studied by recording EJPs during potentiation. The data suggest that potentiation, at least in part, is due to a direct action of the metacerebral cell on the muscle, perhaps on its contractility. Our results suggest the hypothesis that the MCC may be a modulatory neuron that can operate centrally as well as peripherally. We are currently investigating whether the MCC plays a role in mediating behavioral arousal associated with the presentation of food stimuli.

Some Emergent Problems in Neural Control of Molluscan Feeding, A Chairman's Summary

BY

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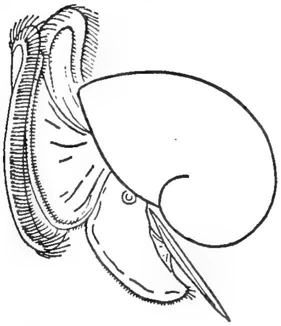
THE MOLLUSKS STUDIED to date provide a spectrum. With respect to initiation of feeding: In *Helisoma* the buccal ganglia initiate the neural signals for rasping movements whenever they are disconnected from the CNS. In *Navanax* the buccal ganglia require a positive stimulus to initiate feeding, although pathways through the cerebral ganglia probably are not required, and thus influences from higher centers may also be inhibitory. *Pleurobranchaea* clearly has neurons in the cerebral ganglia capable of driving the buccal ganglia to generate the feeding rhythm, but as in *Navanax* sensory pathways not involving the cerebral ganglia are also adequate to initiate the activity. The extent of cephalization of control of feeding requires further clarification. With respect to burst formation by mutually excitatory neurons: In *Helisoma* regenerative activity of the electrically coupled and mutually excitatory "cyberchrons" apparently drives feeding. An important issue is how a population of such cells fires bursts of appropriate duration and frequency. Sensory neurons in *Navanax* apparently also show mutually excitatory interactions, and they may function as command elements when prolonged regenerative activity in the population is initiated by evoked activity in a small subgroup of the population. Burst modulator cells of *Pleurobranchaea* may operate in the same manner. Again, mechanisms are not clear for control of duration and intensity of population activity. As yet, little knowledge is available of how motoneurons operate in different patterns for different motor acts. The same muscle is likely to operate in different ways in different stages of feeding or rejection of food. In *Navanax* synaptically controlled uncoupling is suggestive of allowing synchronous and asynchronous activity in different reflexes, but convincing demonstration of this physiological role has remained elusive. Feedback from peripheral receptors that initiates chains of reflexes and preprogrammed fixed action patterns are theoretical poles of a continuum along which the several species appear distributed. Modulation of behavior, as by the metacerebral cell in *Aplysia*, seems to be present as a distinct mode of neural interaction. Yet although activity of this cell may not ordinarily cause feeding, in a near threshold situation it would be expected to do so. It seems likely that a precise differentiation of command, sensory, and modulator elements will not be possible and that the terms will retain usefulness only in so far as the inherent limitations are recognized.



NOTES & NEWS

New Range Extensions for Chitons

(Amphineura : Polyplacophora)

BY

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THE RAPIDITY WITH WHICH developments in marine biology follow extensions of the technological or commercial frontier is often gratifying.

In March 1975 Mr. Roger Dick was serving aboard the Tenneco-owned vessel *Prospector*, which at that time was collecting samples of manganese nodules in the eastern Pacific in an area near 15° N Lat. and 125° W Long. In the course of dredging for nodules at a depth of 4000 m (2167 fathoms) Mr. Dick was able to collect several small marine specimens – a shrimp, some specimens of a brittle star species, several snail species, a species of ubiquitous abyssal bivalve, and a small chiton – all of which he placed in alcohol and eventually delivered to Dr. George E. Radwin, Curator of Marine Invertebrates, San Diego Natural History Museum.

The chiton proved an unusual find as it appears to be a second recorded specimen of *Lepidopleurus (Leptochiton) benthus* (Haddon, 1886). The original specimen was collected by H. M. S. *Challenger* from 2300 fathoms (4246m) at position 35°41′N Lat. and 157°42′E Long. The present specimen is curled; the straight length would measure 7 - 8mm. The cross-section is well-rounded, as noted by Haddon, and the nose plate presents a rounded rather than a straight profile. The sculpture consists of fine round pustules which are generally irregularly scattered, but which tend to form rows aligned longitudinally on the pleural areas and somewhat concentrically on the end plates; this linear formation, however, is neither strong nor consistent. Aside from an understandably shrunken and deformed girdle, the specimen is in good condition.

In a similar fashion, the advent of the new paved Baja California highway has proved beneficial. Previously, a land trip to Bahía de Los Angeles (29° N Lat., 133°35′ W Long.) on the Gulf of California was an arduous trek of several days which militated against transport of heavy equipment. The trip can now be made in one day in a heavily loaded standard vehicle. In May 1975, shortly after the opening of the new road, Mr. and Mrs. C. Shy and Mr. & Mrs. L. Poorman transported boats and dredging equipment to Bahía de Los Angeles and dredged the Bahía for 10 days. In addition to the usual Gulf chitons, another species, *Lepidopleurus (Xiphiozona) heathi* Berry, 1919, was collected, representing a surprisingly large range extension. This chiton, described from off Monterey, California in 15 fathoms (28m), has previously been collected only from the type area and south to off Redondo Beach, California, always in approximately 28m. That geographical range has now been significantly extended to Bahía de Los Angeles, Baja California, Mexico, in the channel between the mainland and Isla Coronado (Isla Smith) at a depth of 28m on a bottom of dead shells and small stones. All specimens taken are absolutely typical in all aspects, and in several cases bear the same touch of lavender coloration that appears on some specimens from Southern California.

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HADDON, ALFRED C.
1886. Report of the scientific results of the voyage of H. M. S. "*Challenger*." XV. – Zoology, iii Polyplacophora, pp. 1 - 47; plts. 1 - 3

Glans carpenteri vs. *Glans subquadrata*: The Rules Concerning Renamed Transient Secondary Homonyms

BY

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Renamed secondary homonyms once transferred out of their condition of homonymy have always created thorny nomenclatural problems. In such cases, workers have often reverted to the original name, and up to the time of the most recent changes in the International Code of Zoological Nomenclature (1972), there was little guidance on the proper course to be taken in the case of taxa so renamed prior to 1961. The recent changes in the Code, and details now becoming evident as to their application, provide more guidance.

In my recent review of the northwest American Carditidae (Coan, 1977), I discussed a species of *Glans* under the name *G. subquadrata* (Carpenter, 1864), having already forwarded an application to the International Commission on Zoological Nomenclature to preserve this commonly used name as would seem to be required by the new rule on secondary homonymy [Art. 59b(i)]. The Secretary of the Commission, Dr. Richard V. Melville has written to me (7 February 1977) providing information with regard to the application of this provision. The upshot of his letter is that we should use *Glans carpenteri* (Lamy, 1922), as the species was renamed when Lamy placed most of the Carditidae in the genus *Cardita*, rather than the older and better known *G. subquadrata*.

The Code provision in question states that "A junior secondary homonym rejected before 1961 is permanently rejected and cannot be restored unless the use of the replacement name is contrary to existing usage. In that case **existing usage is to be maintained** and the **matter is to be referred to the Commission** to designate as the valid name ... whichever name will ... best serve stability and uniformity of nomenclature." (emphasis mine)

In his letter, Dr. Melville points out that the words "contrary to existing usage" are to be interpreted in a rigorous manner, and applications should generally not be submitted to the Commission when "existing usage" is partially divided between the original taxon and its renaming. (The kind of test given for "unused senior synonyms" in Art. 79(b) provides guidance on the usage question.) Melville also indicates that the Commission is inclined, in practice, to give weight to usage outside the taxonomic field in exercising its Plenary Powers in this sort of case. Such non-taxonomic usage is generally not available with our less common marine mollusks.

Thus, for all practical purposes, a taxon renamed as a secondary homonym prior to 1961 is to be considered permanently renamed, even if most workers have reverted to the earlier name when the condition of secondary homonymy ended.

Literature Cited

Coan, Eugene V.
1977. Preliminary review of the northwest American Carditidae. The Veliger 19 (4): 375 - 402; 4 plts. (1 April 1977)

STANFORD COLLECTIONS GO TO THE CALIFORNIA ACADEMY OF SCIENCES

The molluscan shell collection, the type specimen collection, and a major part of the invertebrate fossil collection of the Department of Geology, Stanford University, have been transferred on indefinite loan to the Department of Geology, California Academy of Sciences.

All enquiries, loan requests, etc., relating to the Stanford collections should be directed to the Academy.

Peter Rodda

ANNUAL MEETING OF THE AMERICAN SOCIETY OF ZOOLOGISTS AND SOCIETY OF SYSTEMATIC ZOOLOGY HOSTED BY THE CANADIAN SOCIETY OF ZOOLOGISTS

The annual meeting of the American Society of Zoologists and the Society of Systematic Zoology hosted by the Canadian Society of Zoologists will be held Tuesday to Friday, December 27 to 30, 1977 in Toronto, Canada at the Royal York Hotel.

The following symposia are planned: Comparative Heart Physiology: Cellular Mechanisms of Control, Biology of Air Breathing Fishes, Developmental and Evolutionary Aspects of Brain Endocrine Function, Antigen Recognition, Comparative and Developmental Aspects of Immunity and Disease; Regeneration: Neurotrophic and Morphogenetic Controls, Polyamines in Embryonic Development, Developmental Genetics of the Mexican Axolotl; Skeletal Muscle Tissue: Form and Function; Marine Larvae: Metamorphosis and Settlement; Population Studies: Are There Any General Rules?; Nectar Feeding in Birds: Models for the Ecology and Behavior of Consumers; Numerical Taxonomy, Evolutionary Mechanisms and Processes, and Phenetic and Phylogenetic Concepts and Methods of Classification.

Contributed paper sessions are planned, and the deadline for abstracts is September 1, 1977.

Accommodations at the luxurious Royal York Hotel are $26.- per evening per room with occupancy of 1 to 4 persons. Advance registration (through December 6) is $20.- regular and $10.- for graduate students.

Social events include a Happy Hour in the Exhibit Hall on December 27, a Continental Breakfast in the Exhibit Hall, a Wine and Sherry Reception and Luncheon following the ASZ Presidential Address, and three divisional socials on December 28, a Sandwich Luncheon in the Exhibit Hall and an open party on December 29. A family program is planned and will include a one-day trip to Niagara Falls on December 31. Groups of 50 or more will be provided with chartered bus transportation round trip from the Royal York and lunch at the Revolving Dining Room of the Skylon Tower in Niagara Falls for a total of about $12.-.

Special group air fares will be available from most major cities. Many require only 10 persons travelling on the same flight to Toronto with separate return arrangements. For information contact Ms. Lou Bagnara, Travel Unlimited, 3838 East Fifth Street, Tucson, AZ 85726 (telephone: 602-325-2687) in September or October. Reservations cannot be accepted after November 15.

Members of the three participating Societies will receive abstract forms, housing and advance registration forms, and many details of the arrangements as they become available. Non-members may obtain such information from: Ms. Mary Wiley, Business Manager, American Society of Zoologists, Box 2739 California Lutheran College, Thousand Oaks, CA 91360.

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If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

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We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address).

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

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Supplement to Volume 6: out of print.

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Supplement to Volume 11: $6.-* plus handling charge. [The Biology of *Acmaea* by Prof. D. P. Abbott *et al.*, ed.]

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(Our supply of this supplement is exhausted; however, copies may be available by making application to the Secretary, Hopkins Marine Station, Pacific Grove, California 93950.)

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We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US$12.- to US$20.-, depending on the cost to us.

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A Glossary of A Thousand-and-One Terms Used in Conchology

by WINIFRED H. ARNOLD

originally published as a supplement to volume 7 of the Veliger has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US$ 3.50 postpaid if remittance is sent with the order.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

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We are unable to accept UNESCO coupons in payment, except at a charge of $4.25 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to Mrs. J. DeMouthe Smith, *Manager,* C. M. S., Department of Geology, California Academy of Sciences, Golden Gate Park, San Francisco, CA(lifornia) 94118. However, until further notice, we are suspending the publication of supplements until it will be reasonably certain that we will not be forced to spend many hours in tracing of lost insured or registered parcels and entering claims for indemnification. The special mailing list of members and subscribers who have entered an "including all supplements" will be preserved because of our innate optimism that sometime within our lifetime the postal services throughout the world will return to the former excellent and reliable performance.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims of missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues. This refusal is necessary as we have received an increasing number of "claims" as much as 6 months before the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

At present we are charged a minimum fee of $12.50 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

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is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 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); 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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Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of $5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is $25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

New Postage Rates

Although the Postal Service continues to deteriorate consistently, the postal rates are increased by 30 to 100%. We are, therefore, forced to increase the handling charges as well as the postage charges on the subscription. The following rates will be in effect on all new subscriptions and subscription renewals as of December 28, 1975:
$1.- on subscriptions and memberships in the U. S. A.; $2.50 on memberships and subscriptions to PUAS countries (Mexico, Central and South America and Spain); $3.50 to all other foreign countries, including Canada. We wish to stress that we are NOT INCREASING either membership dues or subscription rates, in spite of increased printing costs. But at the same time, we wish to call the attention to our Endowment Fund, the income from which enables us, in part, to keep these charges at the established levels. Contributions (tax deductible in the U. S. A.) are always welcome.

It has been announced by the Postal Service that no increase in postage rates would be asked during the current year; it was not stressed sufficiently that this applies only to the so-called first class mail. Second class mail rates are "phased," that is, they are scheduled to be increased each year until the rates are sufficiently high to pay the actual cost of handling that type of mail. While it is true that the rates have been very low, it should be borne in mind that the original intent of the special low rates was to aid in the dissemination of knowledge. This philosophy has, seemingly, been abandoned.

The regulations pertaining to second class mailing require "pre-sorting" of the mail which involves a large amount of time, especially if the total number of pieces is too small to warrant the employment of computerization. This requirement seems justified as long as the rates for second class matter remain substantially below those for first class matter. However, our members should be aware of the fact that postal regulations rule that second class matter cannot be forwarded three months after an address change, even though the addressee guarantees forwarding postage (in contrast, first class mail, at least for the time being, is forwarded for one year and that without charge!). Thus, issues mailed to the "old" address will be returned to the publisher if return postage is guaranteed at a rate that is considerably higher; we have been charged as much as $1.45 for such returned copies. There is also a charge of 25¢ for a postal notification of the new address. It must be obvious that we cannot keep absorbing such extra expenses and keep membership dues and subscription rate at the current low rate. We must ask for the wholehearted cooperation of all concerned to help us to hold the line against increases. Also, if a copy is returned we will, as in the past, advise the member of this fact and indicate the total costs incurred for which we must seek reimbursement. If this reimbursement is not made, we cannot continue to send future issues to the delinquent member. Membership will have to be considered as terminated and can be re-instated only upon payment of all arrears. We regret that this apparently hard rule is necessary, but we wish to continue publishing the Veliger – which will not be possible if these rules are not observed.

REGARDING POSTAL SERVICE

Complaints regarding late arrival of our journal are increasing in number, steadily, continually. However, we very conscientiously dispatch our journal on the printed publication dates. What happens after deposition at the Post Office is, of course, beyond our control. From some of our members we have been able to construct a sort of probable delivery schedule. In general, within California, 8 days is usual; outside of California, the time lapse increases with the distance; the East Coast can consider a lapse of "only" two weeks as rapid service; 4 to 5 weeks are not uncommon. Foreign countries may count on a minimum of one month, six weeks being the more usual time requirement and over two months not rare!

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed $200.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, $200.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

BOOKS, PERIODICALS, PAMPHLETS

The Biology of the Mollusca

Second Edition, by R. D. Purchon. Volume 57 of International Series of Monographs in Pure and Applied Biology; Division: Zoology. General Editor: G. A. Kerkut. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt, xxv+560 pp., 1977, $35.-.

The publication of a second edition of Dr. Purchon's valuable "**Biology of the Mollusca**" (first published in 1968 as vol. 40 of the above-mentioned series) should be an event of great importance to students of mollusks. Unfortunately, this so-called "second edition" is but a reprinting of the first edition, with insertions of a very few recent developments. A careful inspection of the chapter bibliographies reveals no more than 4 new citations, which is a small sample of the papers on mollusks that have appeared since 1966, when the author wrote his Preface to the First Edition. As the author candidly states in the preface to this "second edition," the new material comprises only: the time-factor and cyclical patterns of feeding and digestion in bivalves (inserted on pp. 233 - 235); a discussion of the distribution of snails on certain Pacific islands, based largely on a paper by Peake (1969) (see p. 344 and the graph which replaces a map in figure 114); the carnivorous habit in the Verticordiidae (Bivalvia) as elucidated by Allen & Turner (1974) and its bearing on the affinities and origin of the septibranchs; and some minor corrections.

The new discussion of the Verticordiidae leads to an interesting reconsideration of the sub-class Lamellibranchia, which is now considered to include both Verticordiidae and Septibranchia as carnivorous specializations (see pp. 105 and 109 - 111, and altered figures 39 and 47).

Since the changes entered into the second edition are insertions "pasted in," leaving the body of the text unchanged, there have been left a number of minor inconsistencies, particularly relating to the re-institution of the sub-class Lamellibranchia, in which Purchon now includes septibranchs (p. 111, fig. 47). In the first edition, Purchon explicitly rejected the name Lamellibranchia in favor of Polysyringia (filter-feeding bivalves), stating (pp. 101-102) that the majority of bivalves "... constitute the Polysyringia (no other name is available for these bivalves —although the term Lamellibranchia is suitably descriptive it is undesirable since it has long been used as the name of the whole class)." But now, even though the inclusion of the septibranchs renders Lamellibranchia even less suitable, the latter term is restored as the sub-class designation (pp. 105 and 111). This could be mildly confusing to students. Figures 39 and 47 eliminate Septibranchia as a sub-class, but the usage remains in all other parts of the book including the scheme of classification in Table 16 of Appendix B. Likewise, the term Polysyringia continues to be used in the unchanged part of the text.

The lack of any thoroughgoing revision has left certain features of the first edition that might well have been improved. The meaning of the terms Gastrotriteia, Gastropempta, and Gastrotetartika (in figure 47 but with no explanation in text) remains unexplained, and the revised figure even omits reference to the source. The important discussions of the "four minor classes" and "three major classes" which might logically have come early in such a book remain as Appendices A and B.

What these criticisms add up to is not a reflection on the valuable first edition of 1968, but to the fact that the publishers have restricted the "second edition" to a paste-in job, doubtless to avoid the expense of resetting of the work, and this has not permitted the author to do justice to a decade of advance in knowledge of mollusks. Considering that the total new material could have been inserted as an Appendix, or published as a pamphlet for about 35 cents, it is regrettable to see a hardbound "second edition" for 35 dollars. Owners of the first edition need only spend an hour making notes in a library to update their old copies. Is it too much to hope that Pergamon Press will not in future dignify slightly modified reprints by calling them new "editions"?

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Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda)

by S. VAN DER SPOEL. 484 pages; text figures, tables, and charts. Bohn, Scheltema & Holkema, P. O. Box 13079, Utrecht, The Netherlands. $60.00. 1976

I FOUND THIS a difficult book to review. Not so much due to its complexity but rather because van der Spoel's views of biogeography, ecology, behavior, speciation, and of what constitutes a species and how to go about deciding are so much at variance with my own. In situations like this it is difficult to maintain the appropriate objectivity.

The book is meant to be a companion volume to "Euthecosomata, a Group with Remarkable Developmental Stages" published in 1967, and therefore (in spite of its title) contains a section on "Additions to the Euthecosomata," where "newly distinguished taxa," "concised synonymy and short diagnoses" are presented along with many illustrations of the shells of the species (?) or formae (?) of these animals.

But the main body of the book concerns the groups in the title. It is organized into four main sections: an introduction with thoughts on phylogeny and speciation, taxonomy, distribution, and a list of type material. An appendix includes diagrams for the "dispersal" over something called "faunal centers," a large number of maps and some nice illustrations of the animals.

Van der Spoel recognizes what he calls formae in the shell bearing species of these groups. As near as I can make out these represent shell shapes that differ from other specimens of the same species. He names the formae and presents descriptions and keys, in some cases, to the formae. Each form is, presumably, based on a number of specimens that tend to look more or less alike but yet different from other formae. The formae have distributional "centers" and hence a biogeography. While I think he believes that formae tend to intergrade there is little mention of intergradation nor are there numerical or graphical attempts to show how this might occur in space or time. My own impression is that there is a lot of variability in shell shape within some species in both space and time. The scale(s) on which this occurs is so large that our sampling is pretty much inadequate for the purposes of generalizing. For example, I found the charts of distributional centers and diagrams of dispersal to be not very convincing.

This problem of scale of pattern and scale of sampling seems to me to have strongly affected the biogeographic charts of species and formae as well. Van der Spoel does not really tell us the number, distribution and type of samples on which these are based. Further, he does not tell us what the blank areas of the charts mean; are the species-formae really absent, were there adequate samples but no specimens, were no samples taken there? The charts of the Pacific are very different than my own and I am naturally curious as to why this might be so.

I found the synonymies, lists of type specimens, and bibliography to be very thorough and I think that these will be quite helpful to many persons wishing to study these animals. The descriptions of the species are almost entirely qualitative and while helpful are not nearly as useful as the illustrations of the animals.

I don't know whether or not to recommend purchase of this book. It is very expensive, and if the reader can afford to pay for an idiosyncratic view of the taxonomy, biogeography, speciation and behavior of these animals, in order to obtain what appears to be a good list of synonyms, a large bibliography and some nice illustrations, is a judgement beyond my capabilities.

JOHN A. McGOWAN,
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THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

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 specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

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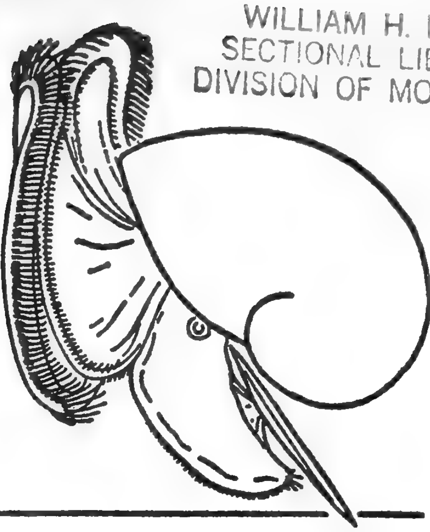

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, *(Subgenus)*
New Taxa

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Freeze-Etching Studies of Pulmonate Spermatozoa

BY

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(4 Plates)

INTRODUCTION

THE LITERATURE DESCRIBING the ultrastructure of pulmonate molluscan spermatozoa has been reviewed by THOMPSON (1973), BACCETTI & AFZELIUS (1976). All of these descriptions have, however, been limited to examination of thin sections necessitating lengthy examination to appreciate the complex helical forms of these gametes. Despite THOMPSON's (*op. cit.*) demonstration of the usefulness of the freeze-etching technique as a means of rapid appreciation of complex three-dimensional forms in molluscan spermatozoa there has been no exhaustive freeze-etching study. Freeze-etching has the advantage that replicas may be produced of membrane surfaces and three-dimensional structures over considerable areas. The most rapid appreciation of the whole cell form may be achieved with the scanning electron microscope MAXWELL (1975) but this technique lacks the resolution to study internal subcellular components. Freeze-etching allows greater resolution, and fractures reveal the three-dimensional organisation of subcellular components. The technique was applied to studies of mature spermatozoa taken from the vas deferens of a basommatophoran and a stylommatophoran pulmonate.

METHODS

Mature spermatozoa of *Arion hortensis* Férussac, 1819 and *Lymnea peregra* (Müller, 1774) were treated in the Balzers 360M freeze-etching unit (THOMPSON, 1971) and the replicas were examined with an AEI 6B or 801 electron microscope.

RESULTS

Lymnea peregra.

The mature spermatozoon has already been examined with the SEM (MAXWELL, 1975) and differs little from the generalized basommatophoran form described by THOMPSON (1973). The head is short and consists of 7 spiral ridges arranged one behind another. Freeze-etching provides much more detailed information about the interrelation of these ridges which prove not to lie parallel to one another but are compressed at the base of the head in the region surrounding the implantation fossa (Figure *1*). Here the width of the helical ridges is reduced from 0.25 μm to 0.16 μm. The helices are discrete and the nuclear surface is smooth except at the anterior tip in the region beneath the digitiform, granular acrosome where there are a large number of small but discrete spiral ridges 56 nm in width (Figure *2*). These ridges are overlaid by the apical acrosome within which little substructure is visible.

The nuclear chromatin forms a basal collar around the shallow implantation fossa which contains the anterior tip of the axoneme of the sperm tail. In regions where the plasmalemma is stripped away and the axoneme has been fractured a fine sculpturing is visible on the base of the nucleus (Figure *3*). This sculpturing consists of a series of parallel ridges of variable number (12 - 18) arranged in a more or less radial manner and showing discrete points of dislocation such that adjacent groups of ridges lie at an obtuse angle to their neighbours. It is unclear whether the sculpturing is a reflection of nuclear packing or an impression left on the base of the nucleus by the closely apposed top of the mitochondrial derivative which was removed in the preparation of the replica.

There are 7 helices in the anterior portion of the mitochondrial derivative with a sinistral pitch of 4.5 μm when viewed from the head posteriad (MAXWELL, 1975). When the plasmalemma is stripped away the helical organisation of the paracrystalline mitochondrial derivative is revealed. While thin sections demonstrate a complex structure (ANDRÉ, 1962), they give no indication of the helical distribution of subunits. Freeze-etched replicas have now demonstrated that the 9 nm globular subunits of the paracrystalline material are arranged with a consistent transverse translocation such that they lie in helically oriented parallel rows running around the flagellum (Figure *4*). In the anterior portion of the sperm tail this orientation parallels that of the 7 underlying mitochondrial helices but in the posterior region where only 2 helices are present there is a difference in helical pitch between the 2 helices and the overlying paracrystalline material. The 2 helices have a pitch of 3 μm (MAXWELL, 1975) and it is apparent (Figure *4*) that the paracrystalline material has a longer pitch. It may be suggested that the paracrystalline material has a constant helical substructure throughout the sperm length and that the pitch of the mitochondrial helices is independent of this.

Also visible in surface fractures are series of more or less regular swellings between the 2 mitochondrial helices of the posterior portion of the sperm tail. In fractures where the outer paracrystalline material is also removed, these swellings can be seen to be due to series of regularly arranged blebs located within the derivative of the mitochondrial cristae lying between the helices. The blebs are disposed in a helical manner around the flagellum and are about 0.05 μm in diameter, spaced at intervals of 0.1 μm (Figure *5*). The mitochondrial helices contain glycogen (ANDERSON & PERSONNE, 1970) and freeze-etching demonstrates a granular form with particles 20 - 30 nm in diameter.

When both mitochondrial paracrystalline layers are removed during the fracture of the frozen specimen the fibres of the axoneme may be exposed directly (Figure *6*). Closely apposed longitudinal structures with very little surface ornamentation are displayed, but no doublet structure or regularly arranged projections are visible. Thin sections indicate that the axonemal doublets are spaced at 17.5 - 20 nm with the dynein arms lying between them (WARNER, 1974). A portion of the outer mitochondrial membrane separates the paracrystalline material and the axoneme in pulmonate spermatozoa and the replicas may thus be interpreted as images of the surface of the outer mitochondrial membrane overlying the axonemal components.

The separation of the doublets and the regularly arranged projections of the dynein arms are visible in parts of the sperm tail lacking any mitochondrial derivative,

Explanation of Figures *1* to *3*

Lymnea peregra

Figure *1*: Longitudinal view of a mature sperm head. The granular acrosome covers the apex and the helices become squashed towards the base. × 120 000

Figure *2*: The 56 nm spiral ridges beneath the acrosome are exposed. A small part of the acrosome is still attached at the right side. × 95 000

Figure *3*: A surface view of the base of the nucleus. Remnants of the axoneme are visible in the implantation fossa, groups of parallel lines are visible around its periphery. There is a marked nuclear collar around the implantation fossa. × 85 000

Explanation of Figures *4* to *6*

Lymnea peregra

Figure *4*: A surface view of the paracrystalline material with small patches of plasmalemma still attached. The difference in pitch of the helical organization of this material and the 2 major helices is displayed. × 27 000

Figure *5*: Longitudinal fractures of 2 sperm tails illustrating the internal mitochondrial structure. The 2 glycogen filled major helices and the regular arrangement between the 2 mitochondrial membranes are displayed. In the right hand specimen the tip of part of the axoneme is exposed. × 26 000

Figure *6*: When all the paracrystalline mitochondrial derivative has been removed, the parallel disposition of the axoneme fibres lying beneath part of the outer mitochondrial membrane is demonstrated. The fibres are discrete but little substructure can be determined. × 75 000

Figure *1*

Figure *2*

Figure *3*

4

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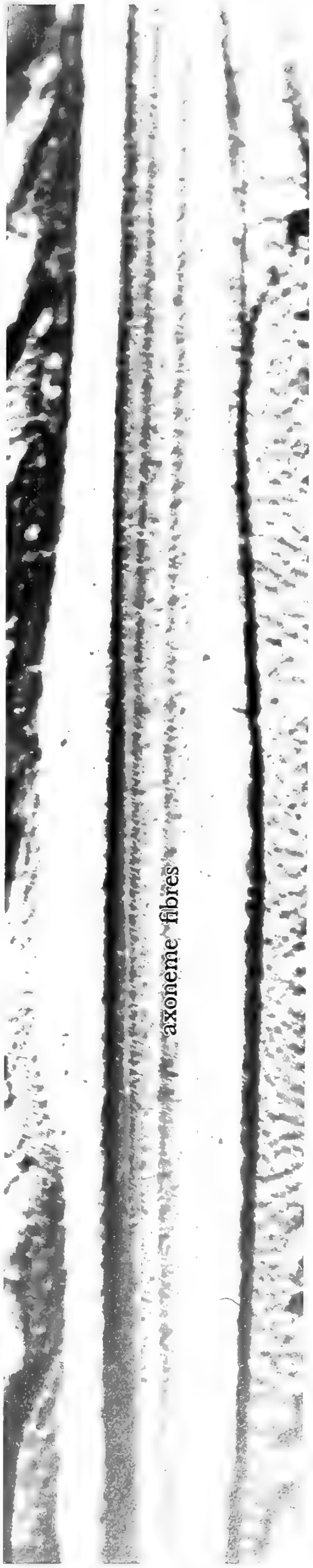

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as occurs in the most posterior portion of the *Lymnea peregra* sperm tail where only a glycogen deposit surrounds the axoneme forming a tube 0.5 µm in diameter (Figure *7*).

Arion hortensis

Freeze-etching confirms the trihelical form of the mature spermatozoon (Maxwell, 1975) but allows a greater insight into the spatial inter-relationships between the spermatozoan organelles. The 3 helices of the head run parallel, differing from the posteriad compression described in *Lymnea*. The helices are 0.35 - 0.4 µm wide and spaced at intervals of 0.1 - 0.15 µm, providing a much coarser structure. It should also be noted that the helices are dextral in orientation when viewed from the front of the head. This is clearly demonstrated in replicas of the mitochondrial region also. There is no surface sculpturing on the *Arion* sperm head, either beneath the acrosome or in the region of the implantation fossa (Figure *8*). However, there is a discrete collar of material surrounding the axoneme in this latter region formed by a thin membranous structure around the implantation fossa (Figure *9*) but it is unclear whether this is a remnant of the nuclear membrane. The implantation fossa is circular in section.

Transverse fractures of the flagellum demonstrate that the axoneme is closely enveloped by the paracrystalline mitochondrial derivative indicating that the separation of the 2 structures often observed in thin section may, to some extent, be an artefact. In the anterior portion of the flagellum the paracrystalline derivative forms a regular circular periaxonemal sleeve in which 8 - 9 layers of material may be counted (Figure *10*). Three structures are attached at the periphery of the paracrystalline sleeve, one large 'major' helix and 2 'minor' helices externally limited by a double layer of paracrystalline material. Transverse fractures indicate a very regular substructure within the paracrystalline derivative which is masked in thin sections where several layers of subunits occur within the thickness of one section.

SEM observations show that 72 µm behind the sperm head the trihelical organisation (Figure *11*) is lost and replaced by a single, large helix. This is confirmed in freeze-etched replicas which emphasize the extent of the glycogen deposit in this region where it lies around the axoneme to cover half of its transverse circumference (Figure *13*). The prominent major helix of the anterior part of the flagellum increases in size and becomes flattened around the axoneme to impose an ellipsoid cross-section. Freeze-etching clearly confirms the helical disposition of this glycogen deposit when examined in a longitudinal fracture (Figure *12*). Both the glycogen deposit and the axoneme are enclosed by portions of the outer mitochondrial membrane resulting in a smooth contour. Two layers of paracrystalline material may be observed, the thinner surrounding the axoneme, the other limiting the whole spermatozoon and enveloping the glycogen deposit.

As in *Lymnea*, the outer mitochondrial membrane is closely apposed to the periphery of the axoneme (Figure *15*). The 20 nm spacing of the doublets is very clear but the precise doublet nature and location of the dynein arms are masked.

DISCUSSION

Application of the freeze-etching technique provides information additional to that obtained with the SEM or thin sectioned studies of pulmonate spermatozoa. The form of the head, and any interspecific differences, can be appreciated in one favourable fracture rather than by a laborious reconstruction using thin sections. Freeze-etching also allows the detection of small surface structures or sculpturing which are undetectable using the SEM or thin sections. In this study it provides evidence of a specialised region at the base of the acrosome in *Lymnea peregra*.

New information is also obtained about the helical disposition of the mitochondrial derivative and its contents. This report includes the first demonstration of a helical arrangement of the subunits of the paracrystalline mitochondrial derivative, and indicates that the helical disposition of these subunits and the mitochondrial helices of André (1962) may not be directly related. Also reported is the regular and close packing of the paracrystalline subunits when observed in transverse fracture and which is masked in thin sections due to the fact that a number of layers of subunits will occur in the thickness of a single section. A previously unreported organisation of the derivatives of the cristae of spermatid mitochondria is demonstrated by freeze-etching where thin section studies had indicated a low order of organisation. In the posterior part of the *Lymnea* spermatozoon the derivatives of the cristae form a double layered structure with regularly spaced concretions of material placed between them and arranged in a helical manner around the flagellum. No such regular organisation has been described previously although the pustulose structure of the *Helix pomatia* spermatozoon (Thompson, 1973) might be comparable.

Explanation of Figures *7* to *11*

Lymnea peregra

Figure *7*: Part of 2 glycogen filled end-pieces demonstrating the granular deposit around the axoneme exposed in the centre of the tube. Regular projections can be observed on the exposed axonemal fibres. × 80000

Arion hortensis

Figure *8*: A mature sperm head illustrating the parallel orientation of the 3 helices and the lack of nuclear surface structure. A small membrane remnant is present at the base of the head, and the periaxonemal collar is visible. The axoneme extends backwards inside the paracrystalline sheath. ×30000

Figure *9*: The base of the sperm head showing the central location of the implantation fossa containing a remnant of the axoneme and the smooth surface of the nuclear base. × 70000

Figure *10*: A transverse fracture of the anterior part of a sperm tail showing the regular organisation of the paracrystalline material and the peripheral location of the 3 mitochondrial helices. × 85000

Figure *11*: External surface of a mature spermatozoon showing the trihelical structure beneath the plasmamembrane. × 48000

ACKNOWLEDGMENTS

I am grateful to Professor H. E. Hinton, F. R. S., Zoology Department, University of Bristol, England, and Dr H. Waters, Ministry of Overseas Development Fatal Leaf Yellowing Research Project, University of the West Indies, Jamaica, for allowing me to use their electron microscopes. I am grateful to the University of the West Indies for study leave to allow me to complete this project.

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Explanation of Figures *12* to *14*

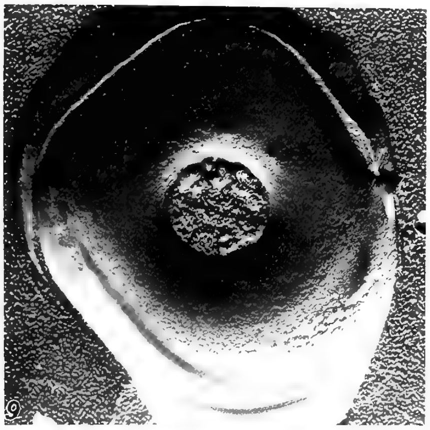
Arion hortensis

Figure *12*: The content of the single helix in the posterior part of the sperm tail is exposed illustrating the axoneme, the 2 layers of paracrystalline material and the spiral glycogen deposit. × 55000

Figure *13*: A transverse fracture of the lower part of a sperm tail showing the ellipsoid transverse form and the extent to which the glycogen deposit surrounds the axoneme. × 100000

Figure *14*: A longitudinal fracture to expose the axoneme fibres enveloped by part of the outer mitochondrial membrane. The fibres and their separation are discrete. The paracrystalline material is very closely applied to the axoneme surface. × 80000


7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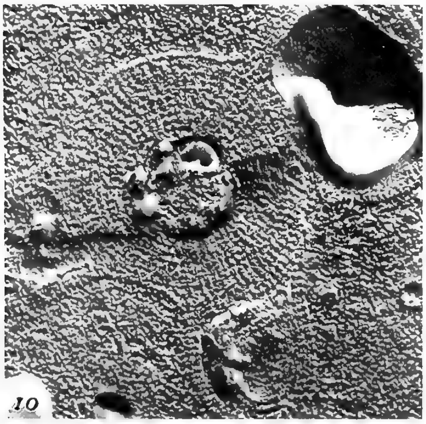
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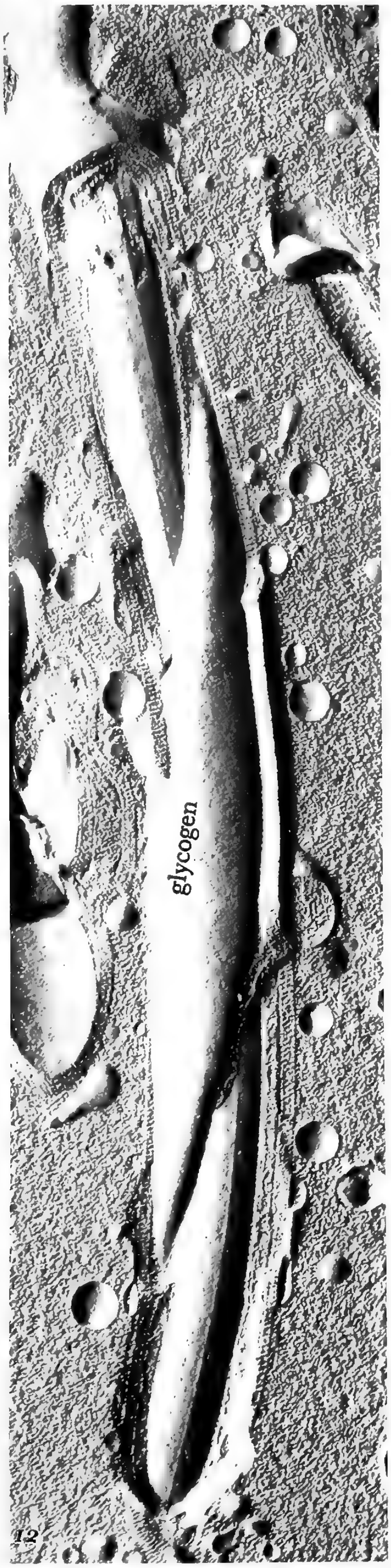

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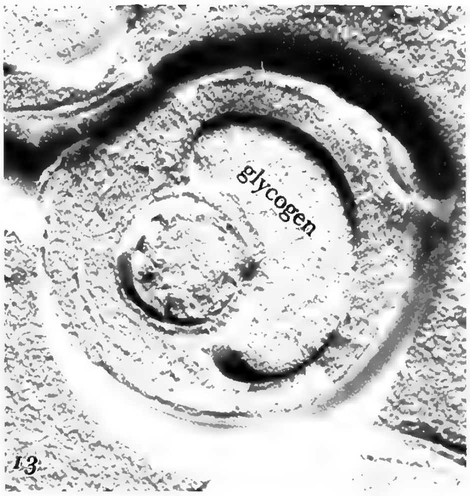

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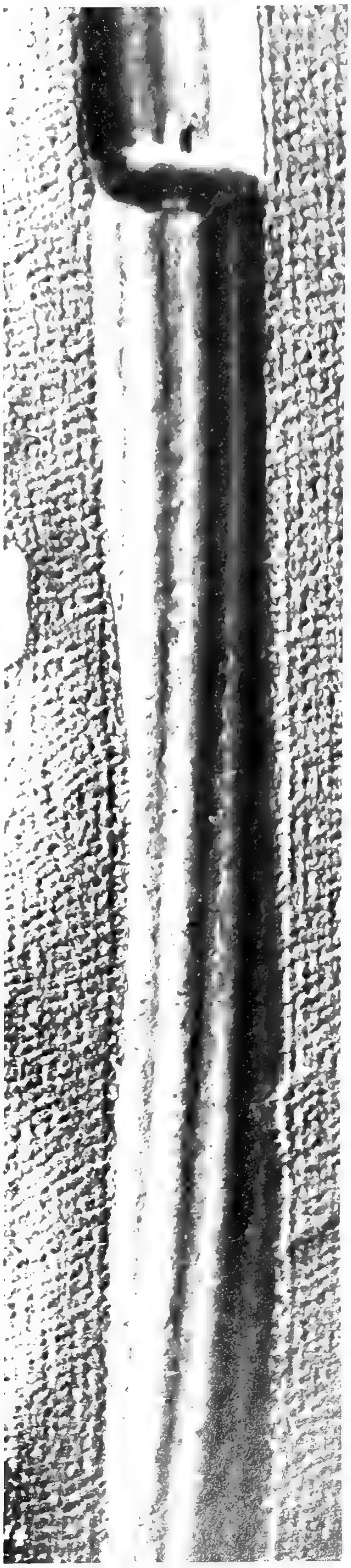

Observations on the Copulatory Behavior of *Littorina rudis* (Maton) and *Littorina nigrolineata* Gray

(Gastropoda : Prosobranchia)

BY

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(4 Text figures)

INTRODUCTION

High intertidal marine snails are active mainly under conditions of high relative humidity, such as occur when the tide recedes and on cool nights (Berry, 1961; own observations). When the time available for movement is limited, as occurs in the supralittoral zone, copulation by males with individuals other than females of their own species will be disadvantageous. Nevertheless, casual observations on the copulatory behaviour of the *Littorina saxatilis* species complex (for a discussion of this group see Heller, 1975; Raffaelli, in prep.) suggested that interspecific copulations were not uncommon. An investigation of the copulatory behaviour of 2 species within the species-complex *L. rudis* (Maton, 1797) and *L. nigrolineata* Gray, 1839 was carried out in Anglesey, North Wales in order to evaluate the extent of copulation by males with individuals other than conspecific females.

METHODS

Observations were made at Trwyn y Penrhyn, Anglesey (Figure 1), a south-east facing, semi-sheltered (3 on Lewis' exposure scale; Lewis, 1964), fucoid dominated boulder shore. On 25th May, 1973, 5th and 15th May, 1975 copulating pairs of *Littorina rudis* and *L. nigrolineata* were collected as the tide receded when animal activity was greatest. Sample sizes are shown in Table 1. Pairs were considered to be copulating only if the penis of one individual was inserted inside the mantle cavity of the other. This was easily seen if the copulating pair was turned apertures uppermost and gently separated. Shell heights (Figure 2) were measured to the nearest 0.1 mm and snails were dissected to determine their sex.

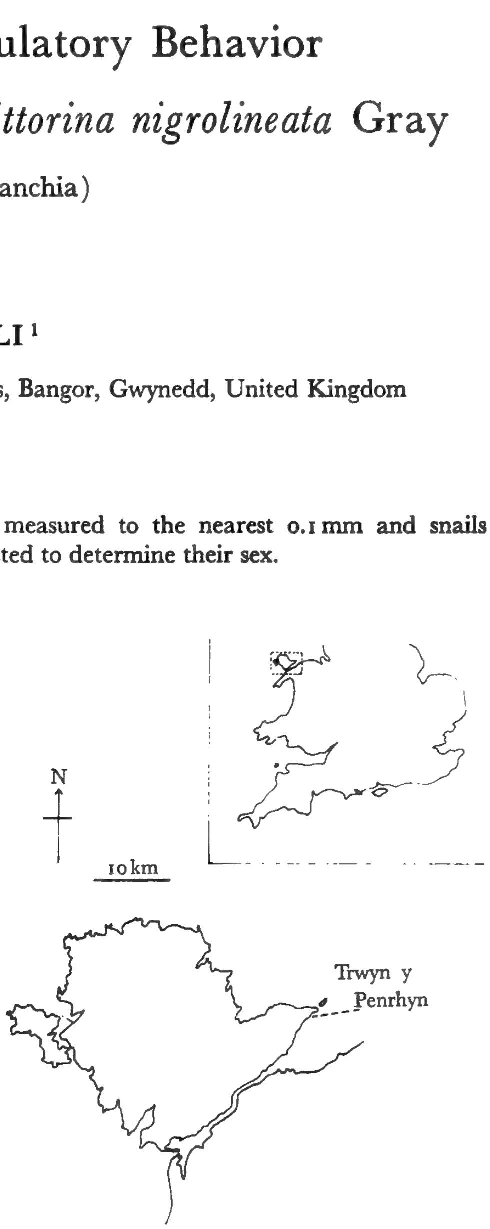

Figure 1

Location of Study Site

RESULTS

Approximately half the copulations in which *Littorina rudis* males were the 'active partners', *i. e.,* their penes were inserted inside the mantle cavity of the partner, involved *L. rudis* females and there was a similar trend

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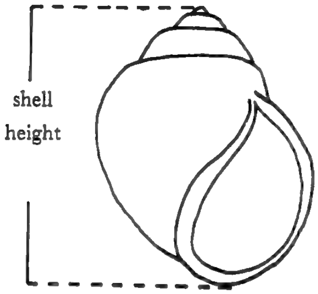

Figure 2

Definition of Shell Height

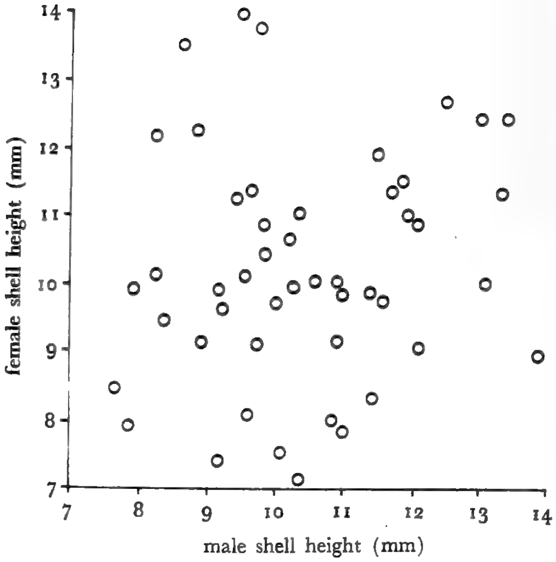

Figure 3

Relationship between size of male and size of female *Littorina rudis* involved in intra-specific copulations

for copulations in which *L. nigrolineata* males were the active partners (Table 1).

Copulations by male *Littorina rudis* and *L. nigrolineata* which did not involve conspecific females were with males of their own species or with females and males of other species.

There was no relationship between the size of male and female *Littorina rudis* and *L. nigrolineata* involved in intraspecific copulations (Figures 3 and 4).

DISCUSSION

Berry (1956) reported copulations between males of *Littorina rudis* and *L. littorea* juveniles. Although Berry (1956, 1961) described his specimens as *L. saxatilis*, subsequent investigation of his population at Whitstable, Kent has shown it to be entirely *L. rudis* (Raffaelli, unpublished, 1975). Copulations by males with males and females of other species and with conspecific males have

Table 1

Frequencies of male × female intraspecific copulations of *Littorina rudis* and *Littorina nigrolineata* at Trwyn y Penrhyn.

Date	Number of copulations by *Littorina rudis* males	Number of intraspecific male × female copulations
25.5.73	15	8
5.5.75	27	14
14.5.75	67	35
Date	**Number of copulations by *Littorina nigrolineata* males**	**Number of intraspecific male × female copulations**
25.5.75	9	3
5.5.75	15	7
14.5.75	12	8

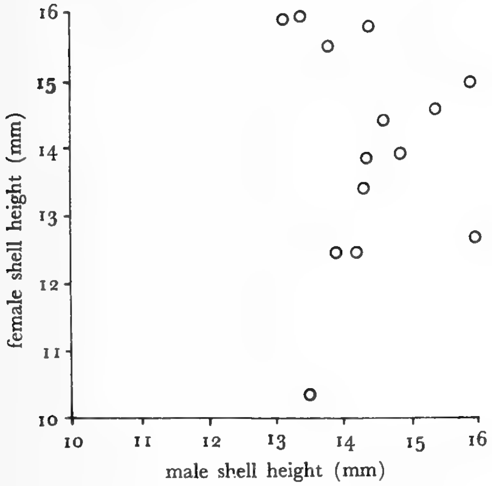

Figure 4

Relationship between size of male and size of female *Littorina nigrolineata* involved in intra-specific copulations

been recorded in *Littorina planaxis* Philippi, 1847 (Gibson, 1964), *L. scabra* (Linnaeus, 1758), *L. pintado* Wood, 1828 and *L. picta* Philippi, 1846 (Struhsaker, 1966), *L. scabra* and *L. irrorata* Say, 1822 (Gallagher & Reid, 1974). I have also observed male *L. mariae* Sacchi & Rastelli, 1966 in copulation with *L. rudis* females at Trwyn y Penrhyn and *L. rudis* males copulating with *L. neritoides* (Linnaeus, 1758) at Trearddur Bay, Anglesey.

There is considerable evidence that *Littorina* species follow mucus trails made by conspecific individuals and that pheromones are involved as specific attractants (Gibson, 1964; Dinter & Manos, 1972; Wells & Buckley, 1972; Dinter, 1974; Hall, 1974). In these studies there was no direct evidence of sex pheromones in the mucus trails. The present paper has shown that males of *L. rudis* and *L. nigrolineata* cannot differentiate between conspecific males and females, at least in the early stages of copulation, supporting the contention that female *Littorina* do not attract males with specific sex pheromones.

Although the copulatory behaviour of *Littorina rudis* and *L. nigrolineata* appears to be inefficient, males copulating with individuals other than conspecific females may not release spermatozoa. In other studies male-male copulations were observed to last for less time than male-female copulations, but these observations were made under laboratory conditions and their relevance to the field situation is not known. Nevertheless, when time available for mating and feeding is limited, *e. g.*, at high shore levels, the time and energy wasted by copulating with the wrong partner may be significant and adversely affect the reproductive success of individuals living at these shore levels.

SUMMARY

The incidence of copulations by male *Littorina rudis* and *L. nigrolineata* with individuals other than conspecific females was found to be high.

There was no relationship between size of male and female individuals involved in intra-specific copulations.

It is considered improbable that mucus trails secreted by *Littorina* species contain sex pheromones.

The inability of males to discriminate between conspecific females and other individuals may significantly lower reproductive success and fitness at higher shore levels.

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The Type Specimens of *Ammonites hoffmanni* Gabb and *Melchiorites indigenes* Anderson

(Cretaceous : Ammonoidea)

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(2 Plates)

THE AUTHORS OF EARLY PUBLICATIONS describing and naming California fossils rarely designated primary type specimens and the existing syntypes for some of these taxa may include specimens referable to 2 or more species. This may reflect the nature of the original collections or the subsequent history of the collections. Much type material has been lost, scattered or mixed with other specimens. In order to achieve nomenclatural stability and taxonomic clarity for these early-described species it has been essential to redescribe existing type material and to designate type specimens. The purpose of this paper is to stabilize the nomenclature of 2 species of desmoceratid ammonoids, *Puzosia hoffmanni* (Gabb, 1864) and *Melchiorites indigenes* Anderson, 1938, from the Lower Cretaceous of northern California.

In proposing a solution to the problem described below we have tried to disturb the present species concept as little as possible. The concepts of these desmoceratid species currently held by most workers in the field are based primarily on ANDERSON (1938), because that paper is generally available and because it contains photographic plates which are superior to the hand-drawn plates in the earlier, scarcer papers.

ANDERSON (1902: 93; 1938: 184, 187) pointed out that the syntypes of *Ammonites hoffmanni* include several distinct species and none closely resembled the figures in Gabb (1864). Anderson also recognized the necessity for selecting a type specimen for *Ammonites hoffmanni* Gabb, and he designated a specimen from the California Academy of Sciences (C. A. S. Geology Type No. 8809) as the lectotype (ANDERSON, 1938: 187; plt. 45, figs. 1, 2). This selection of a lectotype is invalid because the specimen was not chosen from existing syntypes of *A. hoffmanni*. A simple solution to this problem would be to choose, from among the syntypes, a new lectotype that belongs to the same species as Anderson's invalid lectotype. Unfortunately, none of the syntypes of *A. hoffmanni* belongs to the same species as Anderson's lectotype. We exclude Anderson's lectotype from *A. hoffmanni*; at present it belongs to an undescribed taxon. The confused status of *A. hoffmanni* Gabb affects areas far from California. RENZ (1972: 710), following ANDERSON'S (1938) diagnosis, has applied the name *Puzosia hoffmanni* (Gabb) to a specimen from the Lower Cretaceous (Albian) of Venezuela, an action that reinforces the need to clarify this taxon.

The primary types, designated herein, for both *Ammonites hoffmanni* and *Melchiorites indigenes* are chosen from 10 syntypes of *Ammonites hoffmanni* at the Museum of Paleontology, University of California, Berkeley (U. C. M. P.). Four of the syntypes are from the Voy Collection, and these are identified as *Ammonites hoffmanni* on the old labels with the specimens. One of these, U. C. M. P. No. 12091, also has a small label attached to the specimen on which is printed "Collection Pioche." The Voy and Pioche Collections were used by Gabb and others in the description of California fossils. One other syntype, No. 12094, has an old label pasted to it on which is printed "*Ammonites Hoffmanni*." Five additional syntype do not have old labels. All of these specimens are be-

Table 1

Measurements of syntypes of *Ammonites hoffmanni* Gabb, and of other cited specimens. Figures in parentheses express measurements as percentages of shell diameters. Dashes indicate crushed or incomplete specimens from which full sets of measurements could not be made.

	Shell diameter (mm)	Whorl height (mm)	Whorl width (mm)	Umbilical diameter (mm)
Puzosia hoffmanni				
UCMP 12094	110	42 (38)	45 (41)	39 (35)
UCMP 14154	57	22 (39)	22 (39)	20 (35)
UCMP 14839	43	18 (42)	16 (37)	12 (28)
UCMP 14921	43	18 (42)	17 (40)	14 (33)
Puzosia subquadrata				
UCMP 12092	68	31 (46)	27 (40)	18 (26)
UCMP 14155	57	26 (46)	22 (39)	16 (28)
CASG 55399	69	30 (43)	27 (39)	18 (26)
Melchiorites indigenes				
UCMP 14156	–	23 (–)	19 (–)	16 (–)
UCMP 14157	84	34 (40)	– (–)	27 (32)
CASG 8846	78	31 (40)	25 (32)	25 (32)
Melchiorites shastensis				
UCMP 14158	–	20 (–)	17 (–)	13 (–)
CASG 8812	80	36 (45)	– (–)	16 (20)
CASG 8813	48	22 (46)	16 (33)	13 (27)
Melchiorites sp.				
UCMP 12091	80	35 (44)	29 (36)	22 (28)
Lytoceras argonautarum				
UCMP 14153	50	21 (42)	19 (38)	21 (42)

lieved to be from collections made by, or used by, the Second Geological Survey of California (Whitney Survey), and all probably were collected from the Cottonwood Creek district, or adjacent areas, of western Shasta County, California. The 10 syntypes in the U. C. M. P. collection were graciously loaned to us by Joseph Peck. In addition, we have used the paratype of *Melchiorites shastensis*, hypotypes of *Melchiorites indigenes* and *Puzosia subquadrata*, and other specimens from the collection of the Department of Geology, California Academy of Sciences (C. A. S. G.).

The existing syntypes of *Ammonites hoffmanni* include the species discussed below. Measurements of cited specimens are summarized in Table 1.

Puzosia hoffmanni (Gabb, 1864)

(Figures *1* to *5*)

Ammonites hoffmanni Gabb, 1864: 65; plt. 11, figs. 13-13a; plt. 12, fig. 13b
Desmoceras dilleri Anderson, 1902: 97; plt. 4, figs. 116-117; plt. 10, fig. 192
Puzosia dilleri (Anderson). – ANDERSON, 1938: 185; plt. 42, figs. 1 - 3; plt. 46, fig. 1
Puzosia subquadrata (Anderson). – ANDERSON, 1938: 186 (in part); plt. 45, fig. 4

One syntype of *Ammonites hoffmanni* Gabb, 1864, U. C. M. P. No. 12094, is also the holotype of *Desmoceras dilleri* Anderson, 1902 [= *Puzosia dilleri* (Anderson)]. ANDERSON (1938: 185) reports that he found the holotype of *D. dilleri* on the east fork of Huling Creek, Shasta County, but this cannot be true as an old label bearing the name *Ammonites hoffmanni* is glued to the specimen which is surely from Gabb's original lot. The sandstone matrix of the specimen suggests that it could have come from Horsetown, Shasta County, the sole locality for *A. hoffmanni* mentioned by GABB (1864: 65). ANDERSON (1938: plt. 42, figs. 2, 3) figured 2 additional specimens from his collection (C. A. S. G. Type Nos. 8829, 8830) as plesiotypes. Three other syntypes of *A. hoffmanni* (U. C. M. P. Nos. 14154, 14839, and 14921) are clearly specifically identical to these plesiotypes of *Puzosia dilleri* (Anderson).

Thus 4 syntypes of *Ammonites hoffmanni* are identified with *Puzosia dilleri* (Anderson). In order to preserve present nomenclature as much as possible we choose the holotype of *Desmoceras dilleri* Anderson, 1902 [= *Puzosia dilleri* (Anderson)], U. C. M. P. No. 12094, (Figures *1*, *2*) as the **lectotype** for *Ammonites hoffmanni* Gabb, 1864 [= *Puzosia hoffmanni* (Gabb)]. Although this specimen differs considerably from the original figure of Gabb, it has the matrix that is common at the type locality, and it is clearly one of the syntypes because of the old label pasted to it. In addition, other specimens that are conspecific with it have been found at the same stratigraphic level as the principal fossil-bearing strata at Horsetown (*Brewericeras hulenense* zone) (MURPHY, 1956; MURPHY, RODDA & MORTON, 1969). In making this choice we suppress the name *Desmoceras dilleri* Anderson, 1902. The 3 other syntypes, U. C. M. P. Nos. 14154, 14839, 14921 (Figures *3* to *5*) become **paralectotypes** of *Puzosia hoffmanni* (Gabb, 1864).

Puzosia subquadrata (Anderson, 1902)

(Figures *6* to *10*)

Desmoceras subquadrata Anderson, 1902: 96; plt. 4, figs. 118, 119; plt. 10, fig. 193
Puzosia subquadrata (Anderson). – ANDERSON, 1938: 186; plt. 45, figs. 3, 5 (not fig. 4 [= *P. hoffmanni* (Gabb, 1864)])

One syntype of *Ammonites hoffmanni*, U. C. M. P. No. 14155 (Figure *6*), is clearly a specimen of *Puzosia subquadrata* (Anderson) with the characteristic smooth to striate shell and with pronounced constrictions of the internal mold that do not appear on the external shell. The holotype of *Desmoceras subquadrata* ANDERSON (1902: 96; plt. 4, fig. 118; 1938: 186; plt. 45, fig. 3), U. C. M. P. No. 12092, which was probably collected by Anderson from Huling Creek, is refigured here (Figures *7*, *8*). For additional comparison we have illustrated a well preserved specimen of *P. subquadrata*, C. A. S. G. No. 55399 (Figures *9*, *10*).

Melchiorites indigenes Anderson, 1938

(Figures *11* to *14*)

Desmoceras hoffmanni Gabb. – ANDERSON, 1902: 94 (in part); plt. 5, figs. 120-121
Melchiorites indigenes Anderson, 1938: 184; plt. 67, fig. 3; plt. 68, fig. 2

According to ANDERSON (1938: 184), the holotype of *Melchiorites indigenes* was in the collections of the University of California, Berkeley, and it was the same specimen he had figured earlier (1902, plt. 5, figs. 120, 121) as *Desmoceras hoffmanni.* His 1902 drawing seems to be of a single specimen rather than a composite or idealized figure. Unfortunately he did not refigure it photographically in 1938. No specimen with the same shell fracture pattern and of the same size as the figured specimen has been located in the U. C. M. P. collections and the holotype is considered lost. Possibly the holotype of *M. indigenes* was a syntype of *Ammonites hoffmanni.* Two existing syntypes of *A. hoffmanni* (U. C. M. P. Nos. 14157 and 14156) resemble *M. indigenes.* Specimen number 14157 (Figures *11, 12*) closely resembles the original figure of the holotype of *M. indigenes* (Anderson, 1902: plt. 5, fig. 120), and it is from the same general locality. This specimen also closely resembles Anderson's plesiotype of *M. indigenes* (C. A. S. G. Type No. 8846) figured in 1938 (plt. 67, fig. 3), and refigured here (Figure *13*). We therefore designate U. C. M. P. No. 14157 as the **neotype** of *Melchiorites indigenes* Anderson, 1938. Specimen number 14156 (Figure *14*) is similar to specimen 14157, but it is smaller and more poorly preserved.

Melchiorites sp.

(Figure *15*)

Desmoceras hoffmanni Gabb. – Anderson, 1902: 94 (in part); plt. 10, fig. 203. – Anderson, 1938: 187 (in synonymy, reference to Anderson, 1902: plt. 10, fig. 203)
Melchiorites indigenes Anderson, 1938: 183; fig. 3 (8)

Another syntype of *Ammonites hoffmanni,* U. C. M. P. No. 12091, resembles *Melchiorites indigenes,* but it is not clearly identifiable with that taxon. Compared with the neotype of *M. indigenes* it is better preserved, larger, has a greater whorl width, a deeper umbilicus with a steeper umbilical wall, and more sigmoidal constrictions which are more deeply impressed on the internal mold. The suture line of this specimen was illustrated by Anderson (1902: plt. 10, fig. 203), and identified as *Desmoceras hoffmanni.* The same figure was reprinted in reduced size by Anderson (1938: 183; fig. 3, No. 8) and identified as *M. indigenes,* but he also includes the 1902 figure in the synonymy of his revised *Puzosia hoffmanni* (1938:

Explanation of Figures *1* to *10*

Puzosia hoffmanni (Gabb, 1864)

Figure *1*: Lectotype, U. C. M. P. 12094. No locality data. Lateral view. Diameter 110 mm
Figure *2*: Lectotype, U. C. M. P. 12094. Ventral view
Figure *3*: Paralectotype, U. C. M. P. 14839. Cottonwood [Creek], Shasta County. (Voy Collection-. Lateral view. Diameter 43 mm
Figure *4*: Paralectotype, U. C. M. P. 14154. (?) Cottonwood Creek, Shasta County. Lateral view. Diameter 57 mm
Figure *5*: Paralectotype. U. C. M. P. 14921. (?) Hulen [= Huling] Creek, Shasta County. Lateral view. Diameter 43 mm

Puzosia subquadrata (Anderson, 1902)

Figure *6*: Hypotype, U. C. M. P. 14155. (?) Hulen [= Huling] Creek, Shasta County, Lateral view. Diameter 57 mm
Figure *7*: Holotype, U. C. M. P. 12092. Hulen [= Huling] Creek, Shasta County. Ventral view.
Figure *8*: Holotype, U. C. M. P. 12092. Lateral view. Diameter 68 mm
Figure *9*: Hypotype, C. A. S. G. 55399. East Fork of Hulen [= Huling] Creek, Shasta County. Lateral view. Diameter 69 mm
Figure *10*: Hypotype, C. A. S. G. 55399. Ventral view.

Note: For U. C. M. P. specimens the locality data cited in the figure explanations were copied from the labels with the specimens.

Explanation of Figures *11* to *19*

Melchiorites indigenes Anderson, 1938

Figure *11*: Neotype, U. C. M. P. 14157. Cottonwood [Creek], Shasta County (Voy Collection). Ventral view
Figure *12*: Neotype, U. C. M. P. 14157. Lateral view. Diameter 84 mm
Figure *13*: Hypotype, C. A. S. G. Type Collection 8846. Alderson Creek, Shasta County. Lateral view. Diameter 78 mm
Figure *14*: Hypotype, U. C. M. P. 14156. Cottonwood [Creek], Shasta County. (Voy Collection). Lateral view. Diameter (incomplete) 68 mm

Melchiorites sp.

Figure *15*: *Melchiorites* sp. Hypotype, U. C. M. P. 12091. Cottonwood [Creek], Shasta County. (Voy Collection, *ex* Pioche Collection); Lateral view. Diameter 80 mm

Melchiorites shastensis Anderson, 1938

Figure *16*: Paratype, C. A. S. G. Type Collection, 8813. Alderson Creek, Shasta County. Lateral view. Diameter 48 mm
Figure *17*: Hypotype, U. C. M. P. 14158. Cottonwood Creek, Shasta County. Lateral view. Diameter (crushed) 65 mm

Lytoceras argonautarum Anderson, 1902

Figure *18*: Hypotype, U. C. M. P. 14153. Cottonwood Creek, Shasta County. Lateral view. Diameter 50 mm
Figure *19*: Hypotype, U. C. M. P. 14153. Ventral view

Note: For U. C. M. P. specimens the locality data cited in the figure explanations were copied from the labels with the specimens.

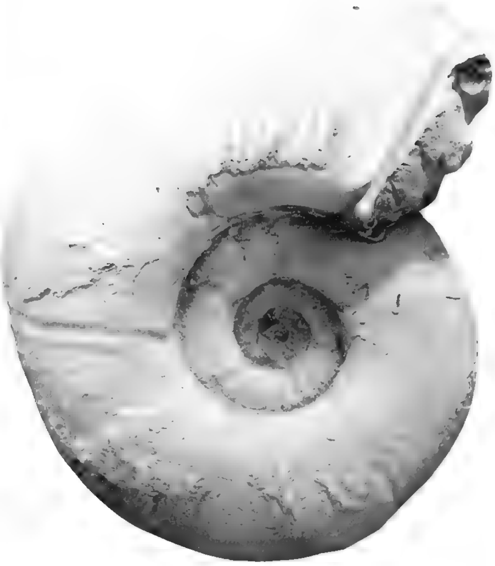

Figure *1*

Figure *2*

Figure *3*

Figure *4*

Figure *5*

Figure *6*

Figure *7*

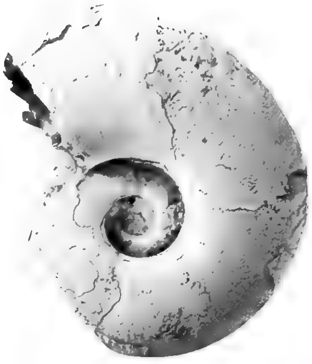

Figure *8*

Figure *9*

Figure *10*

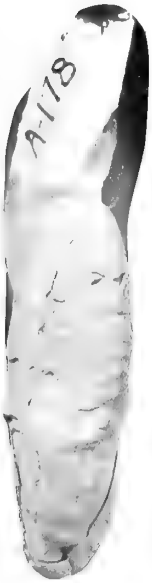

Figure *11*

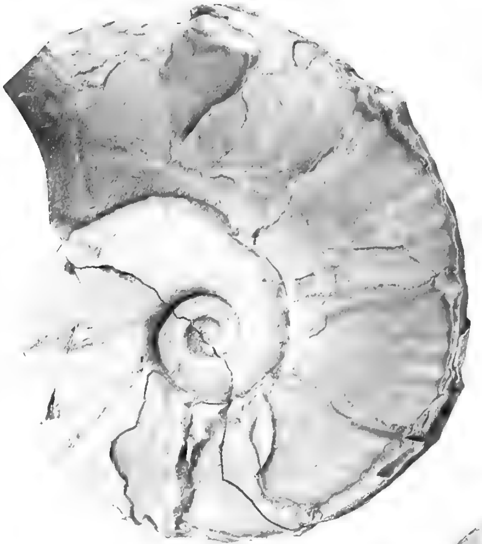

Figure *12*

Figure *13*

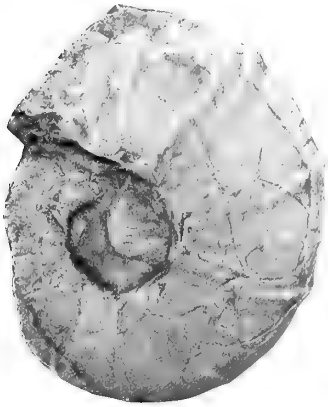

Figure *14*

Figure *15*

Figure *16*

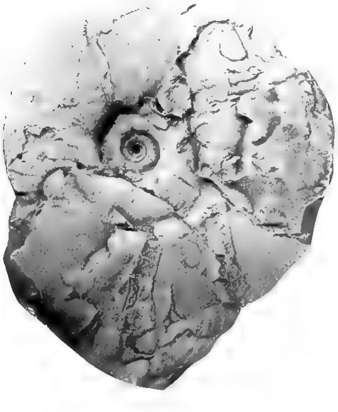

Figure *17*

Figure *18*

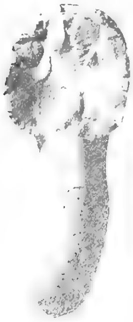

Figure *19*

187). At present we cannot assign this specimen to a named species.

Melchiorites shastensis Anderson, 1938

(Figures *16, 17*)

Melchiorites shastensis Anderson, 1938: 182; plt. 40, figs. 1, 2

The holotype and paratype of *Melchiorites shastensis* ANDERSON (1938: 182; plt. 40, figs. 1, 2) are C. A. S. G. Type Nos. 8812 and 8813 respectively. The paratype of *M. shastensis,* refigured here (Figure *16*), is nearly identical with one syntype of *Ammonites hoffmanni,* U. C. M. P. No. 14158 (Figure *17*), and we exclude this specimen from *Ammonites hoffmanni* Gabb.

Lytoceras argonautarum Anderson, 1902

(Figures *18, 19*)

Lytoceras argonautarum Anderson, 1902: 85; plt. 7, figs. 154, 155

Lytoceras (Argonauticeras) argonautarum Anderson. – ANDERSON, 1938: 149; plt. 17, fig. 3; plt. 19, figs. 1, 2

The remaining syntype of *Ammonites hoffmanni,* U. C. M. P. No. 14153, is a small specimen of the genus *Lytoceras,* doubtless *L. argonautarum* Anderson (1902) because of the very rapid expansion of the whorl and the subquadrate whorl section.

SUMMARY

Ten syntypes of *Ammonites hoffmanni* Gabb, 1864 [= *Puzosia hoffmanni* (Gabb)] are at the University of California, Berkeley, Museum of Paleontology, and No. 12094 is selected as the **lectotype.** This specimen is also the holotype of *Desmoceras dilleri* Anderson, 1902, and this species becomes a junior objective synonym of *A. hoffmanni* Gabb. Three other syntypes belong to *A. hoffmanni.* Two syntypes belong to *Melchiorites indigenes* Anderson, 1938, and No. 14157 is chosen as the **neotype** of this taxon. The other 4 syntypes belong to 4 taxa: *Puzosia subquadrata* (Anderson, 1902), *Melchiorites shastensis* Anderson, 1938, *Melchiorites* sp., and *Lytoceras argonautarum* Anderson, 1902.

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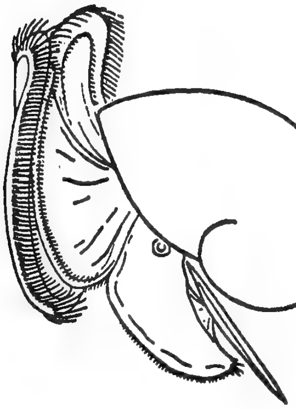

Chiton Fauna of the Galápagos Islands

BY

ALLYN G. SMITH AND ANTONIO J. FERREIRA[1]

(4 Plates)

FOREWORD

On his death, August 18, 1976, Allyn Goodwin Smith left a nearly completed manuscript on the chiton fauna of the Galápagos Islands with the expressed request that I would complete his work and see it published. In humble spirit I strove to carry out his wish. Although in the process alterations were made upon the original manuscript, most of such alterations merely reflect the consensus we had reached in the course of discussions over the contents of the paper. Thus, Allyn's work on the Galápagos chitons is preserved virtually unchanged. The credit is Allyn's, the responsibility mine. A. J. F.

INTRODUCTION

The first collections of Galápagos chitons for scientific purposes were made early in the nineteenth century. The large endemic species, *Chiton sulcatus*, was described in 1815 by Wood and *C. goodalli* by Broderip in 1832, the latter obtained by the famous British collector and conchologist, Hugh Cuming, who probably found *Acanthochitona hirudiniformis* there also. Other species now known to make up the Galápagos chiton fauna are not often collected, or are small and easily overlooked.

The purpose of this report is to assemble such information on Galápagos chitons as has appeared in the literature, supported by specimens in the collection of the California Academy of Sciences and in other institutions, and by personal observations. The principal sources of records and specimens have been the major scientific expeditions to the Islands, the earlier ones having been summarized by Stearns (1893). Since that date collections have been made during the Hopkins-Stanford Expedition in 1898-1899, the California Academy of Sciences Expedition in 1905-1906, the Cambridge Expedition to the Suez Canal in 1924, the Norwegian Zoological Expedition in 1925, the Gifford Pinchot Expedition in 1929, the G. Allan Hancock Expedition of the California Academy of Sciences in 1931-1932, the California Academy of Sciences Expedition under the auspices of Templeton Crocker in 1932, the William K. Vanderbilt South Pacific Expedition in 1933, the George Vanderbilt South Pacific Expedition in 1937, the United States Presidential Cruise in 1938, and the Galápagos International Scientific Project in 1964.

As one of the privileged participants in the Galápagos International Scientific Project (GISP), the senior author (AGS) had the opportunity to collect chitons as well as land and other marine invertebrates and to make field observations during the period January-March, 1964, while this Expedition was headquartered at the Charles Darwin Research Station on Academy Bay, Isla Santa Cruz. Most collections of chitons were made in the intertidal zone supplemented by a limited amount of dredging in 30 m or less. Personal collecting was assisted and augmented by several other GISP scientists and by two enthusiastic local conchologists living in Academy Bay Village — Mrs. Fritz (Carmen) Angermeyer and Mme. André (Jacqueline) De Roy — to whom special thanks are due.

The archipelago of the Galápagos (Archipiélago de Colón) consists of 12 large and several hundred small islands on the equator, some 1000 km west of Ecuador, to which country they belong. Potassium-Argon dating of the geologically oldest flows exposed indicate that the Galápagos Islands have a probable maximum age of 3 000 000 years (Bailey, 1976).

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Table 1

Family, Genus, and Species	Habitat
Lepidopleuridae	
Leptochiton ***albermarlensis*** A. G. Smith & Ferreira, spec. nov.	Dredged, 20 m; endemic?
Ischnochitonidae	
Ischnochiton petaloides (Gould, 1846)	Intertidal zone to 100 m
Chaetopleuridae	
Chaetopleura cf. *C. mixta* (Dall, 1919)	Intertidal zone
Calloplax duncanus (Dall, 1919)	Intertidal zone
Callistoplacidae	
Callistochiton ***carmenae*** A. G. Smith & Ferreira, spec. nov.	Intertidal zone; endemic?
Chitonidae	
Chiton goodalli Broderip, 1832	Intertidal zone; endemic
Chiton sulcatus Wood, 1815	Intertidal zone; endemic
Tonicia forbesii arnheimi Dall, 1903	Intertidal zone to 50 m; endemic
Acanthochitonidae	
Acanthochitona hirudiniformis (Sowerby, 1832)	Intertidal zone
Acanthochitona ***jacquelinae*** A. G. Smith & Ferreira, spec. nov.	Dredged, to 50 m; endemic
Acanthochitona cf. *A. avicula* (Carpenter, 1866)	Intertidal zone

The chiton fauna of the Galápagos Islands is not large; nor is it particularly notable except for the occurrence of 2 large, spectacular species of *Chiton, C. sulcatus* and *C. goodalli*. Other Galápagos chiton species are considerably smaller when adult, and are not especially abundant. Table 1 lists the species making up the Galápagos chiton fauna; to-date, it includes only 11 species in 8 genera, representing 6 families. It seems worth noting that possibly as many as 7 of the total 11 species, or 64%, are endemic to the Galápagos Islands although it is probable that this percentage will be somewhat reduced with more thorough collecting. In spite of the apparent high degree of endemism, however, the Galápagos chiton fauna is essentially Panamic in composition. The influence of the cold, northward flowing Humboldt Current, which impinges on the Galápagos Islands, does not seem to have affected the chitons inasmuch as no species commonly occurring on the coasts of Perú and Chile are found.

SYSTEMATIC TREATMENT

The following account lists the known species of chitons inhabiting the Galápagos Islands, describes 3 considered to be new to science, brings together all published records, and includes comments that may be helpful in adding to the knowledge of each species. The list includes 7 species that have been reported from the Islands, which reflect either erroneous records, misidentifications, or species of such rare occurrence that they cannot be accorded permanent status in the chiton fauna of the archipelago.

POLYPLACOPHORA de Blainville, 1816

NEOLORICATA Bergenhayn, 1955

Lepidopleuridae Pilsbry, 1892

Only one representative of this family has been collected in near shore waters. In addition, one species occurs in very deep water off-shore, although further dredging is likely to produce others.

Leptochiton Gray, 1847

Leptochiton ***albemarlensis*** A. G. Smith & Ferreira, spec. nov.

(Figures *1*, *2*)

Diagnosis: Animal of moderate size, round-backed and cream colored. Over-all decoration of closely spaced, fine granulations on the dorsal side of the valves. Girdle narrow and spiculose.

Description of the Holotype: Holotype a whole animal, preserved dry, the valves all somewhat broken but showing the characters of the species satisfactorily. Color of both valves and girdle a light cream. Valves round-backed, the head valve rounded and somewhat more than semicircular; the intermediate valves have straight, unmucronate posterior margins; the lateral areas hardly raised and set off from the central areas; the tail valve semicircular with a prominent, rounded, centrally-placed mucro. Dorsal sculpture consists of a series of very fine, slightly elongated, unconnected granulations arranged in close diagonal rows. There are 2 - 3 shallow grooves close to the side margins of the valves and parallel to them, which are somewhat better developed on valves ii and vii. The girdle has short, closely set, somewhat appressed, slightly curved or straight, glass-like, blunt-pointed spicules. Dimension are: length, 9.8 mm; width, 5.4 mm; height, 1.5 mm. The holotype is deposited in the California Academy of Sciences Geology Department (CASG) Type Collection, no. 58247.

Type Locality: Dredged in 20 m, Tagus Cove, Isla Isabela (Albemarle Island), Galápagos Islands, 27 January 1968 by André and Jacqueline De Roy. A second disarticulated specimen with all valves badly broken was dredged with the holotype. It is here designated as a paratype (CASG Type Collection no. 58248).

Remarks: This new *Leptochiton* compares most closely in general size and shape with *L. rugatus* (Pilsbry, 1892) from central and southern California and from the Gulf of California. However, the latter species has the granular sculpture of the central areas on the intermediate valves arranged in connected, longitudinal rows, and the girdle is decorated with tiny sand-like granules with no spicules. Because of its spiculose girdle, *L. albemarlensis* may be related to *L. nexus* Carpenter, 1864, from moderately deep water, 37 - 146 m, off Catalina Island, California, which has some girdle spicules along with narrow, striated scales. However, we are not sufficiently acquainted with the detailed characters of *L. nexus*, a poorly known southern California species, to do more than suggest that a possible relationship may exist.

Leptochiton opacus (Dall, 1908)

(Figures *3*, *4*)

Lepidopleurus opacus Dall, 1908: 354-355

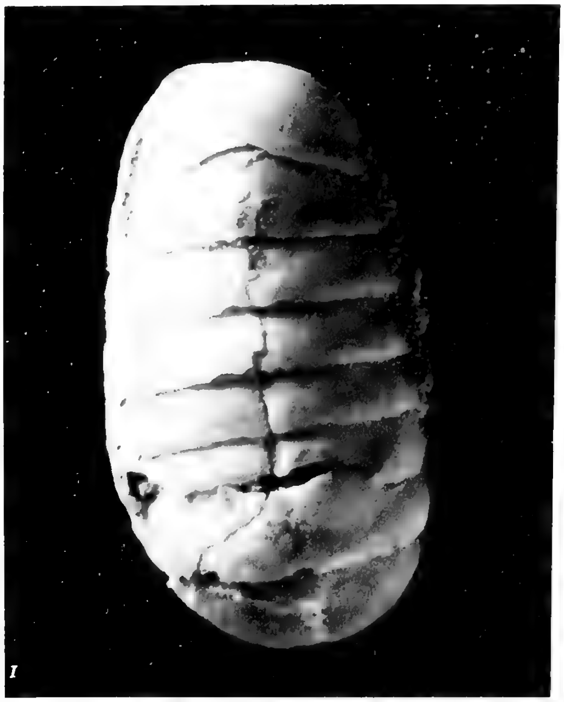
This rare and little-known chiton was dredged by the USS *Albatross* of the United States Fish Commission between the Galápagos Islands and the Peruvian coast in 2005 fathoms (3670 m), ooze, bottom temperature 35.4° F (approx. 2° C) (USFC Sta. 4647). It is illustrated here for the first time. The type lot consists of 2 specimens, preserved dry, that appear to be adults, deposited in the U. S. National Museum of Natural History (USNM 110664). One, considered to be the holotype, is represented by only 7 disarticulated valves, the valve vii being missing. Because of its deep bathyal habitat, *L. opacus* cannot be included properly in the chiton fauna of the Islands, and it is noticed here only because its locality is in the general vicinity.

Ischnochitonidae Dall, 1889

Ischnochitonids are uncommon in the Galápagos Islands. The species most often collected is quite small. Lacking are the larger Panamic species in the genus *Stenoplax* that occur in the Gulf of California and southward, such as *S. limaciformis* (Sowerby, 1832) and *S. magdalenensis* (Hinds, 1843), and in the genus *Lepidozona*, such as *L. clathrata* (Reeve, 1847). The genus *Lepidozona* does not seem to be represented in the Galápagos fauna; specimens previously alluded to as possibly belonging to the genus (Ferreira, 1974: 175) prove to be, on closer investigation, representatives of the genus *Callistochiton*.

Explanation of Figures *1*, *2*, *5*, *13*, *14*

Figure *1*: *Leptochiton* ***albemarlensis*** A. G. Smith & Ferreira, spec. nov. Holotype (CASG Type Collection, No. 58247). Albemarle Island (Isla Isabela), dredged in 20 m, Tagus Cove. Dorsal view; length, 9.8 mm (AJF photograph)
Figure *2*: *Leptochiton* ***albemarlensis*** A. G. Smith & Ferreira, spec. nov. Same as in Figure *1*. Close-up of left side-slope to show detail of sculpture of valves and girdle. (AJF photograph)
Figure *5*: *Ischnochiton (Rhodoplax) petaloides* (Gould, 1846). Lot #3 (CASG 40497). Academy Bay, Isla Santa Cruz, intertidally. Largest specimen, 8.7 mm long (AJF photograph)
Figure *13*: *Chiton goodallii* Broderip, 1832. Academy Bay, Isla Santa Cruz. Dorsal view; length, 104.5 mm (CASG 39264). From CASIZ Color Slide No. 1367 (AGS photograph)
Figure *14*: *Chiton sulcatus* Wood, 1815. Conway Bay, Isla Santa Cruz. Crocker Galápagos Expedition, 1932, coll. Leo G. Hertlein (CASIZ Collection). From CASIZ Color Slide No. 1369 (AGS phot.)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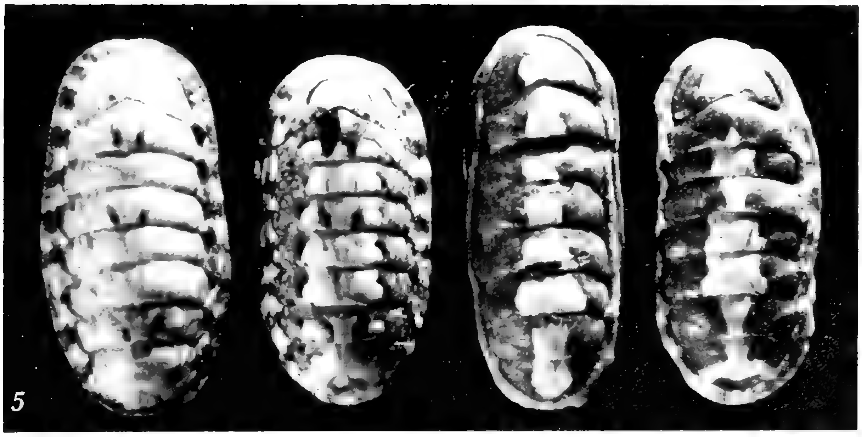
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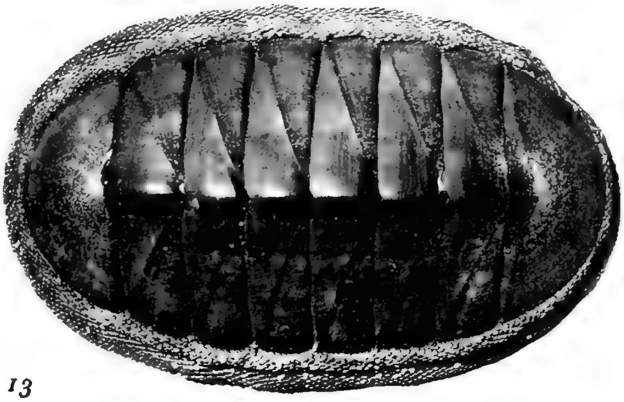
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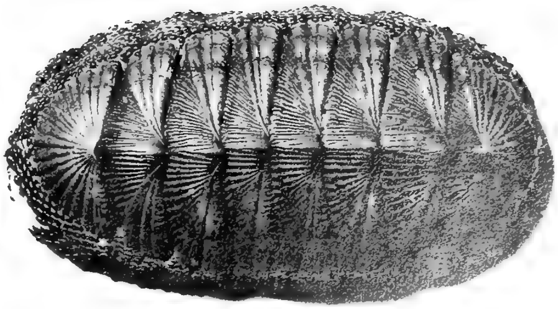
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Ischnochiton Gray, 1847

Ischnochiton (Rhodoplax) petaloides (Gould, 1846)

(Figure 5)

Chiton petaloides Gould, 1846: 6
Radsiella petaloides. Thorpe (in Keen), 1971: 869, no. & fig. 19
Ischnochiton mariposa Dall, 1919: 506-507

In the Galápagos Islands, this small chiton is known to attain an adult length of about 11 mm. It is found sparsely in the intertidal zone, on the underside of rocks, to a depth of at least 100 m. Specimens may be unicolored, or mottled and striped in various light to dark combinations of color; some may have the characteristic electric-blue small spots, but zebra-striped color forms have not yet turned up among the specimens of *Ischnochiton petaloides* collected in the Galápagos Islands.

Ischnochiton petaloides has a unique range (A. G. Smith, 1977). It is known from Hawaii, type locality (Maili, Oahu Id., Hawaiian Islands, *leg.* Kay Gudnason, low intertidal zone, 1974, CASIZ Colln.; lagoon opposite Hawaii Kai, Oahu, and E of Wailupe, Oahu, *leg.* H. Bertsch, Dec. 1976-Jan. 1977, AJF Colln.), the outer coast of Baja California from Punta Abreojos (26°42′N; 113°34.5′W, in 8-10 m, *leg.* J. H. McLean, R/V *Searcher* sta. 1, January 27, 1971, LACM 71-3) southwards to Cabo San Lucas, and throughout the Gulf of California. It is present, although rarely collected in Central America (El Velero, Nicaragua, intertidally, *leg.* A. J. Ferreira, January 21-22, 1974, AJF 132-133; Bahía Herradura, Puntarenas Province, Costa Rica, 10-20 m, *leg.* J. H. McLean, R/V *Searcher* sta. 447, March 9-10, 1972, LA CM 75-52; Tonasi, Las Santar, Bucaru Playa, Panamá, *leg.* E. Bergeron, April 23, 1967, LACM B-23), and in the northern part of South America (El Rubio & Punta Mero, Tumbes Province, Perú, intertidally, *leg.* J. H. McLean, D. Shasky, and Peña, April 16, 1972, LACM 72-85; Lobos de Afuera Islands, Perú, January 17, 1935, LACM-AHF 391-35; Salinas, Ecuador, 2°12′S; 80°58′W, intertidally, *leg.* J. H. McLean, 5-6 March, 1970, LACM 70-9). In the Galápagos Islands, 14 lots of *I. petaloides* were collected by A. G. Smith and others at Isla Santa Cruz, Isla Genovesa, Isla Isabela, Isla San Cristobál, Isla San Salvador, and Isla Rábida. During the California Academy 1932 Expedition, *I. petaloides* was collected at Conway Bay, N side of Isla Santa Cruz, by Leo G. Hertlein (CASG 27232). *Ischnochiton petaloides* is the only chiton so far known that is common to both the Indo-West Pacific (Hawaiian Islands), and the tropical West American provinces; this observation is all the more noteworthy when only a few other mollusks, all gastropods, have been reported to span the faunistic barrier between the two zoogeographic zones (Robertson, 1975).

Except for the relatively smaller size of the specimens examined, and somewhat less variability in colors, *Ischnochiton petaloides* from the Galápagos Islands does not seem to differ from other populations of the same species in the Gulf of California, Central America and Hawaii.

Remarks: The synonymy of *Ischnochiton mariposa* Dall, 1919 was established through the examination and side-by-side comparison of the syntype series of *I. mariposa* (USNM 58865) and the holotype of *Chiton petaloides* Gould, 1846 (USNM 12922) available on loan through the kindness of Dr. Joseph Rosewater. Within the genus *Ischnochiton* the systematic position of the species is, together with *I. eucosmius* Dall, 1919, in the subgenus *Rhodoplax* Thiele, 1893 (Type species, *Chiton squamulosus* C. B. Adams, 1845 [= *I. striolatus* (Gray, 1828)] by SD, herein) established to include relatively small, weakly-sculptured species with striated girdle scales and a tricuspid major lateral radular tooth.

It should be noted that Thorpe *in* Keen (1971: 869) had already placed *Ischnochiton mariposa* in the synonymy of *I. petaloides,* but with a generic change to *Radsiella* Pilsbry (including *Rhodoplax* Thiele, 1893), which cannot be justified inasmuch as *Radsiella* Pilsbry (type species *Ischnochiton tridentatus* Pilsbry, 1893, by OD) was clearly erected to include " ... Ischnochitons (with) insertion-plates of the intermediate valves having two or several slits." (Pilsbry, op. cit. 14: 140), while Thorpe, following Thiele (1929) used the name to signify "American species" which, without supporting evidence, he considered distinct from "Old World species" of *Ischnochiton.*

CHAETOPLEURIDAE Plate, 1899

Chaetopleura Shuttleworth, 1853

Chaetopleura cf. *C. mixta* (Dall, 1919)

(Figures 6, 7)

Tonicia mixta Dall, 1919: 515

The 11 specimens of this small *Chaetopleura,* referred provisionally to *C. mixta,* were collected in the low intertidal zone, under rocks, at 4 different stations in Academy

Bay, Isla Santa Cruz, by Allyn G. Smith and Jacqueline De Roy. The specimens range in length up to a maximum of 9mm. They all have the typical pustulose sculpture occurring on all species in the genus. The mucro of the tail valve is median in position, which places this form of *Chaetopleura* in the typical subgenus. The lateral areas of the intermediate valves are prominent and decorated with 3-4, more or less anastomosing, diagonal rows of rounded, projecting pustules. The central areas have less prominent, closely-set, longitudinal pustular rows. The head valve has 15-18 anastomosing rows of pustules; on the tail valve the pustules are fewer and randomly placed. The girdle is covered with exceedingly small, chaffy, scale-like processes and with numerous, short, curved, glassy spicules; there is a well-developed foot-fringe. Color is a nondescript brownish-green with some lighter maculations. One of the specimens, measuring 6.4mm in length, has a slit formula 8 – 1 – 10.

Remarks: All 11 specimens of the Galápagos *Chaetopleura* appear to be close to *C. mixta* from the Gulf of California, although smaller in average size. Also, the pustules decorating the lateral areas of the valves, and the central areas as well, tend to be slightly shorter in length, a little greater in diameter, and more regularly spaced than they are on *C. mixta*. Thus, if these differences do not turn out to be a criterion of age, or of individual variation within the species based on a study of a larger series of specimens than those now available, this small Galápagos *Chaetopleura* may be in need of a new name.

One might have expected to find *Chaetopleura lurida* (Sowerby, 1832) or a chiton equivalent to this hairy-girdled species in the Galápagos group. But, although abundant in the Panamic region from the Gulf of California to at least Panamá, so far it has not been reported from these islands.

Calloplax Thiele, 1909

Calloplax duncanus (Dall, 1919)

(Figures *8*, *9*)

Callistochiton duncanus Dall, 1919: 512-513 – Thorpe (*in* Keen), 1971: 873

This small, yellowish-white chiton was described by Dall from specimens collected on Duncan Island (Isla Pinzón) by members of the USS *Albatross*. The holotype is in the United States National Museum (USNM 218772). Duncan Island must be regarded, therefore, as the type locality In addition to the holotype, available through the courtesy of Dr. Joseph Rosewater, series of specimens were studied from collecting at Isla Pinzón (CASG 45412), Isla Santa Cruz (ANSP 243647; CASG 40364, 40493, 40497; CASIZ Colln.), Isla Baltra (CASG 42196), Isla Santa Fé (CASG 40365), Isla San Salvador (CASG 42194), Isla Fernandina (CASG 42200), Isla Pinta (CASIZ Colln.).

Remarks: Maximum adult size of *Calloplax duncanus* ordinarily does not exceed 12-13mm. In sculptural details there is a fair amount of individual variation. In some specimens the central areas of the intermediate valves have a longitudinal series of threads only; in others, usually younger animals, there is a weaker series of transverse threads dividing the interspaces between the axials into squarish pits. Some also have over-all finely granular micro-sculpture. The normal number of annulate ribs on the head valve is 9, and on the tail valve 6 as indicated by Dall in his original description. However, these ribs tend to bifurcate (as they do also on the lateral areas of the intermediate valves) with the size and hence the age

Explanation of Figures *3*, *4*, *8*, *9*, *12*, *22*

Figure *3*: *Leptochiton opacus* (Dall, 1908). Holotype (USNM 110664). Dredged in 3667m off the coast of Perú. Side view of curled specimen. From CASIZ Color slide No. 1581 (AGS photog.)

Figure *4*: *Leptochiton opacus* (Dall, 1908). Paratype. Dorsal view of valves i, iv, v(?), and viii; width of valve i, 9.8mm. From CASIZ Color Slide No. 1582 (AGS photograph)

Figure *8*: *Calloplax duncanus* (Dall, 1919). Isla Santa Fé. Dorsal view; length, 10.0mm (CASG 40365). From CASIZ Color Slide No. 1394 (AGS photograph)

Figure *9*: *Calloplax duncanus* (Dall, 1919). Holotype, (USNM 218772). Duncan Island (Isla Pinzón). Dorsal view of valves i, ii, iii, vii (?), and viii; width of valve i, 3.5mm. From CASIZ Color Slide No. 1349 (AGS photograph)

Figure *12*: *Placiphorella blainvillii* (Broderip, 1832). Dredged off Cocos Island, Costa Rica, in 66 fathoms (120.7m) by the USS *Albatross* (USNM 122968). Dorsal view; length, 29mm; width, 27mm. From CASIZ Color Slide No. 1579 (AGS photograph)

Figure *22*: *Acanthochitona* spec. ? "Seymour Bay" [= S. Seymour Channel?], Isla Santa Cruz. Dorsal view of disarticulated valves i, ii, iii (?), vii, and viii (ANSP 153484). From CASIZ Color Slide No. 1351 (AGS photograph)

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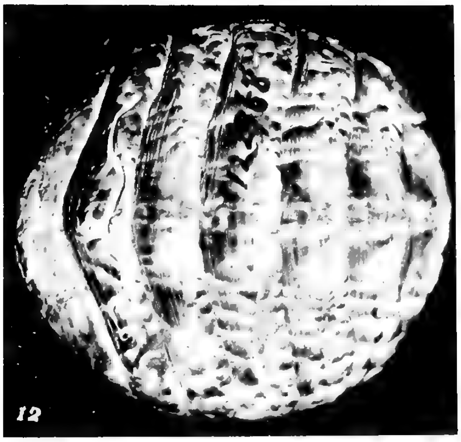

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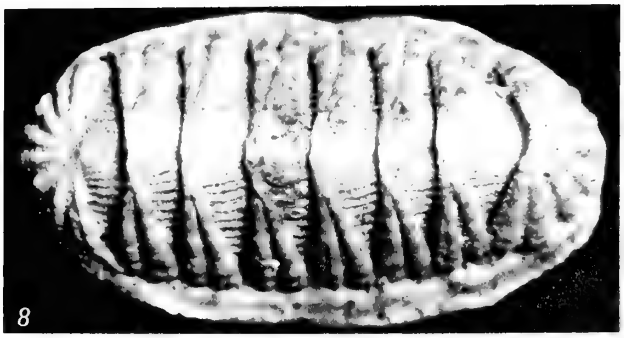

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of the animals, resulting in the rib counts at the valve margins as high as 13 or 14 on both end valves in some instances. While the usual color of the dorsal surfaces of the valves is cream-white, a number of specimens have grayish-green mottlings, and in these the girdles have alternating bands of a similar color. Still fewer animals have light red-brown mottlings on the valves.

The "velvety girdle densely covered with minute whitish spicules" mentioned by Dall in his original description is true of all specimens studied, especially those preserved in alcohol. The girdle "scales" are extremely minute and chaffy, the striation on them being visible only under magnification of more than 400×. This is not the typical girdle decoration on species in the genus *Callistochiton*, which calls for: "Girdle poreless, densely, clothed with minute striated or smooth scales." (PILSBRY, 1893, **14:** 260). In *Callistochiton* species the closely-packed, imbricating scales are "minute" but not so minute as to require high magnification to be visible. In addition, the girdle of *C. duncanus* shows often a fringe of spicules about 100 µm long, and occasional similar spicules interspersed amidst the girdle scales. These spicules are apparently very fragile, and will easily fall off in a dry specimen. Thus, in view of the girdle characteristics, *C. duncanus* cannot be assigned properly to the genus *Callistochiton* s. s., and appears more nearly to fit the requirements of the genus *Calloplax* and hence may be viewed as the Panamic regional counterpart of the Caribbean species, *C. janeirensis* (Gray, 1828).

A disarticulated specimen of *Calloplax duncanus* shows important details: the interior is white; the sutural laminae are wide, separated by a rather narrow and weakly denticulated sinus; the teeth are somewhat thickened outside at the slits which correspond in number and position to the external ribs. Slit formula 7–1–9. The eaves are rather wide, roughened, and grooved. These characteristics of the articulamentum are so much in line with those found in members of the genus *Callistochiton* as to suggest that, for their similarities, *Calloplax* and *Callistochiton* may eventually be considered to belong to the same family Callistoplacidae.

Calloplax janeirensis (Gray, 1828)

Lepidopleurus janeirensis (Gray, 1828). WIMMER, 1879: 506
Chaetopleura janeirensis. STEARNS, 1893: 449

This is an Atlantic species, reported by Wimmer from the Galápagos Islands where its occurrence is questionable. We suspect Wimmer's specimens should be referred now to *Calloplax duncanus* (Dall, 1919).

CALLISTOPLACIDAE Pilsbry, 1893

Callistochiton Carpenter *in* Dall, 1879

Callistochiton carmenae A. G. Smith & Ferreira, spec. nov.

(Figures *10, 11*)

Callistochiton shuttleworthianus Pilsbry, 1893. BERGENHAYN, 1937: 284-285, figs. 3f-3g (girdle scales only)

Diagnosis: Animal small, yellowish-white. Head valve with 12 low, annulate ribs. Lateral areas of intermediate valves with 2 strong radial ribs; central areas with a pitted appearance. Tail valve with a low mucro, slightly anterior, and 10 annular ribs. Girdle clothed with small, imbricating, oval scales.

Description of the Holotype: The holotype is a whole animal, preserved in alcohol, with valves i, ii, and viii disarticulated. Dimensions are 7.8mm in length, and 4.2 mm in width (including girdle). The color is yellowish-white uniformly. The valves are somewhat high-arched, the side slopes gently rounded to a moderately acute jugum. The head valve is semicircular with 12 low, rounded, more or less equally spaced, nodulose, annulate ribs, the posterior ones being strongest and more nodulose. Lateral areas of intermediate valves have 2 strong, radial ribs, the posterior ones heavily nodulose, crenulating the posterior margins of the valves. Sculpture of the central areas consists of about equally and closely spaced diagonal rows of lirae extending from the valve apices and crossed at about right angles by a second series of lirae, forming rounded depressions in the interspaces and giving the central areas a pitted appearance. These lirations become less strong as they cross over the jugal ridges, there being no marked jugal areas. Tail valve has a low rounded mucro positioned slightly anterior to the center of the valve tegmentum, bounded posteriorly by a small semicircular smooth area, and anteriorly by an area sculptured the same as on the central areas of the intermediate valves. The tail valve margin is raised into about 10 short, heavy, somewhat pustulate annular ribs. Internally the valves are white, with a configuration typical for the genus. The slit formula is 12 – 1 – 11. The insertion teeth are slightly thickened at the edges, and weakly festooned, corresponding in position to the ribs in the tegmentum. The girdle is clothed with small, diagonally-placed, overlapping, oval scales, which, under magnification of 200 ×, show 13 or 14 slightly granulose, transverse striae at their tops, while on their sides there is a series of irregularly arranged, rather widely-placed pustules. Girdle width, 0.4 mm.

The holotype was collected at Academy Bay, Isla Santa Cruz (Indefatigable Island), *leg.* A. G. Smith, 15 February 1964 (GISP Sta. G-59), along with a small series of *Calloplax duncanus.* The holotype is deposited in the CASIZ Type Series no. 696. Two dry paratypes are deposited at CASG Type Series no. 58248. Five additional paratypes from the same locality, collected by Carmen Angermeyer, are preserved in alcohol and deposited in the private collection of Glenn and Laura Burghardt, Oakdale, California.

Remarks: Based on the 8 available specimens, animals of this new species vary in length up to 8.7 mm. There is a slight variation in the number of ribs on the head valves, which may range from 10 to 12, and on the tail valves ranging from 8 to 10.

The sculpture on the intermediate and tail valves of *Callistochiton carmenae* differentiates it from other described species in the genus. *Callistochiton carmenae* belongs in the group characterized by having the central areas diagonally ribbed which results in the pitted appearance of the central areas in the intermediate valves; it adds, thus, a fourth species to the group that already includes the West American *C. pulchellus* (Gray, 1828), the Caribbean *C. shuttleworthianus* Pilsbry, 1893, and the Australian *C. antiquus* (Reeve, 1847).

The specimen from Isla Floreana reported by BERGENHAYN (1937) as *Callistochiton shuttleworthianus* Pilsbry, 1893, was located, preserved in alcohol, at the Zoological Museum of Oslo, Norway (No. D 363). The specimen was borrowed for study through the courtesy of Dr. Tor A. Bakke, Curator at the Museum. The specimen was accompanied by a label which read: "Zool. Mus. Oslo nr. D-363 / Callistochiton shuttleworthianus, Pilsbr. / Sted: Floreana, i. strandem / 7-9-1925 / Galapagos – Explg. Bergenhayn dt." The specimen is very small (4.5 mm), completely disarticulated. Slit formula 11 – 1 – 9. The girdle is preserved entire. On the basis of the conchological characters observed, there can be no hesitancy in referring Bergenhayns' Isla Floreana specimen to *Callistochiton carmenae.*

Callistochiton carmenae honors the malacological contributions of Carmen Angermeyer, of Academy Bay, Isla Santa Cruz, who, with her husband, has added much to the knowledge of the invertebrate fauna of the Galápagos Islands through assiduous shore collecting and dredging using their charter vessel, the M/V *Nixe.*

Callistochiton gabbi Pilsbry, 1893

Callistochiton gabbi Pilsbry, 1893. BERGENHAYN, 1937: 282 to 284; figs. 3a-3e (girdle scales only)

No examples of this relatively common Gulf of California *Callistochiton* were collected in the Galápagos Islands in 1964; nor has it been reported since. In all probability, Bergenhayn's record (one 7 mm specimen collected at Isla Floreana) is a misidentification for *Calloplax duncanus.*

MOPALIIDAE Dall, 1889

Placiphorella Carpenter in Dall, 1879

Placiphorella blainvillii (Broderip, 1832)

(Figure *12*)

Chiton blainvillii BRODERIP (*in* BRODERIP & SOWERBY), 1832: 27

Placiphorella blainvillii (Broderip, 1832). DALL, 1909: 246

The type locality is in 17 fathoms (31 m), Inner Lobos Island, Perú, a "few specimens ... while dredging," collected by Hugh Cuming. The United States National Museum mollusk collection contains no specimen from the Galápagos Islands, although it does have one (USNM

Explanation of Figures *17* to *21*

Figure *17*: *Acanthochitona hirudiniformis* (Sowerby, 1832). Academy Bay, Isla Santa Cruz, intertidally. Dorsal view; length, 13.8 mm (CASIZ Collection) (AJF photograph)

Figure *18*: *Acanthochitona jacquelinae* A. G. Smith & Ferreira, spec. nov. Holotype (CASIZ Type Collection No. 967). Dredged in 40 - 50 m, southern end of Academy Bay, Isla Santa Cruz. Dorsal view; length, 8.3 mm (AJF photograph)

Figure *19*: *Acanthochitona jaquelinae* A. G. Smith & Ferreira, spec. nov. Same specimen as Figure *18*. Side view (AJF photogr.)

Figure *20*: *Acanthochitona* cf. *A. avicula* (Carpenter, 1866). Sullivan Bay, Isla San Salvador. Dorsal view of a cobalt-blue adult; length, 18.2 mm (CASG 42193) (AJF photograph)

Figure *21*: *Acanthochitona* cf. *A. avicula* (Carpenter, 1866). Same as Figure *20*. Side view (AJF photograph)

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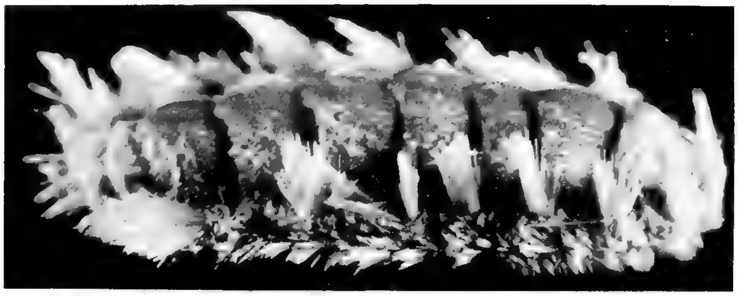

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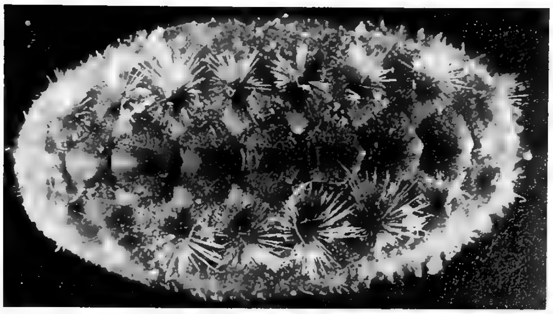

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122968) dredged by the USS *Albatross* in 120m, off Cocos Island, Costa Rica (USFC Sta. 3368) (Figure *12*). Dall's record for *Placiphorella blainvillii,* from "Galápagos, Cocos and Lobos Islands," appears as the only one published. Since there are no museum lots to substantiate the presence of *P. blainvillii* in the Galápagos group, the record remains in need of confirmation.

Chitonidae Rafinesque, 1815

Chiton Linnaeus, 1758

Chiton (Radsia) goodalli Broderip, 1832

(Figure *13*)

Chiton goodalli Broderip (*in* Broderip & Sowerby), 1832: 25 – Sowerby, 1833-1834: 3, 9; plt. 42, fig.34; plt. 43, fig. 40 – Reeve, 1847: spec. no. 8; plt. 2, fig. 8 – Carpenter, 1857a: 180 – Paetel, 1888: 612 – Stearns, 1893: 404, 449 – Pilsbry & Vanatta, 1902: 552 – Dall, 1909: 247 – Schwengel, 1938: 2 – Thorpe (*in* Keen), 1971: 864; fig. 4

Lophyrus goodalli. Carpenter, 1857a: 317, 360 – Wimmer, 1879: 505

Chiton (Lophyrus) goodallii. E. A. Smith, 1877: 71

Chiton (Radsia) chierchiae Nierstrasz, 1908: 158-163; plt. 3, figs. 15-18, 21-28, 30-31

Chiton (Radsia) goodallii. Pilsbry, 1893: **14**: 191; plt. 28, figs. 5-8; plt. 29, fig. 9 – Bartsch & Rehder, 1939: 17 – Leloup, 1955: 1-10; figs. 2a-2c (girdle scales)

This very large, smooth, blackish species heretofore has been considered as being endemic in the Galápagos Islands although there is a recent record of its occurrence on the South American mainland at Santa Elena, Ecuador (Metivier, 1969: 587). Among the Recent Polyplacophora its adult length of 11 to 12.5 cm is exceeded only by the Australian *Acanthozostera gemmata* (Blainville, 1825), which has been reported as long as 15 cm, and the giant *Cryptochiton stelleri* (Middendorff, 1847), which ranges up to 30 cm. *Chiton goodalli* was described by Broderip from specimens supplied by the British conchologist Hugh Cuming, who obtained it during one of his voyages around the world in search of rare shells. Broderip recorded it from Isla San Salvador (James Island), which can be accepted as the type locality. Other records are from Isla Isabella (Pilsbry & Vanatta), Isla Floreana (Bartsch & Rehder), and from Isla San Cristóbal (Schwengel). During the California Academy of Sciences 1905-06 Expedition, W. H. Ochsner collected the species at Isla Isabela (CASG 39557), and at Isla Española (CASG 39556).

In 1964, the senior author encountered *Chiton goodalli* fairly commonly in the intertidal zone in the vicinity of Academy Bay on Isla Santa Cruz. The animals were observed to congregate in groups of a few to a dozen or more in narrow cracks in the lava. At no time were they seen on top of the rocks, which seems to be the normal habitat of the large *Chiton stokesii* Broderip, 1832, on Cocos Island, Costa Rica. Local residents in the vicinity of Academy Bay often prize the large foot of *C. goodalli* as a delicacy; for this reason it was not unusual to find adult specimens drying in the open complete with shells and girdle but with the foot removed.

In a series of adults specimens collected near Nelson's on Academy Bay in 1964 by the senior author, the largest specimen preserved in alcohol in a flattened condition (CASIZ Collection) measures 123 mm in length, 78 mm in width, and 22 mm in height.

Although the dorsal surface in specimens of *Chiton goodalli* normally is quite smooth, some shells exhibit a tendency toward faint, subobsolete ribbing on all valves. This is a sculptural feature, however, that obviously is well within the limits of individual variation for the species.

Fossil Record: Two medium-sized tail valves and an intermediate valve of *Chiton goodalli* were collected in a Pleistocene deposit on Isla San Salvador by the late Leo G. Hertlein during the California Academy's 1931-1932 G. Allan Hancock Galápagos Expedition. This represents the first fossil record for the species. These valves are deposited in the California Academy of Sciences (CASG 27255).

Chiton (Radsia) sulcatus Wood, 1815

(Figure *14*)

Chiton sulcatus Wood, 1815: 16; plt. 3, fig. 1 – Sowerby, 1833-1834: 2, 9; plt. 39, fig. 12 – Reeve, 1847, sp. no. 15; plt. 3, fig. 15 – Stearns, 1893: 404, 408 – Pilsbry & Vanatta, 1902: 552 – Dall, 1909: 247 – Schwengel, 1938: 12 – Thorpe (*in* Keen), 1971: 864, fig. 6 – Metevier, 1969: 586

Lophyrus sulcatus. Carpenter, 1857a: 317, 360 – Wimmer, 1879: 506

Chiton (Lophyrus) sulcatus. E. A. Smith, 1877: 71

Chiton (Radsia) sulcatus. Pilsbry, 1893: **14**: 191-192; plt. 28, figs. 1-4; – Stearns, 1893: 449 – Boone, 1933: 202-203; plt. 127 – Bartsch & Rehder, 1933: 17

This handsome, heavily-sculptured, blue-black chiton has been collected only in the Galápagos Islands. It was described originally by Wood, who said: "This rugged shell is said to inhabit the south seas," a statement now known to be incorrect. It has been reported from Isla Isabela (Bartsch & Rehder; Pilsbry & Vanatta), Isla Floreana (E. A. Smith; Stearns), Isla San Cristóbal (Schwengel), Isla Española (Reeve; Stearns; Wimmer; Boone), Isla Santa Cruz (Stearns), Isla San Salvador (Reeve), Isla Fernandina (Tomlin), and Isla Baltra (Metivier). During the California Academy's 1905-1906 Expedition, W. H. Ochsner collected it on several of these islands, and added Isla Pinzón (CASG).

Isla San Salvador (James Island) may be accepted as the type locality for *Chiton sulcatus* based on Reeve's first localized island record.

In 1964, the senior author found *Chiton sulcatus* in Santa Cruz Island where it was the most abundant species. Generally the shells were clean, without algal or other growths on them. There was some variability noticed in the sculpturing on adult specimens. The largest specimen in the California Academy of Sciences' collection (CASG 39556) was taken on Isla Española by Ochsner; it measures 95 mm in length, 50 mm in width, and 21 mm in height. Most adult specimens are smaller than this.

Chiton sulcatus is active; it has a powerful musculature, clinging to any hard substrate with great tenacity. Once removed, it curls up immediately and will not flatten out readily in a bucket of sea water as many other chitons do. Hence good specimens preserved in a flattened condition are the exception rather than the rule.

Fossil Record: A single, medium-sized tail valve of *Chiton sulcatus* was collected in a Pleistocene beach deposit during the California Academy's 1931-1932 Expedition by Dr. Hertlein (CASG 27250) and represents the first fossil record of the species. This fossil valve, and the 2 of *C. goodalli* previously mentioned, were not included by Hertlein & Strong in their account of the marine Pleistocene mollusks from the Galápagos Islands published in 1939.

Chiton latus Sowerby, 1825

Chiton latus Sowerby, 1825 [not *Chiton latus* Lowe, 1825] – Boone, 1933: 200; plt. 125, fig. B

Boone reported "one large specimen," collected at Gardner Bay, Hood Island, Galápagos Islands, by the *Ara*, February 4, 1928. Mr. William E. Old of the American Museum of Natural History, New York, has seen the Boone specimen and reports it (*in litt.*) to be *Chiton stokesii* Broderip, 1832, quite probably from Cocos Island, Costa Rica, the erroneous record evidently due to a mixing of labels. This species was not collected on Hood Island (Isla Española) by members of the California Academy's 1905-1906 Expedition and has not been reported otherwise from the Galápagos Islands.

According to Pilsbry (1893, **14**: 160-161), *Chiton latus* Sowerby, 1825, is a synonym of *C. magnificus* Deshayes, 1827, which he cites only from Valparaiso, Chile. Thus it is evident that this Chilean species is not a constituent of the Galápagos chiton fauna.

Tonicia Gray, 1847

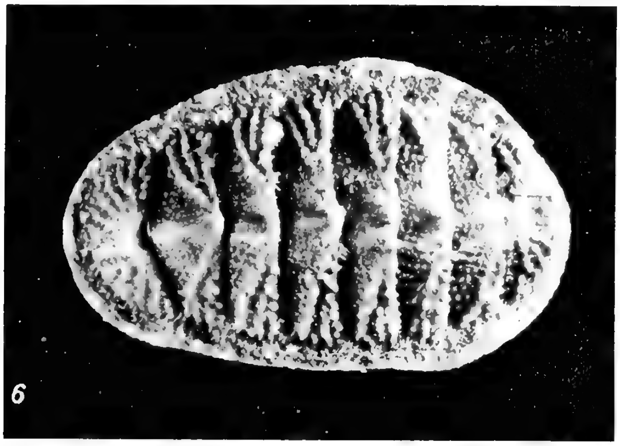
Tonicia forbesii Carpenter, 1857

Tonicia crenulata (Broderip, 1832) [not *Chiton crenulatus* Risso, 1826]. Tomlin, 1927: 154
Tonicia forbesii Carpenter, 1857b: 193

The first Galápagos Island record for this species is by Tomlin who reported it from Isla Floreana under the preoccupied name of *Tonicia crenulata*. Although the species

Explanation of Figures *6, 7, 10, 11, 15, 16*

Figure *6*: *Chaetopleura* cf. *C. mixta* (Dall, 1919). Specimen from Academy Bay, Isla Santa Cruz, low intertidal zone (CASG 40290). Length, 7.3 mm (AJF photograph)
Figure *7*: *Chaetopleura* cf. *C. mixta* (Dall, 1919). Close-up of lateral area and girdle (AJF photograph)
Figure *10*: *Callistochiton carmenae* A. G. Smith & Ferreira, spec. nov. Paratype (CASG Type Collection No. 58248). Academy Bay, Isla Santa Cruz. Dorsal view; length, 9.2 mm (AJF photograph)
Figure *11*: *Callistochiton carmenae* A. G. Smith & Ferreira, spec. nov. Paratype, Burghardt Collection. Academy Bay, Isla Santa Cruz. Close-up of lateral and central areas (AJF photograph)
Figure *15*: *Tonicia forbesii arnheimi* Dall, 1903. Adult specimen from Isla Baltra. Dorsal view; length, 23.3 mm (CASG 40356) (AJF photograph)
Figure *16*: *Tonicia forbesii arnheimi* Dall, 1903. Same. Close-up of lateral areas to show "eyes" (AJF photograph)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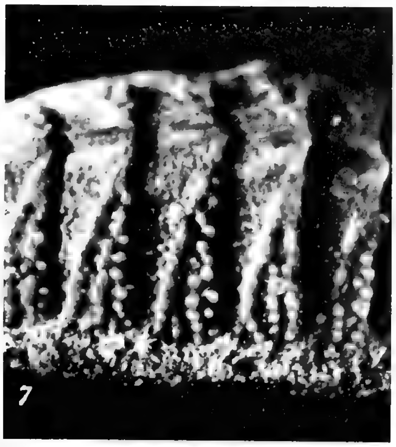
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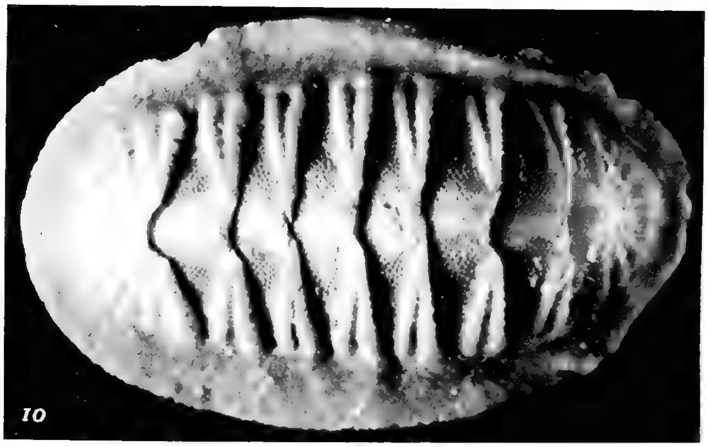
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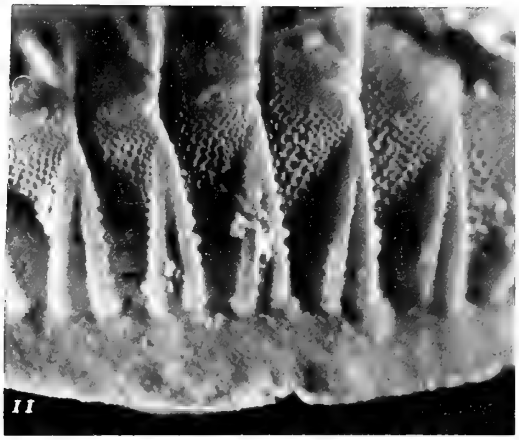
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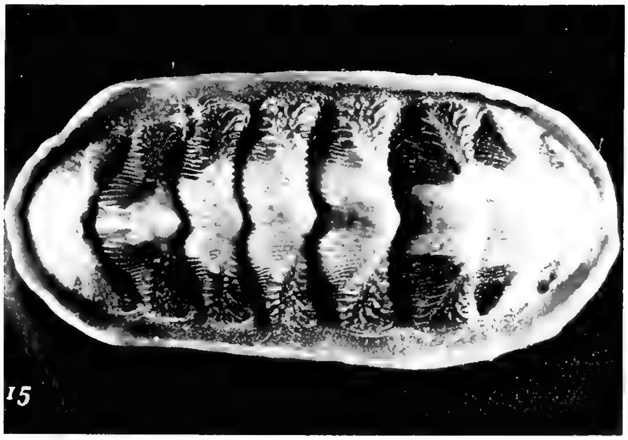
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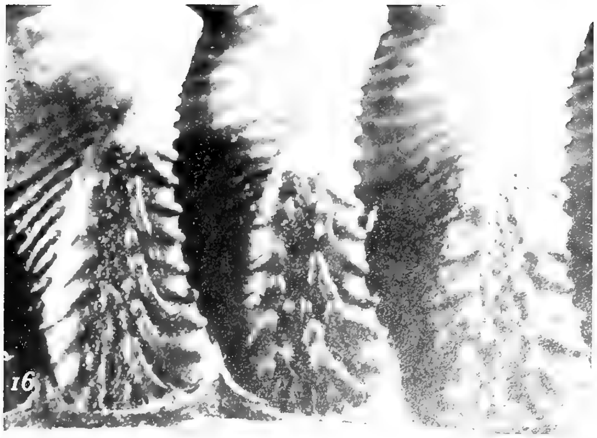
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is relatively common in the Panamic Province from Mazatlán southward, Tonicias are not common in the Galápagos Islands. A number of specimens was collected during the Galápagos International Scientific Project of 1964 and subsequently, both in the low intertidal zone and by dredging. These have been compared with specimens taken at Mazatlán, Barra de Navidad, and Acapulco, México, and also with material from Panamá (Taboga Island) and Nicaragua (San Juan del Sur). This comparison has led to the conclusion that the differences in sculpture and size, as well as color, between Galápagos specimens and those from the mainland, plus the geographical isolation of the Galápagos Islands, warrants the systematic treatment of the Islands' population as a separate geographical subspecies of *T. forbesii.* Fortunately, a name for this subspecies is already available in *T. arnheimi* Dall, 1903; consequently the Galápagos Tonicias related to *T. forbesii* will be treated under that name.

Tonicia forbesii arnheimi Dall, 1903

(Figures *15, 16*)

Tonicia arnheimi Dall, 1903: 37-38 – Thorpe (*in* Keen), 1971: 864

Tonicia arnheimi is based on a single specimen (USNM 170297), examined on a loan obtained through the courtesy of Dr. Joseph Rosewater. The specimen was dredged in "Noyes Cove" in 20 fathoms (36m) by Capt. W. P. Noyes, master of the *Julia E. Whalen*, which carried Messrs. Snodgrass and Heller to the Galápagos Islands under the name of the Hopkins-Stanford Expedition, 1898-1899. The exact location of Noyes Cove is not known but as the Expedition spent some time in Tagus Cove, Isla Isabela, probably it is close by. The holotype of *T. arnheimi* was presented to the U. S. National Museum by Mr. J. S. Arnheim of San Francisco for whom it was named.

Dall described *Tonicia arnheimi* by comparison with *T. crenulata* (= *T. forbesii*) to which he believed it to be closely related. He made a particular point of "the brilliancy in the eye-spots, each situated in a deep, minute pit," which have "a metallic silvery lustre" compared with the black eye spots of *T. forbesii.* This indeed is a striking character in the holotype and on several of the specimens collected recently. This, however, turns out not to be a constant character in the Galápagos specimens of *T. forbesii arnheimi.*

Adult specimens of *Tonicia forbesii arnheimi* average smaller in size than the mainland *T. forbesii.* Also, the Galápagos race has smoother and less prominently incised sculpture on the dorsal surfaces of the valves, and tends to be darker red or pinkish in color. The irregular longitudinal ridges on the central areas of some of the Galápagos specimens are more numerous and closely-set; those from deeper water have smoother sculpture than those living in the low intertidal zone; some have a smooth jugal area, lacking the pair of well-incised grooves on either side of it that is characteristic of mainland shells. Specimens dredged in Academy Bay (lots 13 and 18), and one dredged off Jervis Island (lot 14) agree closely with the holotype of *T. arnheimi.*

Acanthopleura Guilding, 1830

Acanthopleura echinatum (Barnes, 1824)

Chiton echinatus Barnes, 1824: 71; plt. 3, figs. 4a, 4b
Acanthochiton spinifera (Frembly, 1827). Stearns, 1893: 449 (= "*C.*[*hiton*] *aculeatus* Barnes").
Acanthopleura (Corephium) echinata. Dall, 1909: 180, 248
Acanthopleura (Mesotomura) echinatum. Pilsbry, 1893: **14**: 218-219; plt. 47, figs. 6-17

Stearns reported this large South American chiton from the Galápagos Islands based on a specimen in the U. S. National Museum under the name *Acanthochiton spinifera* (USNM 59575). It is a good-sized adult specimen measuring over 100 mm in length, with the upper surface much encrusted. Dall included the Galápagos Islands in citing its range, which extends from Paita, Perú, to Valparaiso, Chile, on the mainland. Pilsbry also includes the Galápagos group for this species based on specimens in the collections of the Academy of Natural Sciences of Philadelphia.

This conspicuous chiton, with a girdle set with sparse, strong, spike-like spines, can hardly be mistaken for any other species. It was not collected by Snodgrass and Heller during the Hopkins-Stanford Expedition of 1898-1899, nor by Ochsner during the 1905-1906 California Academy Expedition. No specimens were collected in Galápagos in 1964 by the senior author, or the local collectors. Why the species has not been collected in the Galápagos Islands in recent years is a mystery. Inclusion of *Acanthopleura echinatum* in the permanent chiton fauna of the Galápagos Islands is therefore withheld pending its possible re-discovery.

Enoplochiton Gray, 1847

Enoplochiton niger (Barnes, 1824)

Chiton niger Barnes, 1824: 71; plt. 3, fig. 3
Tonicia ? coquimbensis (Frembly, 1827). Stearns, 1893: 449
Enoplochiton niger (Barnes, 1824). Pilsbry, 1893: **14**: 252-253; plt. 52, figs. 22-29

Stearns' published record is based on a single adult specimen (USNM 59576). It is the only known one from the Galápagos Islands. The species is a large one with a unique type girdle set with massive, widely-spaced, deeply-imbedded scales. It cannot be mistaken for any other described chiton. Pilsbry records it from Perú and Chile, but not from the Galápagos Islands. The record needs confirming.

Acanthochitonidae Pilsbry, 1893

Acanthochitona Gray, 1821

Acanthochitona hirudiniformis (Sowerby, 1832)

(Figure *17*)

Chiton hirudiniformis Sowerby, (*in* Broderip & Sowerby), 1832: 59 – Sowerby, 1833-1834: 7, 10; plt. 41, fig. 23; plt. 174, fig. 142 – Reeve, 1847: spec. no. 54, plt. 10, fig. 54 – Carpenter, 1857a: 181, 318, 360
Acanthochites hirudiniformis. Wimmer, 1879: 506 – Pilsbry, 1893: **15**: 27; plt. 2, figs. 49, 56 – Pilsbry & Vanatta, 1902: 552 – Dall, 1909: 246
?*Tonicia hirudiniformis.* Stearns, 1893: 449
Acanthochitona hirudiniformis. Thorpe (*in* Keen), 1971: 866, 868, fig. 13 (p. 867)

This species was described by Sowerby from Ancón, Lobos Island, and Paita, Perú, on the mainland of South America, and from Chatham Island (Isla San Cristóbal), Galápagos Islands. His account, which is quite brief, is repeated by Pilsbry in the Manual of Conchology (1893). Pilsbry had specimens from Isla Pinzón, Isla Fernandina, and from Tagus Cove, Isla Isabela, the latter collected by Snodgrass during the 1898-1899 Hopkins-Stanford Expedition; these specimens are in the collection of the Department of Mollusks, Academy of Natural Sciences of Philadelphia. A sizeable series was collected by W. H. Ochsner in Iguana Cove, Isla Isabela (CASG 37082), and on Isla Pinzón (CASG 37268) during the California Academy's 1905-1906 Expedition. Members of the GISP found it on Isla Santa Cruz, Isla Genovesa, and Isla Pinta in 1964.

On Isla Santa Cruz, in 1964, *Acanthochitona hirudiniformis* was found fairly commonly in the general vicinity of Academy Bay from the middle to the low intertidal zone. The species occurs in some abundance on many (and very likely on all) of the islands of the Galápagos Archipelago. The animal is rather small and dark-colored, blending perfectly with the color of the lava blocks on and under which it lives; it escapes notice easily because of the habit of nestling in small depressions. It was observed that young specimens around Academy Bay were subject to considerable predation from large gastropods, including *Thais planospira*, *Th. melones*, *Acanthina muricata*, *Purpura columellaris* and *P. pansa*.

Extended Description: Galápagos specimens of *Acanthochitona hirudiniformis* agree in general with Sowerby's original but brief diagnosis. The valves are arched, not carinated, the intermediate valves only slightly mucronate. The exposed portion of the intermediate valves is subtriangular, usually appearing black when unworn but sometimes with flecks of lighter color. The head valve is semicircular, rounded, and generally has a straight posterior margin. On the intermediate valves and the tail valve the wedge-shaped jugal areas are raised and sharply defined, with a sculpture of transverse growth-lines, faint longitudinal lirae, and occasional remnants of granular sculpture; this is scarcely visible in perfect specimens but more distinct when the dorsal surface is a little worn. The lateropleural areas have an even sculpture of small, closely-spaced, ovate, flat-topped granules. The tail valve has a small, nearly circular tegmentum, the anterior part being a little contracted with the mucro positioned slightly behind the middle. The interior of the valves is blue, more or less purplish at their centers. The insertion plates are long; in the head valve it is about half as long as the tegmentum; in the tail valve it is nearly vertical and deeply sinused in an end view. The slit formula is 5–1–2. The girdle is thick and wide, sepia or brownish in color, and densely covered with very short delicate spicules, giving it a velvety appearance; there is a dense fringe of longer spicules around the periphery. The 18 sutural tufts are colored like the girdle but appear lighter in tone under good lighting; those at the sutures of the intermediate valves are about 5 mm long while those around the head valve are somewhat shorter.

Remarks: There has been some uncertainty concerning the proper identification of *Acanthochitona hirudiniformis*. It is not possible to say with assurance whether Sowerby's figure 142 on plate 2 of the Conchological Illustrations of 1833-1834 (the better of his 2 illustrations) represents a Peruvian or a Galapagan specimen. Because of this uncertainty, PILSBRY (in MS) considered Isla San Cristóbal (Chatham Island) to be the type locality, a suggestion we propose be accepted. This action will establish the Galápagos Islands as the type locality, rather than one of the Peruvian localities (Ancón, Lobos Island, or Paita).

In the California Academy collection there is a series of 3 small, dry, curled specimens of an *Acanthochitona* collected by Don L. Frizzell at Paita, Perú, in 1938. Since they came from one of the original localities for *A. hirudiniformis* cited by Sowerby, a comparison with Galápagos material has some significance. This shows several conchological differences. The specimens from Paita are smaller in size; the oval, flat-topped granules on the latero-pleural areas are slightly larger and are much less numerous, not being as closely spaced. Also, the jugal areas are smaller in extent, especially on valves iv to vii, inclusive, being much narrower. The sutural tufts are whitish rather than sepia or brownish-olive as on Galápagos specimens.

From the above evidence, which admittedly is insufficient, we suspect the specimens from Paita to represent a species of *Acanthochitona* different from the one common to the Galápagos Islands. Should this prove to be the case after study of more and better material from Perú, another name can be allocated to the species from the mainland of South America, which can be selected from *A. coquimbensis* Leloup, 1941, *A. peruvianus* Leloup, 1941, or *A. tabogensis* A. G. Smith, 1961. It should be noted that THORPE (*in* KEEN, 1971) places all 3 of these species in the synonymy of *A. hirudiniformis* without providing any substantiating evidence for these allocations.

Because adequate material from Perú and elsewhere on the mainland south of Panamá does not yet seem to be available, no authoritative judgment can be made at this time. In arriving at a final conclusion, there are several earlier-collected specimens that should be taken into account. As an example, in the mollusk collection of the Academy of Natural Sciences of Philadelphia there are 2 specimens of *Acanthochitona* from Perú (ANSP 35788) received from Dr. T. B. Wilson. The larger specimen measures 36 × 18mm. They were in the old collection of the Philadelphia Academy under the name *Chiton hirudiniformis* and were purchased in London some time between 1846 and 1849, probably from Hugh Cuming. These specimens differ from the Galápagos *A. hirudiniformis* in several sculptural characters and in the girdle decoration, which has stout spines scattered among the finer girdle spicules. They are not mentioned by Pilsbry in the Manual of Conchology. It is possible that Sowerby's figure 142 in the Conchological Illustrations represents this form.

The United States National Museum of Natural History has 3 lots of small Acanthochitonas from South America, 2 of them labeled *Acanthochitona hirudiniformis.* The first (USNM 5804) came from Orange Harbor, Patagonia, collected during the United States Exploring Expedition, and probably identified by P.P. Carpenter. It is a dry, curled specimen in poor condition, the girdle ornamentation being almost completely gone. The second (USNM 19284), identified by Carpenter according to the museum label, came from Valparaiso, Chile, and was also taken during the U. S. Exploring Expedition. It is dry and curled; the valves, which are disarticulated, are much worn and chipped. The third specimen (USNM 218733) is unidentified as to species and came from between Cape Pillar and Cape Horn, collected by Stokes. It is complete and measures 17 × 8.5mm. The tegmentum is light gray to whitish with dark zig-zag markings around the margins of the valves. Sculpture on the latero-pleural areas consists of closely-spaced, small, round granules. So far as can be determined, all of these South American specimens of *Acanthochitona* differ in several respects from *A. hirudiniformis* of the Galápagos Islands and probably represent other species. The Stokes specimen from near Cape Horn possibly can be referred to *A. stygma* (Rochebrune, 1889), an allocation that is problematical as we have not seen authentic specimens of Rochebrune's species.

Acanthochitona jacquelinae A. G. Smith & Ferreira spec. nov.

(Figures *18, 19*)

Diagnosis: This is a small species taken so far only by dredging in 40 to 50m in the southern end of Academy Bay, Isla Santa Cruz, and off Isla San Salvador. Most specimens are reddish in tone although a few are mottled or white. It is characterized mainly by the wide-spreading spicular tufts, which are unusually prominent for such a small sized chiton. This feature is the principal one that distinguishes it from other Acanthochitonas described from the Eastern Pacific.

Description: Animals very small for the genus, generally not exceeding 10mm in length, elongate-ovate, the valves arched but not carinate, intermediate valves mucronate. Color more often mottled with white and reddish tones, with many colored an over-all light orange-red or terra-cotta red; a few specimens are pure white. The girdles are colored the same as the valves and are decorated with the usual spicular tufts or pore-bunches. These tufts are large and wide-spreading for the size of the animal, the spicules being 1.0 to 1.5 mm long, yellowish in tone except those which are white on pure white specimens. The girdles are decorated, in addition, with extremely fine, upward-trending and inward-curving, pointed spicules, sometimes quite numerous close to the side-margins of the valves and surrounding the bases of the pore-bunches. Below these, the girdles have only a few smaller, scattered spicules but they terminate in a well-developed foot-fringe of closely-packed, straight, pointed spicules about half as long as those making up the spicular tufts. The jugal areas of the intermediate valves are quadrilateral, cut into 7 - 10 longitudinal, somewhat beaded lirae by much narrower incised grooves. Latero-pleural areas of intermediate and end valves sculptured with a series of small, round or suboval, slightly convex or flat-topped granules, closely spaced in quincunx rather than in straight rows. The mucro of the tail valve is rounded and centrally placed.

Internally, the valves are orange-red (except in pure white specimens). The combined insertion plates and sutural laminae are not especially wide in relation to the tegmentum area; they are smooth-surfaced, and have the usual 5 – 1 – 2 slit formula. The slits are deep, near parallel-sided, but are not thickened or buttressed at their sides. The anterior sinus of the tail valve is about $\frac{1}{5}$ its entire width.

Type Locality: In 40-50 m (21.3-26.5 fms.) on a broken coralline bottom off Isla Coamaño (Jensen Island) at the southern end of Academy Bay, Isla Santa Cruz, dredged by André and Jacqueline De Roy. A total of 67 specimens was collected in this area, 9 on September 29, and 58 on December 28, 1966.

Type Material: The holotype is an orange specimen from the type locality (CASIZ Type Series no. 967), measuring 8.3 mm in length, 4.2 mm in width, and 1.5 mm in height.

The remainder of the type lot (66 specimens) is hereby designated as paratypes, representative examples of which will be deposited in various museums, and in the private collection of Mme. Jacqueline De Roy.

Other Material: Another specimen, preserved in alcohol, measuring 7.9 mm in length, was dredged in 9 - 18 m (5 - 10 fms.) in Academy Bay on a hard coralline-mud bottom by D. P. Abbott, J. L. Barnard, J. W. Durham and A. G. Smith, 24 February 1964. It was found nestling in a small chunk of hard coralline alga. The basic color of this specimen is white with sea-green markings on valves iii, iv, vii, and viii. The girdle is marbled with reddish brown. The spicular pore bunches are grass-green at their bases, blending into yellowish-white towards their tips. The foot-fringe is colored alternately with lavender and white.

A single, tiny, whitish specimen was dredged in 55 m (30.1 fms.) in Academy Bay near the type locality by the De Roys, 26 April 1967 (CASG 40495). A small curled specimen, preserved dry, was dredged in 25 m off Isla San Salvador by the De Roys, 27 March 1967 (CASG 40323); it has the same reddish color as most of the Academy Bay specimens. A single, pinkish specimen dredged in 20 - 40 m (11 - 22 fms.) off Isla Rábida by the De Roys, 22 March 1967, preserved dry (CASG 40492).

Remarks: This lovely little chiton is distinct and easily separable from any specimens of *Acanthochitona* from the Eastern Pacific known to us. The adequate series at hand, which ranges in length from a little over 1 mm to hardly more than 10 mm, is quite constant in sculptural and other details, although the color varies from mottled reddish and white to over-all light red tones. In the total of 71 specimens available, 39 (55%) are mottled red and white, 25 (35%) are over-all reddish, and 7 (10%) are pure white or yellowish.

*Acanthochitona **jacquelinae*** is most closely related to *A. arragonites* (Carpenter, 1857) from the Gulf of California; both are about the same size. However, it differs from the latter in the following particulars: (1) the jugal tract is finely ribbed longitudinally compared with the smooth jugal tract of *A. arragonites*; (2) the pustules on the latero-pleural areas are smaller and rounder than the more oval shaped pustules in *A. arragonites*, and arranged in quincunx rather than in straight rows; (3) the basic girle spicules generally are sparse and very small whereas in *A. arragonites* they are more numerous and interspersed with spicules of varying sizes. *Acanthochitona **jacquelinae*** differs from *A. avicula* (Carpenter, 1866) in: (1) its much smaller size; (2) much brighter colors, often in tones of red to yellow or white, but not blue (common in *A. avicula*); (3) much smaller and rounder pustules on the latero-pleural areas; (4) thinner and shorter basic girdle spicules, and, in contrast, much longer (for the size of the animal) spicular pore-bunches resulting in a bushier appearance.

*Acanthochitona **jacquelinae*** is named for Mme. Jacqueline De Roy of Academy Bay, Galápagos Islands, who was instrumental in collecting the type lot and who has been contributing much to the knowledge and understanding of the molluscan fauna of the Galápagos Islands.

Acanthochitona cf. *A. avicula* (Carpenter, 1866)

(Figures *20, 21*)

Acanthochites avicula Carpenter, 1866: 211

Ten specimens of a still different *Acanthochitona* have been collected by the De Roys on or in the vicinity of 3 of the larger islands of the Galápagos Archipelago, and 2 of the smaller ones, either in the low intertidal zone, or dredged to a depth of 30m.

The specimens examined are in 6 lots as follows: (1) 2 specimens in alcohol (CASIZ Colln.), collected in Academy Bay, Isla Santa Cruz, 1966; 14mm and 12.1mm long; (2) one specimen, dry (CASG 40494) dredged in 10 - 30m off Beagle Island, 20 March, 1967; length, 7.5 mm; color, whitish with longitudinally arranged light-brown, zig-zag markings on the side-slopes of the valves; pore-bunches of spicules are bluish-green while the other girdle spicules are lavender in tone; (3) 2 specimens, dry (CASG 42194), about 7.5mm in length, collected at low tide in Sullivan Bay, Isla San Salvador, 23 November, 1967; color mottled light green; girdle spicules lavender, pore-bunches colorless; (4) 2 specimens, dry (CASG 42198), dredged in 10m, Tagus Cove, Isla Isabela, 22 January, 1968; one whitish, the other dark slate-grey; (5) 1 specimen, 8.5mm long, dry (CASG 42199) dredged in 8m off Isla Sombrero Chino, 1 February, 1969; mottled whitish and light brown; pore-bunches, lavender; (6) 2 specimens, dry (CASG 42193), collected 2 February 1969, in low intertidal zone, Sullivan Bay, Isla San Salvador; the largest measures 18.2mm in length, 8.2mm in width, and 2.9mm in height (Figures *20, 21*); the spicules in the pore-bunches as well as those covering the girdle are a brilliant iridescent cobalt-blue.

Remarks: All of the specimens at hand for study are small in size (with only one exception which is 18.2mm long), and apparently juveniles. The dorsal sculpture, especially the occurrence of closely-spaced, fine, longitudinal lirae on the well marked jugal areas agrees with a similar sculpture character on specimens of *Acanthochitona avicula* in the California Academy's collections from Mission Bay, San Diego County, California, and from several localities in the Gulf of California, and Scammons Lagoon, Baja California, Mexico. However, the Galápagos specimens do differ from the *A. avicula* of northern waters in the very small size of the spicules covering the girdle; in specimens of *A. avicula* collected in their known range from San Diego to the Gulf of California, the girdle is covered with relatively long and thick spicules, almost the size of the spicules at the fringe, while the examined specimens from the Galápagos Islands show no such a character inasmuch as the girdle is covered with spicules which are quite small and thin. Another possible difference between the northern and the Galápagos populations was found in the examination of the radula: in specimens of *A. avicula* from San Diego and the Gulf of California the radula's median tooth is as wide in the front as (or even narrower than) in the back, whereas the radula of a specimen from the Galápagos Islands (11mm long) has a median tooth which is much wider in the front than in the back. It is interesting to note that in these 2 characters the Galápagos specimens approach *A. hirudiniformis* more than *A. avicula*. However, *A. avicula*, not previously recorded south of the Gulf of California, is given to considerable intraspecific variation (in color, size and shape of the pustules in the latero-pleural areas, degree of striation in the jugal areas, size and color of the pore-bunches spicules), and the distinctions observed in the Galápagos specimens, particularly in view of their being juveniles, do not appear large enough to contradict the notion of conspecificity. Thus, until additional adult specimens of this particular species of *Acanthochitona* can be collected and compared with other described species, it seems best to refer those at hand to *A. avicula* (Carpenter, 1866) subject to a subsequent review.

Acanthochitona species?

(Figure *22*)

In the collection of the Academy of Sciences of Philadelphia is a series of valves (head, tail, and 3 intermediates) of an *Acanthochitona* collected in Seymour Bay, Isla Santa Cruz, under a stone, at low tide, by H. A. Pilsbry, 22 June 1929 (ANSP 153484). The girdle of the specimen is missing. Pilsbry recognized it as a new species, and provided a description which is still in MS at the Philadelphia Academy. According to Pilsbry's description, the species would differ from other Eastern Pacific species in the broad shape of the intermediate valves, the coarser granulations [pustules] of the dorsal surfaces, and the minute girdle spicules, so small that the girdle appeared smooth under a hand lens.

The specimen was borrowed for study and illustration through the courtesy of Dr. R. Tucker Abbott and Mrs. Virginia Orr Maes. Because it is incomplete, and because no other specimens like it have turned up, the above account is included to call attention to the possibility of still another undescribed species of *Acanthochitona* occurring in the chiton fauna of the Galápagos Islands.

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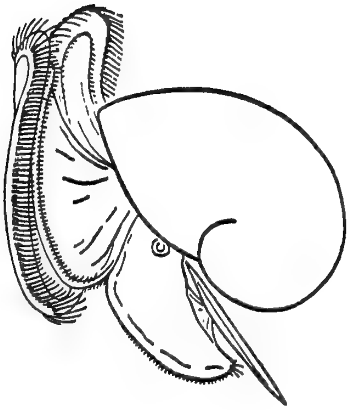

Notes on Sea Hares of South Texas

(Gastropoda : Opisthobranchia)

BY

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THOSE SPECIES OF SEA HARES reported from the South Texas Coast are the source of extensive misidentification and widespread nomenclatural confusion. Synonyms as well as inaccurate descriptions are common in recent literature (BREUER, 1962; ANDREWS, 1971; ABBOTT, 1974; and NECK, 1976). Major scientific works such as those by EALES (1960) and MARCUS (1972) have apparently been overlooked in many instances. The purpose of this paper is to facilitate ease of identification and eliminate nomenclatural confusion with respect to those species currently recognized from South Texas. The results of this study are based on field work conducted in the vicinity of South Padre Island, Cameron County, during the previous 3-year period. It should be noted that frequency of sightings and abundance of specimens of the various species is sporadic and seemingly unpredictable. The following 5 species of sea hares are currently reported from South Texas. The 4 species of *Aplysia* belong to the subgenus *Varria*. Primary synonyms are listed for each species. In several instances new combinations are given due to associated change in the generic name of the taxon.

Aplysia Linnaeus, 1767

Aplysia brasiliana Rang, 1828

Synonymy:

Aplysia livida D'ORBIGNY, 1837: 206
Aplysia cailleti DESHAYES, 1857: 140 (see EALES, 1960: 297)
Aplysia guadeloupensis SOWERBY, 1869: plt. 5 (see EALES, 1960: 297)
Aplysia willcoxi HEILPRIN, 1886: 364; – 1887: 130
Tethys willcoxi var. *perviridis* PILSBRY, 1895: 81
Tethys floridensis PILSBRY, 1895: 82

Remarks: This is the common mottled sea hare extensively referred to as *Aplysia willcoxi* in both the popular and scientific literature. It is currently placed in synonymy with *A. brasiliana* (STRENTH & BLANKENSHIP, in press). Known locally as an "ink-fish" (WHITTEN, ROSENE & HEDGPETH, 1950) or "sea cow," its first report from the Texas Coast is in all likelihood that by REED (1941). This species is an excellent swimmer.

Occurrence: Although it is most abundant from late spring to August, it has been collected at least once in each month over a 2-year period. While this species is generally found to inhabit the bay, it has also been found washed ashore on the beach front, found attached to rocks of the jetties along the Brazos Santiago Pass, and reported from offshore reefs by TUNNELL & CHANEY (1970) along with *A. morio* (as *A. floridensis*).

Aplysia dactylomela Rang, 1828

Synonymy:

Aplysia protea RANG, 1828: 56
Aplysia schrammii DESHAYES, 1857: 140
Aplysia guadeloupensis SOWERBY, 1869; plt. 5 (see EALES, 1960: 307)
Aplysia aequorea HEILPRIN, 1888: 325
Tethys dactylomela var. *aequorea* Heilprin. PILSBRY, 1895: 77
Tethys panamensis PILSBRY, 1895: 88
Aplysia megaptera VERRILL, 1899: 545

Remarks: Commonly known as the spotted or ringed sea hare, this species is distributed worldwide in warm seas. Only those synonyms with specific reference to the Gulf of Mexico or West Indies are given above. Refer to EALES (1960: 307) for a complete listing of worldwide synonyms.

Occurrence: Uncommon, usually found exposed in grass beds at low tide only during late fall and winter. Occasionally found in small groups of 2 or 3, seldom in groups of up to 20.

Aplysia morio Verrill, 1901

Synonymy:

Tethys (Aplysia) morio Verrill, 1901: 25
Tethys modesta Thiele, 1910: 124

Remarks: This is the common "sooty" sea hare reported as *Aplysia floridensis* by Breuer (1962), Tunnell & Chaney (1970), Andrews (1971), and Neck (1976). Living specimens are dark purple to black in coloration. This species, like *Aplysia brasiliana*, is an excellent swimmer.

Occurrence: Sporadically common during summer months of certain years as noted by Breuer (1962). During the course of this study it was noted to be common only during late summer of 1974.

Aplysia donca Marcus & Marcus, 1960

Remarks: This species was described from a single specimen which was "rather small' and "has probably not attained the maximum size of the species" (Marcus & Marcus, 1960). This species differs from *Aplysia morio* with respect to penis morphology, shell foramen and radula formula (Marcus & Marcus, 1960: 253): Due to its similar coloration, possible individual variation of juvenile specimens, and unreliability of both shell foramen (Eales, 1960: 381) and radula formulae (Marcus, 1972: 848; Strenth & Blankenship, in press) as taxonomic characters within the genus, a comparative examination of a juvenile series of *A. morio* from Texas with the type of *A. donca* would appear desirable.

Occurrence: Known only from the single type-specimen collected at Mustang Island, Port Aransas, Texas.

Bursatella Blainville, 1817

Bursatella leachii pleii (Rang, 1828)

Synonymy:

Aplysia pleii Rang, 1828: 70
Bursatella pleii Rang. Gray, 1850: 98
Notarchus pleii, Rang. Mörch, 1863: 25
Notarchus (Aclesia) pleii (Rang). Thiele, 1910: 124

Remarks: Known as the ragged sea hare, the form common to the Gulf of Mexico is just one of a number of subspecies (Eales & Engel, 1935) exhibiting a worldwide circumtropical distribution.

Occurrence: Although occasionally found throughout the year, this species appears most abundant during late fall and winter. Observations in South Texas appear similar to those by Henry (1952) for this species in Florida.

ACKNOWLEDGMENT

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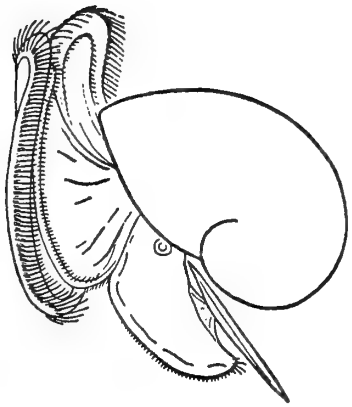

Reevaluation and New Description of the Genus *Bittium* (Cerithiidae)

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(1 Plate)

INTRODUCTION

THE GENUS *Bittium* Gray, 1847 was proposed in manuscript form by Leach for a classification of British mollusca and was subsequently published by GRAY (1847a). Leach's list referred *Bittium* and many other diverse genera to the Purpuridae and under the 65th entry, listed *Bittium reticulatum*, *Murex tuberculare*, *M. adversum*, *M. elegantissimum*, and *M. spenceri*, consecutively. Besides *Bittium reticulatum*, the other species listed by Leach comprise 2 genera, *Triphora* Blainville, 1828 and *Cerithiopsis* Forbes & Hanley, 1853. No description of the genus was given nor was a type-species designated. Three months later, GRAY (1847b: 154) cited only *Bittium reticulatum* (Costa, 1778), which becomes the type-species by subsequent designation (Figure *1*).

To my knowledge, the earliest diagnosis of the genus is that written by H. & A. ADAMS (1854): "Operculigerous lobe with rudimentary expansions on each side and furnished with a roundish, lanceolate cirrhus (Lovén). Operculum subcircular, of four volutions. Shell turreted, many-whorled, granular, often with irregular varices; aperture with a slight canal in front, not produced or recurved; inner lip simple; outer lip acute, not reflexed or expanded." Note that this definition mentions the presence of an anterior canal, a point to which I shall return later. Subsequent classic monographic treatments of the Cerithiidae failed to elaborate on the genus and did not specify further characters.

HISTORICAL REVIEW AND STATUS OF GENUS *Bittium*

There appears to have been some confusion among early workers about the exact placement and rank of *Bittium*. SOWERBY (1855) included *Bittium* in the introductory title of his monograph of *Cerithium* but did not cite it elsewhere in the text; moreover, he referred *Bittium reticulatum* to his "*Cerithiopsis* group." REEVE (1865) did not even mention the name *Bittium*. TRYON (1887) gave it generic recognition but offered no diagnosis. CHENU (1859) appears to have copied the definition of H. & A. ADAMS (1854) but included *Bittium* in the family Potamididae where it was assigned as a subgenus of *Potamidines* (sic) [=*Potamides* Brongniart, 1810], JEFFREYS (1867) lumped *Bittium* under *Cerithium*. DALL (1892) later wrote a diagnosis of the genus *Bittium* that was obviously formulated from his knowledge of Recent and fossil North American species. He mentioned that the last whorl is usually contracted and overhung by its predecessor. This is typical in some individuals of American species, but there is a great deal of variation within specific populations. DALL (*op. cit.*) also noted the close resemblance of *Bittium* to the genera *Diastoma* Deshayes, 1850, *Sandbergeria* Bosquet, 1861, *Alaba* Adams & Adams, 1853, and *Styliferina* A. Adams, 1860 [=*Diala* A. Adams, 1861] and added that the limits of these genera seemed to be quite artificial.

An obvious feature of *Bittium reticulatum*, type-species of *Bittium*, is the presence of a short, shallow, but distinct anterior canal. This was mentioned by H. & A. Adams (1854) in their description of the genus. The presence of an anterior canal is noted in most subsequent treatments of *Bittium* (Chenu, 1859; Tryon, 1887; Bucquoy, Dautzenberg & Dolfus, 1884; Fischer, 1877; Dall, 1892; Cossmann, 1906). Most modern authors also refer to a short anterior canal in their definitions of *Bittium* (Woodring, 1928; Olsson & Harbison, 1953; McLean, 1969; Abbott, 1974) although Keen (1971) regarded it as " a slight anterior notch, not a canal."

Bittium species are frequently referred to other genera. Keen included *Bittium* in the subfamliy Cerithiopsinae but the radulae, larvae and anatomy of *Cerithiopsis* species are far-removed from those of *Bittium* and they should not be considered a closely related group (see Fretter, 1951; Fretter & Pilkington, 1970; Johansson, 1956). Recently, Abbott (1974) referred several American species of *Bittium* to the genus *Diastoma* Deshayes, 1850. His placement of these species was followed by Emerson & Jacobson (1976). Dall (1889) was the first worker to confuse American members of the genus *Bittium* with *Diastoma* Deshayes, 1850 when he referred the common eastern species, *Bittium varium* Pfeiffer, 1840, to *Diastoma*. Dall (1889) noted that Deshayes (1850) considered *Diastoma* to be a rissoid but the former regarded *Diastoma* as a subgroup of *Bittium* and added that *Alaba* Adams & Adams, 1853 was also very similar to *Bittium*. Although *Diastoma* was placed in the Cerithiidae by Fischer (1884) and Cossmann (1889), it is now regarded as a separate family, Diastomatidae (see Ludbrook, 1971). The genus *Diastoma* embraces a group of relatively large snails and is best known from the Eocene of the Paris Basin. Deshayes (1850) designated *Melania costellata* Lamarck, 1804 as the type-species and later (1864, Description des Animaux san Vertèbres, **2:** 413-414) described it in detail. This species is large (about 40mm in length) and the lower portion of the outer lip is a smooth semicircle with no evidence of an anterior canal or even a shallow flared depression. Excellent illustrations of this type-species, cited as *Melania costellata* Lamarck, appear in Favre (1918: plt. 2, figs. 26-30). Ludbrook (1971) has discussed the nomenclatural problems of *Diastoma* in more detail and has pointed out that small cerithiids such as those described from Southern California as *Diastoma fastigiata* (Carpenter, 1864), *D. oldroydae* Bartsch, 1911, and *D. stearnsi* Bartsch, 1911, and an east coast species, *D. virginica* Henderson & Bartsch, 1914 [= *Bittium varium* Pfeiffer] differ from true *Diastoma* by their small size, different sculpture and in the possession of a short, shallow anterior canal. The only living species of *Diastoma*, *D. melanioides* (Reeve, 1849) is found in a very restricted area in south-western Australia and off Eyre Peninsula in South Australia (Ludbrook, 1971). This moderately sized species was figured by Reeve (1849, 5: plt. 1, fig. 3) under his section on *Mesalia* Gray, 1840 and is very unlike the small *Bittium* species of authors. I have been unable to examine a specimen of *Diastoma melanioides* but Cotton (1932) stated that it bears close relationship to fossil species of *Diastoma* even though the upper portion of the outer lip is not as far detached from the body whorl as is the lip in *D. costellata*. It is thus clear that the referral of American species of *Bittium* to *Diastoma* by Dall (1889), Bartsch (1911), Keen (1971), Abbott (1974) and Emerson & Jacobson (1976) should be considered erroneous.

The subgenus *Bittinella* Dall, 1924 was proposed to accommodate *Bittium hiloense* Pilsbry & Vanatta, 1908, from Hawaii. I suggest that this species and *Cerithium zebrum* Kiener, 1841, referred to *Bittium* by Cernohorsky (1972), are merely very small members of the genus *Cerithium* Bruguière. Both species have thick, heavy shells, short, deep anterior canals and thick, crenulated outer lips that are different from most other species of *Bittium*.

Grant & Gale (1931: 731) suggested that many subdivisions of *Bittium* were probably artificial and should be discarded as soon as a natural classification was worked out. My studies on living populations of cerithiids and familiarity with numerous fossil groups and species have convinced me that the adaptive radiation of this large group has led to frequent convergence in shell form, sculpture and radular morphology. Most of the supraspecific taxa proposed for *Bittium* are parochial in conception and scope, are based on specific rather than generic characters and convey misleading or little phylogenetic information. In the interest of pragmatism and taxonomic parsimony I am suggesting that a number of generic and subgeneric taxa be abandoned or synonymized. All species formerly referred to these taxa should be considered as *Bittium* species until the entire group is monographed and subgeneric taxa can be properly evaluated on the basis of more than shell characters.

In order to promote taxonomic stability and to clarify the problems discussed above I herein present a synonymy and redescription of the genus *Bittium*.

SYNONYMY

Cerithiinae Fleming, 1828

Bittium Leach in Gray, 1847

Bittium 1847 (Oct.), Leach in Gray, Ann. Mag. Nat. Hist., **20:** 270. Type-species, *Murex reticulatus* (Montagu, 1803) (= *Strombiformis reticulatus* Costa, 1778), by SD Gray, 1847 (Nov.), Proc. Zool. Soc. London part **15** (178): 154

Cerithiolum 1869, Tiberi, Boll. Malacol. Ital. **2:** 263. Type-species, *Cerithiolum (Strombiformis) reticulatum* (Da Costa, 1778), by OD

Semibittium 1869, Cossmann, Ann. Soc. malac. Belg., Mem. **31:** 29. Type-species, *Cerithium cancellatum* Lamarck, 1804, by OD

Bittiolum 1906, Cossmann, Essais Paléoconch. **7:** 139. Type-species *Bittium podagrinum* Dall, 1892, by OD

Stylidium 1907, Dall in Bartsch, Proc. U. S. Nat. Mus. **33** (1564): 178. Type-species, *Bittium (Stylidium) eschrichti* (Middendorff, 1849), by OD

Lirobittium 1911, Bartsch, Proc. U. S. Nat. Mus. **40** (1826): 384-385. Type-species, *Bittium (Lirobittium) catalinensis* Bartsch, 1907, by OD

Monobittium 1917, Monterosato, Boll. Soc. Zool. Ital. (3) **4:** 20. Type-species, *Manobittium latreillei* (Payraudeau, 1826), by M

Inobittium 1917, Monterosato, Boll. Soc. Zool. Ital. (3) **4:** 20. Type-species, *Inobittium lacteum* (Philippi, 1836) by M

Zebittium 1927, Finlay, Trans. New Zeal Inst. **57:** 381. Type-species *Zebittium exile* (Hutton, 1873), by OD

Cacozeliana 1928, Strand, Arch. Naturgesch. Berlin, **92:** 66. nom. nov. per *Cacozelia* Iredale, 1924, Proc. Linn. Soc. N. S. W. **49:** 246 [*non* Grote, 1878]. Type-species, *Cerithium lacertina* Gould, 1861, by OD

Bittiscalia 1937, Finlay & Marwick, Paleo. Bull. New Zeal. **15:** 44. Type-species, *Bittiscalia simplex* (Marshall, 1917), by OD

Eubittium 1937, Cotton, S. Austral. Natural. **18:** 2 [= *Paracerithium* Cotton, 1932 (*non* Cossmann, 1902)]. Type-species, *Eubittium lawleyanum* (Crosse, 1863), by OD

Brachybittium 1962, Weisbord, Bull. Amer. Paleont. **17** (193): 175-176. Type-species, *Bittium (Brachybittium) caraboboense,* Weisbord, 1962, by OD

Dahlakia 1971, Biggs, Journ. Conchol. **27:** 221. Type-species, *Dahlakia leilae* Biggs, 1971 (= *Cerithium proteum* Jousseaume, 1930), by OD

DESCRIPTION

Shell

Shell small, turreted and elongate, consisting of many moderately inflated or angular whorls (6-10). Sculpture normally reticulate, of varying combinations of spiral cords and axial riblets, frequently beaded at intersections. Usually 3 spiral cords per whorl. Former varices usually present at irregular intervals. Suture distinct, straight. Protoconch about $2\frac{1}{2}$ whorls, smooth, but sometimes with several spiral lirations. Frequently, teleoconch strongly reticulate. Aperture ovate with short, shallow, anterior siphonal canal that is not reflected backwards. Weak anal sinus present. Columella concave and with slight callus. Outer lip thin, smooth and rounded, occasionally flaired at the base on some individuals. Base of last whorl sculptured with 5-6 spiral cords. Last whorl occasionally contracted in some individuals. Periostracum thin.

Animal

Moderate sized foot with ciliated duct on right side terminating in knob-like ovipositor. Operculum thin, corneous, ovate and paucispiral with an excentric nucleus. Snout moderately large, flattened dorso-ventrally. Eyes at bases of tentacles. Mantle cavity deep with long monopectinate ctenidium extending its length, ending at anterior siphon. Osphradium bipectinate. Hypobranchial gland well-developed, large. Intestine wide, rectum distal to end of gonoduct. Feces cylindrical with mucus filament at one end. Pallial gonoducts in both sexes open, consisting of 2 laminae joined dorsally to mantle roof. Males aphallic, producing spermatophores about 1 mm in length containing eupyrene and apyrene spermatozoa. Eupyrene spermatozoa with nucleus about one-twentieth the total length of sperm and with spiral keel on flagellum. Female pallial oviduct a glandular groove between 2 deep laminae joined at dorsal wall and open ventrally. In medial lamina, an open sperm-collecting gutter runs into a ciliated tube that opens into a "bursa" at the proximal end of the medial lamina. Bursa is anterior to 2 seminal receptacles, the 1st of which serves as a receptacle for the spermatophore, in the left wall of the duct and the 2nd along the free edge of the wall. Nervous system characterized by very large nerve ring and large cerebral ganglia. Jaws cuticular, conical and rough surfaced. Stomach with style-sac and large crystalline style.

Radula

Radula taenioglossate, ribbon long, about 50 rows. Rachidian tooth squarish, concave at top with one large central cusp flanked by 3 denticles on each side. Base of rachidian concave with 2 short lateral projections. Lateral tooth rhomboidal, serrated on top with 2 small entocones, large pointed mesocone and 4 small ectocones, respectively. Base of lateral tooth with 2 extensions, 1 at each side; outer basal projection broad, long and extending laterally. Marginal teeth long, curved, spatulate and serrated at tips. Inner marginal tooth serrated with 4 entocones, large pointed mesocone and 3 sharp ectocones. Outer marginal tooth serrated with 4 to 6 entocones, outer surface smooth.

Eggs and Larvae

Eggs tiny, deposited in gelatinous string that may be coiled counterclockwise into a spiral from 3 to 25 mm in length or irregularly folded on itself. Egg mass containing several hundred small, opaque eggs, each about 60-70 μm in diameter. Larvae planktotrophic with bilobed, colorless velum; right velar lobe somewhat larger than left. Larval foot colorless. Larval shell about $2\frac{1}{2}$ whorls, smooth except for median spiral ridge on 2^{nd} whorl. Sutures and columella reddish brown. Outer lip with prominent tongue-shaped beak.

REMARKS

The description given above is based upon *Bittium reticulatum*, *B. varium*, and several other *Bittium* species from throughout the geographic range of the genus. I have attempted to describe the genus as a whole and not just the type-species. I have also endeavored to formulate a holomorphic description, using characters drawn from all phases of development.

A thorough treatment of the anatomy of *Bittium reticulatum* may be found in JOHANSSON (1947; 1948; 1953). MARCUS & MARCUS (1963) wrote an extensive paper on the anatomy of *Bittium varium* in which they also described and figured gametes, egg mass and larvae. The spermatozoa of *B. reticulatum* have been figured by FRANZEN (1955: 411; figs. 31-32) and FRETTER & GRAHAM (1962: 339; fig. 176, 4). MARCUS & MARCUS (1963) indicated that the sperm of *B. varium* are very similar to those of *B. reticulatum*. For further information on the anatomy of *Bittium* and illustrations of internal anatomy see FRETTER & GRAHAM (*op. cit.*). Excellent illustrations and treatments of *Bittium* eggs and larvae may be found in THORSON (1946), LEBOUR (1937), FRETTER & PILKINGTON (1970) and RICHTER & THORSON (1975). The last paper contains good scanning electron micrographs of the larval shell of *Bittium* species and a photograph of a living veliger larva.

The reproductive anatomy of *Bittium reticulatum* and *B. varium*, allopatric species that differ in shell size, shape and sculpture, shows that the structures of these conservative tracts are virtually identical between the 2 species and indicates that they are indeed members of the same genus. There is not a shred of anatomical evidence to support the need of a separate genus to accommodate *Bittium varium* nor is its referral to *Diastoma* justified. Although there is no information about the anatomy of Indo-Pacific and Eastern Pacific species of *Bittium*, it is not unlikely that they are all similar in their anatomy and habits. A small species from the Red Sea that was previously placed in the Potamididae and for which a new genus was created, *Dahlakia* Biggs, 1971, has been found to be a true cerithiid and is now assigned to *Bittium* (HOUBRICK, 1977b, in press). The family Cerithiidae is an old, slowly evolving group of prosobranchs (G. M. Davis, pers. comm.) that has not changed significantly since the Tertiary. Although some groups are now extinct, many living species of cerithiids have records going back to the Eocene (see HOUBRICK, 1977). COSSMANN (1906: 137) has recorded *Bittium* as far back as the Paleocene. Fossil *Bittium* species are conchologically very similar to Recent members.

Bittium is a genus in the family Cerithiidae and is probably very close in affinity to *Cerithium* Bruguière, 1789. Familial or subfamilial status for the *Bittium* group is not warranted because there are no characters, beyond those of size and a shorter canal, to justify such a great taxonomic difference. Examination of living populations of *Bittium* in Florida, Belize, and Enewetak Atoll and anatomical studies reveal only minor differences between these animals and those of the genus *Cerithium* Bruguière. Cerithiids are highly responsive to microhabitat in their shell shape and sculpture, and even anterior canals may be longer or shorter, depending upon the habitat. Inflation of whorls and spire length are highly correlated with different substrates such as sand, algae, rubble or rock. Populations of a given species frequently exhibit striking ecoclines. Shells of *Bittium* species are remarkably polymorphic in shape and sculpture, and subgenera such as *Lirobittium* Bartsch, 1911, *Stylidium* Dall, 1907, and *Semibittium* Cossmann, 1869 have no taxonomic value because the characters separating them (see BARTSCH, 1911: 384) may be found within a single population of one species and are thus not even good criteria for specific determination. *Bittium* is a genus with a cosmopolitan distribution of species and much of the confusion regarding generic and subgeneric placement of many species has resulted from parochial views of the genus. *Bittium* species have a cosmopolitan distribution and supraspecific taxa proposed solely for regional forms while ignoring other geographic areas and the full range of morphologies in the group are of little value (see Figures *1* to *5*).

In conclusion, subgeneric and generic taxa proposed for *Bittium* are based solely upon shell form and sculpture

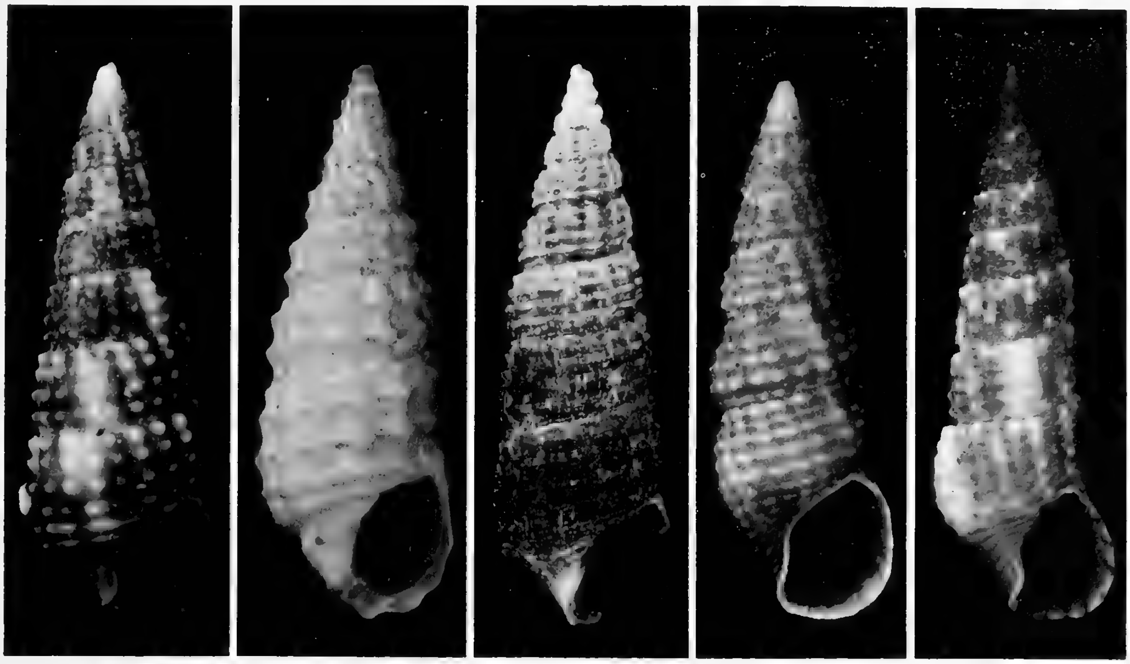

Figure *1* Figure *2* Figure *3* Figure *4* Figure *5*

Bittium species showing variation in shell form and sculpture as found throughout the genus

Figure *1*: ***Bittium reticulaum*** (Costa, 1778), type-species of the genus, from Cartagena, Spain (12×4 mm)
Figure *2*: ***Bittium interfossa*** (Carpenter, 1864) from Catalina Island, California (7.4×2.5 mm)
Figure *3*: ***Bittium quadrifilatum*** (Carpenter, 1864) from Mission Bay, California (10×5.2 mm)
Figure *4*: ***Bittium varium*** (Pfeiffer, 1840) from Sarasota, Florida (5.8×1.9 mm)
Figure *5*: ***Bittium varium*** (Pfeiffer, 1840) from Chincoteague, Virginia, formerly known as ***B. virginicum***, Henderson & Bartsch, 1914 (9.9×2.9 mm)

of regional species groups. In some cases, these sculptural characters are not of sufficient weight to justify specific differences and as a rule, polymorphism has been overlooked. Many of the taxa are provincial in scope and their authors either ignored or have been unaware of *Bittium* species in other parts of the world. In all cases, the criteria and concepts used in the formulation of these taxa ignore anatomy, eggs, larvae, early developmental stages, the fossil record and evolutionary convergence. For these reasons I think it is best to disregard the generic and subgeneric taxa that appear in the above synonymy and to regard all species previously referred to these taxa as *Bittium* species.

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The Chromodoridinae Nudibranchs from the Pacific Coast of America. - Part I. Investigative Methods and Supra-Specific Taxonomy

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(3 Text figures)

INTRODUCTION

Chromodorid nudibranchs are a worldwide tropical group, noted for their distinctive and beautiful color patterns. The group has been studied extensively, with numerous papers in part dealing with members of the Chromodorididae. This contribution is the first in-depth treatment of all the known species of the Chromodoridinae from the Pacific coast of America. Previous studies of this group from American Pacific waters have been based on a very small number of dissected specimens or only a few species (*e.g.*, MacFarland, 1966; Marcus & Marcus, 1967; Bertsch, 1970). Modern reviews of the Chromodorididae from other geographic provinces (Indo-Pacific: Rudman, 1973; Australia: Thompson, 1972; Hawaii: Kay & Young, 1969) are also based upon small numbers of dissected specimens of each species.

By obtaining specimens from several major museums, and making many collecting trips to Mexico and Panama, I have obtained a large quantity of specimens, which I dissected and examined critically. Visual and numerical data obtained from these dissections were used to revise systematically the genera and species of the American Pacific coast Chromodoridinae.

Principles governing the use of the radula in opisthobranch systematics have been proposed by Bertsch (1976 a). This study applies Bertsch's methods of examining opisthobranch radular variation (multiple meristic counts and measurements, ontogenetic patterns, and morphological studies using light microscopy and scanning electron microscopy) to a large group of phylogenetically related nudibranchs. Radular morphology and meristic qualities, and the external coloration are diagnostic characters for each of the 15 species of the Chromodoridinae from the Pacific coast of America.

The following abbreviations refer to the collections from which nudibranch specimens were obtained:

USNM – United States National Museum of Natural History (Smithsonian Institution), Washington, D. C.
CAS – California Academy of Sciences, San Francisco, California
LACM – Los Angeles County Museum of Natural History, Los Angeles, California
HB – Hans Bertsch

MATERIALS AND METHODS

Scanning Electron Microscopy

In the past few years, the scanning electron microscope has become a significant source of visual data for malacologists studying the ultrastructure, taxonomy, and functional morphology of various mollusks. It has been used to depict veligers (Robertson, 1971b), adult shells (*e. g.*, Solem, 1970; Thomas & Bingham, 1972; Margolis & Carver, 1974), chiton girdle scales (Ferreira, 1974, 1976), body soft parts (Arcadi & Hodgkin, 1973; Murray & Lewis, 1974), spermatozoa (Maxwell, 1975), fossil eggs (Tompa, 1976), a fossil radula (Solem & Richardson, 1975), and radulae of living mollusks (*e. g.*, Solem, 1972).

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Because of the SEM's clear resolution in the 300-10000 magnification range and its 3-dimensional imaging of biological samples, it is ideal for studying the total morphology of opisthobranch radulae, the details of individual teeth, and interrelationships between movable parts. THOMPSON & HINTON (1968) published the first scanning electron micrographs of opisthobranch radulae. BERTSCH (1970) first used the SEM to illustrate the radula in a new species description of an opisthobranch. Since then, stereo pair micrographs have been published (BERTSCH *et al.*, 1973), other workers have begun using SEM to illustrate opisthobranch radulae (*e. g.*, MULLINER & SPHON, 1974; BOUCHET, 1975), and scanning electron micrographs have become an established method for presenting information about opisthobranch radulae.

The principles of operation of the SEM and its biological applications are extensively documented. An entry to this literature can be gained by consulting the papers by HAYES (1972, 1973) and EVERHART & HAYES (1972).

The recent increase of published scanning electron micrographs necessitates a few precautionary words about their interpretation. Certain artifacts (avoidable or not) are inherent in the preparation and viewing processes of SEM. CLARK & GLAGOV (1976) have discussed 3 types of artifacts: accretion of extraneous materials, distortion of real cell and tissue surface details during processing, and distortion during viewing (including "charging," cf. PAWLEY, 1972).

There are 2 additional artifacts that can occur by uncritical examination of SEMs: the "2-headed cow" effect (T. L. Hayes, personal communication), and the "other side of the coin." The first artifact involves the interpretation of different planes that are visible in a micrograph. People can easily separate objects seen in the everyday macroscopic world as occurring at different depths in our field of vision (we know that the 2-headed cow is actually 2 cows standing together in opposite directions), but the same phenomenon in the microscope may pass unrecognized and be described as an ultrastructural unit. It is the advantage of the SEM — providing great depth of field with high resolution — which causes this possibility of planar reversibility. Analysis of overlapping and shading on the micrograph will often eliminate this problem, but sometimes it can be resolved only by stereopair or by rotating the specimen 90° so that the planes in question are aligned parallel, rather than perpendicular, to our field of vision.

The second artifact also stems from the imaging properties of the SEM. Image formation occurs by a time sequencing of points on the specimen surface with points on the cathode ray tube. This contrasts with the light and transmission electron microscopes' transparent technique of point-to-point spatial correspondence between the specimen and its image. Because the SEM operates by temporal sequencing across a non-transparent object, the researcher does not know what is on the obverse side of the object being examined. The observer is looking **at** rather rather than **through** the specimen. Prevention of unduly assuming bilaterality requires tilting or rotating the specimen, reorienting the specimen on the mounting platform, or (if the details are large and the specimen thin enough) viewing the specimen with a light microscope.

Specimen Preparation

In this study, I dissected and examined over 270 radulae. By using such a large sample size, by comparing light and scanning electron microscopy, by taking stereo-pair micrographs, and by frequent tilting and rotation of puzzling specimens in the SEM chamber, descriptions of the radular teeth were carried through a rigorous checking to insure their accuracy and usefulness to other researchers.

Radular preparation involved dissecting the buccal mass, dissolving the tissues surrounding the radula with a cold bleach (sodium hypochlorite) solution (cf. LINDBERG, 1977), and then allowing the radula to rinse in a 70% ethanol solution. For light microscopy, the cleaned radula was placed flat on a standard microscope slide, allowed to air dry, and then sealed under a cover slip with Permount mounting fluid.

Radulae that were to be examined with SEM were dissected and cleaned in the same way. After rinsing, each radula was mounted on a petrographic slide without a cover slip, air dried, and then covered with a thin layer of gold by vacuum evaporation to improve specimen conduction and reduce charging. The radular ribbon was bent or torn in places so that lateral views of the teeth could be obtained from the SEM. Any shrinkage or bending caused by the air drying did not significantly distort the rigid teeth shapes; moreover, it often allowed lateral and basal examination of the teeth. Specimens were viewed with a Japan Electron Optics Laboratory Co., Ltd., Scanning Type Electron Microscope Model JSM, at either 10 or 25 kV accelerating voltage. After examination with the SEM, each radula was covered with a cover slip and observed with a light microscope. The gold layer did not interfere with the transparency of the radula to visible light, but enhanced the resolution by acting as a surface stain.

Mounting the radula on the smaller-sized petrographic slide permits successive viewing of the specimen by SEM and light microscopy. The petrographic slide is small enough to fit on the specimen holder inside the SEM vacuum chamber, and is transparent to light. Similar techniques for comparative imaging of the same specimen have been used previously by McDonald & Hayes (1969) and Barber (1972).

Numerical Analysis of Radular Variation

Statistical studies of dentition form an important corpus in the understanding of mammalian taxonomy and vertebrate community structure. Examining large numbers of mammal specimens, authors of new species and revisers have given particular attention to numbers of teeth, means of sizes, and other measurements and counts (the literature is extensive, and only a few citations are necessary; cf. Mooser & Dalquest, 1975, or Villa-R., 1966). Recent papers by Grant (1967), Roughgarden (1974), and Tamsitt (1967) have estimated trophic relationships of vertebrate communities by analysis of the comparative morphology of trophic structures (bird bills, lizard jaws, and bat jaws). Findley (1976) included measurements of feeding structures in his investigation of the phenetic structure of tropical and temperate bat communities.

By contrast, statistical treatment of molluscan teeth has been relied upon much less. Although knowledge of the radula has advanced considerably since Aristotle's brief descriptions of the cephalopod radula ("a minute organ of a fleshy nature, and this it uses as a tongue, for no other tongue does it possess" - Ross, 1952: 50) and that of the "spiral-shaped testaceans" ("Some of these creatures have a mouth and teeth, as the snail; teeth sharp, and small, and delicate" - Ross, *op. cit.*: 55), most treatments of the radula have emphasized just morphology, and not ontogenetic changes nor inter- and intraspecific size variation.

Troschel's works (1856-1863, 1866-1893) are a notable exception, since he gave the sizes of most of his illustrated radulae and even indicated that larger specimens can have correspondingly greater-sized teeth ("Die Breite der Mittelplatte des abgebildeten Exemplars ist 0.085 Millim.; an einem grösseren Exemplare messe ich 0.11 Millim." - vol. I: 111).

In recent years, a number of articles have appeared discussing mathematical variations in radular teeth. Of special note is a series of papers by Schilder & Schilder (1961 a, 1961 b, 1963) and Schilder, Schilder & Houston (1964), in which numerous cowrie radulae are examined by regression analyses and mean sizes to determine sexual dimorphism and correlations between shell and radular sizes. Robertson (1971 a), reviewing reports of sexually dimorphic radulae among the Muricidae and Buccinidae, discusses meristic and morphological sexual dimorphism and population differences in the radulae of a phasianellid; he speculates on the possible evolutionary significance of the dimorphism and illustrates the male and female radulae with scanning electron micrographs. Bandel (1974) and Borkowski (1975) studied the variability of Caribbean Littorinidae radulae. Finally, Bloom (1976) correlated radular tooth curvature (amount of concavity of the inner [sic] margin of the tooth) with sponge prey items of dorid nudibranchs.

Variation in size and number of opisthobranch radular rows and teeth has been considered taxonomically important for over a century. The use of these characters has been primarily typological (in the sense of Dobzhansky, 1970: 126, and Mayr, 1970: 3-5), resulting in the descriptions of intraspecific variations as new species. Some workers have recognized intraspecific and ontogenetic variation: *e. g.*, Engel & Hummelinck (1936: 38) state that the number of teeth per half-row in *Dolabrifera dolabrifera* (Rang,1828) increases with the size of the animal, and Gonor (1961:91) records a similar observation for the tooth rows of *Aplysiopsis smithi* (Marcus, 1961).

Regression analyses of radular size and numerical variables have been applied only recently to opisthobranchs. Beeman (1963) graphed the number of lateral teeth vs. total body length of *Phyllaplysia taylori* Dall, 1900, and Thompson (1958) graphed the estimated age in months vs. number of rows and size of the lateral teeth of *Adalaria proxima* (Alder & Hancock, 1854); neither calculated the regression lines of his plots, but a visual examination of their graphs indicates that their correlations probably are statistically significant.

The first use of regression analysis formulae to prove statistically that the radular sizes and numerical variations of certain opisthobranch species are ontogenetic differences in size was by Bertsch (1976 a). The method has also been applied by Ferreira (1977) to *Triopha maculata* MacFarland, 1905, and *T. catalinae* (Cooper, 1863), and by Bertsch & Meyer (in prep.) to *Discodoris heathi* MacFarland, 1905, and *D. mavis* Marcus & Marcus, 1967. These studies have shown that for certain opisthobranch groups, the size of the radula, and the numbers of rows of teeth and teeth per half-row increase with the age (size) of the animal. Bertsch (1976 a) predicts within which opisthobranch taxa these variations will occur, and gives suggestions to the use of statistical analyses.

In this work, regression analyses are used in conjunction with light and scanning electron microscopy and examination of whole animal morphology to elucidate the taxonomic relationships of a large assemblage of species. Such a multidimensional approach bases the choice of taxonomically important characters on significance and reliability. For instance, dependence on color patterns is usually reliable at the species level for chromodorid nudibranchs, but one must take into account changes in this pattern between juveniles and adults (Haefelfinger, 1959; Ros, 1974: plt. 2) and adult variation. Grouping species on the basis of coloration (Rudman, 1973) is useful for comparative purposes, but does not indicate generic relationships. It is necessary to use multiple parameters for taxonomic evaluations, so that the animals are viewed as biological, genetic, and ecological entities subject to natural variation.

In this study, all measurements and calculations were made at least twice to improve their accuracy. The rows of teeth were counted on both halves of the radula, and the larger number was used for the calculations. Several rows of teeth were counted on each radula, to determine the maximum number of teeth per half-row. All counts of number of teeth per half-row indicate the maximum number found in each radula. Variations in the number of teeth per half-row exist within a radula because of tooth growth posteriorly and tooth wear anteriorly (Bertsch, 1976 a: 119; table 2; fig. 5). Using the maximum number found in the tooth rows eliminates the ontogenetic biases. Length and width maxima were measured on flattened, slide-mounted radulae. The formulae for means, standard deviations, regression analyses, confidence intervals and tests of regression coefficients are presented in Simpson, Roe & Lewontin (1960: 84, 213-230, 238-241); tables of significance probabilities are in the same book (pp. 422, 426).

Radular Teeth

Definitions of Structural Terms

Descriptions of radulae have included a wide variety of terms with inconsistent usage. To help standardize radular descriptions, Figure 1 illustrates the morphological terms used in this paper for the various parts of a chromodorid radular tooth.

The base (Figure 1, a) of the tooth joins the radular ribbon; the functional, rasping part grows upward as the erect shaft (Figure 1, b). The shaft curves postero-dorsally, and terminates in a point.

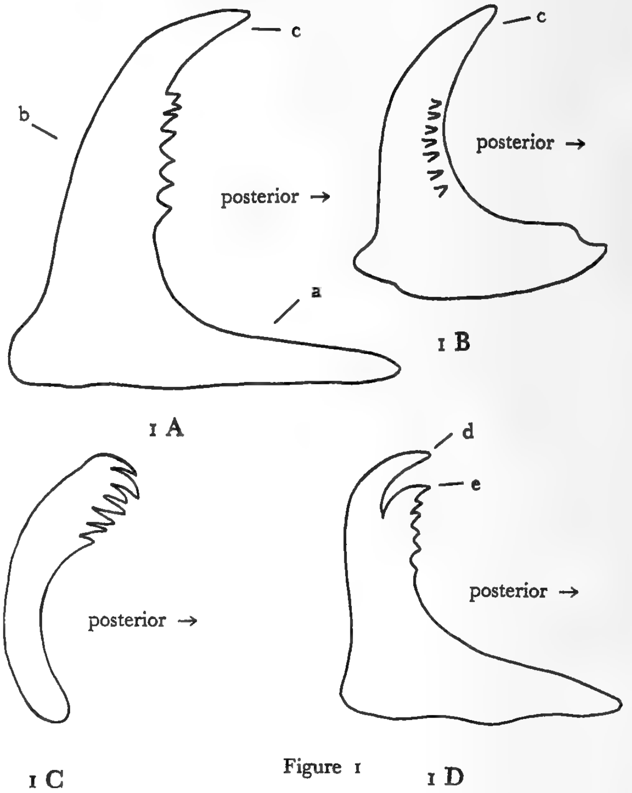

Figure 1

Illustration of structural parts of Chromodoridinae radular teeth

A. Unicuspid tooth with posterior denticulation; a – base; b – erect shaft; c – cusp

B. Unicuspid tooth with lateral denticulation; c – cusp

C. Acuspid tooth (after Bertsch, 1976b)

D. Bicuspid tooth; d – main (or primary) cusp; e – secondary cusp

Careful discrimination of the different sides of the teeth requires orienting the teeth in the resting stage when the radula is not extended. Along the cephalo-caudal axis of the animal's body, the forward, convex surface of the shaft is anterior. The concave side behind the shaft is posterior (termed "inner margin" by Bloom, 1976). The lateral, left and right, sides of the shaft are more properly designated inner and outer faces. The inner face is closest to the rachidian or mid-line of the radula.

Denticles usually occur on the posterior (Figure 1 A) or lateral (Figure 1 B) surfaces of the teeth. When the denticles are significantly smaller than the point on the erect shaft, the point is termed a cusp (Figure 1, c). A unicuspid tooth terminates in one large cusp (Figures 1 A, 1 B), and a bicuspid tooth terminates in 2 cusps larger than the denticles (Figure 1 D). The most distal cusp of a bicuspid tooth is termed the main (or primary) cusp (Figure 1, d), and the more proximal cusp (and also closer to the denticles) is the secondary cusp (Figure 1, e). The shaft of an acuspid tooth (Figure 1 C) terminates in a point smaller than, or of equal size with, the succeeding denticles, and is also called a denticle. Teeth with cusps have a serrate (posterior or lateral) denticulation (Figures 1 A, 1 B, 1 D) and acuspid teeth exhibit pectinate denticulation (Figure 1 C).

TAXONOMIC COVERAGE

Supra-Generic Taxa

GASTROPODA

Subclass Opisthobranchia

Superorder Nudibranchia

HOLOHEPATICA

Doridoidea

CHROMODORIDIDAE

A family of cryptobranch dorid nudibranchs; usually with bright colors and smooth dorsal skin texture (at times the dorsum may have small, low, round tubercles), with lamellate rhinophores and gills surrounding anus. Receptaculum seminis attached to vagina or bursa copulatrix. Radular teeth numerous; erect shaft thicker along antero-posterior axis than laterally; denticles usually present; shaft of tooth may end distally as unicuspid, bicuspid, or acuspid.

Cadlininae

Characters of the family, but usually colored cream or yellow, and dorsal skin surface covered with small, low, round tubercles, or smooth. Rachidian tooth well developed, having a solid erect shaft with pronounced denticulation laterally; lateral teeth unicuspid. Ecologically are predominantly members of temperate, cooler water faunal provinces.

Chromodoridinae

Characters of the family; almost always brightly colored (when seen in laboratory aquaria, intertidally, or at greater depths with artificial lighting). Rachidian tooth not well developed; erect shaft of a small triangular shape, or recurved, thin and narrow; without prominent lateral denticulation. Erect shafts of lateral teeth unicuspid, bicuspid, or acuspid; with lateral or posterior denticles or occasionally smooth.

The familial and subfamilial divisions of the cryptobranch dorid nudibranchs have not been agreed upon consistently in recent literature. ODHNER (*in* FRANC, 1968: 866-867) gives full family status to Echinochilidae (with 2 subfamilies, Echinochilinae and Lissodoridinae) and Chromodorididae (Echinochilidae is based on the rejected genus *Echinochila* Mörch, 1869; the proper name is Cadlinidae; *cf.* ICZN Opinion 812, 1967). Ros (1975: 320-321) uses Cadlinidae and Glossodorididae. KAY & YOUNG (1969) and MARCUS & MARCUS (1967) treat Chromodoridinae as a subfamily of Dorididae. The MARCUSES (*op. cit.*) discuss *Cadlina* Bergh, 1878b, but do not separate the group on a supra-generic level. SCHMEKEL (1972) gives familial status to Chromodorididae and Dorididae. LANCE (*in* KEEN, 1971: 821-823) recognizes Chromodoridinae and Cadlininae as subfamilies of Chromodorididae (but then erroneously places the Discodoridinae and Inudinae within this same family).

The most natural grouping is to separate Dorididae from Chromodorididae at the family level, and retain Chromodoridinae and Cadlininae. There is a suite of characteristics proper to each family and shared by the respective genera and species:

a) **Body Form and Texture.** The Chromodoridinae all have a smooth dorsal surface; some of the Cadlininae show a slightly more rugose texture, with low, rounded tubercles, but members of this group (*e. g.*, *Cadlina evelinae* Marcus, 1958) have a smooth dorsum. The Dorididae tend to have much larger tubercles, and a rougher texture of the dorsum. This difference is not absolute, but in general is a fairly reliable external separation between the families. It is the least important phylogenetic characteristic because some Chromodorididae show a rougher body texture and because smooth body texture occurs in a number of unrelated dorid forms: *e. g.*, *Aphelodoris antillensis* Bergh, 1879b, and *Dendrodoris krebsii* (Mörch, 1863).

b) **Reproductive System.** The triaulic cryptobranch dorid reproductive system exhibits little functional and morphological variation (GHISELIN, 1966: 348-349). However, despite this overall homogeneity, the structural arrangement of parts of the female reproductive organs shows 2 patterns, a chromodorid arrangement and a dorid arrangement. These are fairly significant variations; they are not a loss of parts nor a relative difference in size, but

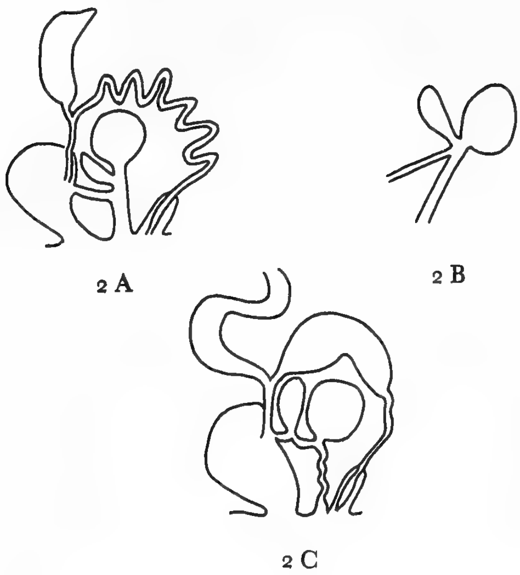

Figure 2

Schematic comparative drawings of Chromodorididae and Dorididae reproductive systems

A. Chromodorididae reproductive system (after Schmekel, 1972: fig. 50).

B. Chromodorididae reproductive system, showing (clockwise from the bottom) vagina, insemination duct, receptaculum seminis and bursa copulatrix attached closely.

C. Dorididae reproductive system (after Schmekel, 1972: fig. 57)

a gestalt configuration. In Chromodorididae (Figure 2 A) the receptaculum seminis is attached to the distal portion of the vagina (near the bursa copulatrix), or to the bursa copulatrix; it is not attached to the central portion of the insemination duct. At times the attachment points of the vagina, receptaculum seminis, and insemination duct are all close together on the bursa copulatrix (Figure 2 B). The typical dorid arrangement (Figure 2 C) has the receptaculum seminis attached near the middle of the insemination duct.

This configuration is uniform throughout the Chromodorididae, and there are only a few exceptions among the other dorids. From tropical west American waters, *Doriopsilla janaina* Marcus & Marcus, 1967, has a chromodorid-type reproductive system (Marcus & Marcus, 1967: 97; fig. 125). It is immediately distinguished from a chromodorid because it is a porostome and it has a rough, highly tubercled dorsum. In 2 Mediterranean species, *Doris verrucosa* Cuvier, 1804 (authorship and date *fide* Schmekel, 1968) and *Doris ocelligera* (Bergh, 1881), the reproductive systems' arrangement approaches that of the Chromodorididae. The receptaculum seminis is attached to the insemination duct near the latter's attachment with the vagina (Schmekel, 1968: figs. 2, 4, 8); a dorsum covered with large tubercles and the shape of the radular teeth clearly separate these species from the Chromodorididae. It is of special note, showing that these are rare exceptions to the general rule, that related species in these genera have the typical Dorididae reproductive system arrangement, with the receptaculum seminis clearly attached to the insemination duct: *cf.* the drawing of *Doriopsilla nigromaculata* (Cockerell, *in* Cockerell & Eliot, 1905) by Marcus & Marcus (1967: 206; fig. 62C) and of *Doris marmorata* Risso, 1818, by Schmekel (1968: figs. 6d and 8).

c) **Radula.** The shape of the lateral teeth is the most characteristic feature of the Chromodorididae. Each tooth (Figure 1) has a thin, knifelike, erect shaft, usually with denticles. By contrast, the teeth of Dorididae (*cf.* Marcus & Marcus, 1967: 81, 83, 86, *etc.*) are much more hook or sickle shaped, and broader laterally than are those of Chromodorididae. In addition, within the Chromodorididae, subfamily and generic separations are based on major differences of radular morphology.

By using jointly the 3 characteristics of body form and texture, reproductive system, and radula, the members of a genus can be placed reliably within (or excluded from) the Chromodorididae. For example, Bergh (1891) established the Chromodorididae as encompassing 5 genera, including *Aphelodoris* Bergh, 1879b. Recent usage justifiably excludes *Aphelodoris* from the Chromodorididae; although the animals have a smooth dorsum, their reproductive system and radular teeth are not chromodorid.

Genera of the Chromodoridinae

Odhner (*in* Franc, 1968: 867) included 3 genera in Chromodorididae which are highly problematic. All 3 (*Ceratodoris* J. E. Gray, *in* M. E. Gray, 1850; *Gruvelia* Risbec, 1928, and *Otinodoris* White, 1948) need further study and adequate descriptions of their radulae and reproductive systems before determining their taxonomic placement. *Rosodoris* Pruvot-Fol, 1954, was originally placed within the Glossodorididae; it is probably not a Chromodorididae, but its familial relationships are uncertain without additional material. *Ceratosoma* Adams & Reeve, 1850, is probably a member of the Chromodorididae, but examination of specimens is required to establish its subfamilial status.

The following 8 genera are what I recognize as comprising the Chromodoridinae, with the distinguishing characteristics of their radulae:

Chromodoris Alder & Hancock, 1855
(xvii)
(type genus of the family and subfamily)

Synonym: *Felimida* Marcus, 1971 (see Thompson, 1972: 398, for additional synonymy).

Type Species: *Doris magnifica* Quoy & Gaimard, 1832 (= *D. quadricolor* Rüppell & Leuckart, 1831).

Radular teeth unicuspid, with serrate denticulation; innermost lateral tooth with denticles on both sides of cusp; strongly recurved erect shafts of approximately 2nd through 8th lateral teeth with denticles on lateral face (some species may have denticles on both sides of the cusps of teeth 1-8); erect shafts of teeth lengthen toward the middle of the half-row, with denticles on posterior surface. Outermost lateral teeth become smaller, and retain denticulation.

Chromolaichma Bertsch, gen. nov.

Type Species: *Casella sedna* Marcus & Marcus, 1967. Also included: *Chromodoris dalli* Bergh, 1879c; *Chromodoris punctilucens* Bergh, 1890a; possibly *Chromodoris youngbleuthi* Kay & Young, 1969.

Radular rows at least 2-3 times greater than maximum number of teeth per half-row; width : length ratio greater than 1:3; small rachidian tooth usually present; radular teeth unicuspid, with lateral serrate denticulation; outermost laterals smooth (with larger radulae, there is a greater number of smooth outer teeth).

Etymology: "Colorful spear-point," derived from *τὸ χρῶμα* (color) and *ἡ αἰχμή* (the point of a spear), referring to the bright colors of the living animals and the elongate, spear-like radula; the letter "*l*" inserted for euphony; generic name feminine.

Mexichromis Bertsch, gen. nov.

Type Species: *Chromodoris antonii* Bertsch, 1976b.
Also included: *Chromodoris porterae* Cockerell, 1901; *Chromodoris tura* Marcus & Marcus, 1967.
Radular teeth acuspid; pectinate denticulation.

Etymology: "Mexican sea-fish," derived from *chromis* (sea-fish); generic name masculine.

Thorunna Bergh, 1877
(plate 58, figures 30-32)

Synonym: *Noumea* Risbec (1928: 165).

Type Species: *Thorunna furtiva* Bergh, 1877.

Radular formula n · 1 · 0 · 1 · n; first innermost lateral tooth with an extremely enlarged base.

Although recent references (*e. g.*, Odhner *in* Franc, 1968: 867; Russell, 1971: 112) cite 1878 as the date of authorship, Bergh published the new names *Thorunna furtiva* in 1877, accompanied by 3 illustrations. Hence the correct date is 1877.

Babaina Odhner, 1968

Odhner *in* Franc, 1968: 867 (not Roller, 1972, which = *Babakina* Roller, 1973).

Type Species: *Glossodoris florens* Baba, 1949 (pp. 53, 143-144).

Also included: *Babaina arbuta* (Burn, 1961), *comb. nov.* (originally *Glossodoris*), and *Babaina daniellae* (Kay & Young, 1969), *comb. nov.* (originally *Hypselodoris*).
Radular teeth have elongate, narrow, erect shafts; bifid (tooth shaft bifurcates distally, but does not have the prominent anterior primary cusp of *Hypselodoris*); without denticulation.

Casella H. & A. Adams, 1854
(p. 57)

Type Species: *Casella gouldii* H. & A. Adams, 1854, = *Doris atromarginata* Cuvier, 1804.
Living animal with a stiff, smooth mantle margin that is lobed.
Radular teeth unicuspid, lateral teeth hook-shaped with denticles on the outer face; rachidian tooth absent. Principal diagnosis of *Casella* rests on the texture of the notum and the notal margin.

Hypselodoris Stimpson, 1855
(pp. 388-389)

Type Species: *Goniodoris obscura* Stimpson 1855.
Radula usually without a median tooth; lateral teeth bicuspid; inner lateral teeth with denticles on outer face; most of the lateral teeth with posterior denticles on the erect shaft below the secondary cusp.

Felimare Marcus & Marcus, 1967
(p. 62)

Type Species: *Felimare bayeri* Marcus & Marcus, 1967. Radula "with a rachidian plate nearly as high as the neighboring teeth, provided with a smooth cusp." The single species in this currently monotypic genus has bicuspid lateral teeth; the inner lateral teeth are without denticles, but the outer laterals are denticulate on the posterior surface of the erect shaft. A number of *Hypselodoris* species possess a similar denticulation pattern. Further study of these species in contrast with those that have denticles on all the lateral teeth, may warrant a re-evaluation of the importance of the enlarged rachidian tooth, and a generic separation based on patterns of denticulation.

These major gestalt patterns of the radulae and their teeth separate the Chromodoridinae into 8 genera. Precise feeding studies are needed to elucidate the functioning differences between these radular patterns. Bloom's (1976) work correlated the degree of bending of radular teeth with division of sponge food resources. Functional morphology studies examining broad patterns of Chromodoridinae radular shapes will show additional separation of feeding resource utilization. For instance, studies of feeding specificity should indicate that members of the Chromodoridinae with narrow, long radulae (*e. g.*, ***Chromolaichma***) will utilize a different sponge prey item than those which have a proportionately wider and shorter radula.

Synopsis of Chromodoridinae Species from the Pacific Coast of America

For comparative purposes, these species are all illustrated in Figure 3.

Chromodoris:
- *Chromodoris baumanni* Bertsch, 1970
- *Chromodoris* sp. (to be named in Part II)
- *Chromodoris marislae* Bertsch, *in* Bertsch *et al.*, 1973
- *Chromodoris mcfarlandi* Cockerell, 1901
- *Chromodoris norrisi* Farmer, 1963
  - Synonyms: *Chromodoris banksi* Farmer, 1963
  - *Chromodoris banksi sonora* Marcus & Marcus, 1967
- *Chromodoris sphoni* (Marcus, 1971)

Chromolaichma:
- ***Chromolaichma*** *sedna* (Marcus & Marcus, 1967)
- ***Chromolaichma*** *dalli* (Bergh, 1879c)

Mexichromis:
- ***Mexichromis*** *antonii* (Bertsch, 1976b)
- ***Mexichromis*** *porterae* (Cockerell, 1901)
- ***Mexichromis*** *tura* (Marcus & Marcus, 1967) (species name ending not changed because of uncertain etymology)

Hypselodoris:
- *Hypselodoris agassizii* (Bergh, 1894)
  - Synonym: *Chromodoris aegialia* Bergh, 1904
- *Hypselodoris californiensis* (Bergh, 1879c)
  - Synonyms: *Chromodoris glauca* Bergh, 1879b (*nomen oblitum*)
  - *Chromodoris universitatis* Cockerell, 1901
- *Hypselodoris* sp. (to be named in Part IV)
- *Hypselodoris lapislazuli* (Bertsch & Ferreira, 1974)

(*Chromodoris juvenca* Bergh, 1898, from Chile, is *Cadlina juvenca*, and hence not a Chromodoridinae.)

Detailed analyses of each species will appear in Parts II, III, and IV.

Because of length considerations, this study[2] will appear as 4 separate articles in this journal.

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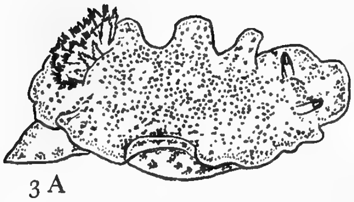
[2] Submitted as a dissertation in partial fulfillment of the requirements for the Ph. D. degree in zoology, University of California, Berkeley.

(on facing page →)

Figure 3

Drawings of living Chromodoridinae from the American Pacific coast

A. *Chromodoris baumanni* (after Marcus & Marcus, 1967: 172)
B. *Chromodoris* sp. (after color transparencies by Alex Kerstitch)
C. *Chromodoris marislae* (after Bertsch *et. al.*, 1973: 294)
D. *Chromodoris mcfarlandi* (after MacFarland, 1966: plt. 22)
E. *Chromodoris norrisi* (after Marcus & Marcus, 1967: 171)
F. *Chromodoris sphoni* (after Marcus, 1971: 356)
G. ***Chromolaichma*** *sedna* (after Marcus & Marcus, 1967: 179)
H. ***Chromolaichma*** *dalli* (after Marcus & Marcus, 1967: 174)
I. ***Mexichromis*** *antonii* (after Bertsch, 1976b: fig. 1)
J. ***Mexichromis*** *porterae* (after MacFarland, 1966: plt. 24)
K. ***Mexichromis*** *tura* (after Marcus & Marcus, 1967: 52)
L. *Hypselodoris agassizii* (after Marcus & Marcus, 1967: 177, fig. 31)
M. *Hypselodoris californiensis* (after MacFarland, 1966: plt. 24)
N. *Hypselodoris* sp. (after Marcus & Marcus, 1967: 177, fig. 30)
O. *Hypselodoris lapislazuli* (after Bertsch & Ferreira, 1974: fig. 1)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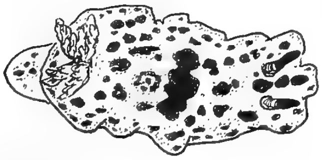
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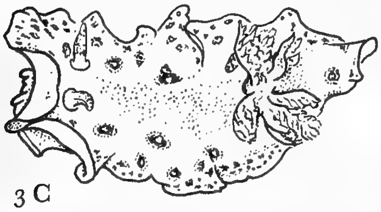
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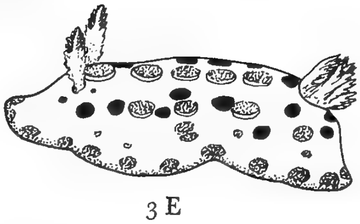
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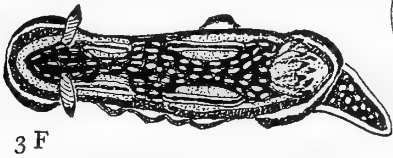
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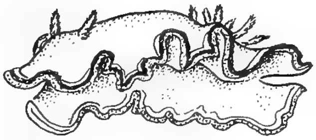
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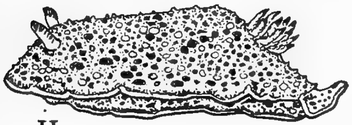
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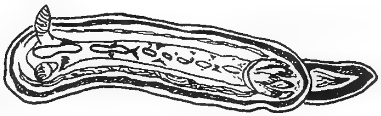
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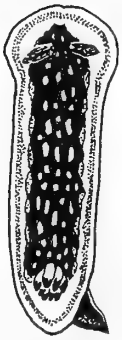
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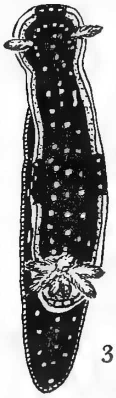
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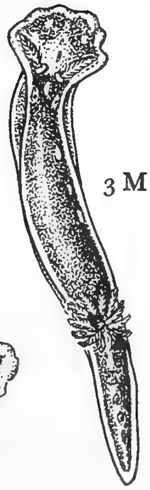
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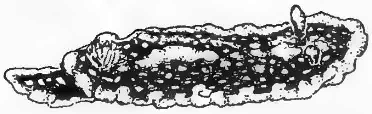
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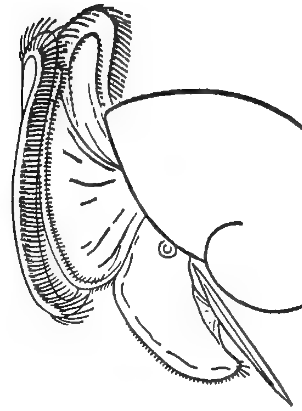

The Family Columbellidae in the Western Atlantic

Part IIa. - The Pyreninae

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(4 Plates)

INTRODUCTION

As noted in the first article of this series (Radwin, 1977), the family Columbellidae is a large cosmopolitan family of small buccinacean gastropods which, since an apparent Eocene origin, have undergone considerable adaptive radiation. The family may be divided into 2 unequal sized subfamilies on the bases of radular dentition and, to a lesser extent, shell morphology (Radwin, *op. cit.*). In Part I most of what is known concerning the phylogeny, ecology, and zoogeography of the family was reported, together with a systematic treatment of the genera and species assignable to the subfamily Columbellinae, the smaller of the 2 columbellid subfamilies. The present contribution continues the systematic treatment, covering the genera *Anachis* H. & A. Adams, 1853; *Costoanachis* Sacco, 1890; *Metulella* Gabb, 1873; *Nassarina* Dall, 1889; *Parvanachis* Radwin, 1968; and *Steironepion* Pilsbry & Lowe, 1932 of the subfamily Pyreninae. A total of at least 22 western Atlantic species is assignable to these genera. Another portion, Part IIb, is projected, which will cover the remaining 9 genera and their complement of at least 17 species in the region.

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Standard abbreviations for museums may be found in part I of this series (The Veliger 19 (4): 409 - 410).

Pyreninae Suter, 1913

Shell small to moderately large (2 - 40mm), fusiform or subfusiform; spire generally high and acute, spire whorls flat to convex in profile, suture varying from very shallow (*Mitrella*), to impressed (*Amphissa*) or incised (*Suturoglypta*); body whorl varying from large and broad (*Cosmioconcha*) to small and slender (*Steironepion*), apertural lip generally denticulate on inner surface, columella either denticulate or smooth; siphonal canal short (*Aesopus*) to moderately long (*Metulella*). Sculpture variable, including axial elements, with or without spiral elements of variable strength. Each radular row with a flat, subrectangular median tooth, not as broad as typical for the Columbellinae, and devoid of cusps and denticles (Figures A3, A4). Median tooth flanked on each side by a single sigmoid, bi- or tricuspid lateral tooth, narrower than that typical for the Columbellinae.

Type genus: *Pyrene* Röding, 1798.

Anachis H. & A. Adams, 1853

Columbella (Anachis) H. & A. Adams, 1853. Gen. Rec. Moll.: 184
Anachis H. & A. Adams. Mörch, 1852. Cat. Conch. ... Yoldi: 254

Type species by SD (Tate, 1868: 13), *Columbella scalarina* Sowerby, 1832 (Figure *24*).
Shell moderate-sized to large (10 - 25 mm in length), and broadly fusiform; spire moderately high and acute, whorls convex, suture distinct, not generally impressed; body whorl ½ the total shell length, heavy, shouldered, aperture wide, siphonal canal short; sculpture consisting of prominent axial ribs. Color pattern of 1 or 2 spiral bands of white on brown or the reverse. Each radular row consists of a single flat, subrectangular median tooth flanked on each side by a sigmoid, distally bicuspid lateral tooth (Figure *29*).

Remarks: Tate's selection of *Columbella scalarina* as the type species of *Anachis* limited the concept of the genus (*s. s.*) to a small number of relatively large species with strong axial ribbing and a prominently shouldered body whorl. Many species previously assigned to *Anachis* are more properly assigned to *Costoanachis* Sacco, 1890, as they are smaller, their axial ribbing is neither as strong nor as consistent and they lack the thickened, shouldered body whorl.

Anachis lyrata (Sowerby, 1832)

(Figure *1*)

Columbella lyrata Sowerby, 1832. Proc. Zool. Soc. London 2: 114 (Panamá Bay, Panamá; **lectotype**, BM(NH) 1966320)
Colombella veleda Duclos, 1846. Illust. Conchyl., plt. 7, figs. 19-20 (type locality here designated as Boa Viagem, Brazil; representation of **lectotype**, Duclos, 1846, Illust. Conch. 4: plt. 7, figs. 19-20)

Shell moderately large (14 - 20 mm in length), and heavy; spire high and acute, whorls slightly shouldered, and somewhat convex, suture impressed; body whorl large and broad, aperture moderately wide, apertural lip thickened and denticulate within, columella straight and denticulate, siphonal canal very short, anal groove present; sculpture of strong axial ribs; color ivory with 1 or 2 spiral rows of brown spots on the axial ribs. Each radular row consists of a flat, subrectangular median tooth, flanked on each side by a single, bicuspid lateral tooth (Figure *30*).

Remarks: Originally described from the Panamic-Pacific province of Central and South America, specimens of this species from the Atlantic coast of South America are indistinguishable from Pacific examples.

This is the only Recent species of *Anachis s. s.* occurring in the western Atlantic. Empty and worn shells of *A. terpsichore*, an Indo-Pacific species have been collected in the Caribbean. These appear to be adventitious ballast records. No fossil record has been found for this species, although its Recent amphi-American distribution would suggest a substantial ancestry.

Western Atlantic Range: Cuba and Central America to Santa Catharina, Brazil (also inhabits the tropical eastern Pacific).

Costoanachis Sacco, 1890

Costoanachis Sacco, 1890 (*in* Bellardi) Mem. Reale Accad. Sci. Torino 6: 57 (type species by SD [Pace, 1902, 5 (1/2): 43] *Columbella (Anachis) turrita* Sacco, 1890, not Sowerby, 1832 (= *Costoanachis* ***saccostata*** nom. nov.). (see Figure *2*)

Shell small to moderate in size (4 - 15 mm in length), and fusiform; spire moderately high, acute, whorls flat to convex, suture shallow to incised or impressed; body whorl equal to or less than ½ total shell length, aperture moderately wide, outer apertural lip generally denticulate within; columella straight, weakly denticulate, siphonal canal short and straight; sculpture of prominent axial ribs, in some cases limited to the body whorl, commonly with sub-

Explanation of Figures *1* to *14*

Figure *1*: *Anachis lyrata* (Sowerby, 1832)
Figure *2*: *Anachis turrita* Sacco, 1890 (*Costoanachis* ***saccostata*** nom. nov.)
Figure *3*: *Costoanachis avara* (Say, 1822)
Figure *4*: *Costoanachis hotessieriana* (Orbigny, 1842)
Figure *5*: *Costoanachis lafresnayi* (Fischer & Bernardi, 1856)
Figure *6*: *Costoanachis lafresnayi* (Fischer & Bernardi, 1856)
Figure *7*: *Costoanachis floridana* (Rehder, 1939)
Figure *8*: *Costoanachis hotessieriana* (Orbigny, 1842)
Figure *9*: *Costoanachis hotessieriana* (Orbigny, 1842)
Figure *10*: *Costoanachis sparsa* (Reeve, 1859)
Figure *11*: *Costoanachis scutulata* (Reeve, 1859)
Figure *12*: *Costoanachis catenata* (Sowerby, 1844)
Figure *13*: *Costoanachis sertularium* (Orbigny, 1839)
Figure *14*: *Costoanachis semiplicata* (Stearns, 1873)

Figure *1*

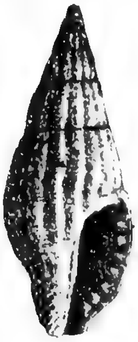


Figure *2*

Figure *3*

Figure *4*

Figure *5*

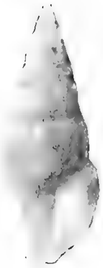


Figure *6*

Figure *7*

Figure *8*

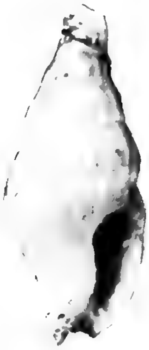


Figure *9*

Figure *10*

Figure *11*

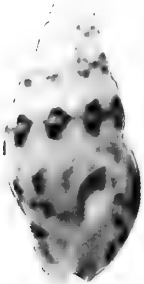


Figure *12*

Figure *13*

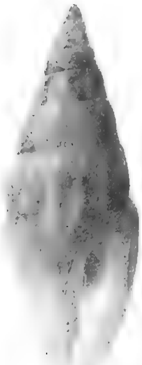


Figure *14*

microscopic spiral grooves between them. Color variable. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a single bi- or tricuspid lateral tooth. These are shorter and more strongly bent than those of *Anachis s. s.*

Remarks: Sacco, in his extremely brief description ("all whorls axially ribbed (except for *C. corrugata* Brocchi)"), apparently did not intend to limit this name to only those species with axial sculpture on every whorl. With the expansion of the original description to include partially ribbed forms, many species previously assigned to *Anachis* but differing from the type species of that genus may now be assigned to *Costoanachis* (*e.g., "A." avara, "A."sertularium, "A." catenata*).

Gardner (1948) and Olsson & Harbison (1953) tacitly accepted this wider interpretation of *Costoanachis* without offering a verbal expansion of the original definition. These authors placed *Anachis obesa* here, an assignment which appears to be incorrect. *Parvanachis* Radwin, 1968 was erected for the group of very small, squat, ribbed, *Anachis*-like forms with ventricose apertural lips, typefied by *A. obesa*.

A new name for *Columbella (Anachis) turrita* Sacco, 1890 is needed, as this name is preoccupied by *Columbella turrita* Sowerby, 1832 (at present assigned to *Strombina*). ***Costoanachis saccostata*** Radwin, nom. nov. is introduced herein as a replacement.

Costoanachis avara (Say, 1822)

(Figure *3*)

Colombella avara Say, 1822. Journ. Acad. Nat. Sci. Phila. 2: 230 (type locality restricted by Scheltema (1968) to "Florida"; lectotype ANSP 16887)

Colombella cleta Duclos, 1846 (*in* Chenu) Illust. Conchyl. plt. 15, figs. 13, 14 (type locality not specified; representation of lectotype, Duclos, 1846, 4: plt. 15, figs. 13, 14)

Anachis avara (Say). Dall, 1889b. Bull. U. S. Nat. Mus. 37: 116

Shell moderate in size (10-20mm in length); spire slightly greater than ½ shell length, whorls convex, suture shallow; body whorl cylindrical, moderately broad, aperture moderately wide, apertural lip slightly thickened, weakly denticulate interiorly, columella straight, nondenticulate; siphonal canal short and straight; sculpture of widely spaced ribs on the body whorl only, all other whorls smooth. Color pattern of irregular brown blotches on a white background. Each row consists of a flat, rectangular median tooth flanked on each side by a single sigmoid, bicuspid lateral tooth (Figure *31*).

Remarks: This species is certainly one of the most common shallow-water columbellids on the U. S. Atlantic coast. It is often confused with *Costoanachis lafresnayi* (= *C. translirata*), another east coast columbellid. *Costoanachis avara* is easily distinguished from *C. lafresnayi* by its lack of all sculpture on all whorls but the last one and by the convexity of its whorls; *C. lafresnayi has* flat-sided completely sculptured spire whorls.

Costoanachis avara has been reported from as far south as Brazil and Argentina (Pilsbry, 1898; Eyerdam, 1950). These reports probably refer to *C. sertulariarum* Orbigny, a related South American species lacking spire sculpture. *Costoanachis avara* differs from *C. sertulariarum* in its larger apical angle, its more convex whorls, and its more impressed suture.

No fossil examples of this species have been reported.

Range: The Gulf of Maine to Miami, Florida on the eastern coast of the United States of America.

Costoanachis catenata (Sowerby, 1844)

(Figure *12*)

Columbella catenata Sowerby, 1844. Proc. Zool. Soc. London 12: 52 (here restricted to Montego Bay, Jamaica; representation of lectotype, Sowerby, 1847, sp. 94, fig 171)

The location of the holotype is unknown. Originally part of the Cuming Collection, the type is not to be found at the British Museum (Natural History) where the Cuming Collection was deposited. Some small parts of the Cuming Collection were sold prior to its acquisition by the BM(NH). This type was apparently in one of those parts.

Shell small (4-7mm in length); spire slightly over ½ total shell length, whorls convex, distinctly shouldered, with impressed suture; body whorl cylindrical, apertural lip strongly denticulate within, columella strongly denticulate, bent at its anterior end, siphonal canal short and bent; sculpture of strong, sharply cut axial ribs with weak intercostal spiral grooves and a single strong subsutural spiral groove; color white with spiral bands of brown or orange "chain-links." Protoconch 2 swollen, translucent-white whorls. The radula of *Costoanachis catenata* was not examined, as none of the specimens examined had been collected alive.

Remarks: This species has been confused with *Costoanachis sparsa* and *C. scutulata* where their ranges overlap in Bermuda. However, the strongly denticulate apertural lip and columella, the strongly bent columella and siphonal canal, the striking patterns of color and sculpture, and a rather distinctive bulbous protoconch serve to distinguish *C. catenata* from these 2 congeners.

No fossil specimens of this species have been reported.

Range: Bermuda and southern Florida to Colón, Panama and Bahía, Brazil.

Costoanachis fenneli Radwin, 1968

(Figure *15*)

Costoanachis fenneli Radwin, 1968. Proc. Biol Soc. Wash. **81**: 147 (Sacco São Francisco, Guanabára, Brazil; holotype, USNM 539122)

Shell small (5 - 7 mm in length); spire acute, slightly more than ½ total shell length, spire whorls slightly convex, suture weakly impressed; body whorl expanded, angular, asymmetrical, left side slightly more expanded than right, outer apertural lip denticulate within, anal sinus strong, columella straight, weakly denticulate; sculpture of strong axial ribs, crossed by fine shallow, spiral grooves; yellowish-white ground color with anastomosing brown blotches; protoconch of almost 3 full, glassy brown whorls. Each radular row consists of a flat subrectangular median tooth flanked on each side by a single sigmoid, bicuspid lateral tooth (Figure *32*).

Remarks: This species is known from a single lot of 35 specimens, collected alive by Dr. Doris Cochrane near Nictheroy, Guanabára State, Brazil in April 1935. Its large, angulate body whorl, prominent axial and distinctive spiral sculpture, color pattern and multiwhorl protoconch distinguish this species from all others.

No fossil examples have been reported.

Known to me only from the type locality, Sacco São Francisco, Guanabára, Brazil.

Costoanachis floridana (Rehder, 1939)

(Figure *7*)

Anachis floridana Rehder, 1939. The Nautilus 53 (1): 20-21; plt. 6 (near Cape Canaveral, Brevard County, Florida; holotype, USNM 473202)

Shell small (6 - 12 mm in length); spire ½ total shell length, whorls slightly convex, suture shallow; body whorl cylindrical and moderately wide, apertural lip slightly thickened, distinctly denticulate within, columella straight, weakly denticulate; sculpture of low, widely spaced axial ribs on only the last 2 whorls, disappearing below the periphery. There are also numerous microscopic spiral lines over the entire adult shell; color pale yellow with irregular blotches of purplish brown. Each radular row consists of a rectangular median tooth flanked on each side by a single sigmoid tricuspid lateral tooth. The 3 cusps of the lateral teeth are very long and strongly curved (Figure *35*).

Remarks: Considered a variety of *Costoanachis avara* by some, *C. floridana* actually appears more closely related, on the basis of the radula and certain shell characters, to *C. sertulariarum*. It may be separated from that species on the basis of geographic distribution (southern Florida vs. Brazil), its smaller size, more convex spire profile, slight differences in lateral radular dentition and presence of microscopic shell sculpture.

Rehder (1939) in his original description of this species states that it differs from *Costoanachis avara* in "lacking the spiral grooves of that species." The holotype of *C. floridana* has distinct spiral sculpture. Although the catalog number and dimensions in the original description agree with those of the labeled holotype, Rehder states that the holotype was collected in Brevard County near Cape Canaveral, Florida. The locality listed with the holotype in the USNM type collection is near S. Jetty, St. John's Bar, Mayport, Duval Co., Fla. This confusion apparently arose because of a mixup in labeling. A lot of *Parvanachis obesa* with a label giving the published type locality of *C. floridana* has been found in the USNM collection.

No fossil examples of this species have been reported.

Range: Off Beaufort, North Carolina to Dade County,

Explanation of Figures *15* to *28*

Figure *15*: *Costoanachis fenneli* Radwin, 1968
Figure *16*: *Steironepion monilifera* (Sowerby, 1844)
Figure *17*: *Steironepion minor* (C. B. Adams, 1845)
Figure *18*: *Anachis scalarina*
Figure *19*: *Metulella columbellata* (Dall, 1889)
Figure *20*: *Nassarina bushii* (Dall, 1889)
Figure *21*: *Nassarina metabrunnea* Dall & Simpson, 1901
Figure *22*: *Parvanachis rhodae* (Radwin, 1968)
Figure *23*: *Nassarina glypta* (Bush, 1885)
Figure *24*: *Parvanachis isabellei* (Orbigny, 1839)
Figure *25*: *Parvanachis isabellei* (Orbigny, 1839)
Figure *26*: *Parvanachis obesa* (C. B. Adams, 1845)
Figure *27*: *Parvanachis ostreicola* (Sowerby, 1885)
Figure *28*: *Parvanachis melvillei* (Strebel, 1905)

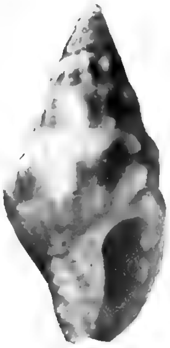


Figure *15*


Figure *16*

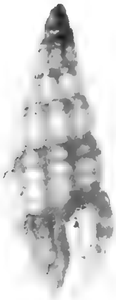


Figure *17*


Figure *18*

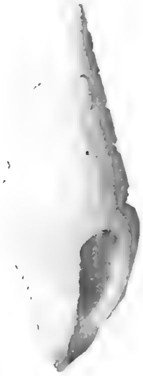
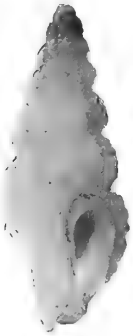


Figure *19*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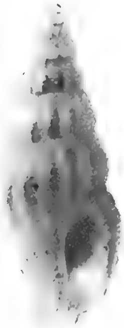
Figure *21*

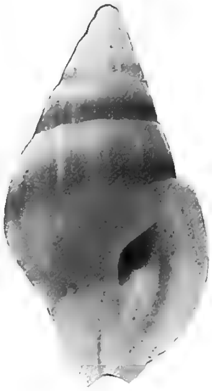
Figure *22*

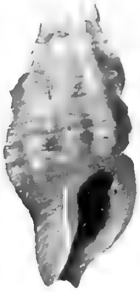
Figure *23*


Figure *24*


Figure *25*


Figure *25*a


Figure *26*

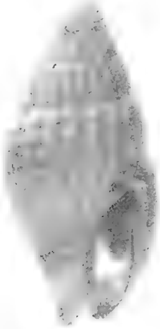
Figure *27*


Figure *28*

Florida, and from Carancahua Bay, Texas to Brownsville, Texas.

Costoanachis lafresnayi (Fischer & Bernardi, 1856)

(Figures *5*, *6*)

Columbella lafresnayi Fisher & Bernardi, 1856. Journ. de Conchyl. 5: 357; plt. 12, figs. 4, 5 (Guadeloupe; holotype, CJC)

Columbella ocellata Reeve, 1859 (not Gmelin, 1791). Conch. Icon., *Columbella*, plt. 37 , fig. 237 (type locality not specified; holotype, BM[NH]

Columbella translirata Ravenel, 1861. Proc. Acad. Nat. Sci. Philadelphia 3: 41-42 (off Charleston, South Carolina; holotype apparently destroyed)

Columbella (Anachis) avara Kobelt, 1897 (not Say, 1822). (*in*) Martini & Chemnitz, Conchyl. Cabinet 3-Id: 62; plt. 8, figs. 8, 9

Moderately large (10 - 16mm in length); spire high (more than ½ total shell length), whorls flat-sided, suture moderately impressed; body whorl fusoid; aperture moderately broad, apertural lip thickened, denticulate interiorly, columella straight and strongly denticulate, siphonal canal short to moderately long, slightly bent; sculpture of numerous prominent axial ribs crossed by weaker spiral grooves; color from straw yellow to chestnut brown with a spiral subsutural row of white spots. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid, bicuspid lateral tooth (Figure *33*).

Remarks: The type of *Columbella translirata* was lost, along with the remainder of Ravenel's types, which were reportedly destroyed during the burning of Atlanta, Georgia in the U. S. Civil War.

This species exhibits a cline in shell characters coincident with apparent tropical submergence from north to south along the Atlantic coast of the United States. In the north, where *Costoanachis lafresnayi* may be collected in moderately shallow water, the shell is relatively broad with a moderately acute apical angle and a very short siphonal canal. Southward, this species inhabits progressively deeper water, to 36m or more. Here the shell is lighter-colored and more slender, with a more acute apical angle and a somewhat longer siphonal canal.

Examples of this species are known from the Pliocene of Florida and are otherwise known only from the Recent.

Range: Grand Manan Island, New Brunswick, Canada to Key West, Florida and Yucatán, Mexico; occasional specimens from Barbados, West Indies.

Costoanachis hotessieriana (Orbigny, 1842)

(Figures *4*, *8*, *9*)

Columbella hotessieriana Orbigny, 1842. *in* Sagra, Hist. Phys. Polit. Nat. Cuba. Atlas, plt. XXI, figs. 37-39 (Guadeloupe; lectotype, BM[NH] 1854.10.4.359; paralectotype BM[NH] 1854.10.4.359/1)

Columbella guildingi Sowerby, 1844. Proc. Zool. Soc. London **12:** 53 (St. Vincent, B. W. I.; holotype, BM[NH] 1966. 448)

Columbella hotessieri Orbigny, 1845. (*in* Sagra), Hist. Fis. Polit. Nat. Cuba. Text, p. 234

Anachis mcgintyi Usticke, 1959. Checklist mar. shells St. Croix, p. 67; plt. III, fig. 15 (St. Croix, Virgin Islands; holotype, Usticke Coll.)

Shell small (6. 0- 7.5mm in length); spire moderately high (about ½ total shell length) and acute, whorls convex, suture impressed; body whorl subcylindrical, apertural lip moderately thickened, denticulate interiorly, columella straight, weakly denticulate, siphonal canal short to moderate in length, slightly bent, anal sinus barely discernible; sculpture of axial ribs crossed by shallow, closely-spaced spiral grooves which become crowded just below the suture; color pattern varying from chocolate brown to light tan with a spiral band of white spots of varying width just above the suture. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid, tricuspid lateral tooth (Figure *34*).

Remarks: First named *Columbella hotessieriana* by Orbigny (1842), this species had its name emended to *C. hotessieri* without explanation by the same author (1845) in subsequent editions of the same work.

Costoanachis scutulata (Reeve, 1859)

(Figure *11*)

Columbella scutulata Reeve, 1859. Conch. Icon. *Columbella.* pl. XXX, spec. 191 (here restricted to Hamilton Harbor, Bermuda; holotype, BM[NH] 1966.48.6)

Columbella (Seminella) catenata Tryon, 1883 (not Sowerby, 1844). Man. Conch. 5: 179; pl. 58, figs. 51-55

Shell moderate in size (7 - 10mm in length); spire slightly less than ½ shell length, whorls slightly convex, shouldered, suture impressed; body whorl cylindrical, aperture moderately broad, apertural lip denticulate interiorly, columella slightly bent, weakly denticulate, siphonal canal very short, anal sinus distinct; sculpture cancellate on first 2 postnuclear whorls, spiral sculpture almost completely obsolete on later whorls where low axial ribs predominate. A single spiral subsutural groove persists to the most recently formed whorl; ground color from light brown to purple black with spiral rows of irregular white blotches below and above the suture. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a bi- or tricuspid sigmoid lateral tooth (Figure *36*).

Remarks: The validity of this species has been in doubt ever since Reeve's original description as a result of his poor figure and his failure to give a type locality. There is little doubt in my mind, after having examined a photograph of the holotype in the British Museum (Natural History), that this name must be applied to a small, somewhat variable species from Bermuda.

Although often considered a variety of *Anachis sparsa* Reeve, 1859, a species with a much greater geographic range, *Costoanachis scutulata* differs from that species in the general appearance of its aperture (especially its distinct anal sinus), its lower, less prominent sculpture, its unusual subsutural groove, its distinctive color pattern, and in minor radular distinctions. Furthermore, *A. sparsa* and *C. scutulata*, although occurring together in several Bermudan localities, have remained distinct, thus apparently ruling out the possibility of interbreeding.

No fossil examples of this species have been reported.

Range: Apparently endemic to the Bermuda Islands.

Costoanachis semiplicata (Stearns, 1873)

(Figure *14*)

Anachis semiplicata Stearns, 1873. Proc. Acad. Nat. Sci. Philadelphia 25: 344 (Tampa Bay, Florida; **lectotype**, US NM 54275)

Anachis avara Tryon, 1883 (not Say, 1822). Man. Conch. 5: 159; plt. 55, fig. 68 only

Shell small to moderate in size (8 - 15 mm in length); spire slightly more than ½ shell length, whorls almost flat-sided, suture shallow; body whorl narrow, aperture moderately wide, apertural lip slightly thickened, distinctly denticulate within, columella straight, weakly denticulate; sculpture of a few widely spaced low axial ribs limited to the body whorl, all spire whorls smooth, colored light green or yellow-grey. Each radular row consists of a flat, rectangular median tooth flanked on each side by a sigmoid, distally bicuspid lateral tooth (Figure *37*).

Remarks: This species has been considered a variety or subspecies of *Anachis avara*, a species that occurs on the east coast of the United States as far south as Matecumbe Key, Florida, whereas *Costoanachis semiplicata* occurs in the Gulf of Mexico and on the west coast of Florida south to Cape Romano. Several shell differences and certain minor radular distinctions serve to differentiate these 2 species. *Costoanachis semiplicata* has a longer, narrower shell form, with fewer, more widely spaced axial ribs than those of *A. avara*. Another form of *C. semiplicata* from the Gulf of Mexico has many, more closely spaced axial ribs. This form has often been called *A. similis* Ravenel, 1861, a name of dubious identity as it was never figured by its author, and its holotype, along with the rest of Ravenel's types was presumably destroyed during the U. S. Civil War.

No fossil examples of this species have been reported.

Range: Boca Grande, southwestern Florida, along the shores of the Gulf of Mexico to Progreso, Yucatán, Mexico.

Costoanachis sertulariarum (Orbigny, 1839)

(Figure *13*)

Buccinum sertulariarum Orbigny, 1839. Voy. Amér. Mérid., Atlas, plt. 61, figs. 13-17 (La Baie de San Blas, Patagonie; holotype, BM[NH] 1854.12.4.451)

Columbella sertulariarum Orbigny, 1841. Voy. Amér. Mérid., text: 431

Columbella avara Kobelt, 1874 (not Say, 1822). Nachr. Malac. Gesell.: 59

Columbella brasiliana Martens, 1897. Arch. Naturgesch. 1 (2): 171-172; plt. 16, fig. 10 (Desterro, Brasil; holotype, BM)

Moderate in size (9 - 12 mm in length); spire about ½ shell length, acute, whorls flat-sided, suture shallow; body whorl cylindrical, aperture moderately wide, interior of

Explanation of Figures *29* to *37*

Figure *29*: *Anachis scalarina* – radular dentition
Figure *30*: *Anachis lyrata* – radular dentition
Figure *31*: *Costoanachis avara* – radular dentition
Figure *32*: *Costoanachis fenneli* – radular dentition
Figure *33*: *Costoanachis lafresnayi* – radular dentition
Figure *34*: *Costoanachis hotessieriana* – radular dentition
Figure *35*: *Costoanachis floridana* – radular dentition
Figure *36*: *Costoanachis scutulata* – radular dentition
Figure *37*: *Costoanachis semiplicata* – radular dentition

Figure 29

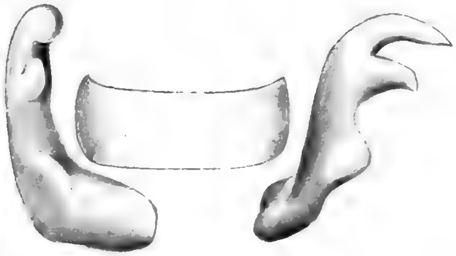

Figure 30

Figure 31

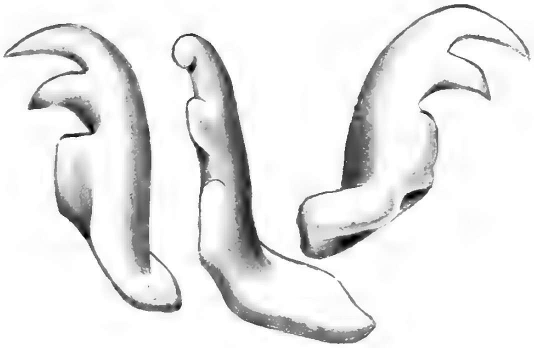

Figure 32

Figure 33

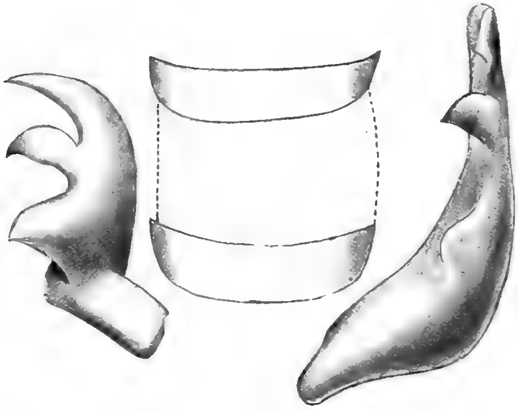

Figure 34

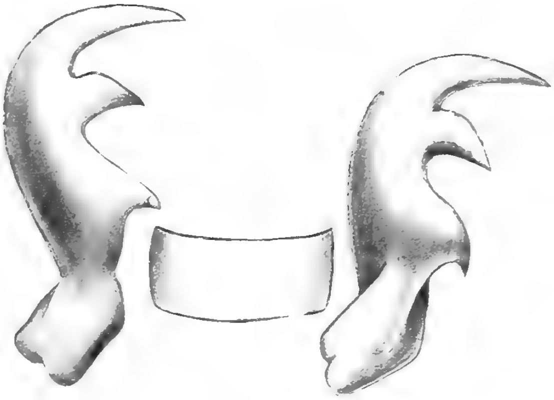

Figure 35

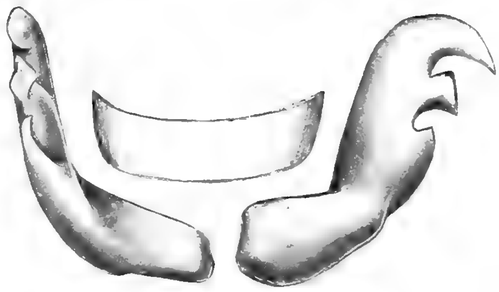

Figure 36

Figure 37

apertural lip denticulate, columella non-denticulate, slightly bent anteriorly; sculpture of sharp axial ribs with microscopic spiral scratches between them limited to the body whorl. Color off-white with random fine brown punctations and larger purple-brown blotches. Each radular row consists of a flat subrectangular median tooth, flanked on each side by a sigmoid lateral tooth with 2 sharp distal cusps and a more rounded proximal projection (Figure *39*).

Remarks: The only specimen of *Costoanachis sertulariarum* from the Orbigny collection in the British Museum (Natural History) is considered the holotype. It must be noted here that the dimensions of the BM(NH) specimen are significantly greater than those given by Orbigny and the type locality is considerably further south than any locality record in the collections examined.

Misidentification of this species is almost certainly responsible for the periodic assertions that *Anachis avara* Say occurs on the Atlantic coast of south-central South America (Kobelt, 1874; Pilsbry, 1898; Eyerdam, 1950; Parodiz, 1962). Although these species are similar in general form, the spire whorls of *Costoanachis sertulariarum* are less convex, its axial ribs are more poorly defined, its columella is not denticulate as in *A. avara,* and there are minor differences in color pattern and radular morphology.

Marcus & Marcus (1962) have described and figured the anatomical features of *Anachis brasiliana* von Martens, a synonym of *Costoanachis sertulariarum.* According to them Orbigny's species has a wider distribution, a larger shell and slightly different body coloration. Although these assertions may have a bearing on the discrepancy between Orbigny's type and other specimens we have seen, the fact is that we have seen no other specimens that agree in size and locale with the type. Unfortunately no living specimens of this species have been available for examination.

There appears to be a close relationship between this species and *Costoanachis floridana* (Rehder, 1939). The primary differences are that *C. floridana* is, on the average, significantly smaller and has a broader apical angle and heavier body whorl, both of which impart a stouter appearance to it. The ranges of the 2 (*C. floridana* – east coast of the United States from North Carolina to southern Florida and on the Texas coast; *C. sertulariarum* – northern Brazil to southern Argentina) do not overlap to my knowledge.

No fossil examples of this species have been reported.

Range: East coast of South America from Rio Grande do Norte, Brazil to Mar del Plata, Argentina.

Costoanachis sparsa (Reeve, 1859)

(Figure *10*)

Columbella sparsa Reeve, 1859. Conch. Icon. *Columbella,* plt. 31, figs. 200a, 200b (here restricted to St. Thomas, Virgin Islands; holotype, BM[NH] 1966484)

Columbella (Seminella) catenata Tryon, 1883. (not Sowerby, 1844). Man. Conch. 5: 179; plt. 58, figs. 51-55

Shell moderately large (8 - 11 mm in length); spire moderately high ($\frac{1}{2}$ shell length), acute, whorls slightly convex, shouldered suture moderately deep; body whorl fusoid, aperture narrow, apertural lip slightly thickened, denticulate interiorly, columella straight, denticulate, siphonal canal short, slightly bent, anal sinus present; sculpture of prominent axial ribs with broad spiral grooves strongest between the ribs; color variable, generally with alternating evenly-spaced squares of orange-brown on a white background. Each radular row consists of a flat, rectangular median tooth, flanked on each side by a sigmoid lateral tooth with 2 sharp distal cusps and one blunt proximal projection (Figure *38*).

Remarks: This is the most variable of all the species of *Costoanachis,* with a typical form as described above and other forms varying in shell proportion and color pattern. The sculpture and shouldering of each whorl are, nevertheless, constant throughout the species.

Although confused by many authors with *Costoanachis catenata* and *C. scutulata,* these 3 species are quite distinct. *Costoanachis catenata* has a unique chain-link color pattern and a bulbous, translucent-white protoconch; *C. scutulata* differs consistently from the others in the weakness and limited extent of its sculpture and its prominent anal sinus; the ribs of *C. scutulata* are low, sinuous, often disappearing below the middle of the body whorl. The color pattern of *C. scutulata* also differs markedly from that of *C. sparsa.* Spiral grooves notably present in the latter species are absent in *C. scutulata.*

No fossil examples of this species have been reported.

Range: Bermuda and Lantana, Florida to Venezuela and (possibly) southern Brazil.

Metulella Gabb, 1873

Metulella Gabb, 1873. Proc. Acad. Nat. Sci. Philadelphia 24: 270 (type species by OD, *Metulella fusiformis* Gabb, 1873)

Shell moderately large to large (10 - 25 mm in length); spire high, acute, whorls flat-sided, suture squarely incised; body whorl fusoid, aperture narrow, strongly constricted anteriorly, outer lip slightly thickened, strongly denticulate on its inner surface, columella straight, weakly callused and weakly denticulate, length of siphonal canal moderate to long; sculpture of strong, closely-spaced axial ribs, crossed by moderately strong spiral cords. Color white to yellow-white. Radular dentition unknown.

Remarks: This genus is almost extinct as the number of species has declined from a high of 4 or 5 in the Pliocene to a single living species today. This living representative of an otherwise extinct genus, *Metulella columbellata* (Dall, 1889a), should present a unique opportunity to establish the relationship of *Metulella* to other fossil and Recent columbellid genera. Unfortunately, no live-collected specimens of the species are known.

Metulella columbellata (Dall, 1889)

(Figure *19*)

Metulella (Nassarina) columbellata Dall, 1889a. Bull. Mus. Comp. Zool. **18**: 182 (off Cape Catoche, Yucatán. Mexico; holotype, USNM 93019)

Shell moderately large (10 - 15 mm in length); spire high, acute, whorls almost flat-sided, suture incised; body whorl fusoid, aperture narrow, strongly constricted anteriorly, outer lip slightly thickened, strongly denticulate on its inner surface, columella straight, weakly denticulate with a thin callus, siphonal canal moderately long; sculpture of strong, closely-spaced axial ribs crossed by moderately strong spiral cords; color white or yellow-white. Radular dentition unknown.

Remarks: This rare species, the only Recent species of *Metulella*, has been encountered more frequently as more deepwater dredging is carried out in the Gulf of Mexico. Unfortunately, the position of *Metulella* must await the description of its anatomy and radular dentition.

The earliest fossil Metulellas are known from the Miocene of the Dominican Republic (*Metulella venusta* Sowerby, *M. williamgabbi* Maury, and *M. fusiformis* Gabb).

Range: Gulf of Mexico (specimens have been seen from Cape Catoche, Yucatán, Mexico – type locality – and off Tampa Bay, Florida.

Nassarina Dall, 1889

Nassaria (Nassarina) Dall, 1889a. Bull. Mus. Comp. Zool. **18**: 182 (type species by OD, *Nassarina bushii* Dall, 1889a)
Pyramimitra (Nassarina) Cossmann, 1901. Essais Paléoconch. Comp. **4**: 128
Nassarina Dall. Woodring, 1928. Carnegie Inst. Wash. Publ. **385**: 279

Shell small (3 - 10 mm in length), fusiform; spire moderately high, acute, whorls convex, suture impressed; body whorl approximately ½ of shell length, outer apertural lip denticulate on its inner surface, aperture long, narrow, constricted anteriorly to form a narrow, bent siphonal canal, columella slightly bent anteriorly, its thin, detached callus forming a prominent keel; sculpture of numerous swollen axial ribs crossed by strong spiral cords. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid, distally bicuspid lateral tooth. The cusps of the laterals are shorter and less bent than those in many other genera.

Remarks: The shell characters by which this genus may be differentiated from other columbellid genera are: 1) possession of both strong spiral and strong axial sculpture, 2) the constricted and elongate siphonal canal, and 3) the keel formed by a thin detached parietal callus.

The genus *Zanassarina* Pilsbry & Lowe, 1932, includes 9 small eastern Pacific nominal species. It was originally erected as a subgenus of *Nassarina* Dall. No currently known Recent western Atlantic columbellid species are assignable here. Its affinities seem to be closer to *Costoanachis* and *Parvanachis* than to *Nassarina.*

Explanation of Figures *38* to *47*

Figure *38*: *Costoanachis sparsa* – radular dentition
Figure *39*: *Costoanachis sertulariarum* – radular dentition
Figure *40*: *Nassarina bushii* – radular dentition
Figure *41*: *Nassarina glypta* – radular dentition
Figure *42*: *Nassarina metabrunnea* – radular dentition
Figure *43*: *Parvanachis isabellei* – radular dentition
Figure *44*: *Parvanachis obesa* – radular dentition
Figure *45*: *Parvanachis ostreicola* – radular dentition
Figure *46*: *Steironepion minor* – radular dentition
Figure *47*: *Steironepion monilifera* – radular dentition

Figure *38*

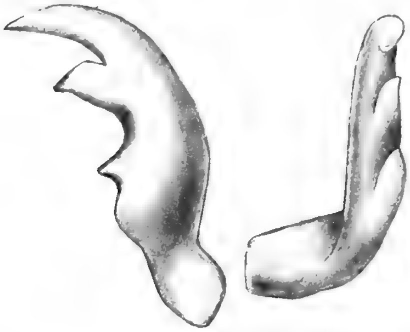

Figure *39*

Figure *40*

Figure *41*

Figure *42*

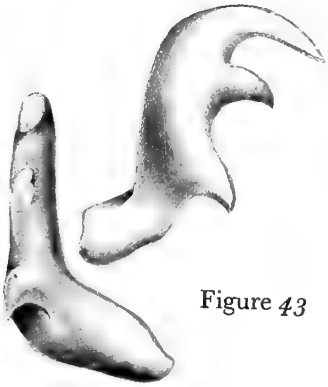

Figure *43*

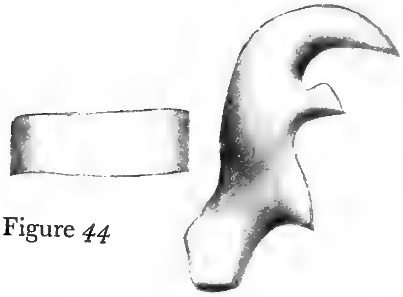

Figure *44*

Figure *45*

Figure *46*

Figure *47*

Nassarina bushii Dall, 1889

(Figure *20*)

Nassaria (Nassarina) bushii Dall, 1889a. Bull. Mus. Comp. Zool. 18: 182; plt. 15, fig. 12 (off western Cuba in the Gulf of Mexico; holotype, USNM 94776)

Shell moderate in size (9 - 10mm in length), fusiform; spire high, moderately acute, whorls convex with strongly impressed suture, body whorl slightly less than ½ total shell length, apertural lip denticulate, thickened, aperture sinuous, narrow, columella bent, nondenticulate, bearing a detached keel, siphonal canal moderately long, bent, and constricted; sculpture of raised axial riblets crossed by strong spiral cords producing a reticulate pattern, within each box formed by the intersection of axial and spiral elements there are microscopic axial scratches. Color white to ivory. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a weakly sigmoid lateral tooth. Each of these bears 2 sharp, distal cusps (Figure *40*).

Remarks: In spite of the unusual shell of *Nassarina*, the form of the radular teeth of *N. bushii*, its type species, leaves no doubt as to the familial assignment of this genus. Comparing the 3 species that Dall originally and subsequently assigned to *Nassarina* (*N. bushii*, *N. glypta*, and *N. metabrunnea*), it appears that a number of features used by him to define the genus are, in fact, only of specific value. Although the other species have the prominent spiral and axial sculpture, elongated siphonal canal, and general shell form of *N. bushii*, type species of *Nassarina*, they nevertheless lack the prominent columellar keel found in that species. Conversely, *N. bushii* lacks the prominent columellar callus found in *N. glypta* and *N. metabrunnea*. A 4th Dall species, *N. grayi*, has proven, on radular evidence, to belong to the Muricidae.

No fossil examples of this species have been reported.

Range: Florida Keys to Barbados; occasionally elsewhere in the Caribbean.

Nassarina glypta (Bush, 1885)

(Figure *23*)

Mangelia glypta Bush, 1885. Ann. Reprt. Comm. Fish for 1883: 461; plt. 4, figs. 5, 5a (off Cape Hatteras, North Carolina; lectotype, USNM 36363)

Nassaria (Nassarina) glypta Bush. Dall, 1889. Bull. Mus. Comp. Zool. 18: 181

Columbella (Atilia?) mystica Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 58 (off Cape Hatteras, North Carolina; holotype, USNM 108321)

Nassarina dalli Olsson & Harbison, 1953. Acad. Nat. Sci. Philadelphia, Monogr. 8: 239; plt. 39, fig. 3 (St. Petersburg, Florida; holotype, ANSP 18100)

Shell tiny (3 - 6mm in length); spire less than ½ shell length, whorls convex, suture impressed; body whorl fusiform, expanded, aperture narrow, apertural lip flaring, thickened, prominently denticulate on its inner surface with a distinct anal notch, columella bent anteriorly, weakly denticulate, siphonal canal moderately long and strongly constricted; sculpture consisting of prominent axial ribs crossed by strong, squared spiral cords. This imparts a grooved appearance to the interspaces. The spiral cords are as prominent between the axial ribs as they are at the intersection. Color deep orange to white. Each radular row consists of a flat, rectangular median tooth, flanked on each side by a sigmoid, distally bicuspid lateral tooth. The cusps of the lateral tooth are short and less bent than in other genera. The broadness of the most proximal of these cusps distinguishes the dentition of this species from its congeners (Figure *41*).

Remarks: The size, sculpture, and the distinct anal notch have caused some workers to assign this species to *Mangelia*, a turrid genus. The radula, however, is clearly columbelloid. One of the most ubiquitous species toward the deeper end of its range (20 - 200m), *Nassarina glypta* has been confused with *Steironepion minor*. These 2 may be distinguished in the following ways: 1) *N. glypta* is found primarily on the Atlantic and Gulf coasts of the U. S., in moderately deep water; *S. minor* is found in shallower water primarily in the Bahamas and the Greater Antilles. 2) The sculpture of *N. glypta* imparts a reticulate appearance to the shell, whereas *S. minor* has a nodulose appearance due to the expansion of its spiral elements on crossing the axial ribs. These nodules of *S. minor* are white, whereas *N. glypta* only exhibits white coloration in exceptional cases and then not solely on the nodules. 3) The lateral radular teeth of *N. glypta* are typical of *Nassarina*, with their short, slightly bent cusps. The lateral radular teeth of *S. minor* differ in having 2 strongly bent distal cusps in addition to a down-hooked proximal cusp, a feature lacking in *N. glypta*.

The earliest known example of this species is from the Pliocene of Florida (St. Petersburg) as *Nassarina dalli* Olsson & Harbison.

Range: East and Gulf Coasts of the United States from Cape Hatteras and the Mouth of the Mississippi River southward to Barbados.

Nassarina metabrunnea Dall & Simpson 1901

(Figure *21*)

Nassarina (Nassarina) metabrunnea Dall & Simpson, 1901. U. S. Fish Comm. Bull. 20 (1): 401; plt. 57, fig. 16 (off Mayaguez Puerto Rico; holotype, USNM 159695)

Shell small (5 - 8mm in length) and fusiform; spire high, acute, whorls convex, suture moderately impressed, body whorl fusoid, aperture rather narrow, outer apertural lip slightly thickened, weakly denticulate interiorly, columella straight, weakly denticulate, bearing a partial, raised keel, anterior siphonal canal long, straight, severely constricted shallow anal sinus present; sculpture of strong, rounded axial ribs crossed by numerous fine, low spiral threads; color white with a brown suffusion near the apex, and notably, at the anterior end of the siphonal canal. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid lateral tooth. Each lateral bears three sharp cusps. The distal one is the longest and sharpest and the most proximal one is down-hooked. The base of the lateral is quite long compared to that of other columbellid species (Figure *42*).

Remarks: This species may be distributed much more widely than reported at present, but has been infrequently collected, probably because of its deepwater habitat (80 to 600m).

Known only from Recent examples.

Range: Florida Keys to Barbados and Curaçao.

Parvanachis Radwin, 1968

Parvanachis Radwin, 1968. Proc. Biol. Soc. Wash. 81: 145-146 (type species by OD, *Buccinum obesum* C. B. Adams, 1845)

Shell small (5 - 10mm in length), obese; spire moderately high and acute, whorls generally flat-sided, suture impressed or incised; body whorl equal in length to spire, interior of apertural lip denticulate, siphonal canal short to moderately short, constricted, columella straight or slightly bent, denticulate; sculpture of prominent axial ribs, generally crossed by spiral cords. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid, tricuspid lateral tooth.

Remarks: This taxon was proposed to include small, stout, prominently ribbed columbellids with inflated body whorls and heavily thickened, flaring apertural lips. The proportions of the shell in this group are considerably different from those in *Anachis* or *Costoanachis* and impart a foreshortened appearance to it. The strongly downhooked proximal cusp of the lateral radular tooth is typical of *Parvanachis* (Figure *43*). These characteristics serve to distinguish *Parvanachis* from *Costoanachis* Sacco, to which *Anachis obesa*, the type species of the present genus, was assigned by Gardner (1948) and others.

Parvanachis isabellei (Orbigny, 1839)

(Figures *24, 25*)

Buccinum isabellei Orbigny, 1839. Voy. Amér. Mérid. Atlas livr. 44; plt. 61, figs. 13-17 (La Baie de San Blas, Patagonie; holotype, BM[NH] 1854.12.4.486)

Nassa isabellei Orbigny, 1845. Voy. Amér. Mérid. 5: 433

Columbella isabellei (Orbigny, 1841). Carcelles, 1944. Rev. Mus. de la Plata (n. s.) Zool. 3: 25

Anachis isabellei (Orbigny, 1841). Parodiz, 1962. The Nautilus 76 (2): 74

Shell small (5 - 6mm in length), obese; spire moderately low (about ½ shell length), subacute, whorls markedly convex, suture impressed; body whorl inflated, aperture broad, apertural lip flaring, denticulate interiorly, columella bent, non-denticulate, siphonal canal short, bent; sculpture generally lacking, where present it consists of weak axial and spiral elements; color straw yellow with irregular brown blotches, one of which is often at the tip of the siphonal canal. Each radular row consists of a subrectangular median tooth, flanked on each side by a sigmoid tricuspid lateral tooth. The proximal cusp is sharply downhooked (Figure *43*).

Remarks: *Parvanachis isabellei* is closely related to *P. obesa* but differs from this species in its thinner, more obese shell, its lack of strong axial sculpture, and less thickened apertural lip. It is also, on the average, consistently larger (5.8mm vs. 5.2mm) and has a range which overlaps that of *P. obesa* without evidence of interbreeding.

Altena (1975) has named the form of this species from the southern Caribbean *Anachis (Parvanachis) radwini* and explains his reasons for considering it distinct. Because species in this group are notoriously variable in shell form, I consider it unwise to depend too heavily on a strict comparison of material in hand with a holotype, especially one that is worn and apparently juvenile. I disagree with Dr. Altena as to the distinctness of *P. radwini* and consider the form to probably be conspecific with *Parvanachis isabellei.*

Range: Uruguay to northern Argentina and the southern Caribbean.

Parvanachis melvillei (Strebel, 1905)

(Figure *28*)

Columbella (Seminella) melvillei Strebel, 1905. Zool. Jahrb. 22 (6): 637; plt. 23, figs. 37a-37f (Straits of Magellan; representation of lectotype, Strebel, 1905, plt. 23, figs. 37a-37f)

Shell very small (3 - 5 mm in length), obese; spire moderately high, acute, whorls weakly convex, suture impressed; body whorl large (more than ½ total shell length), inflated, aperture moderately broad, apertural lip thickened, denticulate on its inner surface, columella straight, weakly denticulate, with a slight callus, siphonal canal short, bent, weak anal groove present; sculpture of numerous, strong axial ribs with many prominent spiral cords, strongest between the axial ribs; color white with orange-brown blotches; protoconch of 3 full whorls. Radula unknown.

Remarks: *Parvanachis melvillei* differs from *P. obesa* in its less inflated body whorl, its less convex spire-whorl profile, its stronger spiral sculpture, and its protoconch, which has one more volution and is higher than that of *P. obesa.*

No fossil examples of this species have been reported.

Range: Uruguay to the southern tip of Argentina.

Parvanachis obesa (C. B. Adams, 1845)

(Figure *26*)

Buccinum obesum C. B. Adams, 1845. Proc. Boston Soc. Nat. Hist. 2: 7 (Jamaica; lectotype, MCZ 156016)

Buccinum concinnum C. B. Adams, 1845. Proc. Boston Soc. Nat. Hist. 2: 2 (not Dillwyn, 1817) (Jamaica; lectotype MCZ 186112)

Columbella costulata C. B. Adams, 1850b. Contrib. to Conch. 1 (4): 58 (not Cantraine, 1835) (Jamaica; lectotype MCZ 186108)

Columbella decipiens C. B. Adams, 1850a. Contrib. to Conch. 1 (4): 55, nom. nov. pro. *Buccinum concinnum* C. B. Adams, 1845, not Dillwyn, 1817

Columbella pygmaea C. B. Adams, 1850b. Contrib. to Conch. 1 (4): 58 (not Sowerby, 1832), nom. nov. pro *Columbella costulata* C. B. Adams, 1850a (not Cantraine, 1835)

Columbella crassilabris Reeve, 1859. Conch. Icon. 11, *Columbella,* spec. 177 (type locality not specified; holotype, BM[NH])

Columbella ornata Ravenel, 1859. 280-282 (South Carolina – fossil; holotype apparently destroyed)

Shell small (4 - 8 mm in length), obese; spire slightly greater than ½ shell length, whorls barely convex with slightly impressed suture; body whorl inflated, aperture broad, apertural lip strongly flared, ventricose and denticulate on its inner surface, columella straight, minutely denticulate; sculpture of prominent axial ribs crossed by strong spiral cords; shell surface glossy with a thin brown periostracum; color pattern ivory with brown markings varying from isolated spots on the apertural lip to a form in which the entire shell is purplish-brown. Each radular row consists of a flat, subrectangular median tooth, flanked on each side by a sigmoid, tricuspid lateral tooth. The proximal cusps are strongly downhooked, a feature common to the entire group (Figure *44*).

Remarks: The commonest and most widespread of western Atlantic columbellids, this species occurs in 3 distinct morphological varieties, 2 of which have overlapping ranges in the Puerto Rico-Virgin Islands area. In this region the "typical" form and a different form with slightly differing shell proportions, a less flaring apertural lip, a more convex spire profile, and a lack of spiral sculpture occur in the same localities. Although there are minor shell differences, the radulae of these 2 forms are indistinguishable. A third form, with a great reduction in sculpture, more convex whorls, an unthickened apertural lip, and a unique color pattern of discrete rows of squarish dark brown spots appear to be limited to the southeastern Caribbean islands from Dominica to Trinidad.

The earliest fossil records of this species are from the Miocene of Florida.

Range: Mouth of Chesapeake Bay (Maryland-Virginia area) to the coast of Central Uruguay.

Parvanachis ostreicola (Sowerby, 1882)

(Figure *27*)

Columbella (Anachis) ostreicola Melvill, 1881. Journ. Conch. 3 (5/6: 160 (nomen nudum) (Key West, Florida; lectotype, BM[NH] 1883.10.22.26)

Columbella (Anachis) ostreicola Sowerby, 1882. Proc. Zool. Soc. London 1882: 116 (Key West, Florida; lectotype, see above)

Anachis ostreicola (Melvill). Dall, 1883. Proc. U. S. Nat. Mus. 6 (21): 342

Anachis obesa ostreicola. Abbott, 1954. Amer. Seashells: 221

Shell minute (3 - 5 mm in length), cylindro-conical; spire moderately high and acute with a convex silhouette, whorls moderately convex, slightly shouldered; body whorl cylindrical, not inflated, aperture narrow to moderately broad, apertural lip denticulate, somewhat thickened but not flaring, columella straight, weakly denticulate; sculpture reticulate, composed of strong axial ribs crossed by prominent spiral cords, single stronger subsutural spiral cord. There is often a peculiar bald (*i. e.*, unsculptured) spot on the abapertural side of the body whorl; color from reddish-brown to deep purple-black. Each radular row consists of a median tooth flanked on each side by a sigmoid, tricuspid, lateral tooth. The 2 distal cusps are sharp and moderately bent, the proximal cusp is strongly downhooked, as in other *Parvanachis* species (Figure *45*).

Remarks: This species has been considered a variety of *Parvanachis obesa*, especially by workers on the Gulf Coast of Texas (Singley, 1898; Pulley, 1953; Parker, 1959, 1960). It differs from that species by its greater proportion of body whorl to spire, a less flaring apertural lip, greater overall convexity of the spire profile, uniform and distinct color pattern, and consistently stronger spiral sculpture.

The habitat of *Parvanachis ostreicola* (on oysters in shallow, mud-bottom areas) also differs substantially from that of *P. obesa* (in deeper water [3 m plus] on sand bottoms).

No fossil examples of this species have been reported.

Range: The Gulf of Mexico from Key West, Florida to Padre Island, Texas.

Parvanachis rhodae (Radwin, 1968)

(Figure *22*)

Anachis (Parvanachis) rhodae Radwin, 1968. Proc. Biol. Soc. Wash. 81:147 (Puerto Plata, Dominican Republic; holotype, MCZ 261478)

Shell moderately small (6 - 8 mm in length), obese; spire high ($\frac{1}{2}$ total shell length), acute, whorls slightly convex, each "set-in" from the one below it imparting a terraced appearance, suture impressed; body whorl large, inflated, apertural lip ventricose, strongly denticulate interiorly, columella with a small but heavy callus, siphonal canal short and sharply bent, slight anal groove present; sculpture of broad low axial ribs and several obsolete spiral grooves at the base of the body whorl; color yellow-white with varying amounts of chestnut-brown blotching; protoconch of one full, bulbous, translucent white whorl. Despite the apparent freshness of most specimens seen, none were collected alive and thus the radular morphology of this species is not known.

Remarks: This species is known only from a single locality, Puerto Plata, Dominican Republic, on the northern coast of Hispaniola.

This species suggests a link between *Strombina (Sincola)* Pilsbry & Olsson, 1941 and *Parvanachis*. It lacks the typical hump and the very strongly callused and emarginate aperture of *Strombina*, but otherwise might be considered quite similar to it in general shell form. On the other hand, the form of the apertural lip strongly resembles that of *P. obesa*, the type of *Parvanachis*. The generic placement of *P. rhodae* must, therefore, remain provisional pending examination of its soft parts and radula.

No fossil examples of this species have been reported.

Range: Known only from the type locality.

Steironepion Pilsbry & Lowe, 1932

Mangelia (Steironepion) Pilsbry & Lowe, 1932. Proc. Acad. Nat. Sci. Philadelphia 84: 57 (type species by OD, *Mangelia melanosticta* Pilsbry & Lowe, 1932 [= ? *Anachis tincta* Carpenter, 1864])

Psarostola Rehder, 1943. Proc. U. S. Nat. Mus. 93 (3161): 198 (type species by OD, *Columbella monilifera* Sowerby, 1844)

Shell small, slender, cylindrical; spire high, subacute, suture incised; body whorl small about $\frac{1}{3}$ total shell length), aperture narrow, weakly sigmoid, siphonal canal short, distinct anal sinus present; sculpture of narrow axial ribs crossed by strong spiral cords forming nodules at the junctions; color generally white with periodic brown or orange markings on the nodules. Radula minute; each row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid lateral tooth which bears 3 sharp cusps; the most proximal of these cusps is sharply downhooked.

Remarks: In the original description of ***Psarostola***, Rehder states that "this species is apparently near *Nassarina* Dall and *Cigclirina* Woodring, but differs from them in that no attenuation of the base into an anterior canal is noticeable on the outer lip." Some specimens collected alive more recently show a distinct anterior canal. Rehder continues with "... being more like *Zanassarina* Pilsbry & Lowe (1932) in this respect; from this it differs in the smaller and more inflated nucleus." While it is true that the type species of *Zanassarina* (*Z. poecila*) has a multiwhorl protoconch of small diameter, other species of that genus described at that time possess protoconchs ranging from one extreme (narrow, multiwhorl in *Z. xeno* and *Z. albipes*) to the other (pauciwhorl, bulbous, in *Z. atella*), not unlike that in *C. monilifera*. *Steironepion melanosticta*, the type species of *Steironepion*, is characterized by a protoconch of nearly 4 whorls with a spiral keel. The western Atlantic species (*S. monilifera* and *S. minor*) both clearly belong to this group on all shell characters and have a protoconch of less than 2 bulbous inflated whorls with no keel. These discrepancies point up the weakness of the protoconch as a taxonomic character in this group.

The genus *Steironepion* is readily identified by its small size, strongly beaded shell sculpture, distinct anal sinus, and the strongly downhooked proximal cusp of the lateral radular tooth.

Steironepion minor (C. B. Adams, 1845)

(Figure *17*)

Pleurotoma minor C. B. Adams, 1845. Proc. Boston Soc. Nat. Hist. 2: 4 (Jamaica; lectotype, MCZ 186122)

Colombella monilifera Duclos, 1846 (not Sowerby, 1844), (*in* Chenu) Illust. Conchyl. plt. 17, figs. 11, 12) (type locality not specified; representation of lectotype, Duclos, 1846, plt. 17, figs. 11, 12).

Shell tiny (4.5 - 5.5 mm in length) and fusoid; spire high (about $\frac{2}{5}$ of total shell length), acute, whorls convex, suture moderately impressed; body whorl short, narrow, aperture slightly sinuous, apertural lip thickened, denticulate on its inner surface, columella straight, weakly denticulate, with a slight callus, siphonal canal bent, short to moderately long; sculpture of low axial riblets crossed by a strong spiral cord forming large nodules at the intersections, 3 rows of major beads and 1 row of minor beads on the body whorl, decreasing to 2 rows and 1 row on the earlier whorls; color orange-brown with white beads. Each radular row has a flat, subrectangular median tooth, flanked on each side by a tricuspid lateral tooth (Figure *46*). The most proximal cusp on the lateral tooth is strongly hooked downward.

Remarks: *Steironepion minor* is often confused with *Nassarina glypta* (Bush). For distinctions see the section on *N. glypta*. An uncommon species, *S. minor* is usually collected in beach-drift and very little live-collected material has been examined.

No fossil examples of this species have been reported.

Range: Central Bahama Islands to the Caribbean coast of Panamá.

Steironepion monilifera (Sowerby, 1844)

(Figure *16*)

Columbella monilifera Sowerby, 1844. Proc. Zool. Soc. London 12: 53 (West Indies; holotype, BM[NH] 1966.4.50)

Pleurotoma fuscolineata C. B. Adams, 1845. Proc. Boston Soc. Nat. Hist. 2: 4 (Jamaica; holotype lost [see Clench & Turner, 1950])

Columbella telea Duclos, 1848. (*in* Chenu) Illust. Conchyl., plt. 25, figs. 13, 14 (type locality not specified; representation of lectotype, Duclos, 1848, plt. 25, figs. 13, 14)

Shell small (4 - 5 mm in length), turrid-like; spire moderately high ($\frac{3}{5}$ of shell length), subacute, whorls slightly convex, suture impressed; body whorl small, narrow, aperture narrow, apertural lip thickened, denticulate on its inner surface, columella almost straight, nondenticulate, siphonal canal short to moderately short, bent, marked anal sinus present; sculpture consisting of strong axial riblets crossed by prominent spiral cords forming nodules at the intersections; color white with brown markings on the first 2 or 3 nodules below the suture. Each radular row consists of a flat, subrectangular median tooth, flanked on each side by a sigmoid, tricuspid lateral tooth that is strongly downhooked (Figure *47*).

Remarks: *Psarostola monilifera sparsipunctata* Rehder, 1943 is said to have a more restricted geographical distribution than the nominate subspecies [*P. m. monilifera* (Sowerby, 1844)], and to be morphologically distinguished from it in having brown spots on only the first 2 nodules, in contrast to the nominate subspecies with 3 rows of spots. Recent collections in the vicinity of the Yucatán Peninsula have extended the range of *Steironepion m. sparsipunctata*. It is probable that the form does not warrant nomenclatural distinction. An eastern Pacific cognate is *Mangelia melanosticta* Pilsbry & Lowe, 1932, the type species of *Steironepion*.

No fossil examples of this species have been reported.

Range: Bermuda and southeastern Florida to Barbados and Panamá.

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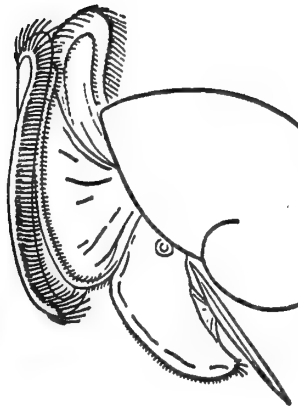

A New Species of *Humboldtiana* (Helminthoglyptidae) from Coahuila, Mexico

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(1 Plate; 1 Text figure)

A RECENT COLLECTION of land snails from Coahuila, Mexico by Dr. David H. Riskind produced a series of large specimens of *Humboldtiana* which, upon cursory examination, appeared to be referable to *H. montezuma* Pilsbry. However, investigations of the genitalia, and a comparison of the shell morphology of the Coahuila specimens to the holotype and 2 paratypes of *H. m. montezuma* reveal that the Riskind specimens represent an undescribed species of *Humboldtiana*.

Humboldtiana riskindi Fullington & Zimmerman, spec. nov.

(Figures *1* to *3* and 7)

Description of Holotype: Shell large and globose; spire elevated with all whorls visible from apertural view; aperture oriented obliquely; embryonic whorl smooth and white; shell entirely devoid of granulations; last ½ turn of embryonic whorl with spiral striae merging with radial striae; remainder of whorls with interrupted, profuse, white striae separated by pronounced grooves; striae continuing over body whorl and into umbilicus and extending through shell forming shallow ridges on inner side; well-developed parietal callus with columella broadly reflected over umbilicus partially concealing the latter in a basal view; parietal wall covered with translucent nacre; 3 narrow, faint bands of brown pigment on body whorl, bottom band disappearing at insertion of upper lip and 2 bands continuing to embryonic whorl; ground color maple; inner aperture wall walnut brown with spiral bands distinctly visible from within; living animal slate gray above, fading to dusky gray or black laterally; sole of foot blue-gray; skin texture heavily corrugated.

Measurements: The holotype is 49.8 mm in diameter, 45.1 mm in height, and has 4½ whorls. Height and diameter of the aperture are 34.5 and 32.7 mm, respectively.

Genitalia: Penis relatively long, 13.0 mm, and bulbous (Figure 7); epiphallus short (8.7 mm), less than ⅙ the length of the flagellum; penis with 5 heavy, longitudinal folds extending up to ½ the penial wall; penial retractor inserted just above the junction of epiphallus and penis; verge short and papilliform with 7 finger-like papillae; 4 dart sacs, equal in size and widely separated (5.0 mm) from mucous gland; vagina long, 15.7 mm.

Type Locality: Coahuila, Mexico, 17 km E Castaños in Cañon Obscuro Chiquillo, Sierra de la Gloria, at 26° 47′25″ N Lat., 101°17′45″ W Long. Approximate elevation 1300 m. D. H. Riskind and T. Wendt, 7 September 1976. The specimens were found aestivating on a north-facing slope of a massive, limestone cliff in a narrow gorge of the Cañon. Vegetation in the Cañon is primarily brushy Tamaulipan woodland with oaks, *Quercus glaucoides*; pistacio, *Pistacia* sp.; chapotillo, *Amyris marshii*; manzanita, *Colubrina gregii*; and guajillo, *Acacia berlandieri*.

Disposition of Specimens: Holotype deposited in Dallas Museum of Natural History, Invertebrate Type Collection No. 5357. Paratypes deposited in the United States National Museum.

Discussion: Members of the helicoid genus *Humboldtiana* are among the largest terrestrial gastropods in North America. The genus includes 27 recognized species distributed from the Trans-Volcanic Belt of central Mexico northward to western Texas (BURCH & THOMPSON, 1957;

Cheatum, 1972; Pilsbry, 1939, 1948; Pratt, 1971; present study).

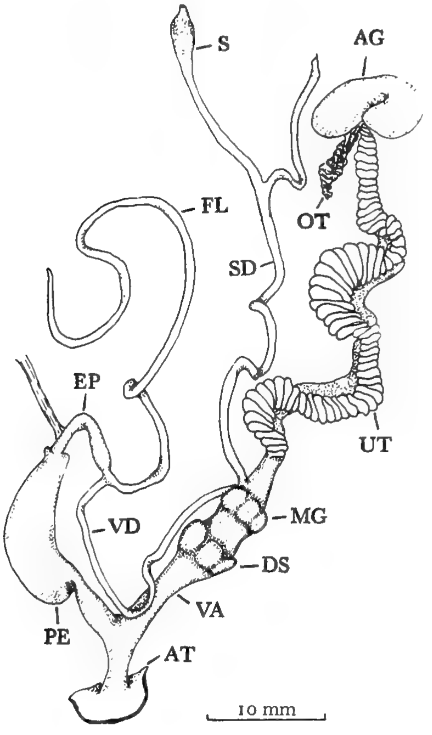

Figure 7

Humboldtiana riskindi Fullington & Zimmerman, spec. nov.

Genitalia of paratype, DMNH 5358

AG – Albumen gland AT – Atrium DS – Dart sac
EP – Epiphallus FL – Flagellum MG – Mucous gland
OV – Ovotestis PE – Penis S – Spermatheca
SD – Spermathecal duct UT – Uterus VA – Vagina
VD – Vas deferens

Ten species are found in Texas, and all occur as insular relicts at elevations above 1200m in isolated mountain ranges west of the Pecos River (Burch & Thompson, 1957; Cheatum, 1972; Pratt, 1971). The remaining Mexican forms are distributed in Mexico, D. F., Hidalgo, and Vera Cruz in the Trans-Volcanic Belt; Queretaro, Guanajuato, San Luis Potosi, and Tamaulipas in the Sierra Madre Oriental; Zacatecas, Durango, and Chihuahua in the Sierra Madre Occidental; and Nuevo Leon and Coahuila in isolated mountain ranges of the Mexican plateau (Burch & Thompson, *op. cit.*). The diversity of available habitats and climatic effects of post-Pleistocene isolation at higher elevations have, no doubt, contributed to the evolution of the diversity of *Humboldtiana* forms in this region.

Humboldtiana riskindi would appear to belong to the loose assemblage of species occurring in the Sierra Madre Oriental and resembles *H. m. montezuma* in certain aspects of shell morphology, including large size and presence of the white striae. In fact, the means for diameter and height of the shell and aperture of the holotype and 2 comparably-sized paratypes of *H. riskindi* are similar to those of the holotype and one paratype of *H. m. montezuma* available to us. Additionally, certain features of the genitalia, including the lengths of the vagina and atrium, spermatheca and duct, and diverticulum of the spermatheca compare favorably with values provided for *H. m. montezuma* by Pilsbry (1948). There are, however, several striking differences which provide distinctness to *H. riskindi*. *Humboldtiana riskindi* differs from *H. m. montezuma* in having white striations higher and more regularly and narrowly spaced; no granulations, these being prominent in *H. m. montezuma*; pigmented bands on the body whorls; depressed whorls, with a ratio of height to diameter of the shell averaging 0.94 (0.91 in *H. m. montezuma*); a ground color of light maple and not vinaceous brown; a well-developed parietal callus and columellar lip; the basal whorl less inflated and rounded, and the columellar lip exposing the umbilicus; the distance across the parietal wall from the insertion of the palatal portion of the lip to the point of insertion of the basal lip narrow, averaging 15.3mm (22.6mm in *H. m. montezuma*); a large, bulbous penis; a short epiphallus, averaging 11.1mm (32mm in *H. m. montezuma*); a long flagellum, averaging 65.3mm (40mm in *H. m. montezuma*); and the dart sacs widely separated from the mucous glands. The most diagnostic features of *H. riskindi* include the lack of granulations, prominent white striae, pigmented bands on the body whorls, a large, bulbous penis, a short epiphallus, and a wide separation between the dart sacs and mucous glands.

Features of the soft anatomy and geographic distribution of *Humboldtiana riskindi* do not provide a clear picture of its taxonomic affinities. The genus *Humboldtiana* has been divided into 2 groups based on the relationship of the dart sacs to the mucous glands (Burch & Thompson, 1957), although Solem (1974) cautions investigators that this feature shows some intraspecific variation. Species such as *H. buffoniana* (Pfeiffer), *H. chrysogona* Pilsbry, 1948, *H. fortis* Pilsbry, 1940, *H. montezuma* Pilsbry, 1940, *H. potosiana* Pilsbry, 1927, *H. striata* Burch & Thompson, 1957, and *H. ultima* Pilsbry, 1927 all have the mucous glands situated closely above the dart sacs. Furthermore, certain forms of this group are characterized by a conspicuous apical chamber in the penis and a short verge (Burch & Thompson, 1957). In contrast, *H. texana* Pilsbry, 1927, *H. chisosensis* Pilsbry, 1927, *H. fasciata* Burch & Thompson, 1957, *H. fullingtoni* Cheatum, *H. globosa* Burch & Thompson, 1957, and *H. agavophila* Pratt, all have widely separated mucous glands and dart sacs. Most of these also have a long verge and only a vestige of the apical chamber of the penis (Burch & Thompson, 1957; Pratt, 1971). *Humboldtiana riskindi* would appear to have features of both groups, *i. e.*, a short verge but a wide separation between the mucous glands and dart sacs and a vestigial apical chamber of the penis. The fact that *H. riskindi* and *H. m. montezuma* differ significantly in 2 of the features indicates the 2 species should be placed in different groups established by Burch & Thompson, (*op. cit.*).

Additionally, the distributions of *Humboldtiana riskindi* and *H. m. montezuma* are not indicative of taxa that are closely related. The latter occurs at about 3000m in southeastern Nuevo Leon in the Sierra Madre Oriental. This continuous cordillera is habitat for at least 8 species of *Humboldtiana* (Burch & Thompson, 1957). *Humboldtiana m. montezuma* and *H. m. inferior* Pilsbry, 1948 and 3 other species, *H. fortis*, *H. chrysogona*, and *H. nuevoleonis* Pilsbry, 1927, occur at the northern end of the cordillera, which extends only into southeastern Coahuila. The type locality of *H. riskindi*, on the other hand, is one of several isolated mountain ranges, the Sierra de la Gloria, that extend in a northwest-southeast direction from the Sierra del Carmen, along the Rio Grande River, to the Sierra Madre Oriental in southeastern Coahuila. Geographically, the Sierra de la Gloria lies in an intermediate position between populations of *Humboldtiana* in the Trans-Pecos of Texas and the Sierra del Carmen, and forms such as *H. fortis*, *H. chrysogona*, and *H. nuevoleonis* in the northern Sierra Madre Oriental. The latter 3 species occur between populations of *H. riskindi* and *H. m. montezuma* and bear no external or anatomical similarity to *H. riskindi*.

Therefore, we are unable to completely elucidate the taxonomic position of *Humboldtiana riskindi*. Anatomically it is unique, resembling *H. m. montezuma* in its large size, but being most similar to *H. texana*, *H. chisosensis*, *H. fullingtoni*, *H. agavophila*, *H. fasciata*, and *H. globosa* in morphology of the genitalia. Additional studies utilizing several forms of *Humboldtiana* in an electrophoretic analysis of protein variation in the genus should provide some insight into this problem. A preliminary report of this research is in preparation.

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Explanation of Figures *1* to *6*

Figure *1*: Holotype, DMNH 5357 of *Humboldtiana riskindi* Fullington & Zimmerman, spec. nov. × 1

Figure *2*: Holotype, DMNH 5357, of *Humboldtiana riskindi* Fullington & Zimmerman, spec. nov. × 1

Figure *3*: Holotype, DMNH 5357, of *Humboldtiana riskindi* Fullington & Zimmerman, spec. nov. × 1

Figure *4*: Holotype, ANSP 164062, of *Humboldtiana montezuma* Pilsbry, 1940 × 1

Figure *5*: Holotype, ANSP 164062, of *Humboldtiana montezuma* Pilsbry, 1940 × 1

Figure *6*: Holotype, ANSP 164062, of *Humboldtiana montezuma* Pilsbry, 1940 × 1

Figure *1*

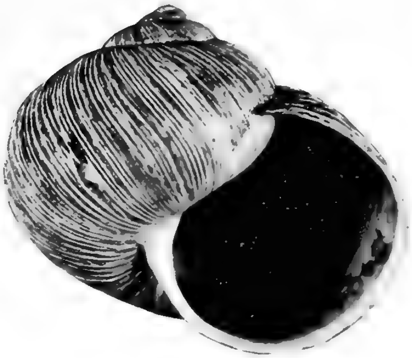

Figure *4*

Figure *2*

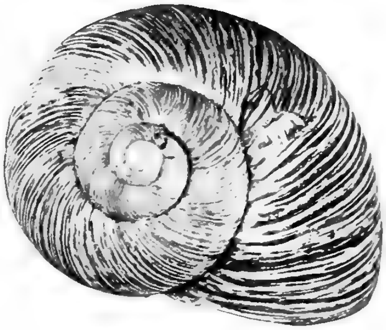

Figure *5*

Figure *3*

Figure *6*

Activity of the Gastropod Mollusk *Olivella biplicata* in Response to a Natural Light/Dark Cycle

BY

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(3 Text figures)

INTRODUCTION

Olivella biplicata (Sowerby, 1825) is a common snail on many sandy beaches along the west coast of North America from Baja California to Vancouver Island, British Columbia (Keen, 1937). It is found both along exposed coastline and in protected bays and estuaries where it lives in relatively clean sands that contain minor amounts of silt and clay (Stohler, 1969; Edwards, 1969b; Johnson, 1971). Its vertical range is from the extreme high of lower low water to the shallow subtidal area (Edwards, *op. cit.*). Previous studies on *O. biplicata* have dealt with reproduction and growth (Stohler, 1959, 1960, 1962, 1969; Edwards, 1968; Zell, 1955), predators (Edwards, 1969a), physiological tolerances (Edwards, 1969b), and the intertidal distribution of size classes (Edwards, 1969b).

In the present paper, a 24-hour activity cycle is reported for *Olivella biplicata*. The general activity cycle is described, activity patterns of individual snails are compared, and interrelationships between the size, sex, and activity of the snails are reported.

MATERIALS AND METHODS

Olivella biplicata were collected in the harbor at Bodega Bay, California. Specimens used in this study were collected intertidally on a sandy spit between the tidal levels of 0.0 and – 0.3 m. The *Olivella* population extended subtidally from this spit down to the bottom of the boat channel (– 6 m to – 7 m). After collection, the animals were maintained in aquaria provided with sand and a constant flow of seawater from the Bodega Marine Laboratory's running seawater system. Experiments were completed within 3 weeks of collection.

The observation chamber was a plexiglass trough (43 × 36 × 14 cm) containing a layer of sand 6 cm deep. The water level was 4 cm above the surface of the sand. Seawater from a constant-level reservoir entered the trough at one end through 4 inlet holes (13 mm diameter) and exited at the opposite end through 4 outlet holes (13 mm diameter). Water flow through the observation chamber was maintained at a rate of 2.5 *l*/min. Water temperature in the trough was usually 1 °C higher than ambient sea-surface temperature, which varied from 11.3 to 14.0 °C during the experiments.

Individual *Olivella biplicata* were identified by writing a number on the shell with a felt-tipped marking pen (black, Color Pen, Perm-color, Esterbrook). All of the numbers remained clearly legible for over a week; however, after 2 weeks, the numbers were beginning to wear off. This marking technique would not be suitable for experiments of longer duration.

Observations at night were made with a flashlight fitted with a red filter (Kodak No. 29, dominant wavelength of 633 nm). In addition to the red filter, 4 sheets of Whatman No. 1 filter paper were placed in the light path to reduce the intensity of illumination and to provide a more uniform light source. The flashlight was powered by 2 standard, "D" batteries (1.5 v each).

RESULTS

General Activity Patterns

Fifty-seven individually numbered *Olivella biplicata* (hereafter *Olivella*) were observed in a large plexiglass chamber, which contained a layer of sand and was provided with running seawater. The observation chamber was located outdoors under an overhang that sheltered the chamber from direct sunlight except during late morning hours. In this location, the animals were exposed to a light/dark cycle that was similar to the natural cycle but with light that was somewhat reduced in intensity. During mid-August (when this experiment was conducted) the animals were exposed to light (> 10 footcandles ≈ 108 lumen per m^2) from approximately 06:15 to 20:15 (Pacific Daylight Time).

After a 24-hour acclimation period in the observation chamber, the snails were observed every hour for 5 days. Since active snails were almost always on the surface of the sand and buried snails rarely moved, the number of snails on the surface was used to quantify the activity of the *Olivella* population. Figure 1 is a summary of the numbers of *Olivella* recorded on the surface at one-hour intervals during the 5 days.

The most striking feature shown by Figure 1 is that the *Olivella* were on the surface and active primarily at night. Fully 88% of the observations of animals on the surface were recorded during the hours of darkness (21:00 through 06:00). Consistently, the number of animals on the surface began to increase at twilight and rapidly reached a maximum, usually within 2 hours of darkness. Similarly, each night the number of animals began to decrease long before the light of dawn. While activity was clearly greatest during the night, it should be noted that some activity was also recorded during each 14-hour daylight period.

Since the numbers of *Olivella* on the surface began to decrease well before dawn and to increase somewhat before complete darkness, it was desirable to directly test the snails' responses to light and to dark. One hundred *Olivella*, which had been in the observation chamber for the 2 previous days, were exposed to complete darkness at 14:00 by covering the chamber with aluminum foil. Two hours later, the cover was removed exposing the animals to ambient, late afternoon lighting conditions (90 footcandles, ≈ 972 lumens per m^2). The results of this experiment are reported in Table 1. It can be seen from Table 1 that before darkening the chamber only 1 of the 100 *Olivella* was on the surface. However, after 2 hours of darkness artificially imposed during the day, 53 of the *Olivella* had emerged and were on the surface. Re-exposure to daylight produced an immediate burial response. Within 2 minutes, over half of the animals had completely buried themselves, and, within 8 minutes, all of them had disappeared under the sand. Light, and the absence of light, clearly has a direct influence on the activity of *Olivella*.

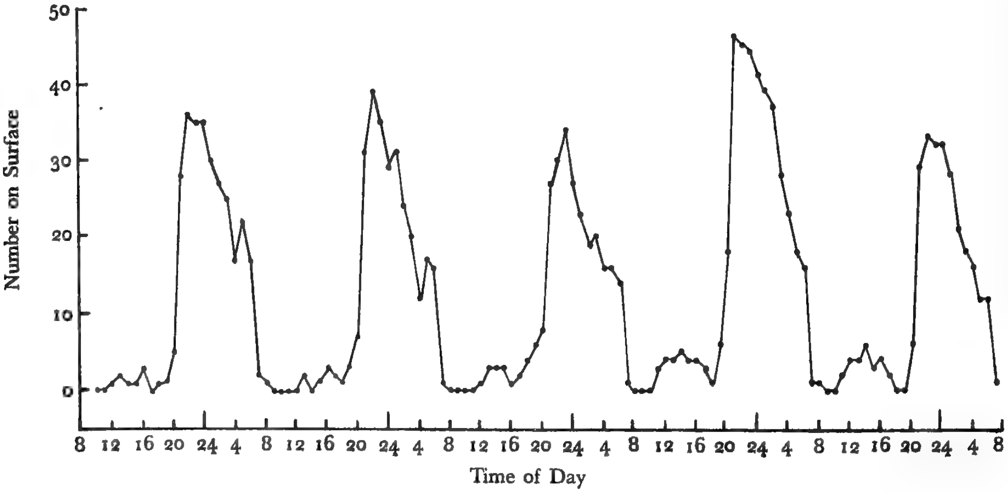

Figure 1

Numbers of *Olivella biplicata* on the surface (N = 57) at 1-hour intervals through 5 complete light/dark cycles. Snails were maintained outdoors and were exposed to daylight (> 100 Lux or > 10 footcandles) from approximately 06:15 to 20:15 (Pacific Daylight Time). A snail was recorded as being on the surface if $\frac{1}{3}$ or more of its shell length was visible.

Table 1

Responses of *Olivella biplicata* to darkness artificially imposed during the day (N = 100), and responses of snails on the surface to daylight (90 footcandles)

Operation	Time	Number on Surface
Chamber darkened	14:00	1
Chamber exposed to daylight	16:00	53
	16:02	20
	16:04	8
	16:06	3
	16:08	0
	16:10	0
	16:20	0

Activity Patterns of Individuals

The general activity pattern of the *Olivella* population (Figure 1) was relatively constant from one 24-hour period to the next. In contrast, the activity patterns of individual snails were extremely variable, and the records of 10 individual *Olivella* are presented in Figure 2 to illustrate this diversity. The median number of times that a snail was recorded on the surface during the 120 hours of observation was 24 times. The activities of many individuals, however, varied widely from this median value. For example, snail #7 was recorded on the surface 53 times (*i. e.*, during almost half of the observations), whereas snail #56 was observed on the surface a total of only 3 times during the 5 days. The percentage of an individual's activity that occurred in the dark or in the light was also variable. Although most of the snails were active primarily or exclusively at night (*e.g.*, snails #10, 23, 25, 29, 32, 46, and 56), several of the snails had activity patterns that were characterized by substantial percentages of daytime activity (*e. g.*, snails #7, 28, and 31). Even among the snails that were active primarily at night, the specifics of the activity patterns varied considerably from individual to individual. For example, snail #29 was not seen on the surface at any time during 2 of the 5 nights of observation, but it was very active during the other 3 nights. In contrast, snail #46 was out on the surface every night, but it stayed out each night for only a short time. All of the *Olivella* were observed on the surface at some time during the 5 days.

While observations at 1-hour intervals gave an adequate picture of an individual's general activity cycle, an hour was a long time compared to the time actually needed for an *Olivella* to bury itself and re-emerge. Was it likely that an animal observed on the surface at 22:00 and again at 23:00 had spent the entire hour on the surface? Or had it perhaps buried itself and re-emerged several times during the hour? To answer these questions,

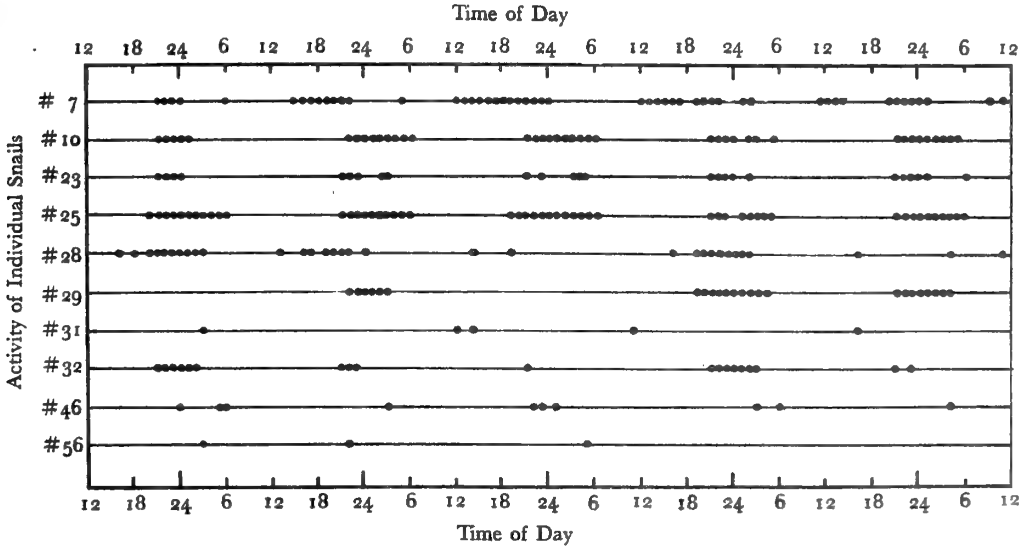

Figure 2

Activity records of 10 *Olivella biplicata* selected to illustrate the diversity of individual activity patterns. Observations were made at 1-hour intervals for 5 complete light/dark cycles. Darkened circles indicate the times that each individual was observed on the surface.

the 57 numbered *Olivella* were observed continuously for one hour (23:00 to 24:00) with data being recorded every 5 minutes. The results were clear. Of the 23 individuals that were on the surface both at the beginning of the observation period ($t = 0$ min.) and at the end ($t = 60$ min.), 20 were on the surface for the entire hour. Of the 35 individuals that appeared on the surface at least once during the hour, only 3 individuals were observed on the surface, then not seen, and later observed again on the surface; furthermore, 2 of these 3 were not seen for only 1 observation, suggesting that they might have been on the surface but overlooked. Almost all of the snails that were observed on the surface were active and moving.

In addition to showing that an individual observed on the surface for 2 consecutive hourly observations was likely to have been on the surface throughout the hour, these short-interval observations provided an important control for possible effects of the red light used to make all of the observations. Table 2 reports the total numbers of *Olivella* on the surface at 5-minute intervals during the hour of observations. There was no significant difference between the numbers of *Olivella* on the surface at the beginning and at the end of the hour ($x^2 = 0.32$; $p > 0.5$). A slight decrease was observed; however, this decline was consistent with the general activity cycle of *Olivella* (Figure 1) in which activity often appeared to decline between 23:00 and 24:00. If there was a response to the red light, it was clearly unlike the strong burial response to daylight that was reported in Table 1. While it is never possible to completely prove "no effect," the conclusion appears justified that the red light did not significantly affect the basic activity pattern of *Olivella*.

Table 2

Numbers of *Olivella biplicata* (N = 57) on the surface recorded at 5-minute intervals during one hour of continuous observation (23:00 to 24:00)

Time (Min. after 23:00)	Number of snails on surface
0	31
5	31
10	31
15	32
20	32
25	33
30	30
35	31
40	30
45	29
50	29
55	27
60	27

Relationships Between Shell Length, Sex, and Activity

Olivella were collected for the preceding experiments without regard to sex or shell length. After the experiments, individuals were measured and sexed. Shell length (apex to siphonal canal) was determined with vernier calipers. The lengths ranged from 18.2 to 27.9 mm ($\overline{X} = 22.7$; $SD = 2.4$). Sex was determined by using the presence or absence of a penis as the test criterion. Using this criterion, the sample of 57 *Olivella* contained 38 females and 19 males. Eleven of the males had functional penes; 8 had rudimentary penes, probably resulting from trematode infections. All animals designated as females were examined under the dissecting microscope to make certain that a penis rudiment had not been overlooked. The total number of times an individual was observed on the surface was taken as a relative measure of its overall activity. These relative activity measures ranged from 3 to 57 times on the surface during the 5-day experiment ($\overline{X} = 25.4$; $SD = 12.4$).

In Figure 3, shell lengths were plotted against the number of times a snail was observed on the surface (*i. e.*, activity). Small snails were generally more active, and activity gradually decreased with increasing shell length. The negative correlation between shell length and activity was highly significant when both males and females were included in the analysis (corr. coeff. $= -0.52$; d. f. $= 55$; $p < 0.001$). A significant correlation was also present when females were considered alone (corr. coeff. $= -0.39$; d. f. $= 36$; $p < 0.05$). A significant correlation was not present between shell length and activity when only males were considered (corr. coeff. $= +0.03$; d. f. $= 17$; $p > 0.5$). The sample linear regression for all of the data (males plus females) was expressed by the equation $Y = 25.2 - 0.1X$.

Males and females were plotted with different symbols in Figure 3, and it was immediately apparent that males in this sample were considerably larger than females. Males had shell lengths averaging 25.3 mm ($N = 19$; $SD = 1.5$), whereas the average shell length of a female was 21.4 mm ($N = 38$; $SD = 1.5$). The difference between the sample means was highly significant (t-test; $p < 0.001$).

Since females were generally smaller than males, and since smaller snails were more active, it was expected that females would be more active than males. This was true. Females were observed on the surface an average of 29.5 times during the 5 days ($SD = 11.6$) compared to only 17.0 times ($SD = 8.9$) for males. The difference between

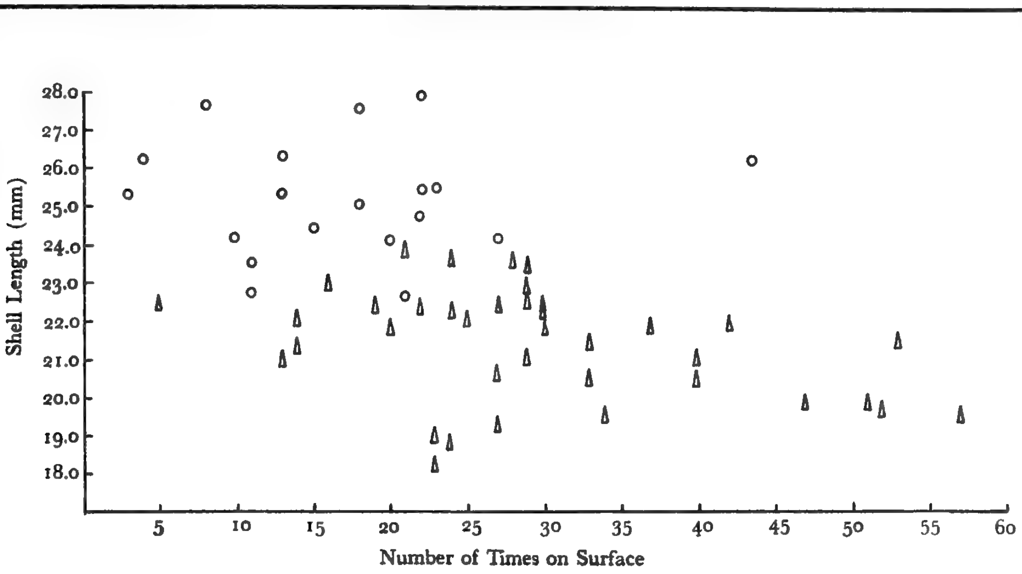

Figure 3

Relationship between shell length and the total number of times a snail was observed on the surface during the 5-day experiment (*i. e.*, activity). Males (○) and females (△) are indicated separately. The correlation is significantly negative when both males and females are included in the analysis (corr. coeff. = -0.52; d. f. = 55; $p < 0.001$). The sample linear regression is expressed by $Y = 25.2 - 0.1X$.

the sample means was again highly significant (t-test; $p < 0.001$). Females tended to be more active both during the day and during the night. This difference was highly significant during the night (t-test; $p < 0.001$). Few individuals were active during the day, however, and the difference in daylight activity between males and females was not statistically significant (Mann-Whitney U test; $p < 0.2$).

While the activities of males and females were clearly different, it was not possible with these data to assess satisfactorily the contribution of sex independently from size effects. There was so little overlap between the size distributions of the 2 sexes (Figure 3) that few males and females of similar size were available for direct comparisons. There was some overlap in size, however, between the 6 smallest and 7 largest females (22.6 to 24.2 mm). When the activities of these 13 animals were compared, females were again found to be more active than males (Mann-Whitney U test; $p < 0.05$).

Although *Olivella* were collected for this study without regard to sex, the sample contained many more females than males. Indeed, the numbers of males and females were significantly different from the 1 : 1 ratio that was expected on the basis of previous work (Edwards, 1968). While this deviation was statistically significant ($X^2 = 6.63$; $p < 0.025$), it may have resulted completely from unintentionally biased sampling related to activity differences between the sexes. Many of the *Olivella* used in this study were collected from the surface of the sand. If it can be assumed that females are generally more active (*i. e.*, spend more time on the surface) than males, then a sample of animals taken from the surface should contain a larger proportion of females than is actually present in the total population.

Field Observations

While a comprehensive field study of *Olivella biplicata*'s activity cycle was not undertaken, numerous trips to the field have provided opportunities to qualitatively confirm the activity cycle. Most of these observations, taken at various times during the day and night, were made at the collecting site, a sandy spit in Bodega Harbor. *Olivella* were observed at this intertidal site during low water when they were still covered by 10 to 50 cm of water. In addition, a few observations were made on subtidal *Olivella* along the bottom of the nearby boat channel (6 to 7 m deep). The *Olivella* population in this channel appears to be continuous with the intertidal population. Both intertidal and subtidal observations confirmed the activity cycle that was seen in the laboratory: many *Olivella* were active on the surface of the sand during the night; few were active during the day.

DISCUSSION

Olivella biplicata maintained under natural lighting conditions were active primarily at night. Most of the snails remained buried in the sand throughout the day, occasionally moving beneath the surface for short distances. At twilight snails began to emerge from the sand, and, within 2 hours, large numbers were moving across the surface. Direct responses were given to light and to dark (Table 1), but *Olivella* also appeared to anticipate changes in the natural lighting cycle (Figure 1): the numbers of animals on the surface always began to increase sometime before dark and always began to fall several hours before dawn. This anticipation suggests the possibility of an endogenous circadian rhythm. Field observations confirmed the general activity cycle. Few snails were seen on the surface during the day, whereas hundreds were seen during the night. Similar field observations have been made by other investigators (Edwards, 1969b; Van Veldhuizen, personal communication).

The nocturnal habit of *Olivella biplicata* may be an evolutionary response to the threat of visual predators. *Olivella biplicata* is a slow-growing animal with a low recruitment and an estimated life-span of greater than 10 years (Stohler, 1962, 1969; Edwards, 1968, 1969a). With a reproductive strategy of this sort, efficient and effective means of avoiding potential predators would appear to be important. Gulls and other shore birds occasionally prey upon *Olivella* species during low tide (Cottam, 1939; Grinnell, Bryant & Storer, 1918; Martin & Uhler, 1939; Edwards, 1969a; Reeder, 1951; Stohler, 1969). Fish are also known to consume these snails (Iverson, 1972; Turner, Ebert & Given, 1969). The numbers of *O. biplicata* actually taken by these visual predators would appear to be very small, however, since adult *O. biplicata* have excellent survivorship (Edwards, 1969).

While the general activity cycle of the *Olivella* population was relatively well-defined and predictable, the activity patterns of the individuals that made up the population were quite variable. A portion of this variability was related to differences in size and sex. Male *Olivella* in this sample were considerably larger than females: males ranged in shell length from 22.7 to 27.9mm, whereas females ranged from 18.2 to 23.9mm. This supports earlier findings (Edwards, 1968, 1969b) that male *Olivella biplicata* grow faster and attain larger maximum sizes than do females. Since both sexes of *O. biplicata* have been reported to mature sexually at a shell length of 16 mm (Edwards, 1968), all of the snails in this sample were of sufficient size to be considered sexually mature.

In the present study, smaller *Olivella* (mostly females) spent more time on the surface and were more active than larger snails (mostly males), and this was true both during the day and during the night. These results are opposite to the results reported by Edwards (1969b); his general conclusion was that large *Olivella* were more active than smaller *Olivella*. Some of the apparent contradiction may be related to differences in the emphasis placed on daytime and nighttime activity in the two studies and also to different lighting conditions. Edwards (*op. cit.*) emphasized activity taking place during daylight hours; in contrast, the present study emphasized the light/dark cycle of activity, and consequently, activity taking place at night. Edwards' experiments were also conducted indoors with lighting provided by a nearby window. He reported that for a short time each morning, the animals were exposed to direct sunlight through this window, and for the rest of the day, they were in shadow. Considering the day as a whole, he concluded that large snails were generally more active than small snails; he added, however, that during the short exposure to direct sunlight, smaller animals were more active and were found more often on the surface than were larger snails. Edwards' results in bright light are in agreement with the conclusions of the present study, which was conducted under relatively bright, outdoor conditions.

While the present study on *Olivella* concentrated specifically on the behavioral effects of a light/dark cycle, many factors in addition to light clearly influence this snail's activity. For intertidal snails, the tidal cycle is probably the most important of these. *Olivella* which are exposed by the receding tide immediately bury themselves in the sand (Stohler, 1969); they remain dormant until the water returns, regardless of the time of day or night (Phillips, unpubl. data). Stohler (*op. cit.*) also reports that similar responses to tidal conditions may occur even when the animals remain covered by several decimeters of water. The presence of food also influences activity; if a piece of crab or mussel meat is placed on the surface of the sand during the day, many of the buried *Olivella* will suddenly emerge and begin searching for the food (Phillips, unpubl. data). Mating condition may influence activity; sometimes during experiments, a male would emerge from the sand to begin courting a particular female that passed by on the surface. Many more factors, such as the amount of turbulence and the presence of potential predators, are probably also important. So, while the light/dark cycle clearly exerts a major influence on the behavior of *Olivella*, the activity patterns of this snail are complex and intricately related to a variety of factors.

SUMMARY

1. The activities of individually marked *Olivella biplicata* were monitored every hour for 5 complete light/dark cycles. The animals were maintained in a plexiglass trough that was supplied with running seawater and located outdoors.
2. The *Olivella* were active primarily at night. During the day, most of the snails remained buried in the sand and rarely moved; at twilight, they began to emerge from the sand, and, within 2 hours of darkness, maximum numbers of snails were active on the surface.
3. While the general activity cycle of the *Olivella* population was well-defined and predictable, the activity patterns of the individuals that made up the population were quite variable. A portion of this variability was related to differences in size and sex.
4. Females in this sample were considerably smaller than males (t-test; $p < 0.001$).
5. Small snails were generally more active than large snails (correlation coefficient $= -0.52$; d. f. $= 55$; $p < 0.001$).
6. Females were more active than males (t-test; $p < 0.001$).
7. Field observations during the day and night confirmed the existence of *Olivella*'s activity cycle.

ACKNOWLEDGMENTS

All of this work was performed at the Bodega Marine Laboratory of the University of California. I wish to thank the Director, Dr. Cadet Hand, for making these facilities available. In addition, I conducted some pilot experiments on the activity of *Olivella biplicata* several years ago at the Hopkins Marine Station of Stanford University. Although none of these pilot experiments is reported in this paper, some of my ideas originated there. I wish, therefore, to acknowledge Dr. Donald P. Abbott and the Director, Dr. John H. Phillips, for their past assistance and support. The field observations of subtidal *Olivella* were made by Mr. Harvey D. Van Veldhuizen.

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Size and Age-Specific Predation by *Lunatia heros* (Say, 1822) on the Surf Clam *Spisula solidissima* (Dillwyn, 1817) off Western Long Island, New York

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(5 Text figures)

INTRODUCTION

The potential importance of the naticid gastropod *Lunatia heros* (Say, 1822) as an important predator on the surf clam *Spisula solidissima* (Dillwyn, 1817) is recognized (Ropes, Chamberlin & Merrill, 1969), but there are little quantitative data on rates of predation or specific predator-prey relationships. *Spisula* is a commercially valuable species and the absence of this information is detrimental to the protection and management of surf clam populations. Part of the problem lies in the difficulties in the quantitative sampling of *Spisula* populations and in the low density of *Spisula* in natural habitats. The commercial hydraulic dredge, which is the standard sampling device for surf clams, does not capture the small individuals, which are washed through the 2-inch (50mm) rings.

In this report, data are presented on the size and age structure of *Spisula* eaten by *Lunatia heros*. The problem of sampling small individuals was partially avoided by the analysis of beached animals and valves. Disadvantages of this approach include: a) no information on the density of living *Spisula* is possible; b) the possibility exists that size/age structure of beach shells may not reflect the population structure offshore due to differential rates of accumulation and destruction; c) the possibility that beach shells originate from areas far distant and therefore do not reflect the age structure of the adjacent nearshore population. The major advantages of the approach taken in this study are the easy availability of size classes of *Spisula* which are not usually captured with commercial gear, and the possibility of collecting large numbers of bored *Spisula* valves which are generally not available in dredged samples.

Because of the location and character of the study area – the extreme SW end of Long Island – some of the disadvantages noted above are minimized. Information on the size structure of the adjacent nearshore populations of *Spisula* is available from a recent NMFS survey of inshore surf clam resources carried out by the author in 1974/1975. From these and other studies of the inner New York Bight, it is evident that the great majority of recent valves washed onto the Rockaway Beach are derived from the extensive populations of small surf clams which occur within 1½ to 5km offshore.

ACKNOWLEDGMENTS

I wish to acknowledge the courtesy of Dr. Jack Pearce, NMFS, Sandy Hook, New Jersey Laboratory for allowing me to examine and measure a collection of surf clams from Twin Gun Beach, New Jersey.

METHODS AND MATERIALS

A. Study Area:

Beach collections of recently washed-up clams were made at Rockaway Beach approximately 1½km east of the Rockaway Point Jetty marking the extreme western tip of Long Island (Figure 1). The Rockaway Peninsula, which at this point is part of the Gateway National Recreation Area, is bounded on the south and west by the lower reaches of New York harbor. Extensive populations of *Spisula* occur directly offshore (south) and in the in-

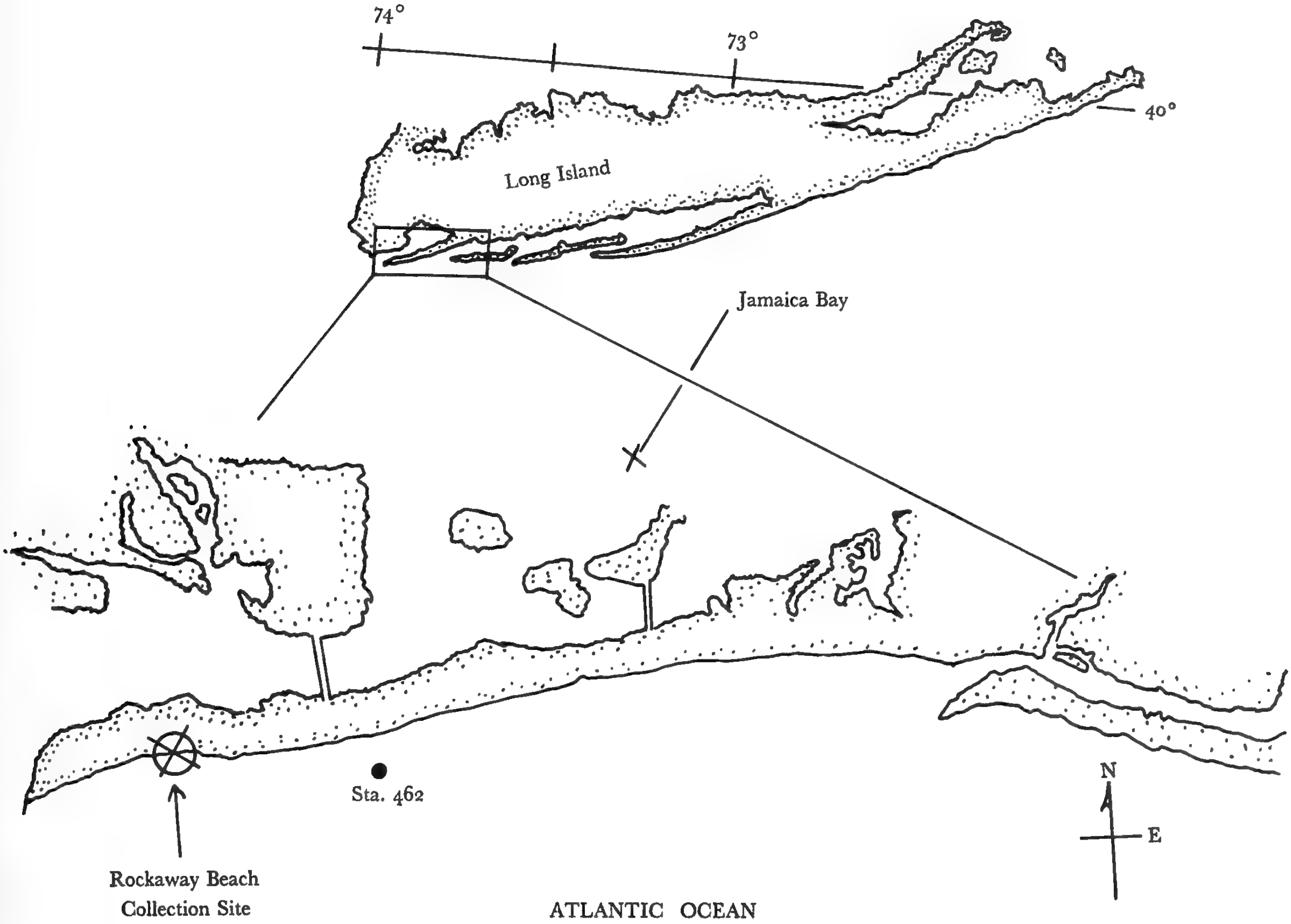


Figure 1

Map of the Study Area

Station 462, located 800 m south of the Rockaway Peninsula, was sampled in August 1974 as part of an NMFS-sponsored survey of the inshore resource of surf clams off Long Island.

shore waters to the east (off the Long Island coast) but not to the west. These clams support a small bait clam fishery centered in nearby Brooklyn. This particular stretch of beach is famous for periodical, massive wash-ups of *Spisula* following winter storms (Jacot, 1920). In fact, living clams are almost always available in small numbers on this beach.

B. Analysis of Bored *Spisula*:

Although the boring snail *Polinices duplicatus* (Say, 1822) occurs occasionally in dredge hauls, no living specimens have been observed during 3 years of observations on this beach. On the other hand, *Lunatia heros* is extremely abundant offshore and is frequently washed up alive at all seasons. Moreover, the occurrence of ***Lunatia*** egg masses in the Spring indicates the abundance of this species nearshore. There is no doubt that this species is primarily responsible for the predation discussed below.

Quantitative collections of bored *Spisula* valves were made in May, 1976. Every bored valve was collected at low tide along an approximately 100 m stretch of beach, between the upper drift line and the water's edge. All valves showing bore holes were collected and returned to the laboratory for analysis. On the same date, 4 1 m² quadrats were sampled near the low water mark to ascertain the size-frequency distribution of all *Spisula* valves regardless of the cause of death.

The shell length corresponding to each observable growth ridge was measured for the 135 bored valves collected in May (see above). This procedure was repeated on 102 paired valves (*i. e.*, one valve of an attached pair) in June, 1976. A similar analysis was carried out on 46 paired valves collected at the same location in July and August, 1976, with the exception that the latter sample was selected on the basis of the clarity of growth ridges, *i. e.*, valves were selected in which all growth ridges were discernible.

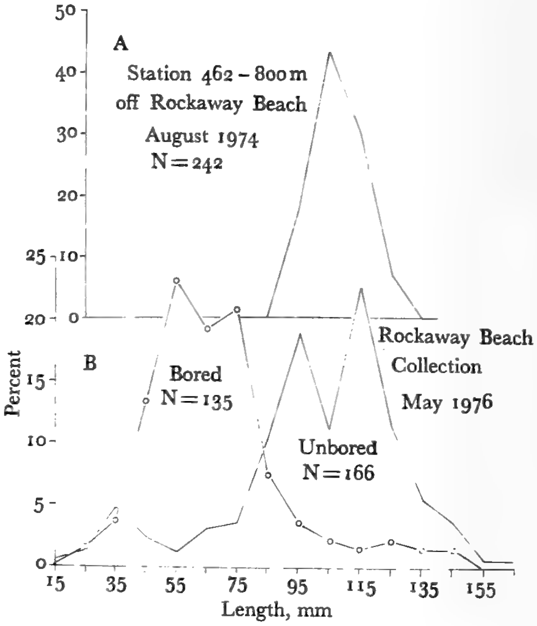


Figure 2

A. The size-frequency distribution of adult clams collected at station 462 off Long Island, August 1974

B. Size-frequency distribution of bored and unbored *Spisula* valves from Rockaway Beach, New York, collected in May, 1976

RESULTS

A. Size Distribution of Rockaway Beach Clams:

West of Jones Inlet, inshore surf clams are generally smaller than those occurring further east (Franz, 1976). Figure 2A shows the length-frequency distribution of clams at station 463 off Rockaway Beach as determined in the National Marine Fisheries Service survey of August, 1974. Figure 2B shows the size distribution of the Rockaway Beach collections of both bored and unbored *Spisula* in May, 1976. There is general agreement in the size range and distribution of unbored beach clams and offshore clams from the NMFS survey with the exception of the absence of clams less than 85 mm in the latter. This is probably due primarily to the inability of the commercial hydraulic clam dredge which was used in the 1974 survey to retain smaller clams. Clams present on the beach in May are considered to be a reasonable sample of the adjacent inshore (800 m) population. Figure 2B also indicates that over 80% of the bored valves are less than 80 mm. Although some bored valves were observed up to about 140 mm.

B. Possible Age Distribution:

In order to determine the age distribution of the bored clams, it is necessary to estimate the age of clams from size-frequency data. At present, the growth rates of ***Spisula*** are uncertain. Growth curves of *S. solidissima* have been proposed by various workers (Belding, 1910; Westman, 1946; Yancey & Welch, 1968; Loesch, 1975) based on the analysis of presumed annual growth ridges on the shell. However, growth estimates of one-year animals in all of the above studies are significantly larger than those observed on the bored Rockaway Beach shells

Table 1

Growth Statistics—Rockaway Beach Clams

Ridge No.	N	Mean (mm)	s.d.	0.05 Confidence Interval
1	46	20.22	2.449	0.730
2	45	37.00	5.543	1.652
3	46	50.56	6.684	1.992
4	46	68.19	6.177	1.842
5	46	81.46	7.092	2.114
6	44	92.89	8.627	3.988
7	31	104.64	7.026	3.582
8	5	115.0	3.937	4.722

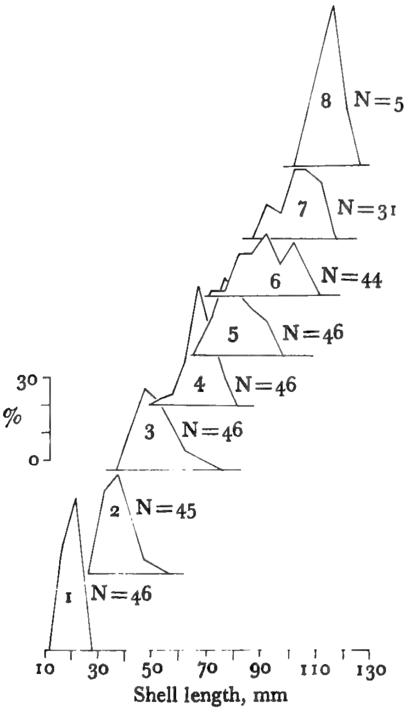
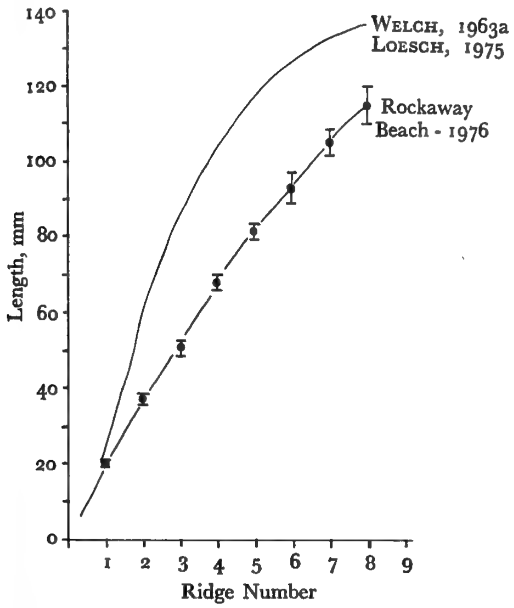


Figure 3

Frequency distribution of shell lengths associated with growth ridges from a suite of paired valves collected on Rockaway Beach in July and August 1976



in the present study. Therefore, a separate analysis of the growth ridges of the Rockaway shells was carried out. It was possible to observe and measure the first 8 growth ridges with relative ease. These data are presented in Table 1 and the frequency distribution of each ridge group (one through eight) is shown in Figure 3. These data are compared in Figure 4 with a growth curve proposed by A. Welch (1963) for a New Jersey population and corrected recently by Loesch (1975). It is clear from these data that the observed growth rates of the Rockaway clams are significantly lower than the rates observed in the other population.

Using the above information on size and presumed age, the probable age of both bored and unbored samples was determined. This indicates (Figure 5) that maximum predation occurred among 3 and 4 year clams, and dropped precipitously in clams older than 5 years.

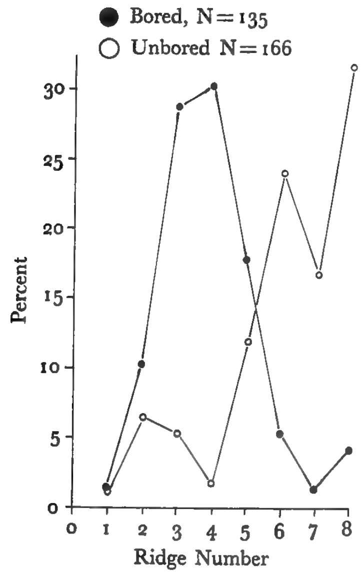


Figure 5

Age distribution of bored and unbored Rockaway Beach valves of *Spisula*

(← adjacent column)

Figure 4

Growth curves corresponding to ridge numbers 1-8 based on analysis of paired Rockaway Beach clams (lower curve). Vertical bars represent 95% confidence intervals of the mean. Upper curve represents comparable portion of a growth curve for offshore New Jersey clams based on Welch (1963) as modified by Loesch (1975)

DISCUSSION

Evidence presented above supports the conclusion that the Rockaway Beach collection of surf clam valves are largely contributed from the adjacent inshore population of living *Spisula*. However, the size distribution of bored valves does not necessarily reflect the true size distribution of prey since there is a chance that very small bored valves are underrepresented on the beach.

It is clear that predation by *Lunatia heros* is most intense on smaller clams (less than 80 mm), and that this component of the population is less than 5 years old. However, it is significant that older and larger clams are not completely immune to attack since bored valves of up to 160 mm were occasionally observed. As emphasized by Edwards (1974, 1976) the existence of an upper critical prey size, beyond which the probability of predation is small, may have been an important component in the evolved reproductive strategies of the bivalve prey of naticid predators. Since it is likely that reproductive output of bivalves such as *Spisula* increases exponentially with increasing body size, the reproductive value of larger individuals, *i. e.*, those which are by virtue of their size relatively immune to attack, is likely to be significantly greater than the reproductive value of smaller animals. This is a factor for consideration in management decisions regarding the establishment of size limits for harvesting surf clams. It may make better sense to harvest populations of predominantly smaller clams – for which man must compete anyhow with *Lunatia* – and conserve populations of predominantly larger clams which are less subject to predation.

Inshore populations of *Spisula* along Long Island differ in size structure. West of Jones Inlet, clams are generally smaller, and the component of very large clams is absent. East of Jones Inlet, the reverse is true, *i. e.*, populations are composed of very large clams with relatively few individuals less than 100 mm (Franz, 1976). There are several alternate explanations for this including differences in settlement and survival of juveniles, differences in fishing intensity, etc. To these must be added the possible role of *Lunatia*. Since predation pressure by *Lunatia* is maximal on small clams, populations of predominantly small to medium clams (less than 100 mm) may suffer greater predation than populations composed of predominantly larger animals. It is reasonable to assume that predator density would also be higher in areas, such as western Long Island, characterized by abundant numbers of smaller clams. If this is true, the absence of larger clams may simply reflect the small proportion of individuals surviving to the critical size of predation immunity. Likewise, predator "carrying capacity" should be lower, off eastern Long Island, where most clams are relatively immune to *Lunatia* predation because of size. This reduction in predator density should increase the probability that small clams can avoid predation and survive to the critical size.

The importance of *Lunatia* as a consumer of surf clam production remains to be determined. In his recent elegant study of the ecology of *Polinices duplicatus*, based on field studies at all seasons, Edwards (1976) has reported that about 100 small *Mya arenaria* are consumed per individual predator per year. If we assume that *L. heros* harvests a comparable quantity of *Spisula*, each *Lunatia* would consume a quantity of clams which, had they reached commercially marketable size, would have been equivalent to about 70*l* (2 bu.) of clams per year. Whether this is a reasonable estimate of the potential role of *Lunatia heros*, and if so, whether this level of predation would constitute a significant proportion of *Spisula* production are problematic. However, *Spisula* shares with many temperate bivalves the characteristic of periodic recruitment. Although spawning occurs annually (Ropes, 1968), significant recruitment does not. The average time span between successful recruitments of *Spisula* is not known but may be as much as 4 or 5 years or perhaps longer. Assuming that *Lunatia* harvest roughly 5% of prey standing stock per annum (*e. g.*, see Green, 1968) and that successful recruitment occurs one year in 5, mortality due to *Lunatia* alone would approach 20% during the intervening years of minimal recruitment. During this time period, of course, other sources of mortality including fishing mortality would continue to occur. If fishing mortality continues at a constant rate during this same time interval, *i. e.*, 5% per annum, then standing stocks could decline as much as 40% due to the combined *Lunatia* and human predation. Under these conditions, the viability of remaining stocks could be endangered.

Review of the size frequency distribution of surf clams from the mid-Atlantic region between 1965 and 1974

(Ropes, 1975) indicated that the components of small to medium clams (less than 125 mm) comprise a small proportion of total clams in all areas surveyed (22% and 11% respectively). Since these are the clams most susceptible to predation, it may be that predation is a primary factor in accounting for skewed size distributions of *Spisula* populations.

The apparently lower growth rate of inshore Rockaway clams relative to other populations, if it can be confirmed by more direct growth studies, is interesting in that it seems to support a suggestion by H. H. Haskin (personal communication) that inshore New Jersey clams are smaller, even stunted, compared with populations from deeper water. Westman (1946) also noted that clams from off Long Beach (western Long Island) tended to exhibit significantly slower growth than populations further east (Jones Beach). The reasons for such differences remain to be discovered but could be related to increased sediment instability and turbulence in shallow waters.

The size of clams at the end of their first growing season (corresponding to ridge No. 1) ranged in this study from about 12 to 28 mm with a mean of 20 mm, a value fairly close to that reported in other studies. The lowest reported value is 10 mm at Boothbay Harbor, Maine (Yancey & Welch, 1968). A sample of small *Spisula* collected in the NMFS survey of inner New York Bight in February 1969 (station 48: Pearce, 1972) averaged 18.1 mm. Likewise, a large homogeneous sample of small *Spisula* from "Twin Gun Beach" near Sandy Hook, New Jersey, collected in November 1969, ranged from 9 - 25 mm with a modal size of 17.5 mm. Ropes & Merrill (1970) reported a dense population of surf clams in October 1964 averaging 21.1 mm at Wallops Island, Virginia, which averaged 22.5 mm by 20 November of that year. Thus, data from a variety of sources indicate that O-class clams in their first season will attain an average size of 10 - 25 mm with the higher averages occurring further south. By the end of the first year, however, the Wallops Island clams noted above attained a length of 44 mm (Ropes & Merrill, *op. cit.*) which agrees also with Welch's data as modified by Loesch (1975). As seen in Figure 4, however, Rockaway clams at 1 year (*i. e.*, at a size about halfway between ridge nos. 1 and 2) are still less than 30 mm. Thus, the low growth rates of the Rockaway inshore clams may reflect a lag in the initiation and rate of new growth in the Spring of their second growing season.

SUMMARY

A comparison of the size distribution of *Spisula* valves with bore holes of *Lunatia heros* with unbored valves indicated that *Lunatia* predation is largely limited to clams less than 80 mm. An analysis of growth ridges on paired, beach-collected Rockaway clam valves indicated an estimated growth rate which is significantly lower than values predicted from other proposed curves available in the literature. Application of the growth information to the collections of bored *Spisula* valves showed that *Lunatia* tends to select clams under 5 years of age. These data suggest that although the adjacent subtidal populations of *Spisula* are susceptible to *Lunatia* predation, populations of predominantly larger clams (> 100 mm) occurring further east on Long Island are substantially immune to *Lunatia* attack. This suggests the possibility that size-specific predation by *Lunatia* may operate to maintain the smaller size structure of western Long Island populations of *Spisula*.

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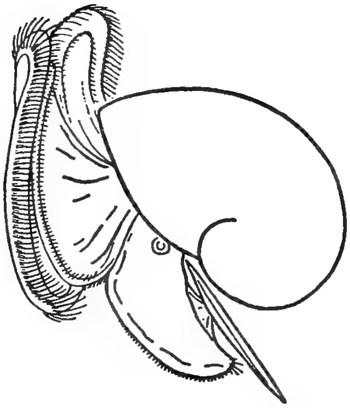

A New Species of *Lithophaga* (Bivalvia) from the Great Barrier Reef, Australia

BY

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(2 Plates)

INTRODUCTION

DURING 1974 I STUDIED the ecology of burrowing bivalves (terminology after CARRIKER & SMITH, 1969: 1011) at the Great Barrier Reef (GBR), where I found 5 *Lithophaga* species restricted to live coral (cf. OTTER, 1937; IREDALE, 1939). One of them is an undescribed species. The species are:

Lithophaga lessepsiana Vaillant, 1865
Lithophaga lima Lamy, 1919
Lithophaga hanleyana sensu Gohar & Soliman, 1963
 (non Reeve, 1857)
Lithophaga simplex Iredale, 1939
Lithophaga kuehnelti Kleemann, spec. nov.

DESCRIPTION OF THE NEW SPECIES

MYTILOIDA

MYTILACEA

MYTILIDAE

Lithophaginae

Lithophaga Röding, 1798

(Leiosolenus) Carpenter, 1857

Lithophaga (Leiosolenus) ***kuehnelti*** Kleemann, spec. nov.

(Figures *1c*, *2*)

Named in honor of Wilhelm Kühnelt with regard to his "Bohrmuschelstudien" I, II, and III (1930, 1933, and 1942, respectively).

Holotype: BM(NH) Reg. No. 1976135; size: length, 28.4mm; height 9.0mm; breadth 8.6mm (Figure *1c*).

Paratypes: NHMW 80635 (dry), NHMW 80636 (formalin), Vienna, Austria.

Type Locality: Heron Island (Lat. 23°27′S; Long. 151°55′E), Capricorn Group, GBR, Queensland, Australia.

Description: Shell small, thin, fragile, translucent, and smooth. Periostracum pale-yellowish, covered by more than one type of calcareous matter. The soft paste-like, non-adhesive deposits are on the dorsal part of the shell as well as on the corresponding part of the burrow. On the ventral part of the burrow, which is free of calcareous deposits, in a few cases a very fine longitudinal ridge can be observed, where the byssus is attached (this species does not rotate). Ventral margin straight, dorsal margin almost parallel; umbonal parts not quite at the anterior end, causing a slight depression in the lateral outline, otherwise both ends of shell rounded. The characteristic feature is the incrustation of the posterior ends of the valves, which is adhesive, rather hard, smooth, thickening towards the ends, and slightly protruding beyond them, where it generally terminates in a conspicuous manner, similar to concave lips of a mouth (Figure *2*). Due to the individual position of the orifice on the coral surface and the angle of the burrow, these lips are modified and rarely equal on both valves of a specimen.

Habitat: *Lithophaga kuehnelti* occurs in *Acropora (Isopora) palifera* (Lamarck) (Figure *3*) at various sites off Heron Island and One Tree Island, both in the Capricorn Group, GBR. Host corals from well exposed sites (in terms of water movement) may be crowded by *L. **kuehnelti***, without showing any harm (cf. WOOD-JONES, 1910: 127). An encrusting *A. palifera* (25×15×9cm) from One Tree Island contained 150 specimens as well as 34 barnacles.

Distribution: At the GBR the species is common in the subtropical part at Heron Island, One Tree Island, and Wistari Reef, all 3 in the Capricorn Group, and less common to rare at the tropical Lizard Island. The local distribution pattern seems to be related to the water movement, but not to the available surface area of the host coral (Kleemann, in prep.). In the bivalve collection of the BM(NH) there is a sample of *Acropora (Isopora) palifera* collected by J. D. Taylor from Addu Atoll, Maldive Islands in May 1975 with 12 specimens of ***Lithophaga kuehnelti*** still in their burrows and 4 loose specimens (BM[NH] Reg. No. 1976134). In the coral collection of the British Museum (Natural History), the following samples contain *L. **kuehnelti***: BM(NH) Reg. No. 1892.6.8.50 and 51, both *A. palifera* from Capricorn Islands, GBR; BM(NH) Reg. No. 1887.1.29.5, *A. palifera* from New Guinea; BM(NH) Reg. No. 1884.12.11.17, *A. palifera* from Shortland Island, Solomon Islands. Other samples of *Acropora-Isopora* were found infested by *Lithophaga*, but without breaking up the corals I could not tell with certainty if the burrower was indeed *Lithophaga* ***kuehnelti***.

COMPARISON WITH OTHER SPECIES

WITH WHICH IT COULD BE CONFUSED

With the conspicuous posterior incrustation present, *Lithophaga **kuehnelti*** can easily be distinguished from other small *Lithophaga* species, such as *L. lessepsiana* Vaillant, 1865 (Figures *1*d, e; *4* a-d), with which it sometimes occurs in *Acropora palifera*. *Lithophaga lessepsiana*, described from *Stylophora pistillata* by Vaillant (1865: 124) can be regarded as the first record of *Lithophaga* from live coral, although not actually stated as such. *Lithophaga **kuehnelti*** can be distinguished from *L. hanleyana* Gohar & Soliman, 1963 by the differences in the patterns of their posterior incrustations (Figures *2*, *4*, *5*). Without its incrustation, *L. **kuehnelti*** is very similar to *L. simplex* Iredale, 1939; this species was determined with reference to Australian Museum Reg. No. C. 105340 (part), as neither the type nor the paratypes could be investigated. The description and figure of *L. simplex* (Iredale, 1939: 421; plt. 6, fig. 25) are inadequate and I consider it worth while to give more details and figures.

Lithophaga (Leiosolenus) simplex Iredale, 1939

(Figures *1*b, *6*a - *6*d, *7*)

= *L. cumingiana* Otter, 1937, not Reeve, but only as described from living *Favia* (BM[NH] Reg. No. 1952.1.29.845-854; one specimen of this lot is shown in Figure *6*a).

Description: Shell thin, fragile, translucent, smooth, with faint growth lines. Periostracum pale-yellowish (colour of the living animal yellowish fluorescent green, except the chalky layers). No real incrustation, but fine, thin, very smooth chalky layer, sometimes covering the whole surface, rarely completely absent, but more often showing bare areas; no tip or prolongation of the posterior end (Figure *8*). Collected specimens reaching 32.4 mm in length. The shell has a straight ventral margin, the dorsal margin is generally angulated (Figures *6*a to *6*c), but is sometimes almost parallel to the former (Figure *6*d). The position of the dorsal angulation is in most cases slightly anterior, rarely posterior to the middle of the

Explanation of Figures *1* to *4*

Figure *1*: *a Lithophaga hanleyana* (Reeve) *sensu* Gohar & Soliman (1963); *b Lithophaga simplex* Iredale; *c Lithophaga **kuehnelti*** Kleemann, spec. nov., holotype (BM[NH] Reg. No. 1976135); *d Lithophaga lessepsiana* Vaillant (host coral *Stylophora pistillata*, Red Sea), part of BM[NH] Reg. No. 1871.9.8.53; *e Lithophaga lessepsiana* Vaillant (host coral *Heteropsammia michelini*, Lizard Island, GBR). Scale in mm.

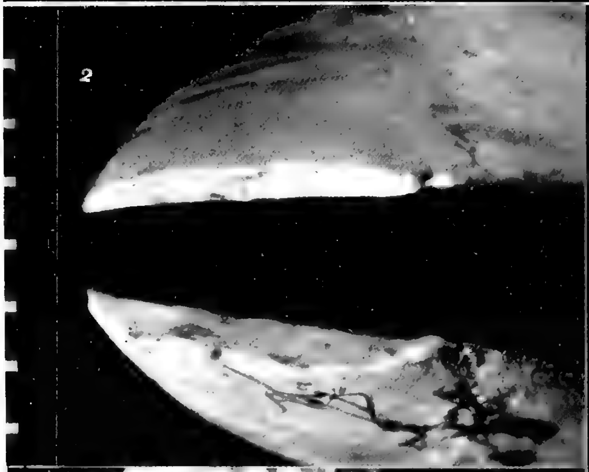
Figure *2*: The conspicuous incrustation of the posterior end of *Lithophaga **kuehnelti***. Scale in mm.

Figure *3*: *Acropora (Isopora) palifera* (Lamarck) *in situ*, showing orifices of burrows. Host coral of *Lithophaga **kuehnelti*** and rarely of *Lithophaga lessepsiana*. ×1.5.

Figure *4*: Four specimens of *Lithophaga lessepsiana*; *c* and *d* are the same as in Figure *1d* and *1e*. Scale in mm.

All photographs, except Figure *3*, by P. Richens, courtesy of the Trustees of the British Museum (Natural History)


1
a
b
c
d
e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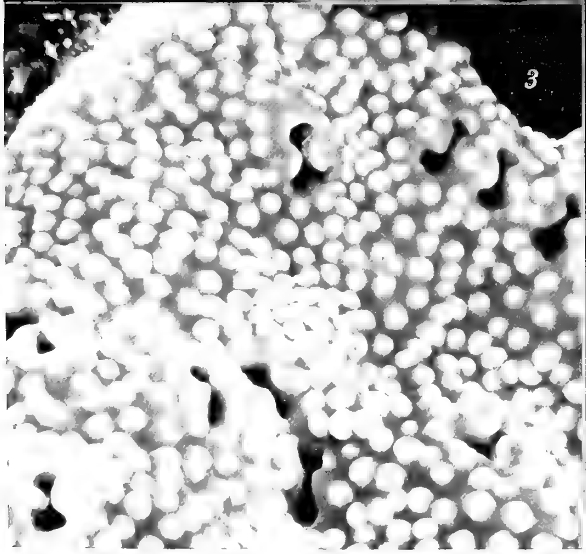
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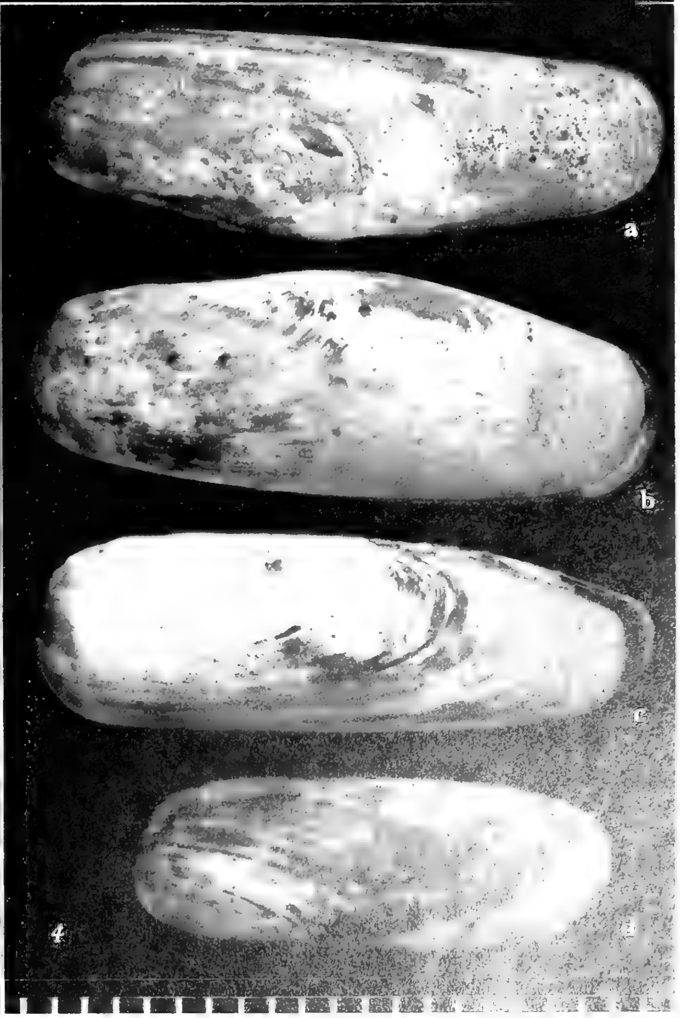
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shell. Siphons with dark pigmentation, edges of the mantle lighter coloured.

Habitat: *Lithophaga simplex* was found in *Porites* and *Symphillia* (Iredale, 1939); in *Favia* (Otter, 1937); in *Porites* (BM[NH] Reg. No. 1976136). I found most of *L. simplex* burrowing in *Favia* (*F. pallida*). Other host corals are *Lobophyllia*, *Symphyllia*, and *Goniastrea retiformis*. The highest population density was observed in a living *Favia* (18 × 12 × 8 cm), inhabited by 63 specimens. Generally infestation is much less, but *Favia* seems to be the preferred host at Lizard Island, GBR. The infested *Porites* samples I examined contained only *L. hanleyana* Gohar & Soliman (Kleemann & Rosen, in prep.) (Figures *1*a, *4*, *5*).

Distribution: Low Island, GBR (Otter, 1937; Iredale, 1939); Palfrey Island (near Lizard Island) in *Favia*; Lizard Island, GBR, in *Favia pallida*, *Symphillia*, and *Lobophyllia*; Wistari Reef, Capricorn Group, GBR, in *Lobophyllia*; One Tree Island, Capricorn Group, GBR, in *Goniastrea retiformis*. In the bivalve collection of the British Museum (Natural History) there is one specimen, BM(NH) Reg. No. 1976136, collected by J. D. Taylor in December 1971 at Pungutiayu, Shimoni, Kenya (Admiralty Chart 998), which in my opinion is a *L. simplex*.

DISCUSSION

All *Lithophaga* species show considerable variation in shape and outline (Figures *4*, *7*; Lynge, 1909: 138 (42); Kleemann, 1974: fig. *3*, *Lithophaga lithophaga* Schalenformen). Sometimes it is obviously influenced by the thickness of the substratum, *e. g.*. *L. kuehnelti* from branched upgrowing forms of *Acropora palifera* are more elongated than those from encrusting colonies of the same host coral. There is also a considerable difference in the relationship between length of the burrow and width of the orifice (Kleemann, in prep.).

The geographical distribution of most subtropical and tropical *Lithophaga* species from dead as well as live coral is fairly wide, but there seems to be a rather distinct difference between Atlantic and Pacific (including the Red Sea) forms.

For the encrusted *Lithophaga* species, in my opinion, the pattern of the calcareous deposits, especially of the posterior end, is the best characteristic for specific determination (Soliman, 1969: 889). Even there we should not be too dogmatic, for observations in the field and many samples have shown that it is impossible to find identical stereotyped copies of a pattern, as would be expected from artificial products. Organisms have individual responses to environmental conditions. The stated differences are not just variations of one species, corresponding to the host coral infested, for *Lithophaga* species appear with the same pattern in different hosts. Furthermore, although rarely observed, one coral can be infested by more than one *Lithophaga* species, *e. g.*, *L. kuehnelti* and *L. lessepsiana* in *Acropora palifera*, as stated above. Gohar & Soliman (1963: 67) stated "a specificity of the boring species to the coral attacked obviously exists," and Soliman (1969: 887) "... and furthermore to a particular coral species." This seems to be the case only for *L. kuehnelti*, but not for any other *Lithophaga* species (Kleemann & Rosen, in prep.).

Some host corals have been given only generic assignments; this list will undoubtedly be extended by further investigations. A full discussion of coral-living *Lithophaga* species and their hosts, with specific determination, is in preparation (Kleemann & Rosen, in prep.).

SUMMARY

Five *Lithophaga* species from the GBR, Australia, are restricted to live host corals. *Lithophaga kuehnelti* infests *Acropora (Isopora) palifera* (Lamarck) at subtropical and tropical sites of the GBR, and was also found on Addu Atoll, Maldive Islands. *Lithophaga kuehnelti* is compared with *L. simplex* Iredale, 1939, for which are presented an extended description, including figures, and more biological data. *Lithophaga* species are recorded from a number of host corals, and in rare cases two *Lithophaga* species occurred in the same host.

ACKNOWLEDGMENTS

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Explanation of Figures 5 to 8

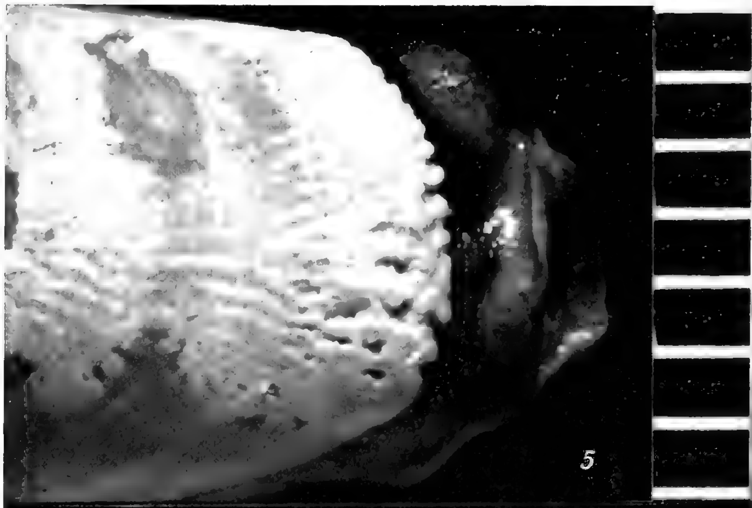
Figure 5: Posterior end of a preserved specimen of *Lithophaga hanleyana* (Reeve) *sensu* GOHAR & SOLIMAN (1963) in lateral view. Scale in mm.

Figure 6: The conspicuous incrustation of the posterior end of *Lithophaga hanleyana* (Reeve) *sensu* GOHAR & SOLIMAN (1963). Scale in mm.

Figure 7: Four specimens of *Lithophaga simplex* Iredale, showing variation in their outline; *a* part of BM[NH] Reg. No. 1952.1.29. 845-854; *b* same specimen as in Figure 1*b*. Scale in mm.

Figure 8: Posterior end of *Lithophaga simplex* Iredale; same specimen as in Figures 1*b* and 7*b*. Scale in mm.

All photographs by P. Richens, courtesy of the Trustees of the British Museum (Natural History)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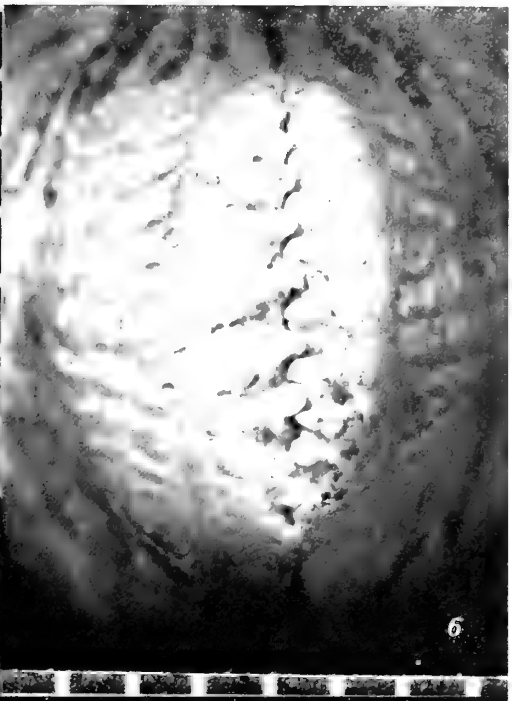
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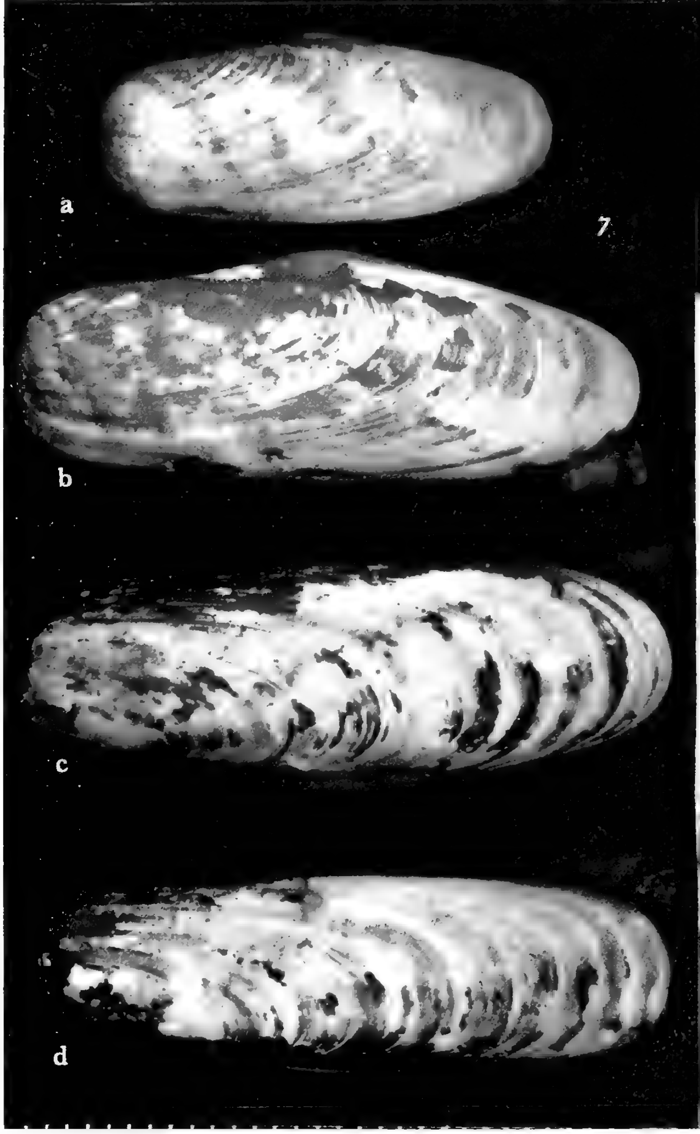
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a
b
c
d


8

The Effects of Season on Visual and Photographic Assessment of Subtidal Geoduck Clam *(Panope generosa* Gould*)* Populations

BY

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(1 Plate)

INTRODUCTION

THE WASHINGTON STATE DEPARTMENT of Fisheries routinely conducts surveys of clam stocks in Puget Sound for management purposes by divers equipped with SCUBA. Geoduck populations [*Panope generosa* (Gould, 1850)] are estimated by visual counts of "shows" (either siphons or marks in the substrate made by siphons) along measured transect lines (GOODWIN, 1973).

Earlier surveys demonstrated that the portion of the geoduck population detected by divers varied widely from 26% to 87% (GOODWIN, 1973). Variability in "showing" has been reported in other clam species (FLOWERS, 1973). Geoducks live permanently buried in the substrate, the average burrow being 52 cm deep in Hood Canal, Washington (ANDERSEN, 1971). When the siphons are extended up to or above the substrate surface and the clams are actively pumping water, they are readily visible to divers. At other times the siphons may be withdrawn below the surface and the siphon holes filled with sand, mud and detritus, leaving no indication of the clam buried below. Frequently marks in the substrate are observed and the presence of geoducks can be verified by divers probing the depression with their fingers. The siphons are large, up to 8 cm across and have a characteristic texture.

The objective of the present study was to more precisely define how the percentage of the geoduck population detected by divers changes seasonally in 2 small subtidal plots. The information developed in this study is used to correct diver survey data to provide more accurate population estimates.

The study area was a delta formed at the mouth of Big Beef Creek in Hood Canal, Washington. The delta has a gentle slope with sand and mud substrate. The study plots were established in a high density geoduck bed at the minus 9.1 m level (calculated from zero tide).

MATERIAL AND METHODS

Geoduck abundance within the 2 plots (each 45.7 m × 1.8 m) was assessed by divers placing small wire stakes next to each siphon observed. This process was repeated on each visit until no unstaked siphons were present. Considerable effort was expended to insure that all geoducks detectable were staked. The total number staked represented the actual geoduck population within the plots. All wire stakes were then removed and the plots allowed to return to normal.

Monthly counts of geoduck siphons were then made from January to December 1974 using our standard transect method and the percentage of the total estimated population observed during each monthly visit calculated. These observations were carried out by 3 divers who alternated between the plots to reduce the chance of bias from an individual diver remembering the location of certain geoducks within the plots.

In addition, 4 small 0.46 m × 0.46 m plots were photographed monthly to further document the seasonal change in "shows." The plots were carefully approached and photographed manually using a Nikonos 35 mm camera with ectachrome film. Tripod-mounted cameras proved unsatisfactory because the slightest disturbance of the bottom caused the clams to retract their siphons. MCERLEAN & HOWARD (1971) found that mechanical disturbance of the bottom affected "shows" of Eastern soft-shell clams (*Mya arenaria*).

RESULTS AND DISCUSSION

The percentage of the geoduck populations detected in the 2 plots varied from a low of 5% in January to a high of 59.8% in May, and averaged 38.0% in Plot A and 36.8%

Table 1

Number of geoducks and percentage of estimated populations
observed in monthly visual counts in two plots near Big Beef Creek, Washington

Date	Plot A (estimated geoduck population = 316)		Plot B (estimated geoduck population = 358)	
1974	Number observed	% observed	Number observed	% observed
				Jan.
Jan.	33	10.4	18	5.0
Feb.	101	32.0	117	32.7
March	142	44.9	169	47.2
April	133	42.1	170	47.5
May	172	54.4	214	59.8
June	168	53.2	178	49.7
July	105	33.2	106	29.6
Aug.	146	46.2	150	41.9
Sept.	144	45.6	174	48.6
Oct.	160	50.6	134	37.4
Nov.	195	30.1	114	31.8
Dec.	41	13.0	37	10.3
Mean		38.0		36.8

in Plot B over the entire year (Table 1). Student's T test was conducted on various combinations of the data using the arc sine transformation as suggested by SOKAL & ROHLF, 1969. Winter data (November-February) from Plot A were compared with winter data from Plot B and no significant differences were found (t = 0.25; d. f = 3). Plot A summer data (March-October) were also tested against summer data from Plot B and no significant differences were found (t = 0.27; d. f = 7). When data from Plots A and B were pooled and winter data tested against those from the summer, the differences were highly significant (t = 6.01; t. f = 11) demonstrating that the siphons were more readily detected by divers in the summer than in the winter.

Data from the photographic plots also demonstrated that geoducks were more easily observed in the summer months than in the winter (Table 2). The seasonal changes are shown in Figures *1*a - *1*d. None of the 5 geoducks present in the 0.45 m × 0.45 m plot can be seen in the February (winter condition) photograph. The May photograph (summer condition) clearly shows 5 clams with their siphons extended. Four can be seen in the July photograph; 3 of these are not distinct. In the November photograph, only 1 siphon mark can be seen.

Several small-scale surveys have been conducted in Puget Sound with underwater television and geoducks were found in water as deep as 60 m. Geoducks living at these depths apparently behave in a similar manner as

Explanation of Figures *1* to *4*

Plot 1: Geoduck Population = 5

Figure *1*: February 1974; no geoducks showing
Figure *2*: May 1974; all 5 geoducks showing, siphons open (pumping water)
Figure *3*: July 1974; 4 of 5 siphons showing, algae covered geoduck in lower left hand corner
Figure *4*: November 1974; 1 out of 5 geoducks showing as a slight mark, siphons are withdrawn, algae cover almost gone

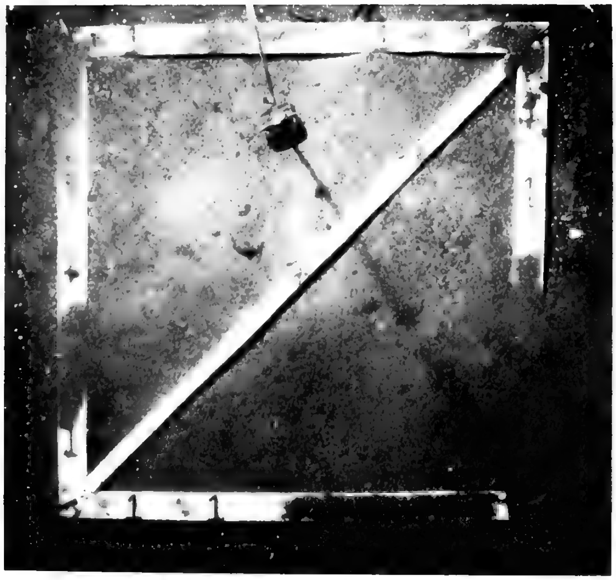

Figure *1*

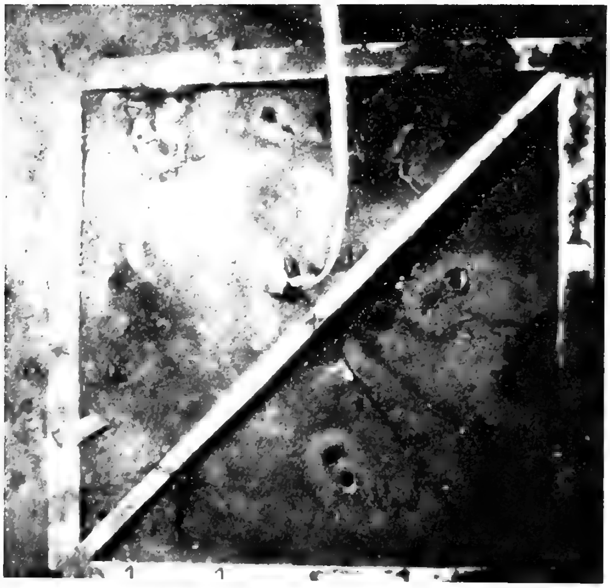

Figure *2*

Figure *3*

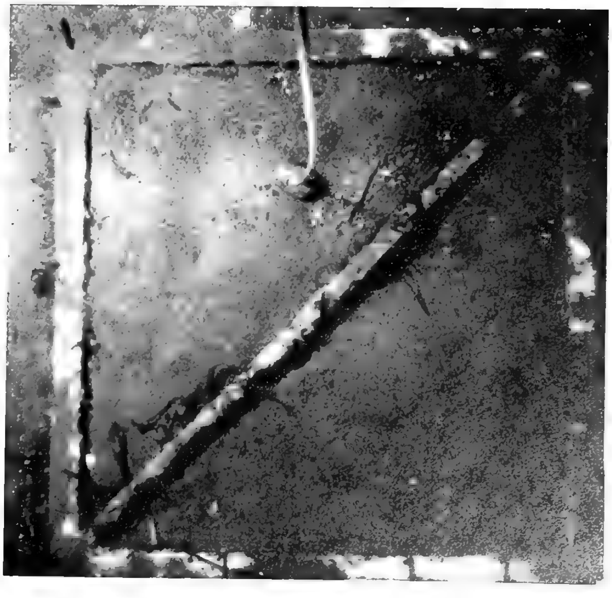

Figure *4*

Table 2

Number of geoducks and percentage of estimated populations observed in monthly photographs at four plots near Big Beef Creek, Washington

Date	Plot 1 (geoduck population = 5)		Plot 2 (geoduck population = 2)		Plot 3 (geoduck population = 3)		Plot 4 (geoduck population = 4)	
1974	number observed	percent observed	number observed	percent observed	number observed	percent observed	number observed	percent observed
Jan.	0	0	0	0	0	0	0	0
Feb.	0	0	0	0	1	33	1	25
March	4	80	2	100	0	0	2	50
April	4	80	1	50	2	66	3	75
May	5	100	2	100	3	100	4	100
June	3	60	2	100	2	66	4	100
July	4	80	0	0	1	33	1	25
Aug.	4	80	1	50	3	100	3	75
Sept.	2	40	2	100	3	100	4	100
Oct.	0	0	1	50	1	33	3	75
Nov.	1	20	0	0	1	33	0	0
Dec.	0	0	0	0	0	0	0	0
Mean		45		46		47		52

those found in shallow water with respect to seasonal "showing." They were readily visible on TV monitors in the summer and fall, but none were apparent during winter surveys in areas containing known geoduck populations.

It is apparent that season has a marked effect on the percentage of geoducks detectable in diver surveys or underwater photographs. Other factors, such as substrate type, algae cover, and water turbidity are probably important too. Differences in seasonal "showing" of geoducks are probably related to availability of food and to water temperature. When food is abundant during the spring and summer, growth of many Pacific Northwest clams is rapid. The reverse of this occurs during the winter (Bourne & Smith, 1972; Nosho & Chew, 1972; Tegelberg, 1964). When geoducks are actively pumping water (feeding) they are readily visible. Temperature may also affect seasonal "showing." I have observed geoducks in temperature controlled spawning experiments in our laboratory. The pumping rate and extension of their siphons is greater as the temperature is elevated up to about 18° C. Above this temperature, pumping is reduced or stopped and the clams begin to suffer mortalities.

Useful survey information of marine benthic organisms can be obtained with visual or photographic techniques, but for accurate results sources of errors need to be defined as well as the behavior of the population studied.

SUMMARY

The ability of divers to detect geoduck siphons on visual transects was found to vary greatly, depending on the season of the year. In the summer months, when the clams are actively pumping water, their siphons are easily seen by divers, but in the winter reduced pumping and retracted siphons make detection difficult. Similar changes in efficiency were noted in underwater photographs. Surveys of marine benthic organisms using direct visual counts, photographs or underwater TV should be corrected with information on the percentage of the actual population detectable.

ACKNOWLEDGMENTS

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I would like to thank Conrad Budd and Robert Dutton for the diving observations and underwater photographs.

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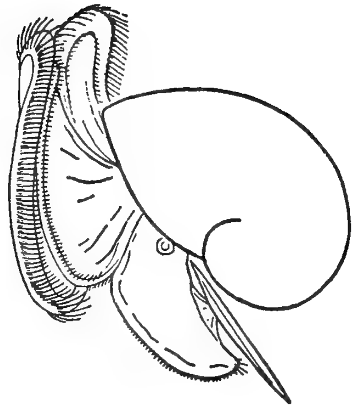

Cypraea: A List of the Species. III.

BY

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(1 Text figure)

THE QUESTION OF JUST which taxa should be considered valid as species of *Cypraea* (*s. l.*) has been subject to confusion ever since the publication of the various editions of the Systema Naturae of Linnaeus, starting more than 200 years ago.

Coming down to more modern times, in the first paper of the present series (DONOHUE, 1965) an analysis was made of the species considered valid by a number of modern authorities. There is no need to go into the details of that analysis again, but merely to summarize the final results, which were given in the form of 4 lists: **1**) 142 "non-controversial" species accepted by both SCHILDER & SCHILDER (1964) and WAGNER & ABBOTT (1964); **2**) 18 "provisional" species accepted by the Schilders but not by Wagner & Abbott; **3**) 18 "provisional species accepted by Wagner & Abbott but not by the Schilders; and **4**) 29 "controversial" species which at one time or another since about 1940 had been accorded specific status by one or more authorities. At that point there were, thus, 142 cowry species for the "lumpers" and 207 for the "splitters."

In the second paper of this series (DONOHUE, 1971) the foregoing analysis was up-dated by a detailed consideration of more recent opinions expressed by 2 of the foremost cypraeologists, viz. SCHILDER (1969) and BURGESS (1970). The net result then was that in Burgess' opinion there were 187 species, plus 4 either "doubtful or provisional," total 191, and that Schilder also accepted 191 taxa, 170 of which were species and 21 were "prospecies." As pointed out at that time this apparent numerical equality of 191 was an accident: some of the species accepted by Schilder were termed doubtful, variants, or not even mentioned by Burgess, while some of the species accepted by Burgess were termed prospecies, subpecies, clines, mutants, or not mentioned by Schilder. The two authorities agreed on 164 species (for the lumpers), with the total number between them being 207 (for the splitters).

Meanwhile, there has appeared a revised (and, alas, final) opinion from SCHILDER & SCHILDER (1971) and an apparently definitive book by TAYLOR & WALLS (1975). It thus becomes necessary to construct a concordance among the classic (and also apparently definitive) work of Burgess and the 2 more recent studies just cited.

Taylor & Walls, in their most welcome book, discuss and figure 187 species. Unfortunately, these 187 are not the the same as the 187 of Burgess, and the new list of the Schilders contains only 164 valid species. In order to express the differences (and agreements) when all 3 sources are considered, a 2-dimensional diagram is required. This is shown in Figure 1, where the 3 circles enclose the species recognized by the Schilders, Taylor & Walls, and Burgess, respectively. Areas of common recognizance occur when the circles overlap; lists of the species which occupy the various areas of Figure 1 are presented in Tables 2 to 5.

To summarize, it is seen that there is now agreement, where all 3 circles overlap, on 158 species, and that Burgess and Taylor & Walls agree on an additional 22 species (Table 2). Furthermore, the Schilders accept 8 more (Table 3), Burgess 7 more (Table 4), and Taylor & Walls 7 more (Table 5), not recognized by either of the others. The total numbers thus are now 158 for the lumpers and 202 for the splitters.

But the story does not stop here. There are, in addition, 10 species described subsequent to the publications of the Schilders and of Burgess, 4 of which also postdate Taylor & Walls. These are presented in Table 6, together with 1 species recently separated by BURGESS (1975). Comments in a recent review by CLOVER (1976) are also included. The total number of species could, accordingly, be as large as 213. I am not sure whether there is more, or less confusion than there was in 1971.

I would like to thank Phillip Clover for many helpful comments he made during the preparation of this paper.

Table 1

Species recognized by Schilder & Schilder, by Burgess, and by Taylor & Walls

achatidea Sowerby, 1837
albuginosa Gray, 1825
algoensis Gray, 1825
amphithales Melvill, 1888
angustata Gmelin, 1791
annettae Dall, 1909
annulus Linnaeus, 1758
arabica Linnaeus, 1758
arabicula Lamarck, 1810
argus Linnaeus, 1758
armeniaca[1] Verco, 1912
artuffeli Jousseaume, 1876
asellus Linnaeus, 1758
aurantium Gmelin, 1791
barclayi Reeve, 1857
beckii Gaskoin, 1836
bistrinotata[2] Schilder & Schilder, 1937
boivini Kiener, 1843
broderipii Sowerby, 1832
camelopardalis Perry, 1811
capensis Gray, 1828
caputdraconis Melvill, 1888
caputserpentis Linnaeus, 1758
carneola Linnaeus, 1758
catholicorum Schilder & Schilder, 1938
caurica Linnaeus, 1758
cernica Sowerby, 1870
cervinetta Kiener, 1843
cervus Linnaeus, 1771
childreni Gray, 1825
chinensis Gmelin, 1791
cicercula[2] Linnaeus, 1758
cinerea Gmelin, 1791
citrina Gray, 1825
clandestina Linnaeus, 1767
contaminata Sowerby, 1832
coxeni Cox, 1873
cribraria Linnnaeus, 1758
cumingii Sowerby, 1832
cylindrica Born, 1778
decipiens Smith, 1880
declivis Sowerby, 1870
depressa Gray, 1824
dillwyni Schilder, 1922
diluculum Reeve, 1845
edentula Gray, 1825
eglantina Duclos, 1833
englerti Summers & Burgess, 1965
erosa Linnaeus, 1758
errones Linnaeus, 1758
erythraeensis Sowerby, 1837
esontropia Duclos, 1833
exusta Sowerby, 1832
felina Gmelin, 1791
fimbriata Gmelin, 1791
flaveola[2] Linnaeus, 1758
friendii Gray, 1831
fultoni Sowerby, 1903
fuscodentata Gray, 1825
fuscorubra Shaw, 1909
gambiensis Shaw, 1909
gangranosa Dillwyn, 1817
gaskoini Reeve, 1846
globulus Linnaeus, 1758
goodallii Sowerby, 1832
gracilis Gaskoin, 1849
guttata Gmelin, 1791
hammondae Iredale, 1939
helvola Linnaeus, 1758
hirasei Roberts, 1913
hirundo Linnaeus, 1758
histrio Gmelin, 1791
hungerfordi Sowerby, 1888
interrupta Gray, 1824
irrorata Gray, 1828
isabella Linnaeus,1758
isabellamexicana[3] Stearns, 1893
katsuae Kuroda, 1960
kieneri Hidalgo, 1906
lamarckii Gray, 1825
langfordi Kuroda, 1938
lentiginosa Gray, 1825
leucodon Broderip, 1828
limacina Lamarck, 1810
lurida Linnaeus, 1758
lutea Gmelin, 1791
lynx Linnaeus, 1758
macandrewi Sowerby, 1870
maculifera Schilder, 1932
mappa Linnaeus, 1758
marginalis Dillwyn, 1827
marginata Gaskoin, 1849
mariae Schilder[4], 1927
martini Schepman, 1907
mauritiana Linnaeus, 1758
microdon Gray, 1828
midwayensis Azuma & Kurohara, 1967
miliaris Gmelin, 1791
minoridens Melvill, 1901
moneta Linnaeus, 1758
mus Linnaeus, 1758
nigropunctata Gray, 1828
nivosa Broderip, 1827
nucleus Linnaeus, 1758
ocellata Linnaeus, 1758
onyx Linnaeus, 1758
ovum Gmelin, 1791
owenii Sowerby, 1837
pantherina Solander[5], 1786
pallida Gray, 1824
pallidula Gaskoin, 1849
petitiana[6] Crosse, 1872
picta Gray, 1824
piperita Gray, 1825
poraria Linnaeus, 1758
porteri Cate, 1966
pulchella Swainson, 1823
pulchra Gray, 1824
pulicaria Reeve, 1846
punctata Linnaeus, 1771
pyriformis Gray, 1824
pyrum Gmelin, 1791
quadrimaculata Gray, 1824
rashleighana Melvill, 1888
reevei Sowerby, 1832
robertsi Hidalgo, 1906
rosselli Cotton, 1848
sanguinolenta Gmelin, 1791
saulae Gaskoin, 1843
schilderorum Iredale, 1939
scurra Gmelin, 1791
spadicea Swainson, 1823
spurca Linnaeus, 1758
staphylaea Linnaeus, 1758
stercoraria Linnaeus, 1758
stolida Linnaeus, 1758
subviridis Reeve, 1835
sulcidentata Gray, 1824
surinamensis Perry, 1811
talpa Linnaeus, 1758
teramachii Kuroda, 1938
teres Gmelin, 1791
tessellata Swainson, 1822
testudinaria Linnaeus, 1758
teulerei Cazenavette, 1845[7]
tigris Linnaeus, 1758
turdus Lamarck, 1810
ursellus Gmelin, 1791
valentia Perry, 1811
ventriculus Lamarck, 1810
venusta Sowerby, 1846
vitellus Linnaeus, 1758
vredenburgi Schilder, 1927
walkeri Sowerby, 1832
xanthodon Sowerby, 1832
zebra Linnaeus, 1758
ziczac Linnaeus, 1758
zonaria Gmelin, 1791

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[1] Given as a subspecies of *hesitata* Iredale, 1916 by Taylor & Walls. However, *armeniaca* is the prior name, so it must be the species name unless both taxa are accorded specific status (as is done by Burgess).

[2] Schilder (1966), after considering the type specimens of Linnaeus, proposed the following name changes:

former name	new name
bistrinotata Schilder & Schilder, 1937	*cicercula* Linnaeus, 1758
cicercula Linnaeus, 1758	*lienardi* Jousseaume, 1874
labrolineata Gaskoin, 1849	*flaveola* Linnaeus, 1758

None of these changes was recognized by either Burgess or Taylor & Walls. The Schilders must have had second thoughts, however, because in Schilder & Schilder (1971) the first 2 of the above changes were not accepted, and only the third was. This is the course adopted in the present paper. It must be remarked that Schilder was not consistent in this matter, for in his 1969 paper he used none of the changes he had proposed in 1966.

[3] Because Stearns hyphenated the name *isabella-mexicana* in his original description, if this taxon is accorded specific status it

Table 2

Species recognized by Taylor & Walls and by Burgess

	Status in Schilder & Schilder
bregeriana Crosse, 1868	subsp. *walkeri*
comptonii Gray, 1847	subsp. *piperita*
cribellum Gaskoin, 1849	subsp. *cribraria*
dayritiana Cate, 1963	syn. *pallidula*
eburnea Barnes, 1824	subsp. *miliaris*
gondwanalandensis Burgess, 1970	[new]
granulata Pease, 1862	subsp. *nucleus*
grayana Schilder, 1936	subsp. *arabica*
humphreysii[8] Gray, 1825	subsp. *lutea*
leviathan Schilder & Schilder, 1937	subsp. *carneola*
luchuana Kuroda, 1966	subsp. *pallidula*
mauiensis Burgess, 1967	subsp. *bistrinotata*
musumea Kuroda & Habe, 1961	syn. *katsuae*
obvelata Lamarck, 1810	subsp. *annulus*
ostergaardi Dall, 1921	subsp. *boivini*
rabaulensis Schilder, 1964	subsp. *katsuae*
semiplota Mighels, 1845	subsp. *limacina*
serrulifera Schilder & Schilder, 1938	subsp. *minoridens*
steineri[9] Cate, 1969	syn. *coxeni*
subteres Weinkauff, 1881	subsp. *teres*
summersi Schilder, 1958	subsp. *pallidula*
thomasi[10] Crosse, 1865	syn. *beckii?*

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[8] As "*yaloka* Steadman & Cotton 1943" in Burgess. CERNOHORSKY (1965) considers *yaloka* a junior synonym of *humphreysi* [sic] and that it does not even merit to be retained as a "form" name.

[9] This unique specimen is considered to be a bulbous form of *coxeni* by CLOVER, 1976.

[10] The specific status of this unique specimen in the British Museum (Natural History) has been the subject of much controversy which will not be detailed here, and which will not be settled until more specimens turn up. Sufficeth to say that it has variously been termed a synonym of *beckii*, *macandrewi*, and *ostergaardi*, as well as a valid species.

Table 3

Species recognized only by Schilder & Schilder

	Burgess	Taylor & Walls
alfredensis Schilder & Schilder, 1929	syn. *edentula*	syn. *edentula*
aurora[11] Lamarck, 1810	syn. *aurantium*	syn. *aurantium*
bicolor Gaskoin, 1849	syn. *piperita*	syn. *piperita*
catei Schilder, 1963	syn. *venusta*	syn. *venusta*
hartsmithi Schilder, 1967	not mentioned	var. *comptoni* [sic]?
listeri Gray, 1824	syn. *felina*	var. *felina*
margarita Dillwyn, 1817	syn. *cicercula?*	subsp. *cicercula*
thersites Gaskoin, 1849	subsp. *friendii?*	subsp. *friendii*

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[11] Why the Schilders separated this taxon from *aurantium* Gmelin, 1791 is a mystery.

Table 4

Species recognized only by Burgess

	Status in both Schilder & Schilder and Taylor & Walls
aequinoctialis Schilder, 1933	subsp. *annettae*
cassiaui Burgess, 1965	subsp. *nucleus*
coheni Burgess, 1965	subsp. *fuscorubra*
coloba Melvill, 1888	subsp. *chinensis*
fernandoi Cate, 1969	subsp. *xanthodon*
hesitata Iredale, 1916	subsp. *armeniaca*
kuroharai Kuroda & Habe, 1961	subsp. *schilderorum*

Table 5

Species recognized only by Taylor & Walls

	Status in	
	Burgess	Schilder & Schilder
bernardi Richard, 1974	[new]	[new]
cruickshanki Kilburn, 1972	[new]	[new]
fischeri Vayssière, 1910	var. *gaskoini*	subsp. *gaskoini*
haddnightae Trenberth, 1973	[new]	[new]
joycae Clover, 1970	[new]	[new]
nebrites Melvill, 1888	syn. *erosa?*	subsp. *erosa*
sakurai Habe, 1970	[new]	[new]

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must be as given here, and and not as *mexicana* as done by the Schilders.

[4] Attributed to Schilder & Schilder, 1927 by BURGESS (1970: 274); the paper cited there, however, is by F. A. Schilder only.

[5] BURGESS (1970: 204) gives the author as Lightfoot, 1786, citing DANCE, 1962 who is said to have said that the date of Solander's death made it impossible for him to have been the author of the pertinent reference.

[6] Considered a "questionable species" by BURGESS (1970: 85) who conjectured that morphological differences between *petitiana* and *pyrum* could be explained if the former were simply a dwarf form of the latter.

[7] Date of *teuleri* given as 1846 by the Schilders. Taylor & Walls give no dates. BURGESS (1970: 58) accepts 1845 as the correct date

Table 6

Additional Species

	Clover	Taylor & Walls
angelicae Clover, 1974	valid	syn. *petitiana*
eugeniae Cate, 1975	semifossil *xanthodon*	[new]
gloriosa Shikama, 1971	form of *gondwanalandensis*	syn. *gondwanalandensis*
jeaniana Cate, 1968	valid	var. *friendii*
ju-kui Shikama, 1974	syn. *cruickshanki*	[overlooked]
kingae Rehner & Wilson, 1975	valid	[new]
lisetae Kilburn, 1975	valid	var. *felina*
maricola Cate, 1976	valid	[new]
perlae Lopez & Chiang, 1975	valid (probably)	[new]
propinqua [12] Garrett, 1879	—	syn. *carneola*
stohleri Cate & Schilder, 1968	syn. *contaminata*	subsp. *pallida*

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[12] Considered separable from *carneola* by BURGESS, 1975 (but not by the Schilders).

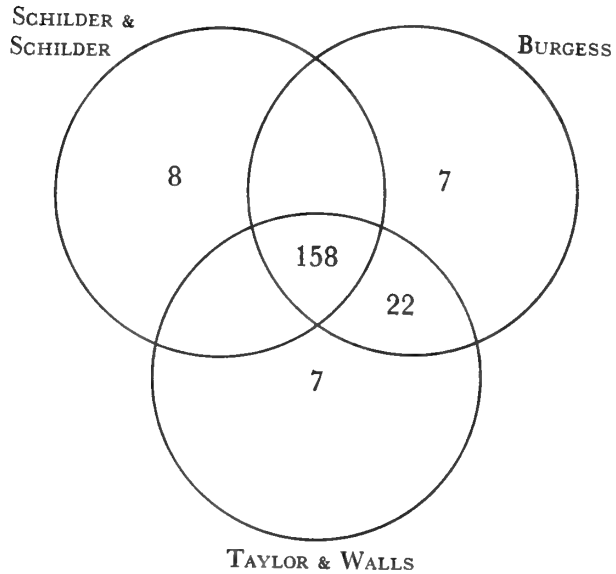

Figure 1

Numbers of species recognized by SCHILDER & SCHILDER (1971), BURGESS (1970), and TAYLOR & WALLS (1975). Number of species accepted by each lies within the respective circles, with acceptances in common as shown.

Addendum on Subspecies: BURGESS (1970) does not recognize subspecies, in distinction from SCHILDER & SCHILDER (1971) and TAYLOR & WALLS (1975). Taylor & Walls list 57 subspecies, and of these the Schilders consider 1 a valid species, 28 are synonyms, and 28 are also subspecies. Conversely, the Schilders list 97 subspecies, and of these Taylor & Walls consider 17 valid species, 25 are synonyms, 30 are also subspecies, 23 are variants, and 2 are not mentioned. Tabulation of these 99 taxa would add an inordinate amount of space to this paper, but interested persons could obtain these by requesting them from me.

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Subtidal Abalone Populations in an Area Inhabited by Sea Otters

BY

JOHN COOPER[1], MARK WIELAND[1] AND ANSON HINES[2]

(2 Text figures)

INTRODUCTION

Lowry & Pearse (1973) determined the population structures and densities in 1972 of 2 species of abalones, *Haliotis rufescens* Swainson, 1822 and *H. walallensis* Stearns, 1899, in the sea otter-inhabited kelp forest at Hopkins Marine Station, Pacific Grove, California. In their study, abalones, as well as sea urchins, were almost always found living in crevices more or less inaccessible to sea otters (*Enhydra lutris* Linnaeus, 1758), and the densities were low in contrast to conditions before sea otters became reestablished, when the bottom "... was covered with urchins and abalones spaced only a few feet apart ..." (McLean, 1962). The size-frequency distribution of *H. rufescens* found by Lowry & Pearse (*op. cit.*) is one of a broad spectrum lacking any distinct modes and reflecting the year-round spawning of this species (Boolootian *et al.*, 1962; Young & DeMartini, 1970). Although we are aware of nothing published on the reproductive cycle and settlement of *H. walallensis*, Lowry & Pearse (*op. cit.*) found this species had a size-frequency distribution with a single, sharp mode at 7.4cm. They suggested that this peak represented a single age-class and hypothesized that *H. walallensis* achieves successful settlement irregularly.

This paper re-examines the densities, population structures and distributions of abalones in the kelp forest at Hopkins Marine Station to see if any changes have occurred since the Lowry & Pearse study. In addition, we test the hypothesis that the single size-frequency mode found by Lowry & Pearse (1973) for *Haliotis walallensis* represents a single age-class by looking for a shift in the mode to a larger size. If the hypothesis were correct, such a shift would reflect continued growth of the abalones in this year-class over the last 4 years, and the appearance of any additional mode in the size-frequency distribution would reflect new successful setlement.

MATERIALS AND METHODS

This study was conducted at the Hopkins Marine Life Refuge, Pacific Grove, California. The study area encompassed 1600 m^2 and was centered at the "100 meter mark" on the black electric cable which runs through the kelp forest adjacent to Hopkins Marine Station (see Figure 1). This area is between and overlaps the 2 transect lines used by Lowry & Pearse (1973). *Haliotis rufescens* and *H. walallensis* were counted and measured *in situ* on scuba dives during July and August, 1976. The 2 species were identified according to Cox (1962) and were distinguished under water by the differences in mantle edge coloration. Densities of the abalones were estimated by counting individuals within 10 m^2 circular plots located by coordinates from a random number table. Notes were taken on the occurrence of abalones within and out of crevices. Abalone sizes were obtained by swimming over the study area and systematically recording maximum shell lengths to the nearest 1 centimeter using calipers. Densities and size-frequency distributions thus obtained were compared with those obtained by Lowry & Pearse (1973).

RESULTS

The mean combined density of both species of abalones was 0.16 per m^2 (s. d. = ± 0.24; n = 25 plots). The

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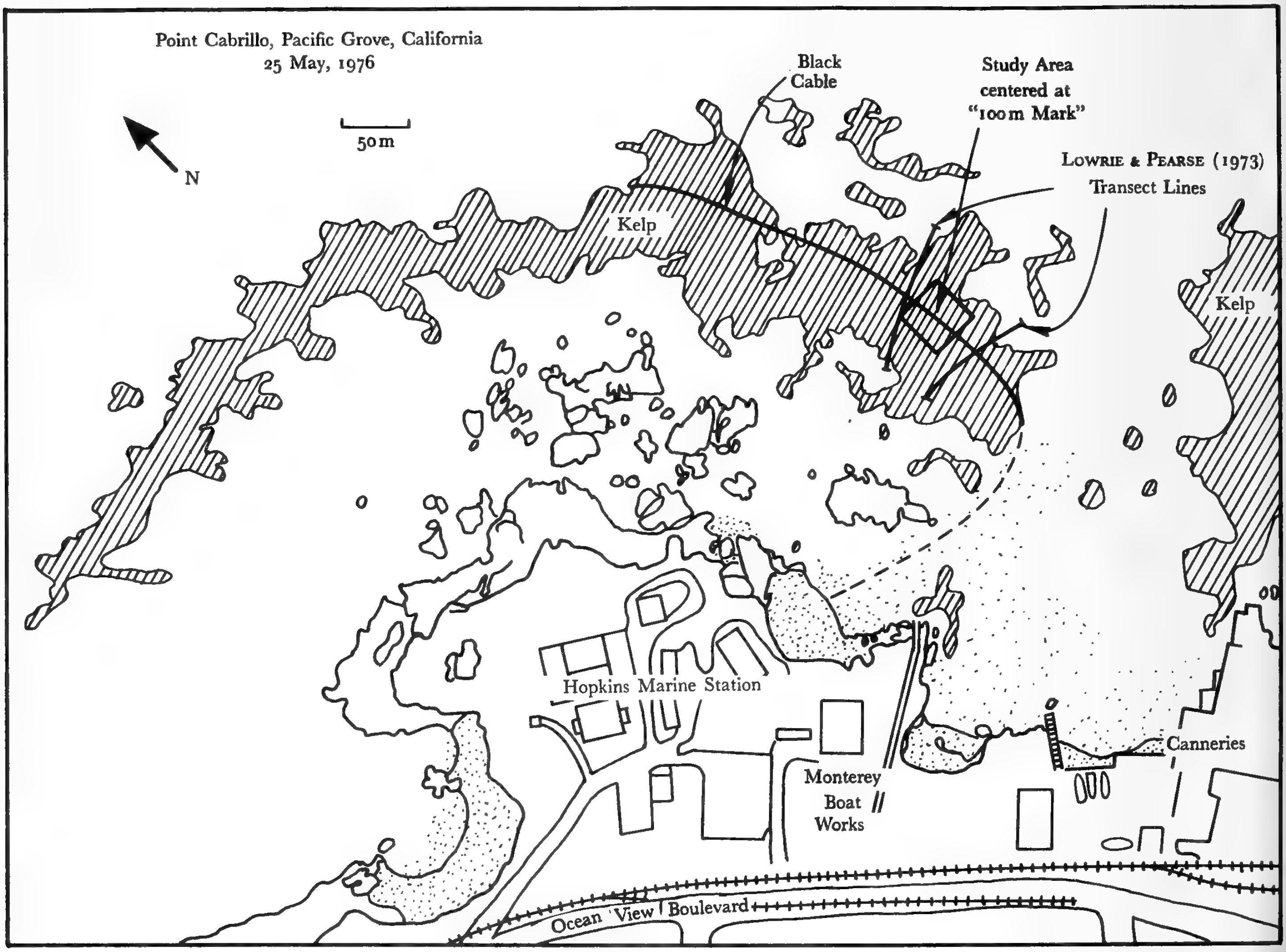

Figure 1

Map of Point Cabrillo, Pacific Grove, California, USA, showing the study area adjacent to Hopkins Marine Station and the location of transect lines used by Lowry & Pearse (1973). The "black cable" is an abandoned heavy electric cable, useful as a reference when diving.

density of *Haliotis rufescens* was 0.08 ± 0.14 per m^2 and of *H. walallensis* was 0.08 ± 0.12 per m^2. These data are not significantly different from those of Lowry & Pearse (1973) (Student t-test, $p > 0.10$) (Table 1).

All individuals observed during this study were crevice-inhabiting, and *Haliotis walallensis* were subjectively judged to be found in shallower cracks than *H. rufescens.*

The size-frequency distribution of *Haliotis rufescens* showed no distinguishable modes over a broad range of sizes, while *H. walallensis* showed a single, distinct mode at 7.5 cm (Figure 2). These frequency distributions are not significantly different from those found by Lowry & Pearse (1973) (Kolomogorov-Smirnov test, $p > 0.20$) (see Figure 2).

Table 1

Densities of Abalones ($\bar{X}$ ± 1 s.d. per m^2)

	Haliotis spp.	*Haliotis rufescens*	*Haliotis walallensis*
Lowry and Pearse (1973) (N = 45 1×10m swath counts)	0.21 ± 0.34	0.15	0.07
This paper (1976) (N = 25 $10m^2$ circular quadrats)	0.16 ± 0.20	0.08 ± 0.14	0.08 ± 0.12

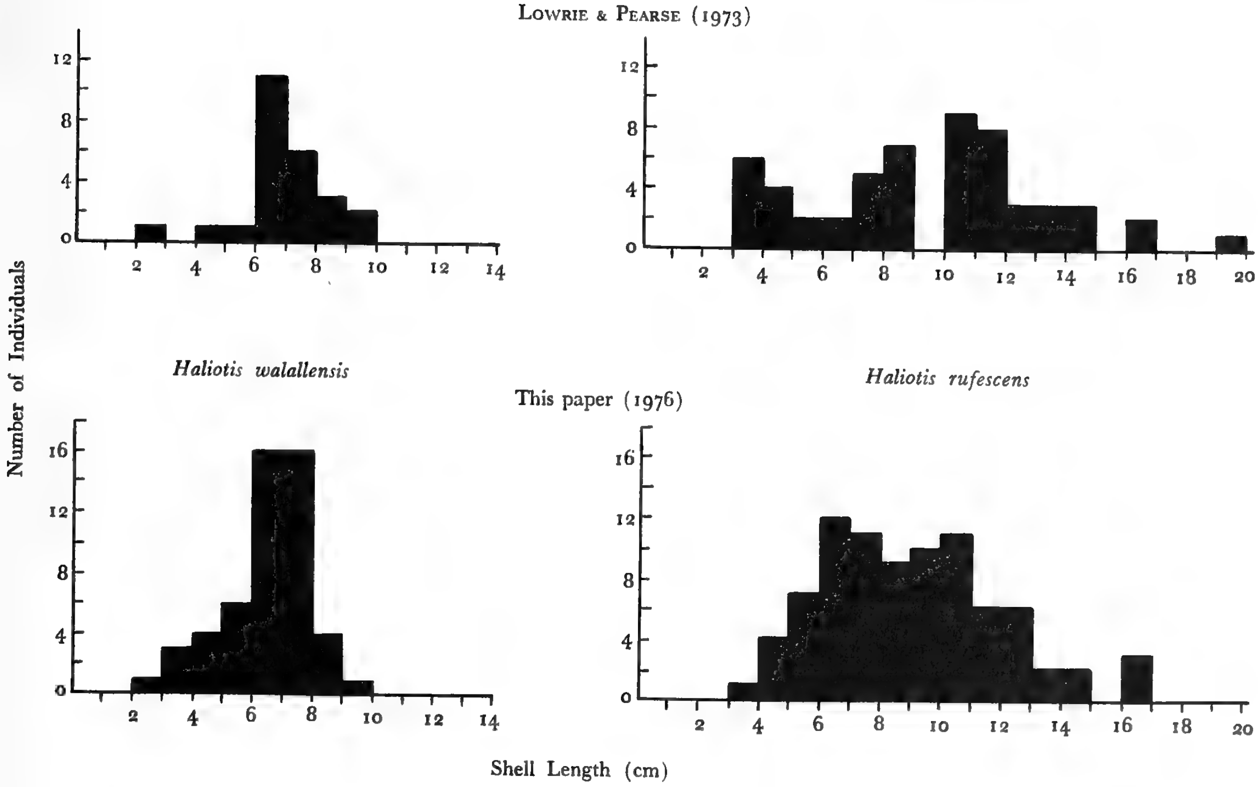

Figure 2

Size-frequency distributions of *Haliotis walallensis* and *Haliotis rufescens* off Hopkins Marine Station in the present study (summer, 1976) and in Lowry & Pearse (1973; data collected in November, 1972). The distributions from the two dates are not significantly different (Kolomogorov-Smirnov test, $p > 0.20$).

DISCUSSION

The densities of *Haliotis rufescens* and *H. walallensis* have remained quite constant over the last 4 years since they were measured by LOWRY & PEARSE (1973). The slight differences in densities between LOWRY & PEARSE (*op. cit.*) and the present paper may be a result of the differences in sampling methods. Lowry & Pearse used belt transects (total sampling area = 3560 m²), while we used random quadrats in a smaller study area. One of their transects had densities (westline = 0.17 per m²) virtually identical to those in the present study, while the other transect densities were somewhat higher (eastline = 0.35 per m²), resulting in a slightly higher overall mean density (0.21 per m²). This stability, coupled with the observation that abalones in the study area continue to be found only in crevices, supports the contention that the crevice-dwelling populations have established a refuge from sea otter predation. Sea otters are, however, continuing to feed on abalones, as well as a wide variety of other invertebrates in Hopkins Marine Life Refuge (Dan Costa, personal communication). Other predators in the area, including sea stars (*Pycnopodia helianthoides* (Brandt, 1835); *Pisaster giganteus* (Stimpson, 1857); and *Orthasterias koehleri* (de Loriol, 1897)), octopuses (*Octopus* spp.), rock crabs (*Cancer antennarius* Stimpson, 1856), and cabezone (*Scorpaenichthys marmoratus* Ayres, 1854), are known to feed on abalone, and all of these predators have ready access to the crevices inhabited by abalone (COX, 1962; FEDER, 1963; O'CONNELL, 1953; personal observations). However, abalones have evolved behavioral responses (clamping down, "running," shell twisting, secretion of mucus, etc.) which minimize their capture (FEDER, *op. cit.*; MONTGOMERY, 1967; personal observations). During other studies in the area, abalones smaller (< 3 cm) than most of those observed in this study have been found on open, exposed surfaces (LOWRY & PEARSE, 1973; Hines & Pearse, unpublished observations). It would be interesting to know if only those recruits which settle in crevices survive, or if abalones settle everywhere and later move into crevices. Our observations agree with LOWRY & PEARSE (*op. cit.*) that *H. walallensis* is found in smaller, that is shallower, cracks than *H. rufescens*. It would also be interesting to know if this difference in crack distribution is the result of competition between the 2 species, differences in crack preference, or perhaps simply a reflection of small abalones (both *H. walallensis* and smaller *H. rufescens*) tending to occur in smaller cracks.

The size-frequency distribution of *Haliotis rufescens* found in this study and that of LOWRY & PEARSE (1973) lack any distinct modes over a wide size range. This is expected from the year-round spawning of this species (BOOLOOTIAN *et al.*, 1962; YOUNG & DEMARTINI, 1970). However, the size-frequency distribution of *H. walallensis* in the present study is also identical to that found 4 years ago by LOWRY & PEARSE (*op. cit.*) with a single, distinct mode at 7.5 cm. This unchanged size-frequency distribution does not support the hypothesis that the *H. walallensis* observed by Lowry & Pearse represented a single age-class resulting from a single earlier successful settlement. Rather, as with *H. rufescens*, *H. walallensis* at Hopkins Marine Life Refuge appears to be in a stable size (age) distribution. LOTKA (1922) showed that a population with constant survivorship and birth rates will reach and maintain a stable age distribution. The stable size (age) distribution of *H. walallensis* and *H. rufescens* thus suggests constant survivorship and recruitment rates for these populations, with recruitment into each size (age) class balanced by losses due to mortality and growth (aging). Finally, it is interesting to note that only one abalone measured in the LOWRY & PEARSE (*op. cit.*) study and none in the present study was larger than legal size (7 inches or 170 mm).

ACKNOWLEDGMENTS

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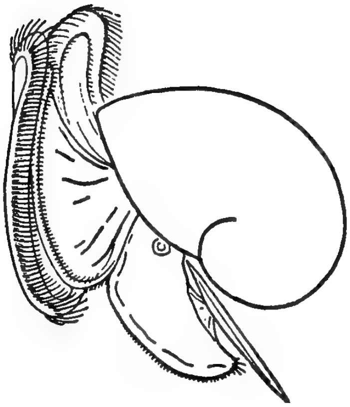

Observations on Feeding, Chemoreception and Toxins in Two Species of *Epitonium*

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

Epitonium tinctum (Carpenter, 1864) and *Epitonium indianorum* (Carpenter, 1864) are small marine mesogastropods often associated with sea anemones. THORSON (1957: 57) reported commonly finding *E. tinctum* at the base of the anemone *Anthopleura xanthogrammica* (Brandt, 1835). HOCHBERG (1971: 23) described *E. tinctum* feeding on the tentacles of *A. elegantissima* (Brandt, 1835). I have made further observations of *E. tinctum* and *E. indianorum* feeding on the tentacles and verrucae of 5 anemone species and have observed that *Epitonium* can apparently locate anemones by using a chemosensory method.

Epitonium species produce a purple dye from the hypobranchial gland area, as do related snails. I have seen this dye staining the foot of an *Epitonium*. Perhaps partly due to speculation by David (*cf.* WILSON & WILSON, 1956: 292) that the purple dye of *Ianthina janthina* (Linnaeus) anaesthetizes the *Velella velella* (Linnaeus) on which it feeds, ROBERTSON (1963: 51) suggests that the dye produced by *Epitonium* species may be anaesthetic. I report here experiments that support this suggestion.

MATERIALS AND METHODS

Epitonium tinctum were collected intertidally at Mussel Point, Monterey Bay, California. *Epitonium indianorum* were collected at depths from 9 to 24m off Mussel Point and at the Pinnacles, near Pescadero Point, Monterey County, California. All collections were made in May 1975.

For experiments on chemosensory perception of anemones, two tanks (approximately 7*l* capacity each), one containing an anemone and one without, were connected by rubber tubing to a glass 'Y' tube. One branch of the Y received water from the anemone's tank, the other from the tank without an anemone. Sea water flowed through the system at a constant rate of about 5m*l* per minute in each branch. *Epitonium* were placed in the junction of the branches of the Y and their positions recorded after 15 minutes. Five sets of experiments were run in which the motion of *E. tinctum* and *E. indianorum* was compared for the anemones *Anthopleura elegantissima*, *A. xanthogrammica*, *Metridium senile* (Verrill, 1865), *Tealia lofotensis* (Gosse, 1858), and *T. crassicornis* (Gosse, 1858). All anemones but *T. crassicornis* had a wet weight of about 30g; the smallest *T. crassicornis* available weighed about 60g. Five *E. tinctum* and 5 *E. indianorum* were used in each set of experiments; each was given 2 runs, for a total of 10 readings for each anemone for each *Epitonium* species. In a control experiment, *Epitonium* were tested when neither tank contained an anemone.

In testing for a possible toxin or anesthetic, 2 types of experiments were carried out. First, to compare the behavior of an *Epitonium* extract to that of previously examined toxins, the ability of *Epitonium* extract to extinguish the compound action potential of the sciatic nerve of the leopard frog, *Rana pipiens*, was tested. The nerve was placed over a set of silver stimulating electrodes and 2 sets of recording electrodes, one on either side of a plastic well which contained the suspected toxin. Supramaximal stimuli were delivered by a Grass SD-5 stimulator. The resulting compound action potential was amplified by a Grass P-8 pre-amplifier and displayed on a Tektronix 502-A dual beam oscilloscope. The ratio between the peaks from the 2 sets of recording electrodes was noted before, and at intervals after the toxin was added, and the oscilloscope image was photographed

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before and after the toxin had taken effect (*cf.* Kao & Fuhrman, 1967: 27). The effect of whole *Epitonium*, and of the pallial area of *Epitonium*, each crushed in amphibian Ringers solution, and of *Epitonium* crushed and then dialysed through Spectrapor tubing (#3. Approx. MW cut-off 3500) against 2000 m*l* of amphibian Ringers solution for 12 - 24 hrs was examined. Both *E. tinctum* and *E. indianorum* were used.

The second set of experiments tested the reaction of an anemone tentacle to administration of *Epitonium* extract. The tip of a severed *Tealia crassicornis* tentacle was tied to a Grass FT-03 force transducer, and the base of the tentacle was attached to a flared piece of capillary tubing over a syringe needle. A short length of rubber tubing connected the needle to the syringe body. Injections of *Epitonium* crushed in sea water, of tryptamine HCl, and of sea water (as a control) were made into the tubing, and the tentacle's response to the injections and to tactile stimulus was recorded on a Grass polygraph.

RESULTS

Feeding Behavior

Generally, *Epitonium tinctum* were found on *Anthopleura elegantissima* and *A. xanthogrammica*, and *E. indianorum* were found on *Tealia crassicornis* and *T. lofotensis*, though there were numerous exceptions. I have found *Epitonium* on the column of an anemone and at the base. However, neither species of *Epitonium* is a permanently attached parasite; I have seen *E. indianorum* 30 cm away from the nearest anemone, and both species frequently crawled about in the tank.

When feeding, an *Epitonium* may position itself on the column, on shell fragments on the column, if these are present, or beside the base of an anemone. The *Epitonium* everts and extends up its long proboscis, which it brandishes until it encounters the tip of a tentacle. When this occurs, the proboscis is slipped over the tentacle, which can be seen inside since the proboscis is quite translucent. One or two minutes later, the anemone contracts in the area of the attacked tentacle, and the proboscis, with the tentacle still visible inside, is retracted. *Epitonium* will also feed in the same manner on the verrucae of anemones, especially the larger species such as *Tealia crassicornis*.

Epitonium tinctum tends to feed on *Anthopleura* sp. and *E. indianorum* on *Tealia* sp. Neither *Epitonium* crawls onto the column of *Metridium* and this anemone is rarely attacked.

Chemosensory Perception

Results of experiments on movement of *Epitonium* with respect to anemones to test chemoreception are listed in Table 1. Of the 4 responses in the table, one is a positive response: motion toward the anemone. Two are avoidances: away from the anemone up the other branch of the Y, or down the Y. The fourth, lack of response, could be due to a variety of factors, possibly including an inability to sense the anemone in that test.

Table 1

Chemosensory Perception of Anemones by two Species of *Epitonium*

Epitonium tinctum or *Epitonium indianorum* were placed at the junction of branches of a Y tube. Sea water from a tank containing one of five species of anemones flowed through one branch of the Y, while sea water from a tank without animals flowed through the other branch. Movement was recorded toward the anemones, away from the anemones up the other branch of the Y, down the Y away from both tanks, or no movement if less than 0.5 cm. The values marked with [1] indicate significant differences from controls with P less than 0.001.

	Epitonium tinctum				*Epitonium indianorum*			
	Toward	Away	Down	No movement	Toward	Away	Down	No movement
Anthopleura elegantissima	9[1]	0	0	1	1	1	4	4
Anthopleura xanthogrammica	7[1]	2	0	1	0	4	4	2
Metridium senile	1	2	5	2	1	4	3	2
Tealia crassicornis	3	10	0	3	11[1]	1	1	3
Tealia lofotensis	3	2	2	3	5	2	2	1
Control	2	0	7	5	4	3	5	3

To see if the positive response of movement toward an anemone was significantly different from movement in control experiments without anemones, I made a X^2 comparison. For the 'expected' value, I took the greater incidence of motion (as a percentage) up either branch of the Y in the absence of an anemone. I compared this value to the incidence of motion toward the anemone for each *Epitonium* species to each anemone species. Using this method, the statistically significant results ($P < 0.001$) are the increased motion of *E. tinctum* toward both *Anthopleura* species and of *E. indianorum* toward *Tealia crassicornis*. P is <0.05 for the increase in motion of *E. indianorum* toward *T. lofotensis*. All other combinations have $P > 0.1$ for increased motion toward the anemone.

Epitonium were apparently able to sense whether the water around them had contained an anemone of the genus with which I had usually found them. Since their information came from the water itself, I assume some chemical derived from the anemone served as the means of location.

Epitonium Toxin

Extracts of *Epitonium* were found to inhibit the amplitude of the compound action potential of the sciatic nerve of *Rana pipiens* (Figure *1*). In this case, the ratio of the spike recorded from a position on the nerve after the toxin well to the spike recorded from before the well decreased from 0.97 in the control to 0.50 after 1 hr, or a decrease of about 48%. The second spike also has been broadened as some of the faster conducting axons were extinguished. Similar results were obtained in other experiments. *Epitonium* extracts had been dialysed for 24 hrs against a total of 2000 m*l* Ringers solution produced results similar to that shown in Figure *1*. Thus the active substance is either a large molecule or is bound to a large molecule.

In another experiment, the pallial area of *Epitonium* crushed in amphibian Ringers solution, decreased the action potential of the nerve by about 60% in 1 hr. Under the same conditions, the remainder of the body had no effect.

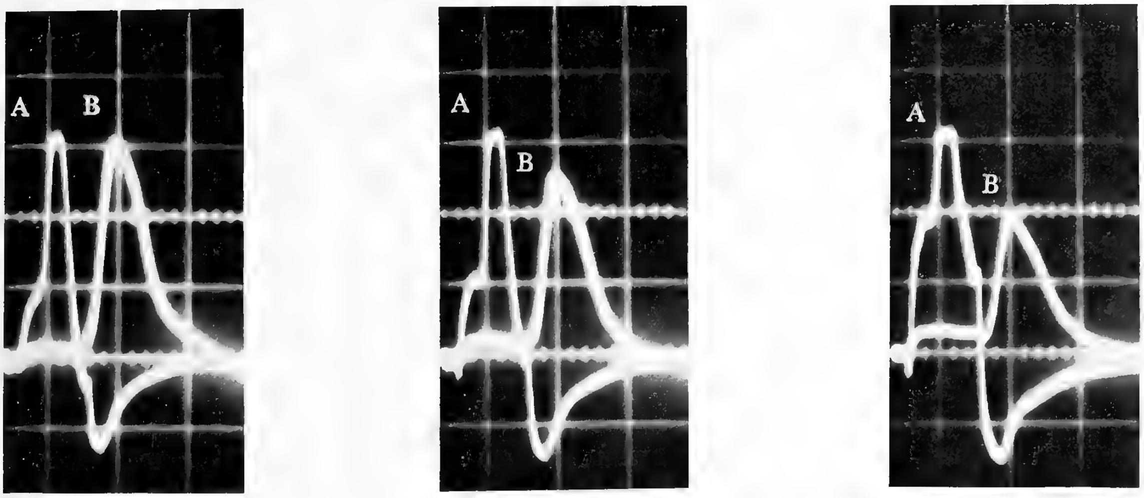
Isolated tentacles from *Tealia crassicornis* exhibited spontaneous contractions and could be stimulated mechanically or by tryptamine (*cf.* Ross, 1960). Extracts of *Epitonium* added to the sea water in which the anemone tentacle was suspended reduced or abolished the spontaneous contractions as well as the response to tryptamine and mechanical stimuli. The results of a representative experiment are shown in Figure 2. In one experiment extracts of *Epitonium* abolished spontaneous contractions for 18 min., after which the rhythm was reestablished. The results suggest that *Epitonium* toxin inhibits some part of the neuromuscular system of the anemone, but further work should be done to localize the site of action.

DISCUSSION

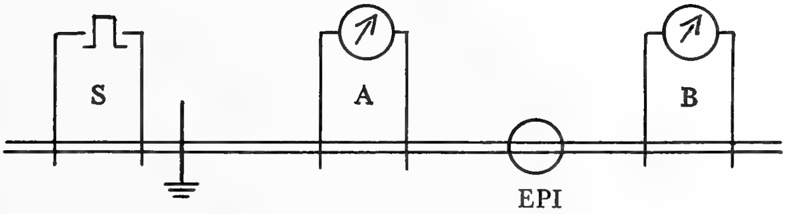
Experimental evidence is presented here for the suggestion made by others (Wilson & Wilson, 1956; Robertson, 1963) that *Epitonium* produces a toxin or anesthetic that paralyzes the anemones on which it feeds, The toxin appears to be either produced or stored in the pallial area, possibly the hypobranchial gland. If the toxin is present in the hypobranchial gland, it may, like the purple dye produced in the gland, sometimes be present on the *Epitonium*'s foot, where it could anesthetize the anemone on which the snail crawls. In this case, *Epitonium* would itself be expected to be resistant to the anesthetic. The toxin may instead be injected when the snail feeds. Robertson (1963: 51) reports that some *Epitonium* possess hollow thorns in the proboscis, presumably to inject a toxin. However, using light microscopy, I was unable to find thorns or a duct which would transport the toxin from the pallial area up the proboscis on *Epitonium indianorum*.

Explanation of Figure *1*

Oscilloscope recordings of the compound action potential of frog sciatic nerve in the arrangement shown in the diagram. The supernatant from 39 mg *Epitonium indianorum* crushed in 1 ml Ringer solution was placed in the cup marked EPI. The spike recorded from the site upstream from the toxin remained essentially unchanged in amplitude, while that recorded from the site downstream from the toxin decreased



Control 30 minutes 1 hour



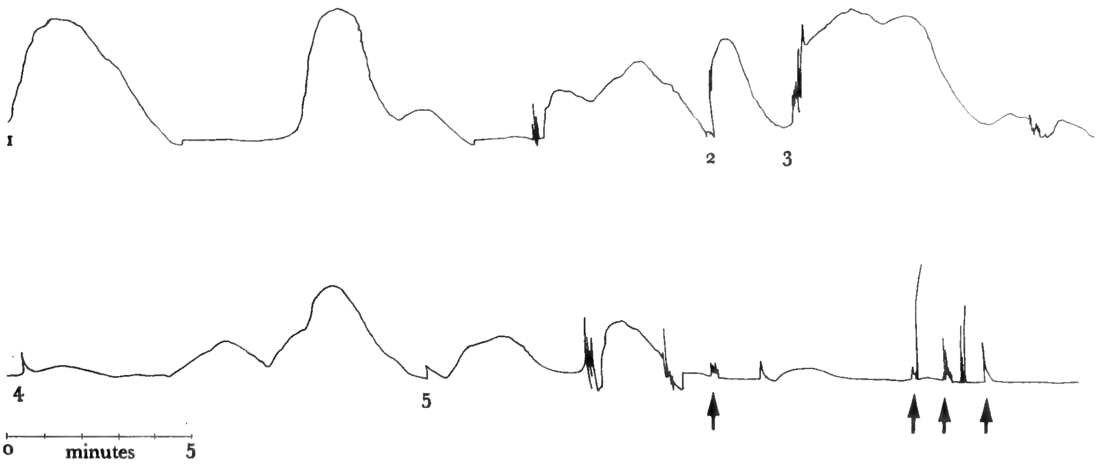


Figure 2

Tracings from polygraph records of contractions of an isolated tentacle from *Tealia crassicornis*.
1. Spontaneous contractions. 2. Contraction in response to tryptamine. 3. Contraction in response to mechanical stimulus (stretch). 4. Addition of extract of *Epitonium*. 5. and subsequent arrows: repeated mechanical stimuli (stretch).

SUMMARY

Epitonium tinctum and *E. indianorum* are two mesogastropods that feed predominantly on the tentacles of certain sea anemones. In the field, the former was generally found on *Anthopleura* species, and the latter on *Tealia* species. Experiments in the laboratory showed that they may locate specific genera of anemones using a chemosensory method. Both *Epitonium* species were found to contain a toxin in the pallial area which is either a large molecule or is bound to a large molecule. The toxin inhibits the compound action potential of frog nerve and may also inhibit the contraction of a tentacle from *Tealia crassicornis*.

NOTE ADDED IN PROOF

After this article was accepted for publication a report by CAREY RESCH SMITH appeared in this Journal (19 (4): 331 - 340) confirming chemical recognition of *Anthopleura elegantissima* and *A. xanthogrammica* by *Epitonium tinctum* (Frederick Fuhrman).

ACKNOWLEDGMENTS

I appreciate the great amount of help I received from Dr. Frederick and Geraldine Fuhrman, of Hopkins Marine Station. I would also like to thank Dr. Myra Keen for use of the Stanford shell collection, and Dr. Nathan Howe for many helpful suggestions. Supported in part by NIH Grant No. GM-16031.

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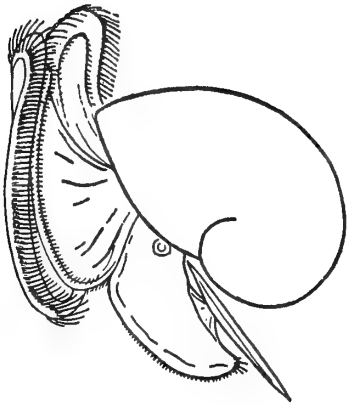

The Development of Conspecific Interactions in Juvenile *Aplysia dactylomela* Rang, 1828: An Observational Study

BY

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(3 Text figures)

INTRODUCTION

THE PURPOSE OF THIS STUDY was to describe developmental changes in the interactions of "juvenile" *Aplysia dactylomela* Rang, 1828. It became possible with the discovery of an apparently "juvenile" population in the Plajita Rosada collection on the southwest coast of Puerto Rico during April and May 1975 (see Figure 1). This was an unusual research opportunity in that the capability of raising sea hares through metamorphosis has been restricted to only a few laboratories in which behavioral development was, to date, not investigated. The methods and procedures used were peculiar to an opportunity such as this, in that they depended on the continued success of finding "juveniles."

Aplysia californica Cooper, 1863 has been raised through metamorphosis and some of the morphological and behavioral changes related to metamorphosis have been described (KRIEGSTEIN, 1976; KRIEGSTEIN *et al.*, 1974). Further progress in the establishment of laboratory cultures of *Aplysia* has been reported by HADFIELD, (1975) and STRENTH & BLANKENSHIP (1976). Recently studies of morphological development have become available for some related opisthobranchs (THOMPSON, 1958, 1962, 1967; TARDY, 1970; BONAR & HADFIELD, 1974), but there are no published studies of behavioral development in the opisthobranchs.

The first occurrence of copulation in *Aplysia* seems to be related to size. Although no data were provided, in a brief report NEWBY (1972) stated that copulation was never observed in animals less than 40 g body weight. SMITH & CAREFOOT (1967) collected small sea hares (1 g - 8 g) and kept these animals together as a group. Copulation was not observed until the 16th day in the laboratory. The body weights at the time of copulation were not reported; however, copulation was observed at about the time the gonads became mature. Thus, it appears that the reproductive behavior develops some time after metamorphosis.

Morphological studies of the bag cells support the notion that the reproductive system as a whole may develop after metamorphosis. The bag cells are a neurohormonal group of the abdominal ganglion which contribute to egg-laying (ARCH, 1976). The cells are few in number and may be non-secretory in small animals (2g). In sea hares larger than 50g, however, secretory granules are present and the number of cells in the cluster increases markedly (FRAZIER, *et al.*, 1967). Thus, some neuroendocrine aspects of egg-laying become functional around the stage when sea hares begin to copulate.

Although the data are scanty, it appears from the above studies that copulation and size might be related. In this study the same sea hares were observed in regular repeated pairings. Systematic observations of their behavior and weight measurements were made.

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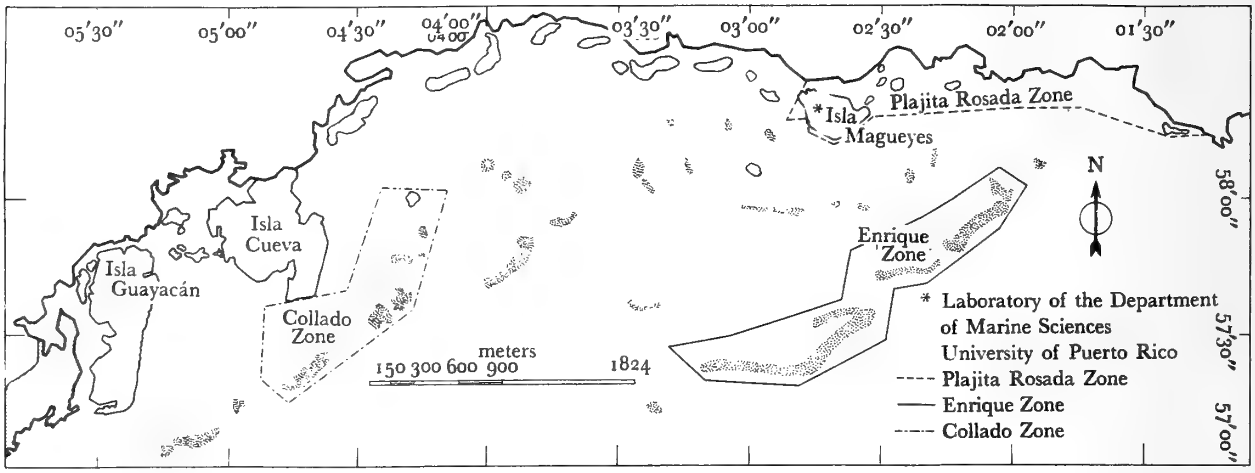

Figure 1

METHODS AND PROCEDURES

A. Subjects and Maintenance

A sample of 56 sea hares was collected off the southwest coast of Puerto Rico at Plajita Rosada. This is a rocky intertidal beach marked by the presence of *Laurencia papilosa* and sargassum (for details of collection see Lederhendler, 1977).

The sea hares were maintained in an indoor laboratory in 1 *l*-capacity aquaria with running sea water and constant daylight illumination. Food was always available and consisted of *Acanthophora spicifera* which was thoroughly rinsed before being placed in the tanks. Wet weights of the animals were measured every other day on a Mettler balance.

To carry out observations of the interindividual behavior, the members of a pair were matched for size. As a result, the smallest animals were paired at the time of collection, to permit a maximum amount of observation during a long period of growth and development.

Five pairs were chosen for observation. These were all from the April and May collections (Figure 2). A failure in the sea water supply cut the period of observation short, resulting in making only 15 to 22 days available in which a total of 22 paired observations were made.

B. Apparatus and Procedure

Observations occurred between 5:00 p.m. and 7:30 p.m. under a 60-watt fluorescent bulb. The animals were paired by their size. Two pairs were observed for 30

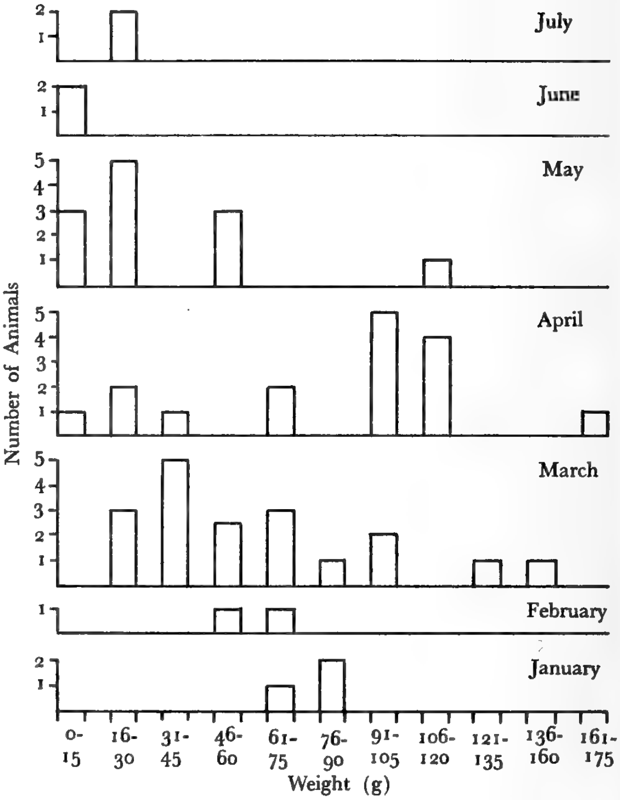

Figure 2

Frequency Distribution of Initial Weights of *Aplysia dactylomela* Collected at Plajita Rosada, Puerto Rico (N = 56) minutes every 6 days; 2 pairs were observed every other day. The 5th pair was observed as individuals on experimental day 1 and then every 6 days (Table 1). A circular bowl 30 cm in diameter and 10.2 cm high was filled with fresh sea water to a depth of 8 cm. The animals were taken from their home tanks and weighed. The observation began immediately upon the introduction of the second animal.

Table 1

Characteristics of Five Pairs of Pre-Copulatory *Aplysia dactylomela* Observed Repeatedly in Different Frequencies

	Initial weight (g)	Number of pairings	Interval between pairings
Pair 1			
Partner A	14	4	6 days
Partner B	16		
Pair 2			
Partner A	25	3	6 days
Partner B	26		
Pair 3			
Partner A	13	2	6 days[2]
Partner B	16		
Pair 4			
Partner A	6	7	2 days
Partner B	11		
Pair 5			
Partner A	21	6	2 days
Partner B	24		

[2] Unpaired on first experimental day.

The frequency and duration of contact and copulation as well as more detailed aspects of the interactions were recorded. Contact was defined as any part of an individual touching any other part of another individual. A sea hare initiated contact if it approached the other and touched it with any part of the body. Approach was defined as any locomotion which decreased the interindividual distance while oriented toward the second individual. Reciprocal contact occurred when both animals initiated the contact. Copulation was said to occur upon the intromission of one animal's penis into the common genital opening of the partner. Under the observational conditions described above, this could be determined exactly. If a pair was still in contact or copulating by the end of the observation, spotchecks every 5 minutes continued until the animals separated.

Table 2

Patterns of Contact and Copulation of "Juvenile" *Aplysia dactylomela* Paired Every Two Days

	Pairing						
	1	2	3	4	5	6	7
Pair 4							
Number of Contacts Initiated By Partner A	0	0	0	3	1	4	0
Number of Contacts Initiated By Partner B	1	3	2	6	2	2	3
Number of Contacts Initiated Reciprocally	0	1	1	0	2	2	2
Pair 5							
Number of Contacts Initiated By Partner A	2	0	0	2	0	0	—
Number of Contacts Initiated By Partner B	0	0	0	0	0	0	—
Number of Contacts Initiated Reciprocally	1	0	1	1	1	2	—
Sperm Recipient	—	—	B	B	B	A	—

C. Sample Characteristics

Figure 2 shows the distribution of weights for the population from which the experimental subjects were selected. The median weight of the entire group was 56 g. The experimental sea hares were collected in April and May when most of the population (15 out of 28) were below 60 g. The median weight of the experimental animals was 16 g.

Only 1 pair of the 56 animals from Plajita Rosada was found copulating and no other animals were found in contact even though most were collected near each other, within approximately 75 m of coastline.

RESULTS

Figure 3a - 3e shows the growth curves and duration of contact and copulation with repeated pairings for each pair in the study. As these data indicate, copulation occurred in only 1 pair (5). There appears to be a tendency for longer contact interaction with increasing size where-

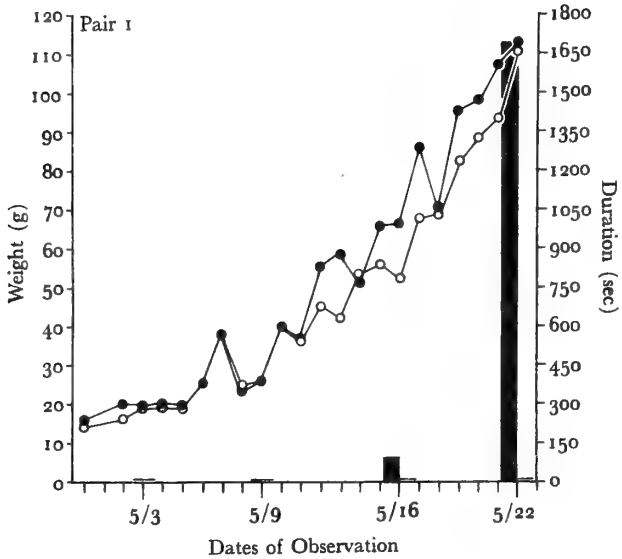

Figure 3a

Total duration (sec) of contact (solid bar) and weight changes of immature *Aplysia dactylomela* found at Plajita Rosada, Puerto Rico.

Copulation did not occur

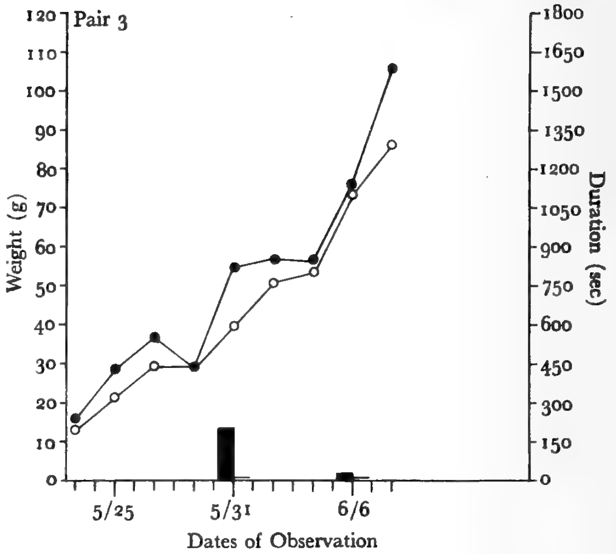

Figure 3c

Total duration (sec) of contact (solid bar) and weight changes of *Aplysia dactylomela* found at Plajita Rosada, Puerto Rico.

Copulation did not occur

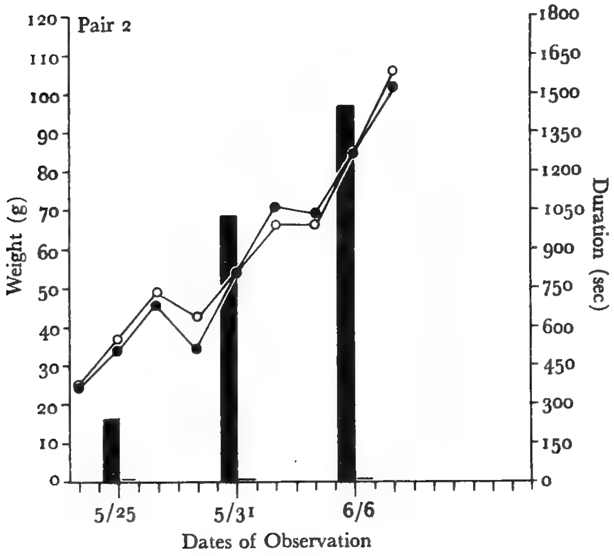

Figure 3b

Total duration (sec) of contact (solid bar) and weight changes of *Aplysia dactylomela* found at Plajita Rosada, Puerto Rico.

Copulation did not occur

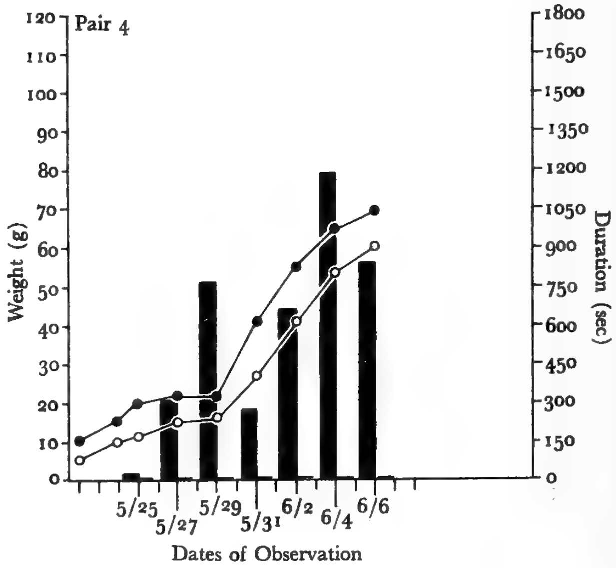

Figure 3d

Total duration (sec) of contact (solid bar) and weight changes of *Aplysia dactylomela* found at Plajita Rosada, Puerto Rico.

Copulation did not occur

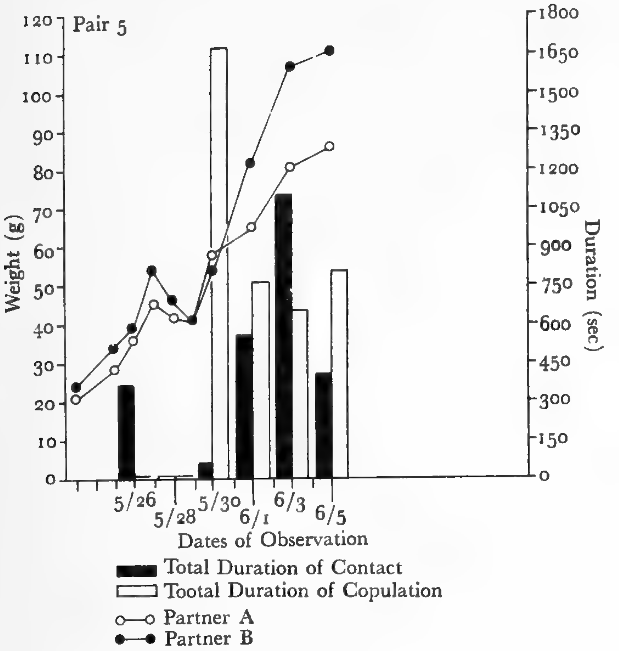

Figure 3e

Total duration (sec) of contact (solid bar), copulation (open bar) and weight changes of *Aplysia dactylomela* found at Plajita Rosada, Puerto Rico

ever there is a consistent tendency to contact at all.

Pairs 4 (Figure 3d) and 5 (Figure 3e) each had 7 and 6 observations respectively. This permitted somewhat more detailed statements about the interactions. As Table 2 shows, pairs 4 and 5 were different in their patterns of contact. In pair 4, a single contact, initiated by B, occurred early during the initial pairing and lasted for 35 seconds. The animals weighed 11 g and 20g respectively during this observation. During the 1st 3 pairings, 2 contacts were initiated mutually; 6 other contacts were initiated only by Partner B (1 in the 1st, 3 in the 2nd, and 2 in the 3rd pairing). In the 4th observation B initiated 6 out of 9 contacts. In the 5th, B initiated 2 contacts, A initiated 1, and 2 were mutually initiated. In the 6th pairing, out of 8 separate contacts, B initiated only 2, 4 were initiated by A, and 2 were mutual. But in the 7th pairing B initiated 3 out 5 contacts where 2 were mutually initiated. Thus, out of 27 separate contacts which were not initiated by both animals (total of 8), B initiated 19 and A initiated 8.

In pair 5, contact occurred during the 1st observation when the pair weighed 28g and 34g respectively. There was no contact during the 2nd pairing. Considering all 6 observations, 6 contacts were initiated reciprocally and 4 were not. These 4 were all initiated by partner A, who was also the sperm donor in 3 of the 4 observation periods where copulation occurred. Partner B became the sperm donor only after A had assumed that role 3 times. The animals contacted shortly after the 3rd pairing and began to copulate after 90 seconds of the observation period had elapsed. At this time, they weighed 53g and 58g respectively. Copulation occurred in each of the next 3 pairings. The 4 copulations lasted for 43, 12, 21 and 49 minutes respectively. It is noteworthy that when partner B assumed the sperm donor role the duration increased to a level equivalent to the first copulation when A was the sperm donor.

DISCUSSION

The *Aplysia* observed in this study were assumed to be pre-copulatory because of the following: 1. Of 56 animals collected from the same location, only one pair was found copulating in the field; these 2 individuals weighed 47g and 55g respectively. In addition, none of the animals found in the field was in contact, although many were near each other. 2. Most of the sea hares did not copulate with repeated pairings in the laboratory. 3. None of the animals laid eggs while they were in the laboratory. Together with their small size when collected, these observations suggest that they were not reproductively mature.

Although only 1 of the 5 pairs copulated, it shared some characteristics with those that did not copulate, such as change in weight, duration of contacts, etc. However, it is useful to examine this pair in detail. For example, Frazier *et al.* (1967) found that the bag cells of *A. californica* begin to contain neurosecretory granules when animals reached 50g in weight. Copulation occurred after each animal of pair 5 passed the 50g mark in body weight, indicating that this may be a necessary but not sufficient condition for copulation to occur, as all pairs reached that weight before observations ended.

In the one pair which copulated, the animal which was the sperm recipient was heavier at the start (B). Following the first copulation there was a spurt in its growth rate in comparison with its partner (A's), and their congruent pre-copulatory pattern of weight change. If the spurt in weight proves reliably associated with copulation, the onset of egg-laying (which may depend on bag-cell hormones) could be related to copulation and the contacts which precede it.

LEDEHENDLER *et al.* (1976) found that in reproductively mature *Aplysia dactylomela* animals which behave more consistently in the sperm recipient role copulate with more partners than the consistent sperm donors. They suggest that this may be based on a feedback system related to amount of sperm received. In the observations recorded here, role reversal occurred after 3 copulations in which the same roles were assumed. This is consistent with the function of such a feedback system. These observations are considered preliminary but indicate directions for further research on the possible interdependence of social stimulation and physiology in the development of reproductive processes in this species.

ACKNOWLEDGMENTS

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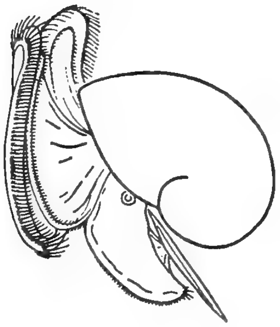

NOTES & NEWS

Direct Development in the Intertidal Gastropod *Batillaria zonalis* (Bruguière, 1792)

BY

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(1 Text figure)

THE MUD SNAIL *Batillaria zonalis* (Bruguière, 1792), a native of Japan, was introduced to North America with the Japanese oyster, *Crassostrea gigas* (Thunberg, 1793) (QUAYLE, 1964). Well established populations of *B. zonalis* can be found on mud flats from California to British Columbia (MACDONALD, 1969) wherever Japanese oysters were planted, but not in other suitable habitats. Nothing is known about the breeding habits and early life history of this mollusk. On the basis of *B. zonalis*' discrete distribution, QUAYLE (*op. cit.*) suggested that it may have either a direct development or a short pelagic life.

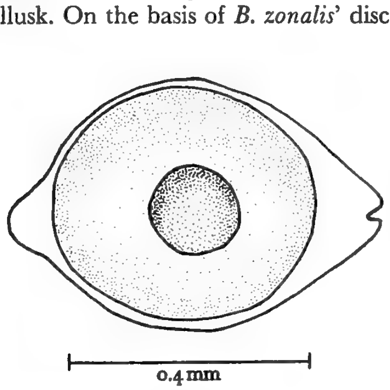

Figure 1

Egg Capsule of *Batillaria zonalis* (Bruguière, 1792)

Adult *Batillaria zonalis* were collected from Fanny Bay (49°18'N Lat.; 124°48'W Long.) on June 25, 1976 and maintained in filtered sea water at 22° C. Seven days after the collection *B. zonalis* released sedentary egg capsules measuring 0.4 mm wide and 0.6 - 0.7 mm long. Detritus and mud adhere to egg capsules thus enabling them to anchor to the sediment or other substrates. Each capsule contained 1 zygote measuring 0.13 mm in diameter. One end of the capsule is notched and the other nippled (Figure 1). Three days after the deposition of egg capsules embryos were moving in 67 out of 70 capsules. Larval shells were observed by day 7 and on day 11 juvenile snails crawled out of their capsules. The juvenile snails were 0.3 mm long and appeared to be benthic and not equipped for pelagic life. The absence of a pelagic dispersal stage might be a controlling factor in preventing *B. zonalis* from spreading to other suitable mud flats.

We thank Dr. Dan B. Quayle for reading the manuscript.

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A New Sea-Floor Oasis

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RECENT EXPLORATION of the sea-bottom along the Galápagos rift zone has revealed a rich fauna. This find is second only to the discovery in the 1950s of *Neopilina* west of Costa Rica. At depths of around 2500 m (1400 fathoms), hot springs along the rift somehow make possible a bottom fauna of spectacular size and abundance. In February, 1977 an expedition funded by the International Decade of Ocean Exploration (National Science Foundation), jointly sponsored by Oregon State University, Woods Hole, Massachusetts Institute of Technology, and Scripps Institution, with participation by others, such as Prof. Tjeerd van Andel of Stanford University, made several dives in a submersible craft, the "*Alvin*," to study the hot springs.

The bottom fauna surrounding the springs came as a surprise, and only a few specimens could be recovered with the equipment on the "*Alvin*." Photographs made during the dives reveal crabs, tube worms, limpet-like mollusks, abundant large clams and mussels, and others. Dr. van Andel reported seeing large gastropods up to 5 cm long grazing on a black slime on the rocks. All of the invertebrates seen were of phenomenal size. One *Calyptogena* shell that was recovered intact measures more than 25 cm in length, and the 2 valves weigh 525 g (18 oz.). Bottom temperature around the springs is 10° C, whereas the surrounding water is about 2° C. Fish were abundant, also, and sessile organisms such as hydroids, bryozoans, crinoids, and sea anemones were observed. Water from the springs is of normal salinity, low in oxygen, rich in manganese and iron, and markedly radioactive.

This find may give us a whole new direction in our efforts to explain faunal movements of the past. It also underscores the need for further study to reveal how such abundant life can be nourished in an oxygen-poor environment so far away from the photic zone. The area is about 320 km (200 miles) ENE of the Galápagos Islands, where 3 large plates of the earth's crust are gradually moving apart (hence the term "rift zone").

A Color Variant of *Conus bulbus* Reeve

BY

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(3 Text figures)

Although many species of *Conus* are known to be highly variable in color pattern, the West African *C. bulbus* does not seem to be particularly noted for color variants. All specimens that I have seen have a pattern of longitudinal bars with some degree of variation in the nature of the bars. Recently I purchased a specimen of *C. bulbus* with a highly unusual and apparently previously unreported color pattern. While it has the characteristic shape and spire of *C. bulbus*, the longitudinal bars are broken up into small dashes. At first glance, the dashes appear to be arranged in spiral lines. Closer examination shows that traces of the longitudinal bars may still be seen near the anterior end of the shell. I do not know how common this color variant is but it is the first I have seen among the more than 50 *C. bulbus* I have had an opportunity to examine.

Figure 1
Conus bulbus, usual phenotype from Luciras Bay, Angola

Figure 2
Conus bulbus, usual phenotype from Lobito Harbor, Angola

Figure 3
Conus bulbus, color variant from Lobito Harbor, Angola
All Figures ×1.5

The Identity of *Conus fulmineus* Gmelin

BY

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(1 Text figure)

Kohn (1966) reviewed the nomenclatural history of *Conus fulmineus* Gmelin, 1791. He (Kohn) designated plt. 58, fig. 644 of Martini (1773) as the lectotype of this species. Kohn (1966, 1968) noted that *C. fulmineus*, although considered a provisionally valid species, is not represented by any specimens that he knew of. Recently, shell dealers and collectors have been identifying a West Pacific cone (figured by HINTON, 1972: plt. 34, fig. 13) as *C. fulmineus*. This identification is certainly erroneous. The figure of the lectotype of *C. fulmineus* (KOHN, 1966; 1968) shows a cone with an elevated, sharp pointed, scalariform spire. The body of the shell is marked by numerous interrupted spiral lines which are at intervals covered by longitudinal brown bars. The specimens erroneously identified as *C. fulmineus* lack interrupted spiral lines. They also have 2 irregular brown bands, one of which covers the posterior half of the body, the other on the anterior half leaving white near midbody. They do not have longitudinal bars that run the length of the whorl. The identity of this species is currently under study and at present I know of no name that has been applied to it.

Figure 1

In the last few years, several specimens have come to my attention which appear to be conspecific with the lectotype of *Conus fulmineus*. A specimen at present in my private reference collection is shown in Figure 1. The color pattern and the elevated, scalariform spire closely resemble the lectotype and general proportions are also similar. The only difference of importance is that the shoulder is more angular on this specimen than the shoulder of the lectotype. This difference could well be due to artistic inaccuracy, or possibly the lectotype was beach worn. The close resemblance in other major features outweighs this difference and specimens similar to the one shown in Figure 1 should be considered *C. fulmineus* Gmelin. Synonyms of *C. fulmineus* include *C. fulgurans* Hwass, 1792 which was also based on the Martini figure (KOHN, 1968), *C. selectus* A. Adams, 1855 from Malacca, *C. lentiginosus* Reeve, 1844 and *C. optabilis* A. Adams, 1853. The latter 2 species were described from shells lacking locality data. The geographic range of *C. fulmineus* is uncertain, but specimens that I have seen have been from the Indian Ocean in the vicinity of the Indian subcontinent. The specimen figured here was trawled from an unknown depth by fishermen near Madras, India.

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MARTINI, FRIEDRICH HEINRICH WILHELM
1773. Neues systematisches Conchylien-Cabinet. 2. Nürnberg.

W. S. M.

AT THE TENTH ANNUAL meeting of the Western Society of Malacologists the following slate of officers was elected to serve during the fiscal year 1977/1978:

President:	Dr. Peter D'Eliscu
First Vice-President:	Barry Roth
Second Vice-President:	Dr. Vida Kenk
Secretary:	Salle Crittenden
Treasurer:	Carol Skoglund
Members-at-Large:	Sally Bennett Patrick LaFollette

The Eleventh Annual Meeting will be held at Santa Clara University, Santa Clara, California 95053 from Wednesday, June 28 to Saturday, July 1, 1978.

The Society elected Mr. Emery Perkins Chace, the oldest living, active conchologist in the United States, and Dr. Wendell Oliver Gregg to Honorary Life Membership.

Another Generous Contribution from the San Diego Shell Club

After our July issue had come back from the printer, we received a very generous donation to our Endowment Fund from the San Diego Shell Club. It was, therefore, impossible for us to express our thanks to the Club and its members until now. As in the past number of years, the continued generosity of our friends helps us to keep the membership dues at their low level in spite of the uninterrupted steady rise in costs of paper and printing. Thus, our thanks to the Club is not only on behalf of the journal itself but also on behalf of the many members of the California Malacozoological Society.

Moving?

If your address is changed it will be important to notify us of the new address at least **six weeks** before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address – $1.-

change of address and re-mailing of a returned issue – $2.75 minimum, but not more than actual costs to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address).

New Postage Rates

The U. S. Postal Service has increased second class mail rates, effective on July 6, 1977. We will, however, not increase our charges for mailing The Veliger, but must insist that we are reimbursed in all cases for returned copies and for the expenses involved in remailing such copies to a new address. It is very important for our members to realize: a) the postal service will not forward any mail other than first class for more than 90 days, even though forwarding postage may be guaranteed by the addressee; and b) it is totally impossible for us to make changes in addresses in less than 6 weeks.

We must make an address change even if only one digit in the ZIP code is changed, and the cost to us is the same as for a completely new address.

Under no circumstances are we able to supply free replacement copies of issues that fail to reach their proper destination. However, we will ship by insured mail replacement copies at half the announced single copy rate of the particular issue plus postage. We have developed a triple check system so that, if we say that a copy has been mailed, we are absolutely certain that we delivered that copy to the post office in Berkeley and on the date we indicate. From our experience with the loss of insured mail, we are tempted to suggest that subscribers figure on a 10% reserve fund for the purchase of replacement copies. The only alternative remaining would be for us to increase subscription rates and membership dues by at least 10%. This, however, does not seem quite fair to us as some of our subscribers in almost 20 years have never failed to receive their copies.

On July 6 the rates for book parcels and the library rate have been increased. This necessitates that we must increase the postage charges on back volumes, supplements and individual back numbers. The charges stated must be increased by 20¢ for one item and by 8¢ for each additional item.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $4.25 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

California Malacozoological Society, Inc.
announces

Backnumbers of

THE VELIGER

and other publications

Volumes 1 through 8: out of print

Volume 9: $22.- Volume 10: out of print
Volumes 11 and 12: out of print
Volume 13: $24.- Volume 14: $28.-
Volume 15: $28.- Volume 16: $32.-
Volume 17: $34.- Volume 18: $34.-
Volume 19: $34.-

We now have a limited number of volumes 9, 11, 13, 14 to 18 available bound in full library buckram, black with gold title. These volumes sell as follows: Volume 9 at $27.-; Volumes 11 and 13 at $29.- each; Volumes 14 and 15 at $33.-; Volume 16 at $38; Volumes 17, 18, 19 at $41.75; to this we must add a handling charge of $2.75 per volume for shipment to domestic addresses and $4.75 for shipment to any foreign address. Further, we must collect the appropriate amount of sales tax on the price of the bound volumes sold to California residents.

Supplements

Supplement to Volume 3: $6.-* plus handling charge
[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;
Part 2: The Anaspidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

[The two parts are available separately at $3.- each plus a handling charge (see below). If purchased separately, each part is subject to the California State sales tax if mailed to California addresses].

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announcement below.

Supplement to Volume 11: $6.-* plus handling charge.
[The Biology of *Acmaea* by Prof. D. P. Abbott *et al.*, ed.]

Supplement to Volume 14: $6.-* plus handling charge.
[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 15: $15.-* plus handling charges as follows: $1.50 for addresses in the United States of America; $3.00 for all other addresses.
[A systematic Revision of the Recent Cypraeid Family Ovulidae by Crawford Neill Cate]

Supplement to Volume 16: $8.-* plus handling charge.
[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]

Supplement to Volume 17: $3.-* plus handling charge.
[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Supplement to Volume 18: $10.-* plus handling charge.
[The Biology of Chitons by Robin Burnett *et al.*].

(Our supply of this supplement is exhausted; however, copies may be available by making application to the Secretary, Hopkins Marine Station, Pacific Grove, California 93950.)

Unless otherwise specified, the following guidelines for estimating the handling charges should be used: Minimum for U. S. A. $2.-. If an order is for 2 or more items, add $0.40 for each. Minimum for all foreign countries $4.-; add $0.55 for each item in addition to the first one. These charges reflect the latest increases in fees by the U. S. Postal Service.

These handling charges must, however, remain subject to change without prior notice, depending on the vagaries of rate-fixing by the postal service.

Items marked with * are subject to sales tax in the State of California; residents of that State please add the appropriate amount to their remittances.

Prices subject to change without notice.

Send orders with remittance to:

Mrs. J. DeMouthe Smith, Department of Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. Please make remittance payable to C. M. S., Inc. in U. S. $, net and free of any fees to the Society.

Shipments of material ordered are made once a month.

We are forced to adopt this measure because of the continual cut-back in personnel at the U. S. Post Office with the amount of time wasted standing in line having increased to intolerable lengths. Since it requires the same amount of time to mail 20 packages as it takes to mail one, the saving of time by our reduced mailing schedule is obvious. It becomes glaringly obvious that with the increase in postage rates and fees, the service is deteriorating at increasing rapidity. Although we spend much of our time complaining, one voice is not enough to bring about a change.

Subscription rate to Volume 20 remains the same.

We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US$12.- to US$20.-, depending on the cost to us.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

A Glossary of A Thousand-and-One Terms Used in Conchology

by WINIFRED H. ARNOLD

originally published as a supplement to volume 7 of the Veliger, has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US$ 3.50 postpaid if remittance is sent with the order.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. 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:

Volume 1: $1.50
Volume 2: $3.00
Volume 3: $3.00
Volume 4: $4.50
Volume 5: $4.50
Volume 6: $4.50
Volume 7: $6.00
Volume 8: $6.00
Volume 10: $9.00
Volume 11: $9.00
Volume 12: $9.00
Supplement to Volume 6: $1.50; to Volume 18: $3.00

California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, P. O. Box 243, Santa Maria, CA 93454.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from the Society at prices indicated elsewhere in the NOTES & NEWS section.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of $1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to Mrs. J. DeMouthe Smith, *Manager,* C. M. S., Department of Geology, California Academy of Sciences, Golden Gate Park, San Francisco, CA(lifornia) 94118. However, until further notice, we are suspending the publication of supplements until it will be reasonably certain that we will not be forced to spend many hours in tracing of lost insured or registered parcels and entering claims for indemnification. The special mailing list of members and subscribers who have entered an "including all supplements" will be preserved because of our innate optimism that sometime within our lifetime the postal services throughout the world will return to the former excellent and reliable performance.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims of missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues. This refusal is necessary as we have received an increasing number of "claims" as much as 6 months **before** the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

At present we are charged a minimum fee of $12.50 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 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); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of $1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of $5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is $25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

REGARDING POSTAL SERVICE

Complaints regarding late arrival of our journal are increasing in number, steadily, continually. However, we very conscientiously dispatch our journal on the printed publication dates. What happens after deposition at the Post Office is, of course, beyond our control. From some of our members we have been able to construct a sort of probable delivery schedule. In general, within California, 8 days is usual; outside of California, the time lapse increases with the distance; the East Coast can consider a lapse of "only" two weeks as rapid service; 4 to 5 weeks are not uncommon. Foreign countries may count on a minimum of one month, six weeks being the more usual time requirement and over two months not rare!

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed $200.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, $200.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office, in other words, it is destroyed.

Publication Date of THE VELIGER

The publication date of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

INFORMATION DESK

What's the Difference?

Telegraphic Style versus Normal Style

BY

A. MYRA KEEN

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In systematic work telegraphic style is generally adopted for the descriptions of taxa, yet few style manuals give discussions on how and when to use it. A compact or condensed manner of writing, telegraphic style omits verbs or uses them only as present participles, and articles often are omitted also. Sentences tend to run together, separated by commas and semicolons rather than periods. The subject of each phrase or sentence is stated early, usually as the first word. This is an appropriate style for descriptions of species and for tabular matter that follows – statements of type locality, distribution, type repositories, etc. In adopting the style one needs to remember to be consistent within the paragraph and not switch from telegraphic to normal until one is ready to go on in normal style to conclude the section or the paper.

As a sample and as evidence of how much space can be saved by use of telegraphic style, here is a somewhat abridged and emended description from a recent issue of The Veliger, followed by a transcription into normal style:

> Shell large, elongate, strong; protoconch of about 2 smooth, convex whorls, followed by 9 gently convex whorls forming a high, pointed teleoconch; suture slightly indented; sculpture consisting of heavy axial ribs (12 on penultimate whorl), and microscopic lines of growth throughout, bent forward at suture, with a few fine spirals at base ...

Paraphrase in normal style:

> The shell is large, elongate, and strong. The protoconch has about two smooth, convex whorls, followed by nine gently convex whorls that make up a high, pointed teleoconch. The suture is slightly indented. The sculpture consists of heavy axial ribs, of which there are twelve on the penultimate whorl. Microscopic lines of growth are present over the entire shell and are bent forward at the suture. A few fine spiral threads are present at the base ...

BOOKS, PERIODICALS, PAMPHLETS

Living Marine Molluscs

by C. M. Yonge & T. E. Thompson. Collins, London, 288 pages, 16 plates (8 in color), 162 text figures, clothbound, $13.95, 1976.

This is a richly interesting and valuable book for any invertebrate zoologist, marine biologist, or professional or amateur malacologist. Co-authored by T. E. Thompson, who contributed two excellent chapters on opisthobranchs, it must be regarded as largely the work of C. M. Yonge, who furnished the remaining 16 chapters and epilogue. The focus on living marine molluscs and their adaptive radiation has been achieved, in part, by a clear limitation of the aspects of molluscan biology that are covered in detail. Thus, there is little on internal anatomy and the physiological functioning of circulatory, respiratory, digestive, and excretory systems; the complexities of stomach morphology and the details of ctenidial structure in bivalves are not spelled out (they have been well covered by other authors); there is little discussion of systematics and phylogeny; there is, of course, no discussion of the highly successful land and fresh-water pulmonates; and at first glance the book might appear to be strongly devoted to British molluscs. Yonge and Thompson view the Mollusca from the outside, or from within the mantle cavity, where the former is so much at home. What has resulted from their selective omissions is a finely balanced account of the astonishing adaptive radiation of the Mollusca, by authors who have a feel for the subject. In short, they give an unsurpassed picture of what molluscs are all about, and the varied ways in which they make a living. British examples are used where appropriate, but the authors, notably Yonge, draw heavily upon experience on the California coast, the Australian Barrier Reef, and other regions. The book is written in clear, simple language, no more technical than necessary, but that does not imply that it is intended for the beginner. Without some basic knowledge of molluscs, one could be overwhelmed in the accounts of so many and diverse adaptations. The breadth of the book will make it appeal to any malacozoologist, since it presents so well-balanced an overview of the evolutionary achievements of so diverse a phylum.

There are a few minor errors: the reference on p. 84 to fig. 3 should be to fig. 4; on p. 178 reference to fig. 160 should be to fig. 162; and on p. 125 a reference to *Limapontia depressa* (fig. 65) sends one to a picture of *Alderia modesta*. That the motion-detecting eyes of scallops, with their unique reflecting-telescope focusing, should be said to be "similar" (p. 257) to the box-camera eyes of cephalopods is a bit too much of an oversimplification. But only a dour New England reviewer would call attention to the typographical error (p. 211) that designates the familiar quohog or little-neck or hard clam (*Mercenaria mercenaria*) as a soft-shelled clam (this name being used at the Hub of the Universe for *Mya arenaria*, also long-necked clam, which passes in Britain as the sand gaper).

The book is well-illustrated and indexed. It is by all means highly recommended, to be read and enjoyed.

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Berkeley, California 94720

Checklist and Bibliography of the Tertiary and Quaternary Mollusca of Japan 1950 - 1974

by Koichiro Masuda & Hiroshi Noda. 494 pages, 4 text figures. Saito Ho-On Kai, 20-1, Honcho-2 chome, Sendai, Japan. 15 December 1976

This comprehensive volume complements the 1952 Hatai & Nisiyama checklist of Japanese Tertiary mollusks described and illustrated through 1949. It is an alphabetic listing of nearly 5000 fossil mollusks described or illustrated during the 25 year period 1950 - 1974. Mollusks from Tertiary and Quaternary formations are listed separately by taxonomic order and by geologic period. The format is similar to that of the well-known catalogue of Tertiary mollusks of California by A. M. Keen and Herdis Bentson published in 1944. Masuda and Noda have indicated taxonomic revisions and corrections, where appropriate, following the author's original citation and an indication of geologic age, formation, and geographic location. A bibliography of papers dealing with Cenozoic mollusks of Japan accompanies the checklist; part of the bibliography covers papers on fossil mollusks from neighboring countries, another deals with topical studies such as biogeochemistry, absolute age dating, and shell structure.

This excellent report, together with the earlier companion volume, will be especially valuable to paleontologists studying the systematics and biogeography of molluscan faunas of the circum-North Pacific area, as well as to neontologists interested in the origin and migrational history of modern molluscan faunas of this region.

Warren O. Addicott

Directory of Palaeontologists of the World Third Edition, 1976

by Ephraim Gerry. 3rd edition, 1976. Universitetsforlaget, P. O. Box 307, Blindern, Oslo 3, Norway. 1976. US$9.50.

The third edition published under the auspices of the International Palaeontological Association, includes names and addresses of some 6000 paleontologists throughout the world. It represents a much more complete compilation than the 1968 edition which included only about half as many names. Following the alphabetic listing of paleontologists, is a listing of specialists by taxonomic specialization. This section includes several specialty subheadings under each phylum or plant group. Finally, there is a geographic listing, by countries and provinces, states or cities, of institutions at which paleontologists work.

Warren O. Addicott

The Biogeography and Numerical Taxonomy of the Oegopsid Squid Family Ommastrephidae in the Pacific Ocean

by John H. Wormuth. Bulletin of the Scripps Institution of Oceanography vol. 23: 1 - 90; 22 text figs.; 15 tables. $5.00 from Univ. Calif. Press, Berkeley or Los Angeles. [2223 Fulton Street, Berkeley, CA 94720]. 22 Nov. 1976

A partly confused and contradictory taxonomic arrangement within the squid family Ommastrephidae is studied on the basis of as large a quantity of material as could be assembled and also on the basis of numerous characters that could be 'measured' accurately in one way or another. The result of this approach was a clarification of many obscure relationships and a partial rectification of taxonomic problems, as well as the recognition that more work along the same lines will be needed for an eventual total resolution of the problems of interspecific relationships.

R. Stohler

Das grosse Buch der Meeres Muscheln

by S. PETER DANCE. Translated and re-worked by RUDO VON COSEL. 304 pages; 1520 color photographs and 73 pen and ink drawings. Eugen Ulmer, P. O. Box 1032, 7000 Stuttgart 1, West Germany. DM 88.- (ca. $40.-)

In recent years the frequency of publication of books in the German language on mollusks has increased; not only the monographic works such as 'Das Tierreich' and the indispensable work of Thiele-Zilch, but a number of books aimed at the collector have appeared. On a recent visit to Switzerland we noticed in the show windows of book stores several books of this latter category by German authors. A still more recent development is the appearance of translations of books by American and English authors. Some of these are straight translations, taking over all the errors of the original works. Others, however, show that considerable effort has been expended in reviewing the original work during the task of translation and errors have been eliminated as far as possible. This is the case in the present book.

The systematic portion of the book is preceded by a preface from the pen of the well-known malacozoologist Wulff Emmo Ankel, an introduction including brief chapters on systematics and nomenclature, morphology, biology, on collecting and preparing shells, an historical review and a plea for conservation. A key with excellent explanatory figures completes this 34 page introduction. The 250 pages of the systematic portion are followed by an appendix containing accounts of species not included in the original work, a glossary and a bibliography. This part is organized into separate lists of works relating to the different geographical regions and contains some brief, but trenchant comments. The index concludes the volume.

It seems probable that this volume will be of value to many collectors who have at least a working knowledge of the German language as the descriptions and comments are written in a relatively uninvolved style. There is not a single sentence that can be called overly long – in contrast to the German style of about 50 or 60 years ago, when it seems that a sentence of less than a page-length was considered poor style.

R. Stohler

Type Specimens of Invertebrates (excluding Insects) Held at the Royal Scottish Museum, Edinburgh

by G. SMALDON, D. HEPPELL and K. R. WATT. Royal Scottish Museum Information Series, Natural History 4: 118 pp. August 1976

This well organized, large-sized (21×30 cm) publication includes 21 pages devoted to the mollusks. The following quotes from the introduction to the list are of great importance because they indicate the scope of the list as well as what further discoveries in the holdings of the Museum may be made:

"As a number of hitherto unrecognized type-specimens came to light as a direct result of investigation for the purposes of this Catalogue it is expected that further research will reveal the status of other similar material in certain of the collections. This is particularly likely in the case of early collections such as those of L Dufresne, E Forbes, R K Greville and W Nicol ... In general, paratypes have not been included ... The 'Scotia' collections ... contain a number of potential types awaiting description. ... In two cases as yet unpublished lectotype designations are included while a third lectotype (for *Cerithium angustissimum* Forbes) is designated herein."

There are very valuable annotations for many of the taxa listed. It seems to us that this particular list might well serve as a sample for similar contributions from other museums.

R. Stohler

Simposio sui molluschi terrestri e dulcicoli dell'Italia Settentrionale

Proceedings of the Societa Malacologica Italiana, Gruppo Naturalistico Mantovano. 103 pp.; numerous illustrations.

Eleven papers presented at the symposium on terrestrial and freshwater mollusks are presented; of these 10 are in Italian and one in English. All articles have at least 2 summaries in languages other than Italian. One of these summaries in each case is in English. This will facilitate the use of this interesting collection of papers presented at the symposium held at Mantua on May 10 and 11, 1975. Interested workers should inquire of Dr. Dario Franchini, 37, Via Cremona, 46100, Mantova, Italy about cost and availability of this volume.

R. Stohler

The Western Society of Malacologists, Annual Report

Pacific Grove, California, June 23-26, 1976. Volume 9
71 pages; 4 photographs, 12 October 1976

Abstracts and full texts of papers presented at the 9th annual meeting, as well as some brief resumés of business transactions are contained in this publication. It is distributed to members of the Society; available at $5.- to non-members from Dr. Eugene Coan, 891 San Jude Ave., Palo Alto, CA(lifornia) 94306.

R. Stohler

Catalogo de los Moluscos Terrestres Cubanos del Genero *Cerion* (Mollusca-Pulmonata-Ceriidae) (con una Bibliografia General) – Catalogo de la Fauna Cubana – XXXVII

by Miguel L. Jaume Garcia. Ciencias Biologicas (4) **51**: 46 pp. April 1975

Of the total of 46 pages, 24 are devoted to a taxonomic, ecologic and zoogeographical discussion of the 147 species and subspecies, and keys to the 3 subgenera. The remainder of the pamphlet is taken up by an apparently complete bibliography of the family in the West Indies.

R. Stohler

Muscheln und Schnecken des Meeres

by R. Tucker Abbott. German translation by Dr. Heinz Schröder; illustrations by George and Marita Sandström. Bunte Delphin-Bücherei Nr. 28. 160 pp.; numerous color illustrations; price unknown. 1976.

This pocketbook is essentially the same as the one published a few years earlier in the Golden Press series. The illustrations are, for the most part, well done. However, in contrast to the American version of this work, there are no translations of the scientific names, creating so-called 'common names', but the few German names that do appear in the booklet are genuine vernacular names.

This booklet will be of use to general collectors whose command of the German language is better than that of the English language.

R. Stohler

Über Ammoniten des Schwäbischen Juras

by Bernhard Ziegler. pp. 3 to 35; 5 plates; 22 text figs.

Die entrollten Ammoniten des Schwäbischen Juras

by Gerhard Dietl. pp. 36 to 43; 1 plate; 4 text figs.

both papers in Stuttgarter Beiträge zur Naturkunde, ser. C, Nr. 4. 1975

These two beautifully illustrated and clearly written articles are obviously intended for the interested layman as well as for the specialist, be the latter paleontologist or geologist.

R. Stohler

Pacific Marine Life

by Charles J. DeLuca and Diana MacIntyre DeLuca. Charles E. Tuttle Company, Rutland, Vermont 05701. 66 pages; 1 map; numerous text figs. $2.75. 30 Aug. 1976

This small pocket book has the ambitious subtitle: A Survey of Pacific Ocean Invertebrates. Pages 29 to 44 are devoted to the mollusks. Within this limited space the very large phylum of the Mollusca can be treated only most sketchily and this the authors accomplish by apparently leaning heavily on Spencer Tinker's book "Pacific Sea Shells." The approach, however, is much more in a popular vein than is Mr. Tinker's work. In the hands of young children this small book will do no damage, probably.

R. Stohler

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. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

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 specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

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A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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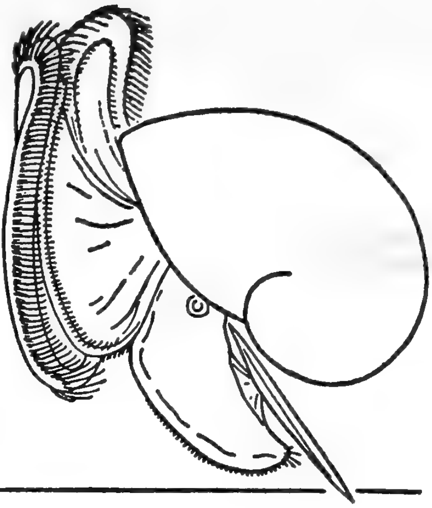

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
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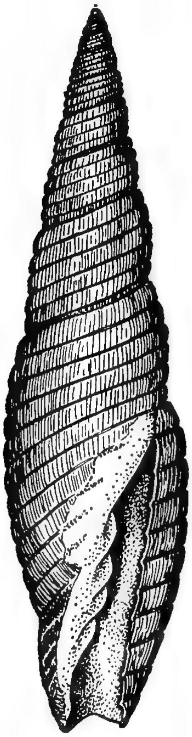

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The Samoan Land Snail Genus *Ostodes*

(Mollusca : Prosobranchia : Poteriidae)

BY

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Department of Zoology, Field Museum of Natural History
Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605

(2 Plates; 36 Text figures)

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I. INTRODUCTION

This report is modified from a dissertation submitted in 1973, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, to the Graduate School of Northwestern University, Evanston, Illinois. It revises the species of the land snail genus *Ostodes* Gould, 1862, which is found only in Western Samoa and American Samoa. Three new species, *Ostodes* ***reticulatus***, *O.* ***exasperatus***, and *O.* ***llanero***, are described, and the previously compound species *O. plicatus* (Gould, 1848) is redefined. Investigation showed that there are species recognition differences in terminal structures of the genitalia. While the presence of such differences is well known in pulmonate land snails, this is, to my knowledge, the first report of this phenomenon in land prosobranchs.

The work is based upon materials in the mollusk collection of the Field Museum of Natural History, Chicago. The methodology used required having shells and soft parts associated at the start of data capture. Material in the Museum of Comparative Zoology, Harvard University, and Bernice P. Bishop Museum is stored with the shells in one cabinet and the soft parts in another; therefore loans of anatomical materials from those institutions were not requested.

In the absence of personal field work, no information on niche differentiation can be presented. Some data on the anatomy of extralimital Pacific island taxa and one Neotropical taxon are presented for establishing outgroup comparisons.

The members of my committee, Dr. Frank A. Brown, Jr., Dr. Olin Rulon, and Dr. Alan Solem have given advice and counsel, and have been most patient with a very protracted period of study. Drs. Kenneth J. Boss, of the Museum of Comparative Zoology, Harvard University; Frank Climo, Dominion Museum, Wellington, New Zealand; Joseph Rosewater, United States National Museum; Bertram Woodland and Carol Jones, Field Museum of Natural History; Shi-Kuei Wu, University of Colorado, Boulder; and Frederick Schramm, Eastern Illinois University, Charleton, loaned specimens or gave advice. Dr. Winston Ponder, Australian Museum, Sydney, allowed me to examine the holotype of *Cyclostoma brazieri* Cox, 1870.

Mrs. Carole W. Christman bore patiently with my inexperienced dissections, and taught me a great deal in the process of producing the illustrations. Her artistic skill was available through the generosity of my father, Frederick K. Leisch, whose timely gift to the Field Museum was used in part to support Mrs. Christman's work. Mr. Fred Huysmans and Mr. John Bayalis of Field Museum of Natural History prepared the photographic prints used in this paper. Elizabeth Liebman drew some of the quantitative diagrams.

I am indebted to Dr. Solem for the SEM photographs of the radulae, to Dorothy Karall and Claire Kryczka for mounting figures, and to Jayne Freshour for manuscript typing. Miss Evelyn Patterson and Mr. Vic Snodgrass helped with translations from the Latin. Barbara Walden assisted in labeling figures and cataloguing.

Finally, I wish to thank my husband, Joseph B. Girardi, who refused to let me quit when I got discouraged, helped with German translations, and put up with sloppy housewifery while I studied; and my daughters, Stephanie and Susan, who bore cheerfully with their part-time mother.

II. HISTORICAL REVIEW OF CYCLOPHORID CLASSIFICATION

The family Cyclophoridae was first established by Gray (1847: 181 – 182). It included a miscellany of genera previously included in Cyclostomacea of earlier authors such as Anton (1839: 52 – 54). Over the next few years, additional genera were added by various authors, the placement being based entirely on shell characters. Pfeiffer (1852: 14) formally grouped the Cyclophoridae and the Pomatiasidae into the superfamily Cyclostomacea. He divided the Cyclophoridae into 4 groups that were roughly equivalent to modern subfamilies, which he named Cyclotea, Diplommatinea, Cyclophorea, and Pupinea. Fischer (1885: 739) separated the Cyclophoridae from the Cyclostomatidae on animal and radular characters.

Kobelt (1902: 336, 484, 231) recognized 3 additional subfamilies – Alycaeinae, Craspedopomatinae, and Neocyclotinae, giving great importance to zoogeographic factors. Thiele (1929: 94 – 113) essentially utilized Kobelt's system.

The first substantial innovation was by Tielecke (1940). His work was based on consideration of male and female reproductive systems, central nervous system, and organs in the pallial cavity, particularly the kidney and circulatory system. He felt strongly that anatomical differences were more fundamental than similarities in shell and radular characters, and that Thiele's system was artificial. On the basis of his findings he re-grouped the cyclophorids into a superfamily with 5 families: Cyclophoridae (with 2 subfamilies); Maizaniidae (which Thiele, 1929, had considered to be a subgenus of *Ostodes*); Poteriidae (with all the New World and Pacific Island helicoid tropical genera, including *Ostodes*); Pupinidae (with 2 subfamilies); and Cochlostomatidae, also with 2 subfamilies. Because he derived information from 3 separate organ-systems, Tielecke's work is the most extensive and the soundest yet done on this group.

Torre, Bartsch, & Morrison (1942) used only shell and opercular characters in classifying the American Cyclophoridae into 4 subfamilies: Megalomastominae (elongate shells with corneous operculum); Diplommatininae (pupoidal shell); Amphicyclotinae (helicoid shells with corneous operculum); and Aperostominae (helicoid shells with calcareous operculum).

Morrison (1955) described the external male reproductive systems of several American cyclophorids, and grouped all the genera into 2 families: the Amphicyclotidae with an enclosed, tubular vas deferens; and the Neocyclotidae, with an open seminal groove ascending the penis.

Thompson (1967, 1969) used the concept of a single large family, Cyclophoridae, recognizing the subfamilies Megalomastominae, Neocyclotinae, and Crocidopominae in Neotropical taxa, based on several characters in both male and female reproductive anatomy.

My own work has been mostly at the species level. I agree with Solem (1959: 182 and unpublished MS.) that the change from open seminal groove to closed vas deferens is by itself insufficient grounds for separation of families. I accept Tielecke's system and consider the cyclophorids as a superfamily containing 5 families, as follows (Tielecke, 1940: 365, 366): Cyclophoridae, with subfamilies Cyclophorinae and Spirostomatinae; Maizaniidae; Poteriidae; Pupinidae, with subfamilies Pupinellinae and Pupininae; and Cochlostomatidae, with subfamilies Diplommatininae and Cochlostomatinae.

The family Poteriidae has representatives in Central America, South America, the West Indies and the South Pacific. It is characterized anatomically in the male by the location of the penis on the dorsal mid-line of the head, behind the tentacles, while in the female the oviduct, seminal receptacle, and bursa copulatrix all enter the uterus via a common genital duct. Tielecke dissected four of the genera: *Poteria* Gray, 1850, from Jamaica; *Amphicyclotus* Crosse & Fischer, 1879, from Central America; *Aperostoma* Troschel, 1847 (as *Cyrtotoma* Mörch, 1852) from Mexico; and *Ostodes* Gould, 1862 from Samoa. Thompson (1967, 1969) has dissected additional taxa, although coming to very different systematic conclusions.

III. PREVIOUS STUDIES OF THE GENUS *Ostodes*

Early work was purely descriptive, as expeditions and traders brought back material for study. The 1840's to 1870's were the height of land snail descriptive work, with full-time efforts devoted simply to naming the flood of new materials. Because the association of some names with actual populations has presented problems, detailed itemization of early descriptions is necessary.

Between 1838 and 1842, the United States Exploring Expedition, under the command of Charles Wilkes, visited various South Pacific Islands, including Upolu, Western Samoa. Shells were collected principally by J. P. Couthouy, assisted by C. D. Pickering (anthropologist), Joseph Drayton (artist), and W. D. Brackenridge (botanist). Upon the Expedition's return, the mollusk collection was shunted from one depository to another, badly mishandled, and finally turned over (in part) to Augustus A. Gould for study and description (Johnson, 1964: 6–11). Gould read his descriptions of *Cyclostoma tiara, C. strigatum,* and *C. plicatum* in 1847. His descriptions were published the following year (Gould, 1848), and subsequently expanded in the text of the U. S. Exploring Expedition (Gould, 1852). The Expedition's Atlas of Shells finally appeared several years later (Gould, 1860), with the three species of *Ostodes* illustrated on plate 8.

Recluz (1851: 213; plt. 6, figs. 10, 11) described and figured *Cyclostoma apiae,* collected by M. Charbonnier, from Apia, Upolu. Pfeiffer (1854: 301–302; plt. 40, figs. 13, 14) described and figured *Cyclostoma pulverulentum* from Upolu, and in the same year Hombron & Jacquinot (1854: 50, plt. 12, figs. 25–28) described and figured *Cyclostoma albida* from Samoa, without further locality. Souverbie (1858: 294; plt. 8, fig. 6) published a description and illustration of *Cyclostoma gassiesi* from an unknown locality.

Gould (1862: 283) proposed the generic name *Ostodes* for the group of 7 Samoan species previously included in Pfeiffer's *Cyclophorus,* section 6. The cited differences of these 7 species from those remaining in *Cyclophorus* were the elongated shell form, simple aperture, deep, spiral umbilicus, and closer resemblance to the assimineid genus *Omphalotropis.*

Mousson (1865: 180) described *Cyclophorus upolensis,* collected on Upolu by M. Graeffe. Four years later the same author (Mousson, 1869: 351; plt. 14, fig. 9) described *Cyclophorus* (*Ostodes*) *adjunctus* from Tutuila, Samoa. Cox (1870: 85) described *Cyclostoma brazieri,* collected by Brazier from under decaying logs on the mountains of Upolu, Navigator's Islands (Samoa). I have examined the holotype of *C. brazieri,* (Australian Museum C64837) and find it to be definitely not an *Ostodes,* nor even a poteriid; it probably belongs to the Assimineidae.

Garrett (1887: 124–153) published the only geographical survey of Samoan land snails, drawing on his own experiences and collections in the field.

Kobelt (1902: 153) summarized the genus and listed 16 Polynesian species. Thiele (1929: 99) combined *Ostodes* with an African genus, *Maizania,* and figured a radula from the latter group.

Only one of the above authors gave data on other than shell, operculum, and radula. Gould (1852: 103) reported that the animal of *Ostodes plicatus* had a long muzzle like a proboscis, long tapering tentacles, and distinct eyes. Its foot was "pale ochreous, upper part of head, neck, and sides a faint red."

Tielecke (1940) examined the anatomy, at least in part, of cyclophorids belonging to 44 species and 19 genera. Most of the material came from the Sunda-Archipel Expedition of Dr. Rensch, and some from the collection of Dr. Degner in the Zoologisches Museum, Hamburg. Specimens identified as *Ostodes strigatus* were available from Apia, Upolu. Their true identity is uncertain, since *O. strigatus,* although originally described from Upolu, is now known only from Tutuila, American Samoa. Tielecke examined the male and female reproductive tracts, the central nervous system, and the pallial cavity, particularly in reference to the kidney and circulatory system.

Clench (1949: 4–29) revised the Pacific Island cyclophorids in the collection of the Bernice P. Bishop Museum, Honolulu. He worked only with shell, operculum, and radula, and did not study the soft anatomy. Clench described and figured 3 new species (*Ostodes cookei, O. savaii,* and *O. garretti*), and refigured 5 previously known species. Earlier authors, such as PEASE (1871: 475), had synonymized *O. plicatus* and *O. strigatus*, but CLENCH (1949: 14) stated that they were distinct and that Gould "was in error in assigning this species [*O. strigatus*] to Upolu rather than to Tutuila." Clench synonymized *Cyclostoma gassiesi* with *Ostodes plicatus*. I have seen some of the material studied by Clench. Of the 15 shells in one lot identified as *O. plicatus* (MCZ 140507), two are *O. plicatus*, the rest are *O. gassiesi*. Since anatomical data led to my recognition of their distinctness, this confusion could only be expected. From extralimital areas, Clench described a number of species and genera. These are mentioned in the section below on other Pacific Island poteriid genera.

IV. MATERIAL STUDIED

Most of this study was based on some 900 live-collected snails in the collection of Field Museum of Natural History, Chicago (hereafter FMNH). These specimens were collected on Upolu and Savaii, Western Samoa, by Dr. Alan Solem and Mr. Laurie Price in October through December 1965, and by Mr. Price on Tutuila in March and April 1975. This field work was supported by National Science Foundation Grant GB-6779 to the Field Museum in support of research by Dr. Solem, and by Office of Endangered Species contract 14-16-0008-873 to Field Museum to survey endangered land snails of American Samoa. The animals had been drowned in water to which chloral hydrate had been added as a relaxant, and then preserved in 70% ethyl alcohol. Shells and soft parts were stored together.

Specimens of poteriids from New Caledonia and the New Hebrides in the Field Museum collection were dissected for comparative purposes, as were specimens of *Mexcyclotus panamensis*, from Panama. The latter are figured for outgroup comparison.

Some shell material was borrowed from the Museum of Comparative Zoology (hereafter MCZ), Harvard University, and from the United States National Museum (hereafter USNM), Washington, to check on published identifications and to verify some of my own identifications.

V. METHODS

For each specimen whose sex could be determined, 10 shell parameters were recorded. Height, diameter, umbilical width, and horizontal diameter of the aperture were measured with a vernier caliper or (for very small specimens) an ocular micrometer. Whorl count, and both dorsal and ventral sculptural elements were counted with a binocular microscope at 10X magnification, spire angle was estimated by holding the shell against a printed protractor, and thickness of the parietal callus was estimated on a scale of one to three (one indicating a very thin callus, and three indicating a parietal callus as thick as the outer rim of the aperture). The character of the umbilical margin was scored as being smoothly rounded, sharply angled, or bordered by a rim composed of the innermost ventral spiral lira. Ratios of shell height to diameter, and of shell diameter to umbilical width were calculated for each specimen.

Empty shells, and snails that had been so severely contracted during preservation that they could not be extracted for sexing, were not measured in detail. Where many specimens in a lot were severely contracted, some shells were broken after measurement to allow sexing.

Specimens were accepted as adult that had started a changed pattern in growth, indicated by the following 3 features: (1) thickening of the parietal callus; (2) a change in the sculptural pattern on the terminal portion of the body whorl; and (3) an increase in the rate of decoiling resulting in the last portion of the body whorl being inset under the periphery of the penultimate whorl. In many snails the onset of reproductive activity is marked by just these alterations in growth patterns, when the energy budget of the individual shifts from individual growth to production of the next generation. Characteristic external genital features of both male and female *Ostodes* develop while the shell is still very small, although the internal reproductive systems remain small and undeveloped. Neither material nor time was available for determining exactly when sperm and egg production begins; much larger samples, preserved for histological examination, would be required to establish the degree of correlation between shell growth changes and onset of reproductive activity. In the absence of such material, specimens showing the growth changes were classed as mature, while those without the changes were considered juvenile. Only adult shells are cited in the species diagnoses, and means and standard deviations of populations are based on adult materials only.

For males, the penis was measured with an ocular micrometer, the lengths of the thick proximal trunk and the tapering distal thread were recorded, and the ratio of thread to trunk was calculated. For female snails, shapes and orientations of anus and vaginal orifice profiles were noted.

Internal reproductive anatomy was studied by dissecting, where possible, at least three males and three females of each species. Drawings were rendered by close collaboration of artist and investigator, with the specimen being dissected in progressive stages so that the artist could depict internal structures and fine details. The method of preservation used precluded histological studies.

Opercula were removed and studied for approximately 25% of the specimens. Examples of each opercular type were studied with both ordinary and polarized light, then embedded in paraffin and sectioned. The presence of calcium deposit was tested for with dilute HCl.

Radulae of *Ostodes gassiesi, O.* ***reticulatus****, O. plicatus* and *O.* ***llanero****,* as well as *Gonatorhaphe* sp. and *Gassiesia* sp., were prepared and photographed by Dr. Alan Solem with a scanning electron microscope as part of a cooperative research program between Field Museum of Natural History and the American Dental Association. Preparation technique was that of Solem (1972).

VI. SYSTEMATIC REVIEW

A. Variations in Structural Features

The basic systems used in species separation and classification are: (1) the shell; (2) the operculum; (3) the radula; and (4) the gross anatomy. The patterns of variation within *Ostodes* are here reviewed in order of their initial use in systematics.

1. SHELL FORM AND ORNAMENTATION

The basic shell form in *Ostodes* is turbinate. The form varies from species to species, with *O. gassiesi* and *O. plicatus* adults being narrowly turbinate (taller than wide), *O. savaii* being of approximately equal height and width, and the other species being more or less broadly turbinate, with *O. garretti* having the least elevation of the spire. Juveniles of all species, even *O. gassiesi* and *O. plicatus,* are broadly turbinate, wider than high (Figure 1).

The periphery of the body whorl in *Ostodes tiara, O. garretti, O. adjunctus,* and the "smooth" form of *O. upolensis* varies from moderately to sharply carinate. Adults of all the other species have round-shouldered body whorls, even when the early whorls were carinate.

Ostodes gassiesi, O. plicatus, O. savaii, O. tiara, and *O. garretti* have deep, narrow umbilici (mean D/U ratio 3.31). *O. strigatus, O.* ***exasperatus****, O.* ***reticulatus****, O. adjunctus, O. upolensis,* and *O.* ***llanero*** have wide open umbilici, with a mean D/U ratio of 2.76. The width of the umbilicus is affected by 2 factors: the rate of whorl translation (rate of decoiling) and the size of the generating curve, as measured by the diameter of the aperture (Raup & Stanley, 1971: 158). In two species with equal-sized apertures, that which decoils faster will have the smaller umbilicus. In two species with equal rates of whorl translation, the one with the larger generating curve will have the smaller umbilicus. Of the 2 factors, the rate of decoiling has the greater influence in *Ostodes*. Table 1 shows

Figure 1

Shell outlines of *Ostodes gassiesi*

a – juvenile b – adult

the species of *Ostodes* arranged, from the top down, in order of increasing size of umbilicus: *O. gassiesi* with the smallest umbilicus at the top, ***O. llanero*** and the "stepped" form of *O. upolensis* at the bottom. (Table 1 compares juveniles of ***O. llanero*** with adults of the other species; Figure 23 compares the same specimens of ***O. llanero*** with juveniles of the other species. The relative position of ***O. llanero*** with respect to the other species is the same. It therefore seems reasonable to assume that, if adults of ***O. llanero*** had been available for examination, they would still have fallen at the bottom of Table 1.) This arrangement also puts the species generally in order of rate of decoiling, fastest at the top and slowest at the bottom, and in approximate order of size of aperture, largest at the top, smallest at the bottom. If the data for pairs of similar species, such as *O. tiara* and *O. garretti*, or *O. savaii* and ***O. exasperatus***, be compared, it will be seen that that species of the pair which decoils faster will have a smaller umbilicus and usually also a larger aperture.

The pair for which the above statement does not hold true is the 2 forms of *Ostodes upolensis*. The stepped form decoils much faster than the smooth form (Figure 24) and should therefore logically have a smaller umbilicus. Instead, its umbilicus is larger than that of the smooth form, which would lead one to suspect it must therefore have a much smaller aperture. Not so; the stepped form has a larger aperture than the smooth form. The reasons for this apparent violation of the rules governing shell morphology can be seen in the silhouette of the smooth form (Figure 24b). Unlike most other species of *Ostodes* and the stepped form of *O. upolensis*, this form retains a pronounced peripheral carina which persists into adulthood. The carina protrudes sideways and increases the diameter of the shell in proportion to its umbilicus. Also, the inset of the terminal portion of the body whorl under the penultimate whorl is proportionally much greater in the smooth form of *O. upolensis* than in the other species of *Ostodes*, so that the umbilicus is impinged on and made smaller.

The aperture ranges in shape from round to very slightly compressed, and is appressed to the penultimate whorl. The outer apertural lip is simple, with no flange or ornamentation. The thickness of the parietal callus varies with the species and the age of the individual.

The spire and early whorls are smooth in all species of *Ostodes*. Although the smoothness might be due to wear, I think it is more likely the true primary condition of the shell because (a) it is seen even in very small, unworn juveniles and (b) the sculpture shows a distinct pattern of beginning from a smooth surface, as discussed below.

Except for *Ostodes cookei*, which is smooth, *Ostodes* shells are ornamented with spiral lirae, radial plicae, or both, according to the species. All species (except *O. cookei*) have spiral lirae, although they are quite unobtrusive in *O. plicatus*. The first spiral lira begins low down on the whorl, just above the suture, at about the beginning of the third whorl. The second spiral thread starts a little further along the whorl, and a little higher up, and so forth, until the full complement of spiral lirae is present by about the start of the fourth whorl. The spiral lirae are usually evenly distributed on the whorl, except in *O. gassiesi*, where they are clustered on the lower portion. The spirals continue in juvenile shells right up to the aperture; in adults, they fade out a few millimeters

Table 1

Mean Diameters of Umbilicus and Aperture in Relation to Shell Diameter in *Ostodes*

Species	N	D/U	D/A	H/D	Spire angle (°)
Ostodes					
gassiesi	126	3.42 ± .04	2.40 ± .01	1.07 ± .01	80 ± 0.5
tiara	15	3.38 ± .12	2.40 ± .03	0.79 ± .01	107 ± 0.9
plicatus	57	3.37 ± .05	2.37 ± .02	1.06 ± .01	81 ± 1.1
savaii	103	3.18 ± .04	2.43 ± .01	0.98 ± .01	86 ± 0.7
garretti	4	3.18	2.51	0.78	108
adjunctus	17	3.02 ± .09	2.74 ± .05	0.75 ± .01	92 ± 1.9
exasperatus	24	2.98 ± .09	2.51 ± .02	0.92 ± .01	90 ± 1.6
upolensis (smooth)	10	2.91 ± .19	2.61 ± .21	0.76 ± .05	98 ± 4.0
strigatus	84	2.89 ± .02	2.57 ± .01	0.91 ± .01	86 ± 0.8
reticulatus	12	2.78 ± .04	2.55 ± .03	0.93 ± .02	92 ± 1.3
upolensis (stepped)	12	2.37 ± .08	2.55 ± .03	0.78 ± .01	98 ± 2.6
llanero	3	2.37	2.61	0.70	110

before the aperture, at about the point where the body whorl is indented under the penultimate whorl. This probably marks the point at which reproductive maturity is reached. The spirals are continued on the lower palatal surface in *O.* ***reticulatus****, O.* ***exasperatus****, O.* ***llanero****,* and *O. adjunctus.* There may be traces of spirals on the ventral surface in *O. upolensis, O. savaii, O. tiara,* and *O. garretti,* but the lower surface of *O. gassiesi* and *O. strigatus* is almost always smooth, while that of *O. plicatus* shows only radial plicae.

Radial plicae are an important element in the ornamentation of *Ostodes gassiesi* and *O.* ***reticulatus****,* and are the major sculptural element of *O. plicatus.* In *O. plicatus* they are close-spaced, moderately broad and in high relief. They continue over the shoulder of the body whorl, across the ventral surface and down into the umbilicus. At the edge of the umbilicus, the radial plicae may sometimes be pinched into an acute angle, but they do not form a true rim around the umbilicus in the same way that a spiral lira would. The radial plicae of *O. gassiesi* are somewhat broader and shallower than those of *O. plicatus*; they hardly ever continue onto the lower palatal surface of the shell. The radial plicae of *O.* ***reticulatus*** are somewhat more widely spaced and a little narrower, so that there are definite valleys between them. The crossing of these valleys by the overlying spiral lirae creates the reticulated surface which gives the shell its name; it is particularly noticeable on the ventral surface of the shell. Radial plicae are but poorly defined in *O. strigatus, O. savaii,* and *O. upolensis,* and are absent in *O.* ***exasperatus****, O.* ***llanero****, O. adjunctus, O. garretti,* and adults of *O. tiara.*

The periostracum in *Ostodes* varies from light yellow to moderately dark brown. It is adherent in *O. gassiesi* and *O. tiara,* but is deciduous in the other species. Possibly the most deciduous periostracum is that of *O. plicatus.*

The color of most *Ostodes* shells is white, off-white or cream-color. The only exceptions are *O. gassiesi, O. adjunctus,* and *O. plicatus,* which (sometimes, half the time, and often, respectively) have pink or red spires. If a pink spire of *O. plicatus* be broken, and the broken edge examined under the microscope, it will be seen that the shell is composed of three layers: the inner and outer layers are a translucent white, but the middle layer is a very intense rose-red to salmon color. It looks pinkish from the outside of the shell because of the white layer covering it. In *O. adjunctus,* the color is deeper and the inner white layer is absent.

Shells of *Ostodes* are subject to wear in varying degrees. The factor of wear is important because a badly worn shell is very difficult to place with certainty within a species, especially if it is empty so that anatomical information is lacking. Of all the *Ostodes, O.* ***reticulatus*** and *O. upolensis* seem to show the greatest resistance to wear, while *O. tiara* and *O. garretti* are most apt to be found badly worn. MOUSSON (1865: 179) says of *O. tiara* that even fresh specimens are almost always badly worn, with not only the periostracum missing, but most of the sculptural elements also gone, so that the shell presents a bony-looking, matte surface. This may reflect space niche differences in microhabitat selection, but no data on this aspect are available.

2. OPERCULA

(Figures 2, 3)

CLENCH (1949) described the opercula of *Ostodes adjunctus, O. cookei, O.* ***plicatus****, O. strigatus, O. tiara,* and *O. upolensis,* and figured but did not describe that of *O. savaii.* He mentioned only one type of operculum for each species. The only differences between species cited were concerned with the degree of central depression and the character of the nucleus.

During this study, 198 *Ostodes* opercula were studied in detail. This sampling consisted of adult examples of both sexes from all species except *O.* ***llanero****,* for which only juveniles were available. Although all opercula were found to be circular, corneous, and transparent, there were 6 variations of this pattern. They are:

Type A-1: laminate, thin (Figure 2)

Of fairly uniform thickness throughout except for very thin and fragile outermost edge, which resembles cellophane in texture and transparency. Slight thickening sometimes found just inside this "cellophane edge." No spiral structure can be seen with either ordinary or polarized light. Central portion of operculum often shows inclusions resembling air-bubbles or fragments of mucus. Disconnected fragments of spiral lamellae occasionally seen around outer margin. Thin horizontal layering seen in cross-section. Specimen illustrated, 5.1 mm in diameter.

Type A-2: laminate, thick (Figure 2)

Cross section shows approximately same number of horizontal layers as in type A-1, but each layer is much thicker. Operculum thicker in center and near outer rim than in circum-central area. Upper surface flat or very slightly concave. No spiral structure apparent in central part, which shows inclusions as in type A-1. Three or 4 spiral lamellae may be seen around outer edges. No "cellophane edge." Lower surface shows large central papilla, formed by a dipping-down of the horizontal layers, and

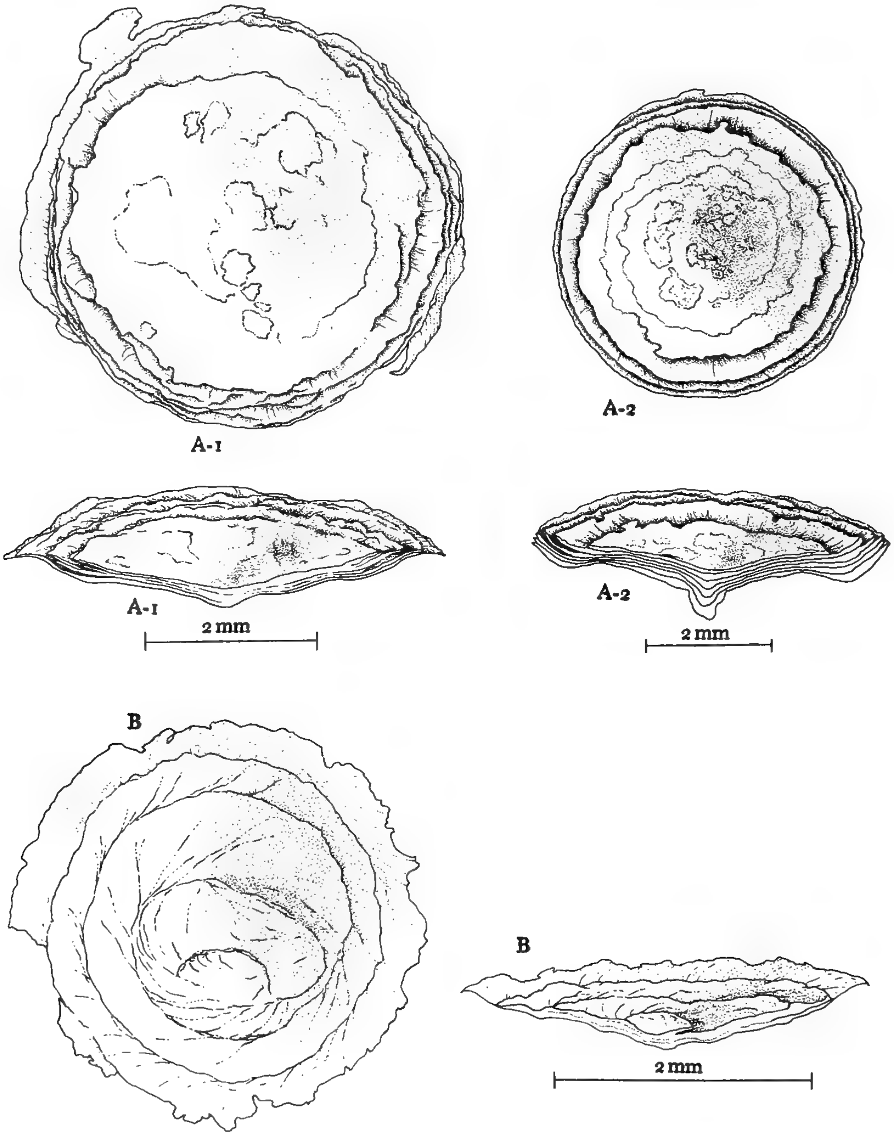


Figure 2

Opercular Types A – 1, A – 2, and B

many faint, fine, closely-spaced radial lines, like brushmarks in wet paint. With transmitted polarized light, many faint, closely-spaced spiral lines can be detected, apparently within the body of the operculum, as they do not show on either surface in any kind of reflected light. Specimen illustrated, 5.9 mm in diameter.

Type B: oligogyrous (Figure 2)

Extremely thin throughout; sometimes flat, sometimes cup-shaped, with flat central portion and edges turned up all around; in *Ostodes strigatus,* may be so acutely concave as to approach a cone-shape. Few (3 – 5) broad, irregular spirals from center to edge. Nucleus often somewhat off-

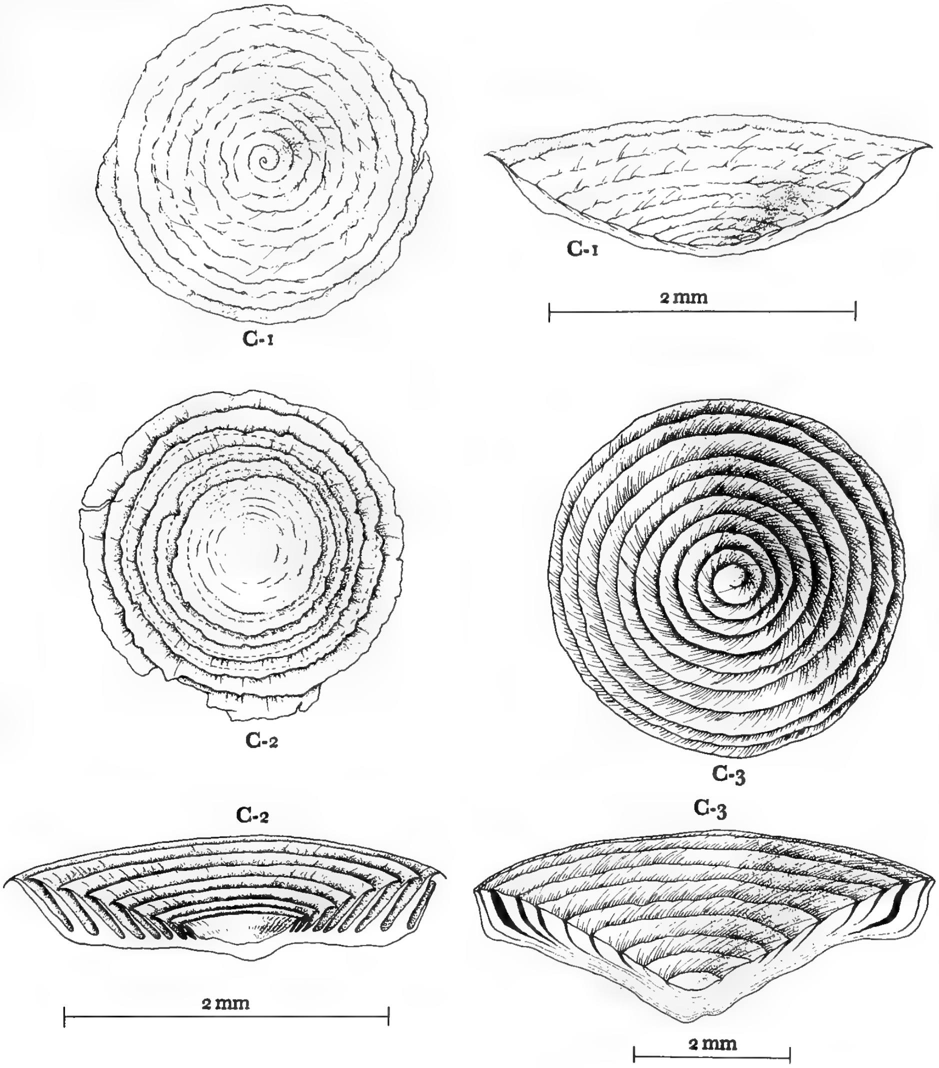


Figure 3

Opercular Types C – 1, C – 2, and C – 3

center. Strongest features of upper surface are many irregularly placed, raised, radial cords. They show up quite well under ordinary light, and are of extreme brightness with transmitted polarized light. Cords occasionally emphasized by parallel (*i.e.,* radial) inclusions of opaque, white, non-calcareous material, possibly mucus. Underside irregular in contour and without elements of true radial or spiral relief. Only very faint traces of horizontal layering seen in cross-section. Specimen illustrated, 3.7 mm in diameter.

Type C-1: polygyrous, thin (Figure 3)

Thin and flexible, of fairly uniform thickness throughout, except for "cellophane edge." No central papilla on undersurface. Flat or concave, depending on contracture of specimen. Upper surface shows many narrow, tightly organized, clearly defined spirals, lying flat and slightly overlapping. Many of these opercula, especially those found in *Ostodes plicatus* and *O. upolensis,* show a silvery, iridescent sheen on the upper surface, which obscures the spirals under ordinary light. With transmitted polarized light, the sheen disappears and the spirals are revealed. Specimen illustrated, 2.3 mm in diameter.

Type C-2: polygyrous, thick, flat (Figure 3)

Basically flat, with slightly concave central portion; nearly all examples about 4 times as thick near outer margin as through center. Many spiral lamellae, elevated at about 45° angle, surrounding smooth, depressed, central portion. Lamellae thick at base, with outer edges very thin and flexible, curving over inter-lamellar air-space, to touch next outermost lamella and producing a smooth outer surface like that of type C-1. Specimen illustrated, 2.7 mm in diameter.

Type C-3: polygyrous, thick, concave (Figure 3)

Of more uniform thickness from center to edge than type C-2, showing horizontal layering in base more clearly. Most have pronounced central papilla; all very deeply concave. Upper surface resembles type C-1 in having many narrow, clearly defined, tightly organized spirals. Inner structure closer to type C-2 in that spiral lamellae stand up from their bases. Lamellae differ from those of type C-2 in 3 ways: they are generally stouter and heavier; they are differently shaped, being thicker at the upper surface than at the base, and having no thin, overhanging edge; and the spaces between lamellae are not air-spaces, but are filled with an opaque white material, which is not calcareous; it may be mucus. Specimen illustrated 6 mm in diameter.

Discussion: The 6 opercular types are not sex-linked, and are not species-specific. Table 2 lists the distribution of opercular types by species. Three species, *Ostodes* ***llanero***, *O.* ***reticulatus***, and *O. upolensis*, are known to have only one type of operculum. However, in each case, the opercular type concerned is also found in at least 3 other species. Larger samples of these 3 species probably would include additional opercular types. One type of operculum, type C-3, has been found only in *O. tiara*, which also shows type A-2. I would expect to find additional examples of type C-3 in *O. garretti*, if more individuals of that species were available for examination. Type C-3 is a large, heavy operculum, which would accord as well with the large, heavy shell of *O. garretti*, as do the already-found types A-2 and C-2. From available evidence, I conclude that in *Ostodes* opercular type is not, as has been previously indicated, a diagnostic character at the species level.

The only correlation found between opercular type and habitat is in the 6 specimens of *Ostodes savaii* which had type C-2 opercula. These 6 snails came from a collection station (Station 32, Savaii) having a more pronounced dry season than the other stations on the same island. No species other than *O. savaii* were found there. Of 7 specimens examined for opercula from this lot, 6 had type C-2; the 7th, as well as all other specimens of *O. savaii*, from more uniformly humid places, had thinner opercula (types A-1, B and C-1). A thick operculum would of course convey a selective advantage in a dry season, offering rather more protection against desiccation.

Even this correlation breaks down, however, on Upolu. Of 21 collection stations on that island, there is a cluster of 5 (Stations 5, 7, 14, 16, and 17) that has the same climate

Table 2

Distribution of Opercular Types by Species

Species	A-1	A-2	B	C-1	C-2	C-3	Totals
Ostodes							
adjunctus			1	14			15
exasperatus	7	2	4	3	7		23
garretti	1	2			1		4
gassiesi	19		9	7			35
llanero					3		3
plicatus	8			11			19
reticulatus	8						8
savaii	14		3	7	6		30
strigatus	7	3	15	16	2		43
tiara		3				5	8
upolensis				10			10
Totals	64	10	32	68	19	5	198

as Station 32 on Savaii. Of 17 snails examined for opercula from these 5 stations, 15 were found to have thin opercula. One individual from Station 14 had a thick operculum that appeared to be of type C-1, but with many added layers. There were no upstanding lamellae, as in types C-2 and C-3, there was no central papilla, as in type A-2, and the layers themselves were no thicker than usual for type C-1; there were simply more of them. One individual from Station 17 had a similarly thickened operculum, resembling type A-1, but with many more layers than normal. The "dry stations" on Upolu are in somewhat denser forest than the one "dry station" on Savaii; perhaps there is enough difference in micro-habitat to decrease the selection pressure for thick types of operculum.

As to the very peculiar opercula designated type B, I think it is unlikely that they are replacements for opercula accidentally torn off: Fretter & Graham (1962: 82) describe a replacement operculum as being thickest in the middle and tapering towards the edges, and without "differentiation of structure apart from being laminated," which description does not fit type B at all. It is possible that type B opercula are the product of some disease process or injury to the snail, although no gross abnormalities of shell or body were observed in the snails from which they were taken. Of 43 animals of *Ostodes strigatus* examined for opercula, 15 had type B opercula, and of these, 8 were so deeply concave as to be cone-shaped, with the greatest diameter of the operculum much less than the diameter of the aperture. The snails with these peculiar opercula looked perfectly normal, except that the back of the foot, beneath the operculum, was deeply hollowed out to accept the pointed end of the cone. One such snail, a female, was very carefully dissected, in search of any anatomical abnormality; none was found, except for the hollow place in the foot. Two of the cone-shaped opercula were greatly thickened by a multiplication of layers. Two other very thick opercula were found in *O. strigatus;* one was type B (ordinary flat form), and the other was type A-1.

The 6 opercular types described above have been observed. The reasons for their existence remain to be explained. It would seem that protection against desiccation or predation could be achieved as effectively by a simple multiplication of layers as by the more elaborate methods of thickening each layer as in type A-2 or creating upstanding lamellae, as in types C-2 and C-3. I have no explanation of these differences.

3. RADULAE

(Figures *37–48*)

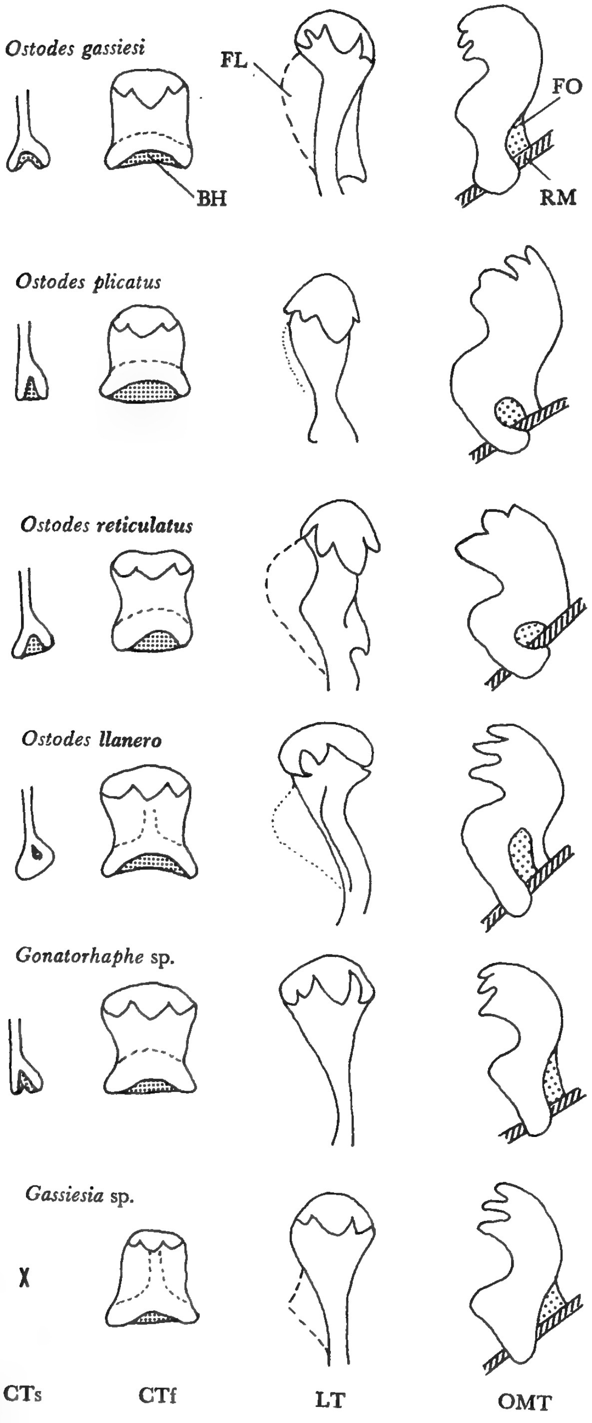
Cyclophorid snails have a taenioglossate radula, with one lateral tooth and two marginal teeth on either side of the central tooth. Photographs taken with a scanning electron microscope (SEM) show slight differences between genera and species which have not heretofore been noticed. For this study, SEM photographs were taken of the radulae from *Ostodes gassiesi, O. plicatus, O. **reticulatus,*** and *O. **llanero,*** plus examples of *Gonatorhaphe* sp. and *Gassiesia* sp. for comparison. The results are summarized below.

Central (rachidian) tooth: In all species examined, the central tooth is tricuspid. The base of the tooth is greatly thickened and deeply hollowed-out from below, with a smaller hollow on each side. When the radula is in the folded position, the central teeth lie in their longitudinal row without touching each other, the curved top of one resting in the space made available by the hollowing of the base of the next anterior tooth (Figure *41*). The shape of the central tooth varies slightly among the species studied. In *Ostodes gassiesi* it is peg-like, appearing of equal width at the level of the cusps, in the middle of the shank, and at the base. The other 3 species of *Ostodes* show central teeth that are slightly flared at the base, and *O. **reticulatus*** and *O. **llanero*** also show a slight narrowing above the flare. In *Gonatorhaphe* there is a pronounced narrowing above a moderately flared base. *Gassiesia* shows no narrowing, but a very strong flare is present.

Lateral tooth: The lateral teeth are about twice the length of the central teeth. When the teeth are not in use, the top of each lateral tooth rests against the shank of the tooth next anterior to it, at about the mid-point of the shank (Figures *37, 41*). In the 4 species of *Ostodes* that were examined, the lateral tooth has 4 cusps, of which the most medial is the smallest and the third from the inside is by far the largest. All *Ostodes* lateral teeth have long, slender shanks. In *O. gassiesi* and *O. **reticulatus,*** there is a medially projecting flange that seems to join the tooth to the radular membrane. The flange is less clearly seen in the photographs of *O. plicatus* and *O. **llanero,*** but it is shown in Thiele's drawing of the radula of *Maizania preussi* (Thiele, 1929: 99; fig. 76). In *Gonatorhaphe* sp. the lateral tooth still has 4 cusps, but the medial one is much reduced. The shank is long and slender, and there is no flange. In *Gassiesia* sp. the long shank has a flange, but the tooth has only 3 cusps – the most medial cusp has disappeared altogether.

Marginal teeth: The viewing angles are such that the inner marginal tooth cannot be seen consistently and clearly enough for comparative discussion. The outer marginal tooth is seen clearly, however, and shows more variation than any of the other radular teeth. The tooth always has 3 (some views of *Ostodes gassiesi* seem to show 4) cusps. The cusps are pointed, except in *O. plicatus,* where the outermost one is truncated. Below the outermost cusp, the outline of the tooth is first deeply indented and then protrudes into a sharply angled "shoulder." In the folded position, the outer edge of the inner marginal tooth is cradled in the indentation of the outer marginal tooth (see Figures *38* and *46*). Below the "shoulder" a shank of moderate length connects the tooth to the radular membrane. In the lower extremity of the shank there is a foramen through which the radular membrane passes. This arrangement permits the tooth to grasp the edge of the membrane firmly, but with the potential for a great deal of movement, due to the size and shape of the foramen. The angles of the indentation and "shoulder," as well as the character of the foramen, vary from species to species, and are summarized in Table 3. The functional significance of the differences in the foramen is unknown.

Discussion: Figure 4 shows 3 teeth from one row of the radula of each of the 6 species studied, presented together for ease of comparison. The differences between the 4 species of *Ostodes* are so slight that I do not feel they could be used as a diagnostic character. The teeth of *Gonotorhaphe* seem to be a sort of mixture: the central tooth resembles that of *O.* ***reticulatus,*** the lateral tooth resembles the lateral tooth of *O.* ***llanero,*** and the outer marginal tooth is very similar to the corresponding tooth of *O. gassiesi.* I would hesitate to try to differentiate between *Gonotorhaphe* and *Ostodes* on the basis of their teeth. The teeth of *Gassiesia,* however, are very different from those of the other 2 genera. The strongly flaring central tooth; the lateral tooth with only 3, not 4, cusps; and the very broad, low foramen in the outer marginal tooth set this



(← adjacent column)

Figure 4

Comparison of Radular Teeth of Six Poteriid Species

BH – basal hollow CTf – frontal view of central tooth
CTs – side view of central tooth FL – flange FO – foramen
LT – lateral tooth OMT – outer marginal tooth
RM – radular membrane

Table 3

Character of Outer Marginal Tooth

Species	Angle of indentation	Angle of shoulder	Character of foramen
Ostodes gassiesi	30°–45°	60°–90°	broad, squarish
Ostodes plicatus	75°	90°	broad, low
Ostodes reticulatus	60°	90°	broad, low
Ostodes llanero	45°	90°	tall and narrow
Gonatorhaphe sp.	45°	90°	very tall, pointed top
Gassiesia sp.	60°	90°	very broad, low

radula apart from the others quite clearly. These radular differences are sufficiently clear-cut to be a useful diagnostic character.

4. GROSS ANATOMY

a. General: Uppermost part of visceral hump occupied entirely by testis in male; in female, ovary lies on columellar side, digestive gland on outer side. Middle portion of visceral hump occupied entirely by digestive system in both sexes, except for passage of gonoduct on columellar aspect. Lowest part of visceral mass in both sexes has reproductive organs on columellar side, digestive system on outer side.

Position of organs in pallial cavity as follows: on right side, gonoduct runs below rectum from mantle line nearly to anterior opening of cavity. On left, kidney lies between layers of mantle, extending forward to about middle of pallial cavity. Pallial renal orifice not located. Pericardial cavity, with heart, nestles against lower middle portion of kidney. Hypobranchial gland J-shaped, beginning to left of mid-line, passing transversely behind kidney, then turning to run anteriorly between upper renal margin and rectum. Point of origin of transverse portion, and length and thickness of anterior portion of hypobranchial gland differ in the several species, and will be discussed individually. Anterior portion of mantle thin, fragile, vascular, except for thickened leading edge.

b. Digestive system: In female, digestive gland reaches apex of visceral mass, surrounding ovary for approximately first whorl, except on columellar side. In male, digestive gland begins at lower edge of testis. Stomach embedded in outer side of digestive gland and visible through integument. In both sexes, stomach and digestive gland together occupy entire lumen of whorl, in middle section of visceral hump, except for passage of gonoduct and esophagus on columellar side. Massed loops of intestine occupy outer half of anterior visceral hump, with most distal segment crossing from left to right just behind mantle cavity. Intestine continues forward as rectum between layers of mantle on right side. Anal orifice just inside leading edge of mantle. In males, anal orifice points straight forward. In females, orientation of anal orifice and degree of hypertrophy of its edges are species-specific.

c. Male reproductive system (Figure 5): Testis fills entire lumen of first 1–2 whorls, depending on age of individual. Color ranges from uniform creamy white through tan and brown to very dark grey. Younger individuals have smaller and lighter-colored testes. Color caused by pigment granules which appear on surfaces of testicular tissue lobules, and in interlobular spaces. In young adults they are light brown, small in size, and scattered sparsely but fairly evenly, giving whole organ a tan color, rather than the cream of the juvenile. As snail ages, granules increase in size, number, and intensity of color, causing whole organ to appear darker and darker. In an occasional individual, the granules will cluster into scattered black blotches; sometimes granules are also found on the inner surface of the encapsulating membrane. The pigment granules, whether clustered or single, are not usually firmly adherent to testicular tissue, but may be picked off fairly easily, revealing tissue itself, still creamy white underneath.

Testicular tissue consists of a number of multiple-branched trees of digitiform alveoli, arranged in a single row on the outer side of a single collecting tube, which runs down the columellar side of the whorl. Each major alveolar trunk or duct divides into 2 equal main branches, which in turn divide and re-divide fairly symmetrically. Outermost tips of the terminal alveoli give surface of the organ a lobulated appearance. There are at least 3 major alveolar ducts near anterior end of testis, with an undetermined number of progressively smaller ducts running back toward the posterior tip of the organ. Even in deeply pigmented testes, the collecting tube, and in some cases, the major ducts, are without pigment granules and thus appear white.

Collecting tube runs forward as seminal vesicle on columellar side of visceral mass. In central visceral section, it lies lateral to the esophagus and ventral to the stomach.

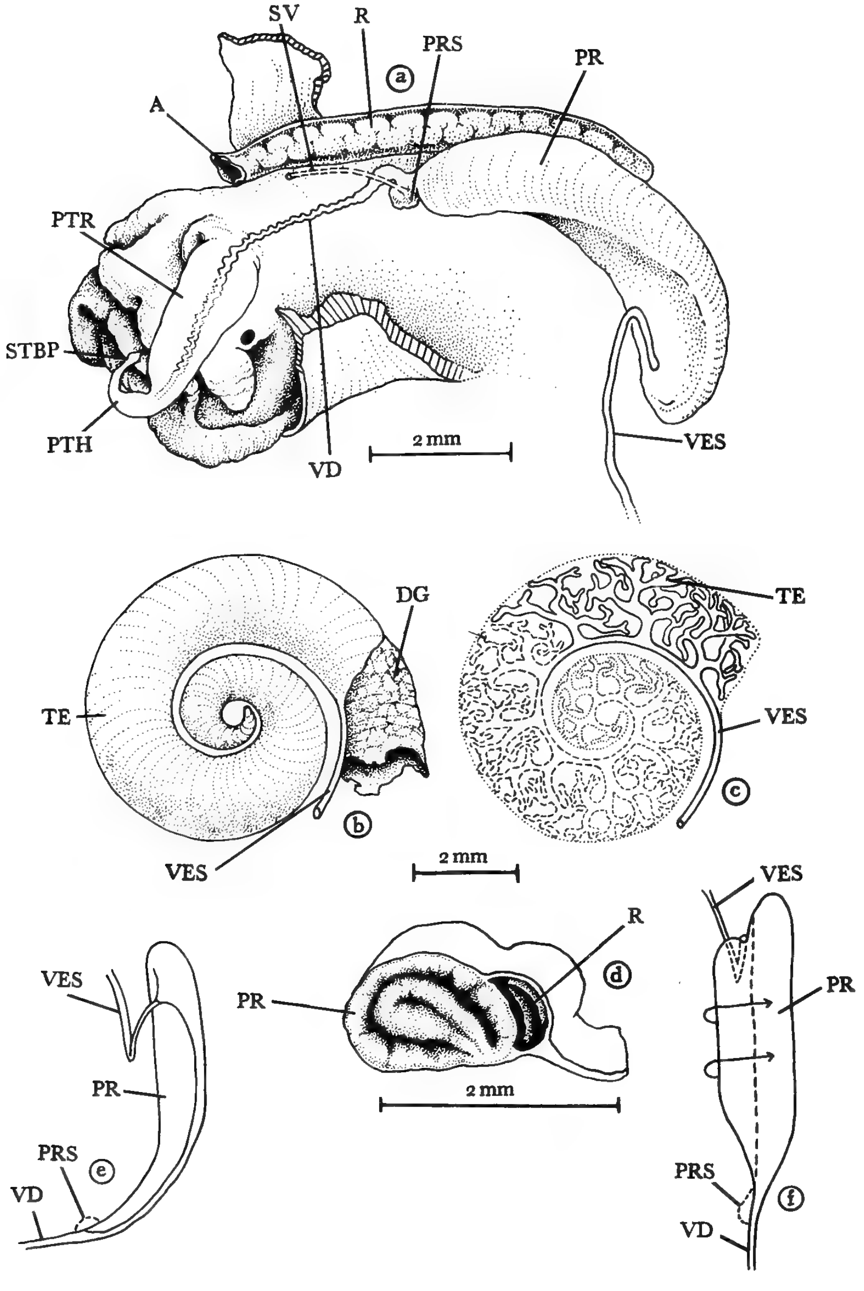


Figure 5

Elements of the male reproductive system in *Ostodes*

a – generalized composite male, view from above b – testis external appearance; c – testis, internal arrangement, diagrammatic; d – cross-section of prostate; e – diagram showing folded structure of prostate, seen from underside; f – diagram showing prostate unfolded, seen from underside [for explanation of abbreviations see Appendix on foldout]

After passing proximal tip of prostate, it turns sharply upon itself and runs back to enter ventral surface of prostate slightly anterior to its proximal end.

Prostate creamy white, visible through integument on columellar side of body. Structure of prostate resembles a sandwich, sealed around the edges, and folded in half longitudinally, slightly off center. This structure gives a cross-section with 2 layers of bread (prostatic tissue) in the middle, the sandwich filling (lumen of the prostate) lying in a U-shape, and another layer of bread (prostatic tissue) around the outside of the U (see Figures 5d, 5e, 5f). Most proximal portion of prostate, which lies beneath distal end of digestive gland, is flattened dorso-ventrally, more anterior portions oval to round. Medial upper aspect of prostate touching intestinal loops.

Prostate enters pallial cavity on right side, within mantle wall, below rectum and in angle formed by juncture of mantle and body. Prostate terminates in a blunt tip at about mid-point of pallial cavity. In some specimens, the prostatic tip is truncated. In others, there is a constriction of the medial half of the organ, a short distance behind the tip, resulting in the presence of a small pouch or sac on the anterior medial corner of the prostate. The presence of this sac is in part a function of age, in part of species. Juveniles almost never have sacs; adults are more likely to have sacs in some species than in others. Table 4 shows the frequency of occurrence of sacs, and also of a small, fragile duct, of varying origin and termination, which appears to be a "safety-valve" for venting excess sperm (see Fretter & Graham, 1962: 345, 348). There is no correlation between presence or absence of a sac and presence or absence of a "safety-valve." If a "safety-valve" occurs in a specimen having a sac, the most usual origin of the duct is the dorsum of the sac. In a snail without a sac, the most usual origin of the duct is the medial anterior corner of the truncated prostate. In either case, the duct usually runs laterally and anteriorly across the base of the vas deferens, and terminates beneath and slightly behind the anal orifice. Variations from these patterns are mentioned in the species descriptions.

Table 4

Prostatic Characters (mixed ages)

Species	Presence of Sac	Presence of "Safety-Valve"
Ostodes		
adjunctus	0 of 4	0 of 4
exasperatus	2 of 5	1 of 5
garretti	2 of 2	1 of 2
gassiesi	11 of 15	2 of 14
llanero	0 of 1	0 of 1
plicatus	1 of 5	4 of 5
reticulatus	3 of 3	3 of 3
savaii	10 of 13	5 of 14
strigatus	0 of 6	0 of 6
tiara ("smooth")	1 of 5	4 of 5
tiara ("bumpy")	1 of 1	1 of 1
upolensis	3 of 4	4 of 4

Vas deferens originates from anterior lateral corner of prostate. It is a closed tube running anteriorly and medially beneath the skin to the base of the penis, where it passes upwards, lying at first near the surface, but penetrating progressively more deeply, to reach the center of the penis about half-way up the trunk. Tielecke (1940: 332) states that males of *Ostodes strigatus* have an open sperm groove. I have not seen the specimens on which he based his statement, and so do not know what species he actually had before him. The 64 males of *O. strigatus* available to me agree with Gould's original description and figure for *O. strigatus* (Gould, 1848: 204–205; 1852: 102–103; 1860: plt. 8, figs. 117, 117a, 117b), and they all have closed vasa deferentia.

Penis on cephalic mid-line, just posterior to tentacles. Base usually thick, somewhat rugose, probably partly contractile but not introversible. The ovoid to rounded trunk narrows gradually to abruptly into a thin distal thread, which may be long or short in proportion to the trunk. Some specimens have a sub-terminal bulb or swelling on the thread; there is no correlation between presence or absence of a bulb and length of thread. Penis usually carried folded sharply back from its base, the whole length of the trunk lying flat along the neck and body inside the mantle cavity. There is another sharp fold at the base of the distal thread, which lies folded against the trunk, the tip pointing forward. In the case of a very long thread, or a thread with a sub-terminal bulb, the tip sometimes may be found folded under. The ratio of thread-length (including taper) to trunk-length is diagnostic at the species level. Ratios for adults of the several species are found in Table 5. For discussion purposes, a specimen is considered to have a short thread if the ratio of thread to trunk is 1/1.6 or more. This ratio was chosen as the dividing point because, on a graph showing the thread to trunk ratio of every available specimen of *Ostodes gassiesi* (a consistently short-threaded species) and *O. plicatus* (a consistently long-threaded species), 95% of *O. gassiesi* specimens had ratios of 1/1.7 or more, while 97% of *O. plicatus* specimens had ratios of 1/1.5 or less. Although the lengths of thread and trunk differ from species to species, the total length of the penis is fairly uniform, at least among the mid-sized species (Figure 6).

Table 5

Penial Characters

Species	Bulb present on thread (mixed ages)	Ratio of thread length to trunk length (adult)					
		Short thread			Long thread		
		N	Range	Mean	N	Range	Mean
Ostodes							
adjunctus	0 of 11	2	1/1.7-1/1.5	1/2.1	9	1/0.5-1/1.5	1/0.97
exasperatus							
(Upolu)	1 of 4	0	—	—	4	1/1.05-1/1.5	1/1.22
(Savaii)	4 of 6	4	1/2.5-1/7.3	1/4.68	2	both 1/1.5	1/1.5
garretti	0 of 2	0	—	—	2	1/1.4-1/1.6	1/1.5
gassiesi							
(all)	7 of 12	53	1/1.7-1/11	1/4.73	3	1/0.86-1/1.43	1/1.12
(Upolu)	5 of 7	36	1/1.7-1/10	1/3.8	2	1/0.86-1/1.43	1/1.13
(Savaii)	2 of 5	17	1/2.7-1/11	1/6.7	1	—	1/1.1
llanero	0 of 1	0	—	—	1	—	approx. 1/1.2
plicatus	0 of 5	1	—	1/1.7	31	1/0.25-1/1.5	1/0.98
reticulatus	0 of 3	0	—	—	5	1/0.46-1/1.25	1/0.91
savaii							
(all)	11 of 23	43	1/1.7-1/10	1/3.66	7	1/1 -1/1.5	1/1.3
(Upolu)	2 of 5	14	1/2.0-1/4.5	1/3.0	2	1/1.38-1/1.5	1/1.44
(Savaii)	9 of 17	29	1/1.7-1/10	1/3.97	5	1/1 -1/1.5	1/1.24
strigatus	0 of 43	0	—	—	43	1/0.31-1/1.20	1/0.60
tiara							
("smooth")	0 of 6	0	—	—	6	1/0.54-1/1.5	1/0.93
("bumpy")	2 of 2	2	thread/collar/trunk		0	—	—
			1/0.22/1.67				
				1/0.2/1.8			
			1/0.22/1.85				
upolensis	0 of 2	1	—	1/2.2	6	1/0.54-1/1.5	1/1.15

In both *Ostodes gassiesi* and *O. savaii,* short-threaded specimens from Savaii have shorter threads than comparable individuals from Upolu. I have been unable to find any reason for this difference. There are no important conchological differences between snails from the two islands, nor are there significant differences between long-thread and short-thread snails of the same species. In *O. exasperatus,* all males from Upolu are long-threaded, while the Savaii population has 67% with short threads. The shells from the two populations are not significantly different, and the female reproductive systems are virtually identical.

Explanation of Figures 37 to 42

Figure 37: *Ostodes gassiesi,* central tooth and tetracuspid lateral teeth × 477

Figure 38: *Ostodes gassiesi,* radula in folded position, showing edge of radular membrane and foramina in outer marginal teeth × 509

Figure 39: *Ostodes plicatus,* central tooth, showing hollowed-out base; tetracuspid lateral teeth and inner marginal teeth × 478

Figure 40: *Ostodes plicatus,* edge of radular membrane and outer marginal teeth with foramina × 360

Figure 41: *Ostodes reticulatus,* central teeth, tetracuspid lateral teeth, and inner marginal teeth × 368

Figure 42: *Ostodes reticulatus,* outer marginal teeth, showing foramina × 1115


37


38


39


40


41


42

Ostodes tiara presents special problems. Sixteen male specimens, 9 adults and 7 juveniles, from 5 different localities, were examined. One was a freak, having a penis with three threads. Ten, 6 adults and 4 juveniles, had standard long-thread penes. These (Figure 7a) are referred to in the tables as "smooth." Some males with "smooth" penes were found at each of the 5 localities. At Station 8, on Upolu, in addition to 3 males with "smooth" penes, 2 adults and 3 juveniles were found with a very different type of penis, referred to as "bumpy." The trunk is surmounted by a white bump, resembling a knuckle. Beyond the bump is a constricted portion, or collar, which may be slightly reddish, and which is followed by a short swollen area which tapers to a short thread with a sub-terminal bulb (Figure 7b). Males with this type of penis have umbilici averaging 15.4% larger than those of "smooth" penis males. The females from Station 8 also had larger umbilici than females from the other stations. No other statistically significant conchological differences were found, nor did the female reproductive systems from Station 8 have any unusual features.

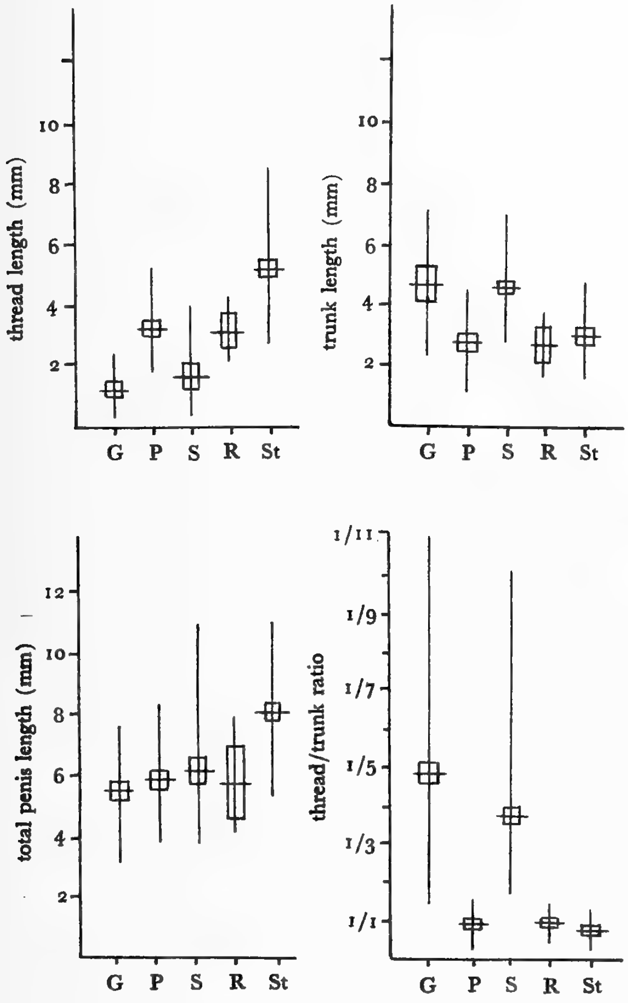


Figure 6

Lengths of penis thread, penis trunk, and whole penis, and ratios of thread length to trunk length, in five mid-sized species of *Ostodes*

G – *Ostodes gassiesi*; P – *O. plicatus*; R – *O. reticulatus* S – *O. savaii*; St – *O. strigatus* — vertical line – range of measurements; horizontal line – mean; hollow box – two standard errors of the mean on either side of the mean

d. Female reproductive system (Figures 8, a, b; 9): Ovary begins slightly anterior to apex of visceral hump and occupies columellar side for approximately one whorl. Ovarian tissue composed of a mass of white granules of irregularly spherical contour, held together by an encapsulating membrane, but not otherwise macroscopically organized. There is no system of collecting tubules equivalent to that of the male testis. The ovary tapers anteriorly to a blunt point, with the encapsulating membrane continuing forward as the oviduct. Oviduct lies on columellar side of body, lateral to esophagus and ventral to stomach and digestive gland, running anteriorly nearly to mantle line, then reflexing sharply upon itself and continuing up to approximately the level of the uterine fundus; reflexes again and runs downward for a short distance.

Slightly below level of uterine fundus, oviduct becomes progressively thicker and begins to fold upon itself accordion-fashion in a single plane. There are from 3 to 6 foldings, each slightly deeper than the preceding one. The folds nearest the columella are laid down even with each other, with the increasing depth of the folds producing a triangular mass, lying ventral to the uterus, its long axis parallel to the long axis of the visceral hump. The folds are held together by an encapsulating membrane which is transparent and covered with brown speckles, which are most numerous in the valleys between folds. I believe that this area of folded oviduct serves as a seminal receptacle (Figure 9a).

Distal to the seminal receptacle, the now quite thick oviduct is joined, on its lateral aspect, by an equally thick duct which leads away from the columella to a large, heavily pigmented, bulbous structure, which I believe to be a bursa copulatrix. It lies partly beneath the uterus but mostly ventral to the mass of intestinal loops. If distended, it can often be seen through the integument of the visceral mass, just behind the kidney at the mantle line. If not distended, it resembles a collapsed balloon, lying beneath the intestine. The pigment particles lie

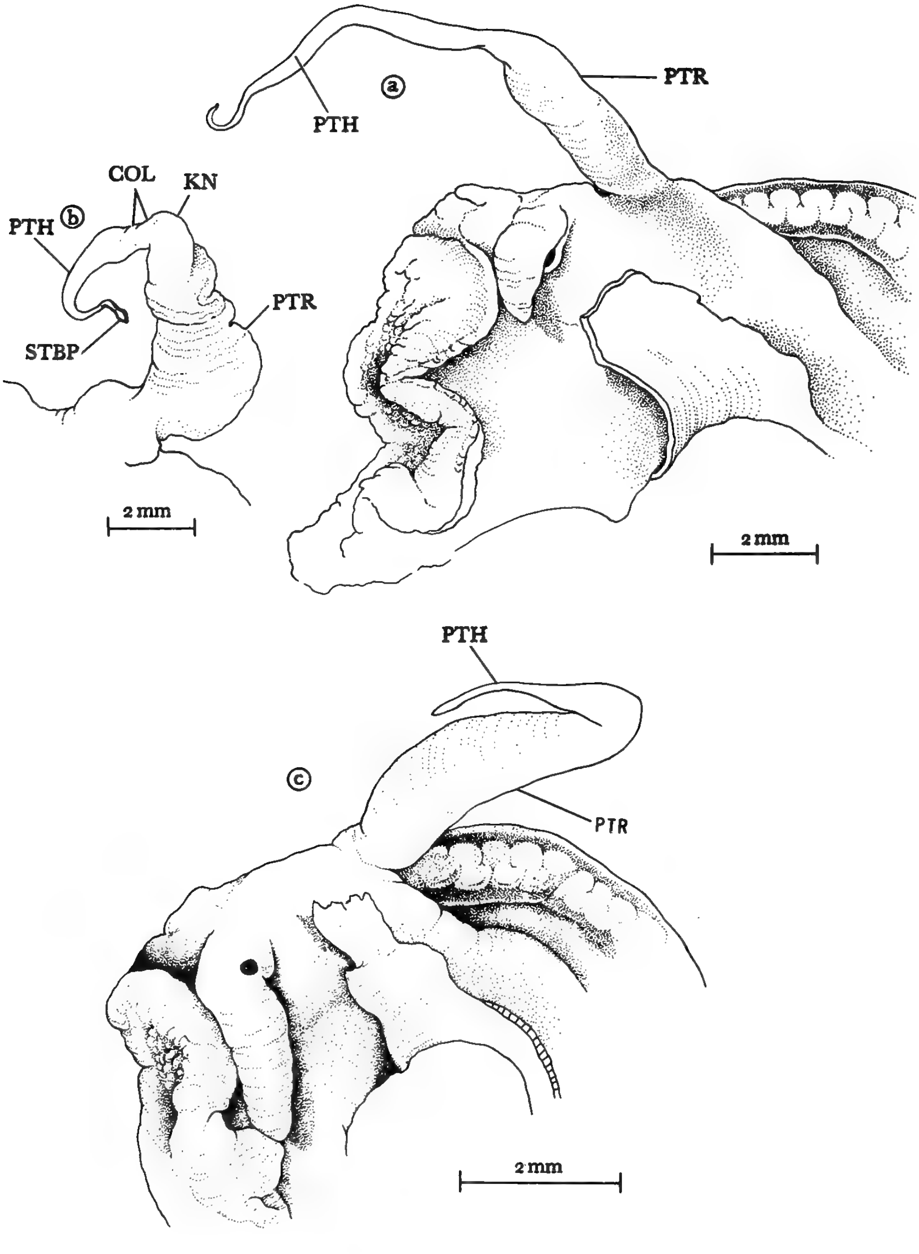


Figure 7

Penis types in *Ostodes tiara* and *Ostodes garretti*
a – *O. tiara*, "smooth"; b – *O. tiara*, "bumpy";
c – *O. garretti*
[for explanation of abbreviations see Appendix on foldout]

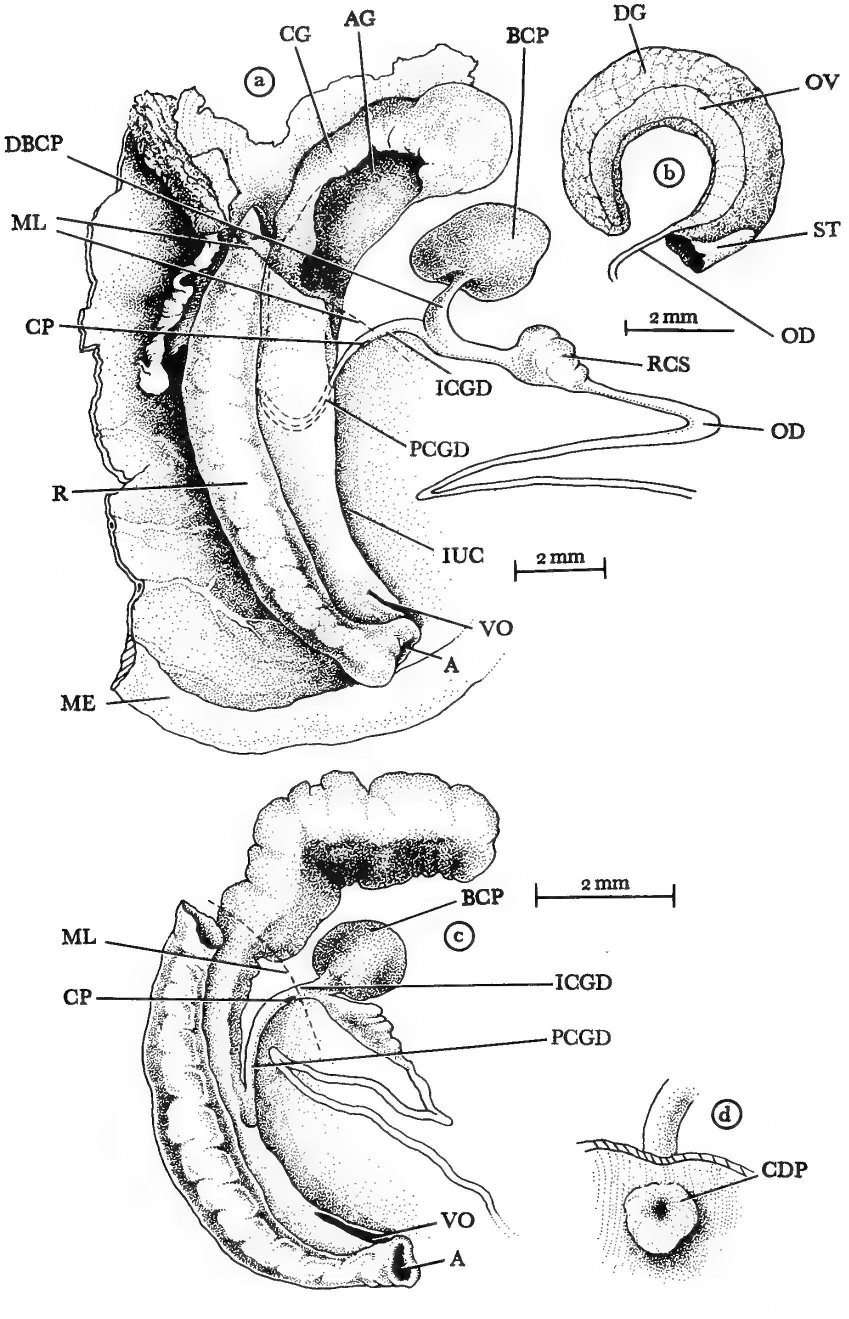


Figure 8

Female reproductive system in *Ostodes tiara* and *Ostodes garretti*

a – *O. tiara*; b – *O. tiara*, ovary; c – *O. garretti*;
d – *O. garretti*, entrance of common genital duct into uterus
[for explanation of abbreviations see Appendix on foldout]

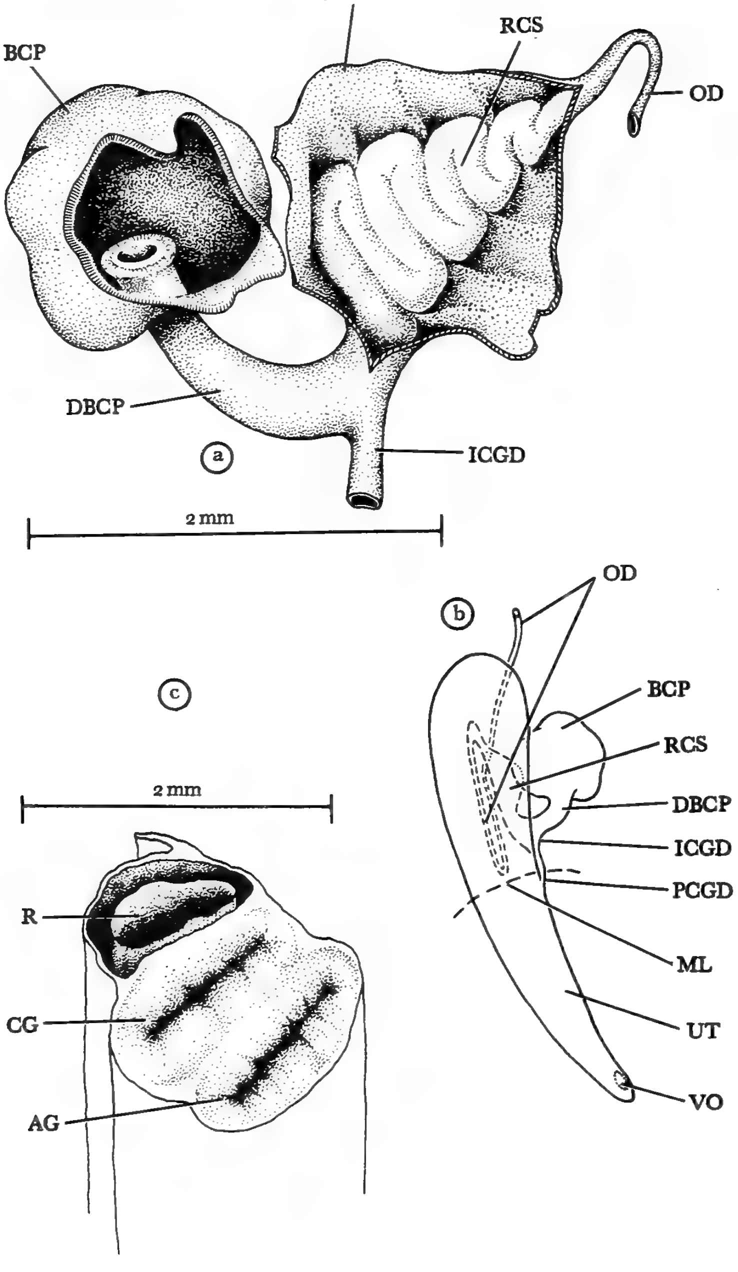


Figure 9

Generalized details of female reproductive system in *Ostodes*

a – cutaway views of bursa copulatrix and seminal receptacle
b – diagram showing elements of reproductive system in true anatomical relationship
c – cross-section of uterus
[for explanation of abbreviations see Appendix on foldout]

partly on the covering membrane, and partly on the outer surface of the wall itself. The walls are thick and soft, and appear to be constructed of fibers laid vertically to the lumen of the organ. The inner surface is soft and creamy white. The duct protrudes part way into the lumen, which is sometimes found filled with a pearly white amorphous mass.

Previous workers do not agree concerning the probable function and nomenclature of the folded oviducal area and pigmented sac. TIELECKE (1940: 331–332) called the folded area of *Ostodes strigatus* a seminal receptacle and the pigmented sac a bursa copulatrix. THOMPSON (1969: 40–41), working on Central American cyclophorids, called the folded area an albumin gland and the pigmented sac a seminal receptacle. Neither gives histological details to support his conclusions.

Work on *Pomatias elegans* (CREEK, 1951) and *Acme fusca* (CREEK, 1953) did involve histological examination of the entire genital tract, extensive tissue staining studies, and laboratory observations of breeding and egg laying. In *Pomatias elegans* there is a widened muscular section of the renal oviduct which functions as a seminal receptacle, its walls being covered with large numbers of orientated sperm at all seasons of the year (CREEK, 1951: 606). There is a sac at the posterior end of the pallial oviduct, which although homologous with the seminal receptacle of many other gastropods, functions as a bursa copulatrix (CREEK, *op. cit.*: 636). This bursa opens directly into the mantle cavity, and the penis is actually inserted into this sac at copulation (CREEK, *op. cit.*: 606). In *Acme fusca,* however, the bursa opens to the mantle cavity by means of a duct, and the penis probably does not actually enter it during copulation (CREEK, 1953: 234). As in *Pomatias,* the anterior portion of the renal oviduct is convoluted and slightly swollen. This area, homologous to the seminal receptacle of *Pomatias,* probably functions in *Acme* as a fertilization chamber, as it has been found to contain ingesting cells for the disposal of excess sperm.

The structures in *Ostodes* are very similar to those found in *Acme.* Both genera show a thickening of the anterior renal oviduct; both have a sac-like structure located near the upper end of the uterus; both have a duct leading from the mantle cavity to the sac, the renal oviduct, and the uterus. I do not know exactly where fertilization takes place, but the pigmented sac in *Ostodes* certainly seems to function as a bursa copulatrix, and I therefore agree with Tielecke and call the thickened area of the renal oviduct the seminal receptacle.

Distal to the entrance of the duct from the bursa copulatrix, the oviduct, now a common genital duct, again becomes thin and fragile. The length of the common duct, from the junction of the ducts from bursa and receptacle to the mantle line, varies greatly from species to species (see descriptions). The common duct enters the pallial cavity and continues downward along the medial margin of the uterus, to which it is bound by a thin sheet of tissue. There is a small hole, the copulatory pore, in the medial aspect of the genital duct. This is located between the posterior margin of the mantle cavity and the point of entry of the genital duct into the uterus, its position varying with the species. The copulatory pore is the posterior termination of a channel which is formed by an overlayment of the uterus onto the right side of the mantle cavity floor. The medial margin of the channel is formed by a very slight ridge in the body tissues, and when the mantle is in its normal position (not laid back as for dissection) the channel would function as a closed tube. There is no grossly visible specialization of the tissues forming the channel floor. Whether this channel serves to guide the penis to the copulatory pore, or as a passageway for sperm deposited at its anterior end, must remain a matter for speculation until behavioral studies can be made.

Uterus lies along columellar side of body, partly within visceral hump beneath most anterior portion of digestive gland, and partly at right side of pallial cavity, below rectum. Uterus bi-lobed, ventral lobe occupying the middle half to three-fourths of dorsal lobe length. Dorsal lobe overlies upper end of ventral lobe, folding upon itself to form entire uterine fundus, and continuing forward, past anterior end of ventral lobe, to form entire vaginal portion of uterus. In cross-section (Figure 9c) it is seen that the two lobes are entirely separate, except for a proximal end-to-end anastomosis, so that the lumen of the uterus is one continuous passage from the anterior end of the ventral lobe, up around the fundus, and down the length of the dorsal lobe to the vaginal orifice. The texture of the two lobes is quite different. The ventral lobe is composed of firm, densely packed, fine-grained tissue which is often pink in color, especially near the anterior end. The tissues of the dorsal lobe are creamy white, and appear softer, more friable, and more loosely organized. Dorsal lobe passes forward, beneath the rectum, toward the front of the pallial cavity. Vaginal orifice near anus. The shapes, sizes, and orientations of these 2 openings are species-specific, and will be discussed in the species descriptions.

5. SEXUAL DIMORPHISM

For this study, there were available 13 populations of *Ostodes* which contained both adult males and adult females. Ten of the 12 species were included in the 13 populations: *O. plicatus, O. reticulatus, O. upolensis, O.*

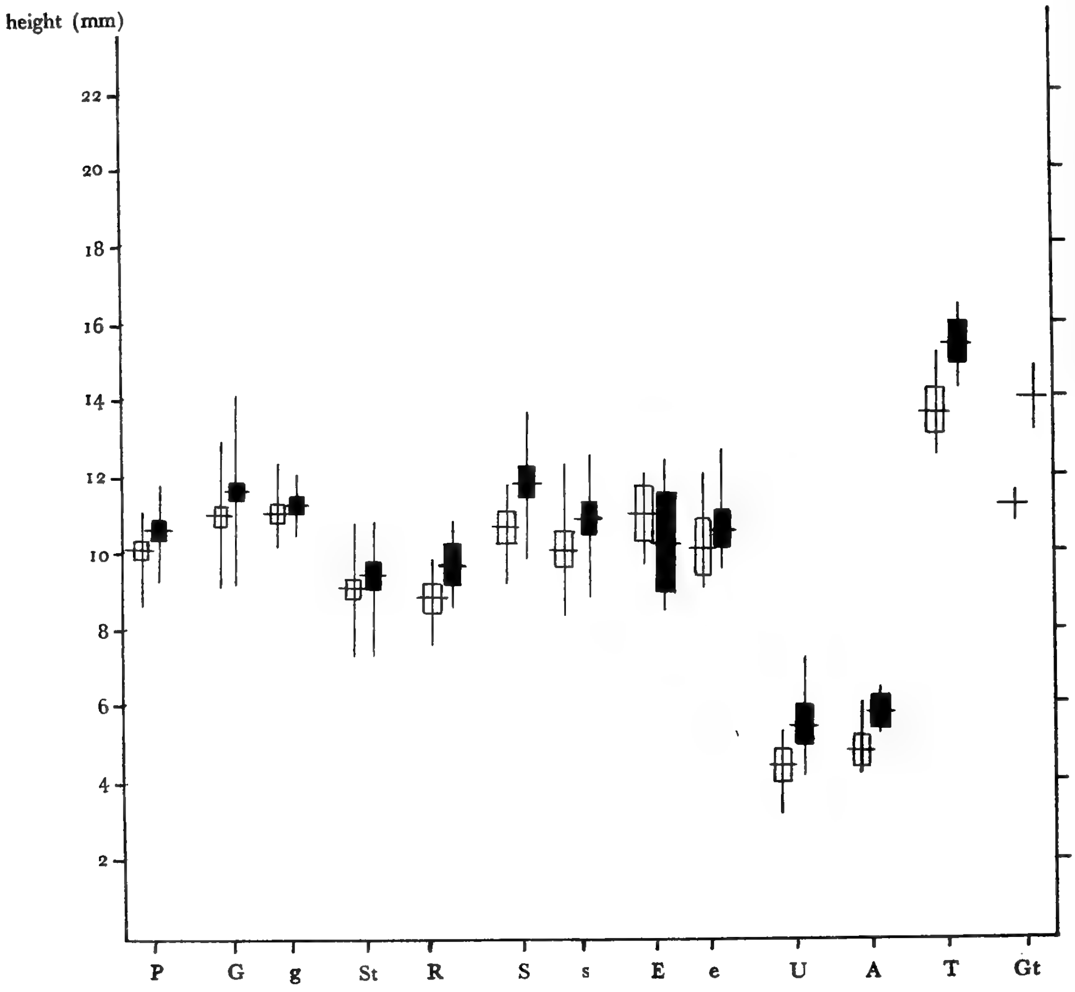


Figure 10a

Sexual dimorphism in height in ten species of *Ostodes* (adults)
A – *Ostodes adjunctus*; E – *O. exasperatus*, Upolu population; e – *O. exasperatus*, Savaii population; G – *O. gassiesi*, Upolu population; g – *O. gassiesi*, Savaii population; Gt – *O. garretti*; P – *O. plicatus*; R – *O. reticulatus*; S – *O. savaii*, Upolu population; s – *O. savaii*, Savaii population; St – *O. strigatus*; T – *O. tiara*; U – *O. upolensis*. Vertical line – range of measurements; horizontal line – mean; box – two standard errors of mean on either side of mean; hollow box – male; solid box – female

tiara, O. garretti, O. adjunctus, and *O. strigatus* were represented by one population each, while *O. gassiesi, O. savaii,* and *O.* ***exasperatus*** were represented by one population from Upolu and another from Savaii. Only juvenile shells of *O.* ***llanero*** were available, and only one empty shell of *O. cookei* was seen.

When the shell measurements of males and females of the above-named 13 populations are examined, the usual pattern is seen to be that females are both taller and wider than males of approximately the same whorl-count (Figures 10a, b). The only population in which this situation is reversed is that of *Ostodes* ***exasperatus*** on Upolu; at a very

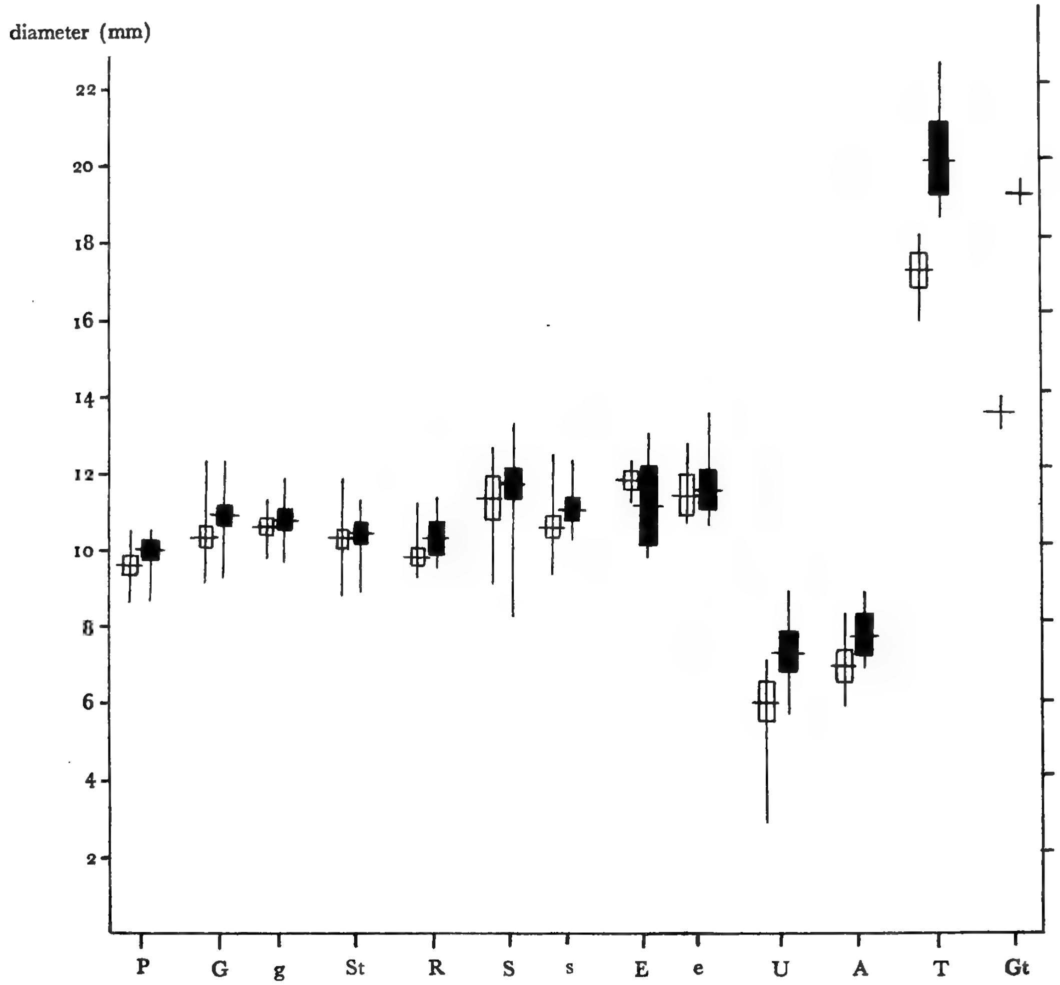


Figure 10b

Sexual dimorphism in diameter in ten species of *Ostodes* (adults)
[for explanation of symbols see Figure 10a]

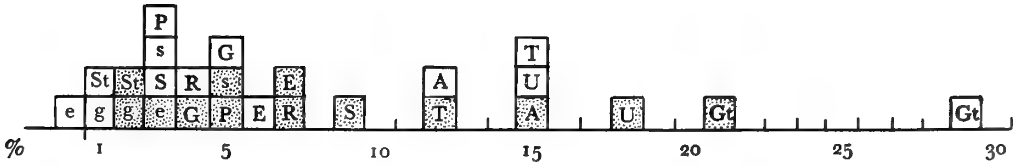


Figure 11

Percentage differences in mean height and diameter between males and females in 13 populations of *Ostodes*. Species designations as in Figure 10a

☐ difference in diameter ▨ difference in height slightly lower whorl-count, males average 0.75 mm higher and 0.69 mm wider than females. The Savaii population of *O.* ***exasperatus*** follows the usual pattern of larger females.

Male-female differences in height are slightly greater than differences in diameter in 10 of the 13 populations. The differences are usually rather small, nearly three-fourths of them being 9% or less, with the remainder widely scattered between 12% and 29%. Figure 11 shows the distribution of percentage differences. It is interesting that the greatest differences occur in the smallest and largest species; in little *Ostodes upolensis,* females average 18% taller and 15% wider than males; in *O. adjunctus,* the differences are 15% and 12%, respectively. In the largest species, *O. tiara,* females are 12% taller and 15% wider. The greatest differences of all occur in the second-largest species, *O. garretti;* its females are 21% taller and 29% wider than males at very nearly the same whorl count ($\bar{X}W = 5.22$ female, 5.19 male).

B. Systematic Accounts

1. THE GENUS *Ostodes* Gould, 1862

GOULD, 1862, Proc. Boston Soc. Nat. Hist., **8:** 283; KOBELT & VON MÖLLENDORFF, 1897, Deutsche Malak. Ges., Nachr., **29:** 112; KOBELT, 1902, Das Tierreich, **16:** 153, fig. 32 (*O. plicatus*); THIELE, 1929, Handb. syst. Weicht., **1:** 99; TIELECKE, 1940, Arch. f. Naturgesch., N. F., **9:** 331, 332, 350, 361, 362, 364, figs. 7, 8, 19 (*O. strigatus* [?], male and female genitalia and nervous system); CLENCH, 1949, Bull. B. P. Bishop Mus., **196:** 9-10.

Type species: *Cyclostoma strigatum* Gould, 1848, by OD.

Shell narrowly to broadly turbinate, spire elevated. Thin and fragile to thick, heavy, and strong. Small (3.2 mm high X 2.8 mm wide) to large (12.5 mm X 22.5 mm). Females average larger than males at same whorl-count, except Upolu population of *Ostodes* ***exasperatus.*** Four to 6 whorls, spire angle 70° – 120°. Aperture round, holostomatous, appressed to whorl above; outer lip simple, parietal callus thin to thick. Umbilicus deep, narrow to wide; may be smoothly rounded, sharply angled, or bordered by rim. Apical whorls smooth. Later whorls show spiral lirae, radial plicae, or both, except *O. cookei,* which is smooth. Terminal portion of body whorl of adults indented under penultimate whorl, except *O. adjunctus.* Periostracum thin, yellowish to dark brown, adherent or deciduous. Color cream to dirty white, sometimes with pink to red spire. Operculum round, corneous, transparent, thin to thick, with many or few volutions, or laminate.

Penis external, on dorsal midline of head behind tentacles, with closed vas deferens and terminal thread. Oviduct, seminal receptacle, and bursa copulatrix discharge into uterus via common genital duct, wherein is copulatory pore.

2. KEY TO THE SPECIES

1 a	Adult shell smaller than 7.5 mm high by 8 mm wide	2
b	Adult shell larger than above	4
2 a	Shell smooth	*O. cookei*
b	Shell with distinct sculpture	3
3 a	Strong spiral sculpture on ventral surface, umbilicus with bordering rim; from Tutuila	*O. adjunctus*
b	Ventral spirals weak or absent, umbilicus without a rim; from Upolu or Savaii	*O. upolensis*
4 a	Shell as high as or higher than wide	5
b	Shell wider than high	7
5 a	Shell with very prominent radial plicae	6
b	Radial plicae weak or absent, spiral lirae strong	*O. savaii*
6 a	Radial plicae very prominent, spiral lirae evenly distributed on whorls, ventral surface with radial plicae; females with rectum and vagina bent downward, males with long-threaded penes	*O. plicatus*
b	Radial plicae broad and low, spiral lirae concentrated on lower half of whorl, ventral surface smooth; females with straight anus and vagina, males with short-threaded penes	*O. gassiesi*
7 a	Radial plicae and spiral lirae of approximately equal prominence, making a reticulated surface	*O.* ***reticulatus***
b	Spiral lirae predominant	8
8 a	Spire angle less than 100°	9
b	Spire angle more than 100°	10
9 a	Ventral surface smooth; from Tutuila	*O. strigatus*
b	Ventral surface with spiral sculpture; from Upolu or Savaii	*O.* ***exasperatus***
10 a	Shell smaller than 10.5 mm high by 13 mm wide	*O.* ***llanero***
b	Shell larger than above	11
11 a	Posterior part of hypobranchial gland thick and heavy; from Upolu	*O. tiara*
b	Posterior part of hypobranchial gland much reduced; from Savaii	*O. garretti*

3. CRITERIA FOR SPECIES RECOGNITION

In order for 2 taxa to be recognized as separate species, they must display significant differences, not only in the shell, but also in the anatomy. The greater the number of differences in unrelated systems, and the greater the magnitude of the differences, the greater the probability that the 2 taxa really are different. To illustrate, let us consider 3 specific cases: one in which a few important differences made the species decision easy; one in which a number of smaller differences made the separation harder; and one in which the differences were deemed insufficient to warrant separation of taxa.

The first case is that of *Ostodes plicatus* vs. *O. gassiesi.* Both taxa have shells of approximately the same size and shape – higher than wide, and with narrow umbilici. Neither has any sculptural element that is totally lacking in the other; the conchological differences lie in the distribution of the spiral lirae, and the distribution and relative prominence of the radial plicae. The shell differences, though present and consistent, would not be sufficient ground for separating the 2 taxa, were it not for anatomical differences of much greater magnitude. In *O. plicatus,* the males almost always have penes with long, bulbless threads, and the females almost always have a distinctive downward bend in the terminal portions of rectum and vagina. In *O. gassiesi,* the female openings point directly forward, and the males have short-threaded penes, often with sub-terminal bulbs. The relatively minor differences in sculpture, plus the major differences in genitalia, give ample evidence for the designation of these 2 taxa as separate species.

The second case, that of *Ostodes savaii* vs. *O.* ***exasperatus*** is less clear-cut. Individuals of *O.* ***exasperatus*** differ conchologically from those of *O. savaii* in height, width, umbilical diameter, and contour – all elements which are influenced by the single factor of rate of decoiling – and in having more whorls for their size than does *O. savaii* (Figure 12). They also differ in sculpture, in that radial plicae are totally lacking in *O.* ***exasperatus,*** while they are present, though unobtrusive, in *O. savaii.* In addition, *O.* ***exasperatus*** shows stronger spiral lirae on its ventral surface than does *O. savaii.* There are also differences in the anatomy: in the female, the proportions of the proximal and distal portions of the pallial common duct are different in the 2 taxa, and the male shows differences in proportions of penis thread to trunk, and in the slenderness or thickness of the penial trunk. Here are four areas of slight difference – shell shape, shell sculpture, male anatomy, and female anatomy – which together are sufficient to warrant separation of the 2 species.

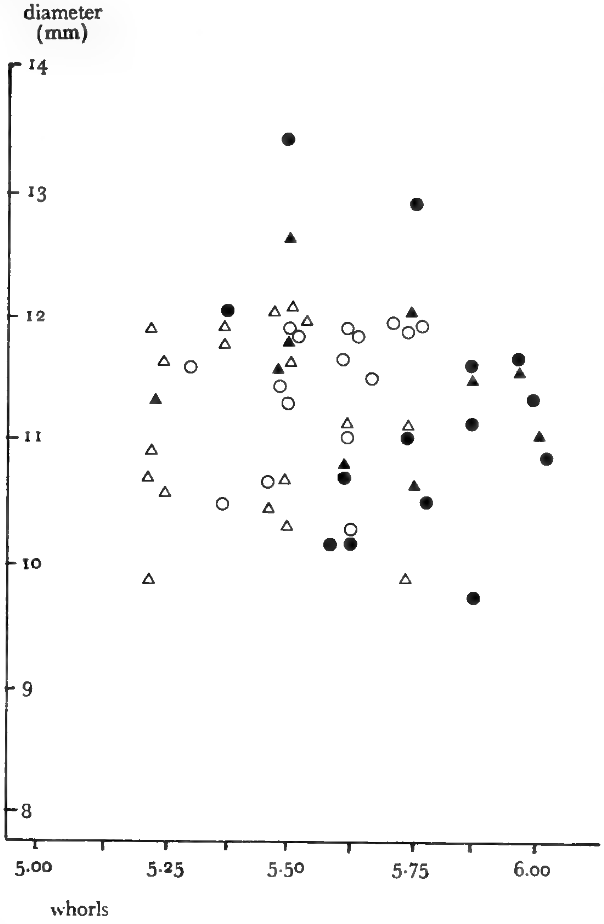


Figure 12

Relationship of whorl-count to diameter in *Ostodes savaii* and *Ostodes* ***exasperatus***

△ – *Ostodes savaii,* male ○ – *Ostodes savaii,* female
▲ – *Ostodes* ***exasperatus,*** male ● – *O.* ***exasperatus,*** female

In the third example, the two forms of *Ostodes upolensis* were not deemed different enough to warrant their separation. As in the preceding example the differing appearances of the 2 types of shell are caused primarily by a single factor – the rate of decoiling. The size, the contour, and the width of the umbilicus are all determined in part by the rate of decoiling, and hence differences between them must be considered as having only a single cause. The anatomical differences observed in the 2 forms are in size only – not in shape or location – and are so slight as to be statistically insignificant. There are no significant differences in sculpture. The single important difference between the forms – the rate of decoiling – was not thought sufficient to warrant separation of the taxon into 2 species, as it was unaccompanied by any significant differences in sculpture or anatomy.

4. SPECIES DIAGNOSES AND DISTRIBUTIONAL DATA

a. *Ostodes plicatus* (Gould, 1848)

(Figures 13a, b; 14b; 15c, d, e)

Cyclostoma plicatum Gould, 1848, Proc. Boston Soc. Nat. Hist., 2: 205 – Upolu; Gould, 1852, U. S. Expl. Exped., 12: 103–104: Gould, 1860, Atlas of Shells, U. S. Expl. Exped., plt. 8, figs. 118, 118a, 118b.

Cyclostoma apiae Récluz, 1851, Journ. de Conch., 2: 213, 214; plt. 6, figs. 10, 11 – Apia, Upolu.

Cyclophorus apiae (Récluz), Gray, 1852, Cat. Phan., pp. 57–58 – Pacific Islands, Upolu; Pfeiffer, 1852, Mon. Pneum., 1: 83 – Upolu.

Cyclostoma pulverulentum Philippi, 1854, *in* Pfeiffer, Conch. Cab., 1 [19(1)]: 301–302, plt. 40, figs. 13, 14 – Upolu.

Cyclophorus plicatus (Gould), Reeve, 1862, Conch. Icon., XIII: sp. 58, plt. 14, fig. 58.

Cyclophorus strigatus (Gould), Mousson, 1865, Journ. de Conch., 13: 179–180 – Upolu and Manua, Western Samoa – partly.

Cyclophorus (Ostodes) strigatus (Gould), Mousson, 1869, Journ. de Conch., 17: 350–351, Upolu, Savaii, Tutuila – partly.

Ostodes strigatus (Gould), Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 147–148 – Upolu, Tutuila, Savaii – partly.

Ostodes plicatus (Gould), Kobelt, 1902, Das Tierreich, 16: 156, fig. 32 (p. 153) – Samoa (Upolu); Clench, 1949, Bull. B. P. Bishop Mus., 196: 15–17 – partly.

Diagnosis: Shell narrowly turbinate, height of adults 9.0–11.6 mm {10.45 mm}[1], diameter 8.8–10.6 mm {9.8 mm} with $5\frac{1}{8}$–6 whorls {$5\frac{5}{8}$}. Whorls with rounded shoulders, suture slightly incised. Usually (85%) higher than wide; H/D ratio 0.92–1.19 {1.06}. (Juveniles, especially males, often wider than high.) Spire angle 70°–100° {81°}. Umbilicus deep, narrow, margin either smoothly rounded or pinched into an acute angle, but usually without a bordering rim. D/U ratio 2.69–4.46 {3.37}. Aperture round, holostomatous, slightly appressed to whorl above. Parietal callus of adults approximately as thick as outer lip. Early whorls smooth. Body whorl with 4–12 {7.1} fine, evenly spaced spiral threads on upper palatal surface, 6–14 {9.3} spiral threads on lower palatal surface, crossing 15–27 {21.0} broad, strong, close-set radial plicae on upper surface, of which 13–23 {17.4} continue across rounded ventral surface and enter umbilicus. Color often salmon to rose pink on apex and spire, otherwise cream-color; body whorl nearly always cream-color. Periostracum thin, transparent, yellowish-brown, deciduous. Opercular types, A-1 and C-1.

Hypobranchial gland with moderately heavy posterior (transverse) portion, beginning well over to left side; anterior portion much reduced. Males have long-threaded penes without bulbs. Prostatic sac seldom present, "safety-valve" nearly always present; "valve" larger, sturdier, more obvious than in any other species. Female internal common duct very long (1.15 X diameter of bursa copulatrix). Pallial common duct very short, with copulatory pore immediately below mantle line, and entry of common duct into uterus immediately below pore, via slightly elevated oval papilla at 30° angle from long axis of uterus. Anus shows slight hypertrophy of upper margin. Vaginal orifice simply a round hole on the distal end of the uterus, equal in diameter to diameter of uterus. Terminal portions of both rectum and vagina bent sharply downward, at an angle approaching 90° in 80% of specimens seen. This bend is absolutely diagnostic of this species, as it occurs in no other. In the 20% without the bend, the anus points straight ahead, the uterus tapers to a point below the anus, and the vaginal orifice is a small hole on the ventral surface of the uterus.

Comparative remarks: Differing emphasis and distribution of sculptural elements on the body whorls are the chief conchological differences between *Ostodes plicatus* (Figure 13) and the most similar species, *O. gassiesi* (Clench, 1949: fig. 7a). Some of the material used by Clench in his work on *O. plicatus* was lent to me and proved to contain examples of both *O. plicatus* and *O. gassiesi*. In *O. plicatus*, the spiral threads are rather unobtrusive and evenly distributed over the entire height of the body whorl; in *O. gassiesi* they are clustered on the lower half, and are stronger. The radial plicae are much stronger in *O. plicatus;* they are narrower and much more numerous, and continue across the lower surface of the shell, which is smooth, or marked only by very faint spirals in *O. gassiesi*. The strong radial plicae also serve to differentiate *O. plicatus* from *O. strigatus, O. savaii, O. llanero,* and *O. exasperatus,* in all of which the radials are very weak or absent. In addition, the latter 4 species are usually as wide as or wider than tall, whereas *O. plicatus* is usually taller than wide. The sculpture of *O. plicatus* also differs considerably from the cross-hatched

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[1] Data in braces { } represent the means of the preceding data

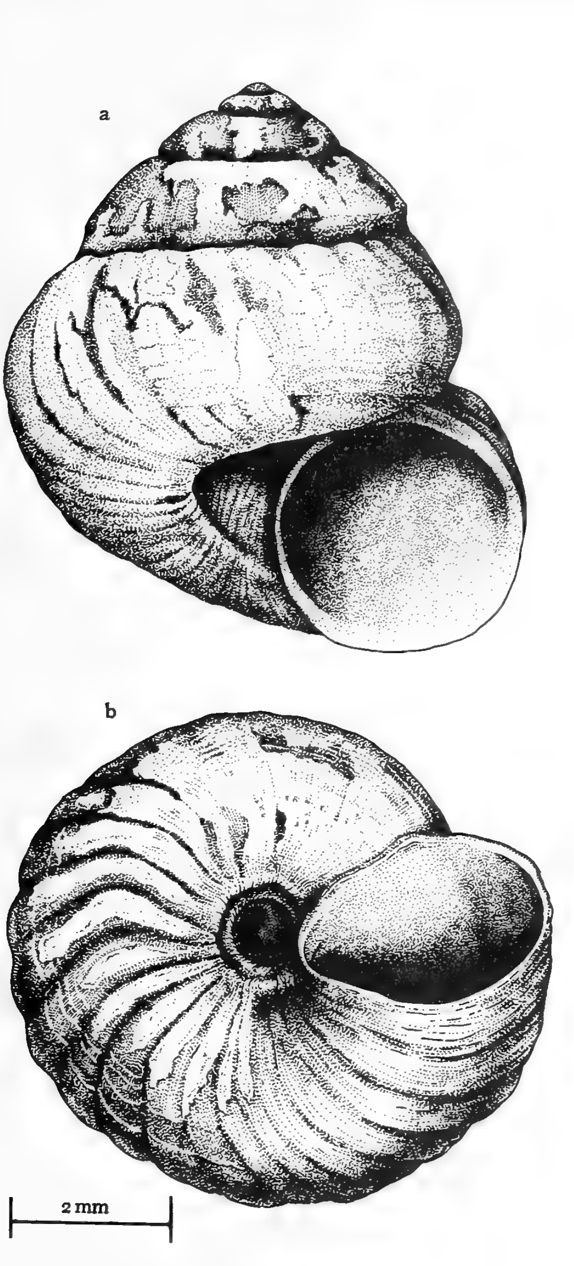

Figure 13

Ostodes plicatus

a – Shell seen from side b – shell seen from below

surface of *O.* ***reticulatus,*** which is a slightly smaller shell, wider than tall, with a much wider umbilicus. *Ostodes plicatus* is, of course, larger than *O. upolensis, O. adjunctus,* and *O. cookei,* and smaller than *O. garretti* and *O. tiara.*

In anatomy, although the reduced anterior portion of the hypobranchial gland is fairly distinctive, *Ostodes plicatus* is set off from other species of similar size chiefly by the reproductive systems. *Ostodes plicatus* males have longer penial threads, on the average, than do males of any species of comparable size except *O. strigatus* and *O.* ***reticulatus.*** In the female reproductive systems, the downward bend of the terminal portions of rectum and vagina is unique to *O. plicatus;* in the unusual specimen in which the downward bend is lacking, the individual could still be distinguished from *O.* ***reticulatus*** and *O. strigatus* by the proportionate lengths of the common ducts. The interior common duct in *O. plicatus* is slightly longer than the diameter of its bursa copulatrix (as is that of *O. strigatus*), while that of *O.* ***reticulatus*** is less than one-half as long as its bursa is wide; the pallial common duct is very short in *O. plicatus,* but nearly 4 times the diameter of the copulatory pore in *O.* ***reticulatus,*** and 15 times the pore-diameter in *O. strigatus.*

Ostodes plicatus and *O. gassiesi* approach each other very closely in conchological characters. An empty shell, especially a worn shell, might well be impossible to assign with certainty to either species. The anatomy, however, is quite distinctive, and there should be no difficulty in identifying any whole specimen.

Range: Upolu, Western Samoa. Northeastern foothills, central uplands, and southern lowlands near coast. Altitude range 15 m – 750 m.

Material: Upolu: Station 2, 1.2 km above Afiamalu seismographic station, at 720 m elevation, on right side of road in dense forest (6 specimens, FMNH 159173); Station 8, 1.2 km above Afiamalu seismographic station, at 720 m elevation, on both sides of road in mixed to good forest (7 specimens, FMNH 170546, 159183, 159166); Station 9, Tafatafa, at 15 m elevation, in heavy forest (28 specimens, FMNH 152941, 159171): Station 18, at foot of Mount Solaua, at 180 – 240 m elevation, under *Ficus* tree in banana patch at edge of forest (59 specimens, FMNH 152894, 152842, 159163, 153107); Station 19, rim of Lake Lanuot'o crater, at 750 m elevation (1 specimen, FMNH 152836); Station 39, top of range above Solaua, at 600 m elevation, narrow ridge in heavy forest (6 specimens, FMNH 152588).

Totals: 107 specimens: 33 adult males, 24 adult females, 5 juvenile males, 4 juvenile females, 5 accidentally broken, 17 not sexed, 19 empty.

b. *Ostodes gassiesi* (Souverbie, 1858)

(Figures 1a, b; 14a; 15a, b)

Cyclostoma gassiesi Souverbie, 1858, Journ. de Conch., 7: 294, plt. 8, figs. 6 a, 6 b. Locality unknown.

Ostodes gassiesi (Souverbie), Kobelt, 1902, Das Tierreich, 16: 155 – Polynesia.

Ostodes plicatus (Gould), Clench, 1949, Bull. B. P. Bishop Mus., **196:** 15–17, fig. 7 a – partly.

Diagnosis: Shell narrowly turbinate, height of adults 9.2–14.6 mm {11.3 mm}, diameter 9.0–12.2 mm {10.6 mm}, with 5⅛ to 6⅛ whorls {5⅝}. Whorls with rounded shoulders, suture slightly incised, ventral surface rounded. Usually (87%) higher than wide; H/D ratio 0.91–1.31 {1.07}. Spire angle 70°–100° {80°}. Umbilicus deep, narrow, margin usually smoothly rounded and without bordering rim. D/U ratio 2.75–4.61 {3.42}. Aperture round, holostomatous, slightly appressed to whorl above, parietal callus of adults not quite as thick as outer lip of aperture. Early whorls usually smooth. Body whorl with 3–9 {5.6} strong, narrow, spiral threads clustered on lower half of upper palatal surface, crossing 14–23 {17.6} broad radial plicae. At maturity, spiral threads fade out completely, radial plicae become broader, flatter, further apart and less definite, underlying numerous fine radial growth lines. Lower palatal surface usually smooth: occasionally shows faint traces of spiral lirae without relief. Rarely shows pink on apex and spire; generally cream-color; periostracum thin, brown, adherent. Opercular types A-1, B, C-1.

Juveniles differ from above in that they are usually wider than high (H/D ratio 0.79–1.07, mean 0.95), the body whorl has a sharply angled periphery, and the ventral surface is almost flat. Compare Figures 1a and 1b.

Hypobranchial gland large and prominent posteriorly, beginning well over to left side. Anterior portion tapers smoothly and is quite short, ending opposite middle of kidney. Males have short-threaded penes, often with subterminal bulb. Prostatic sac present frequently, "safety-valve" seldom. If "safety-valve" is present, it does not cross over the vas deferens to terminate behind and below anus, as usual, but is either very short, terminating on top of the vas, or if longer, runs down the medial aspect of the vas and terminates about midway between the anterior end of the prostate and the base of the penis. Female internal common duct short, only about ⅘ as long as bursa copulatrix is wide. Pallial common duct also short; copulatory pore down from mantle line only by its own diameter, with entry of common duct into uterus 1.5 pore diameters below pore. Common duct enters uterus via an elongate oval papilla, slightly elevated, its long axis at right angles to long axis of uterus. Anus a simple tube, pointing directly forward without hypertrophy of lips. Vaginal orifice a broad triangular slit, apex inward, its length 1.6 times the width of the uterus at the inner end of orifice.

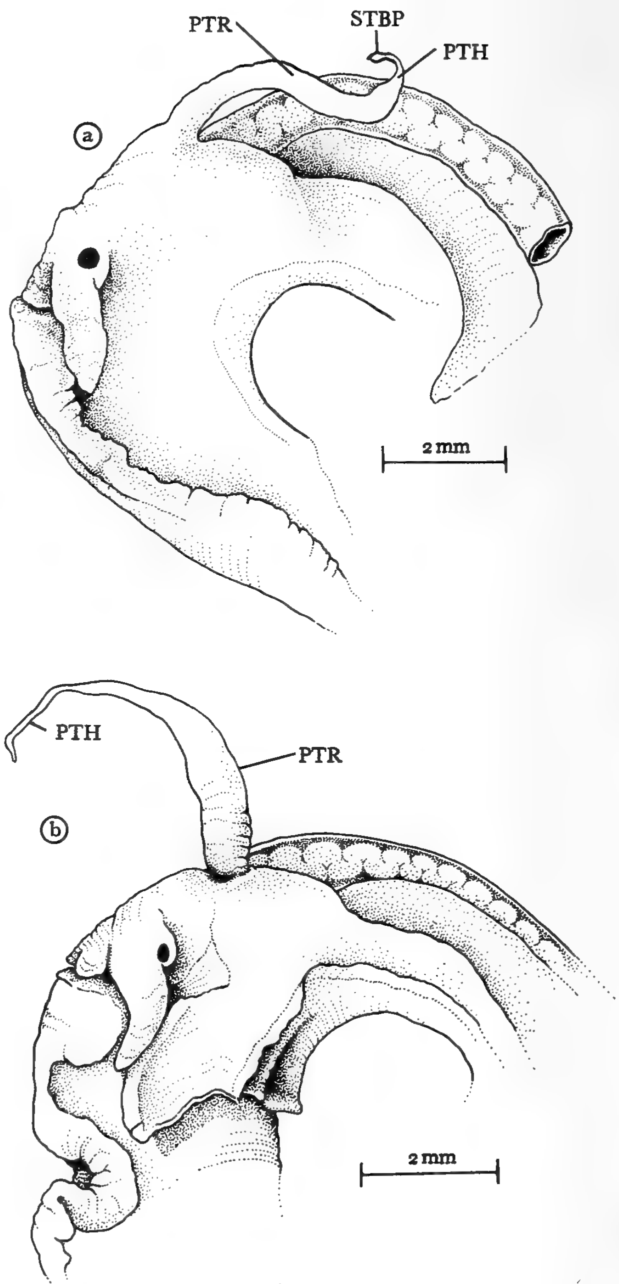

Figure 14

Males of (a) *Ostodes gassiesi* and (b) *Ostodes plicatus*
[for explanation of abbreviations see Appendix on foldout]

Comparative remarks: For the conchological differences between *Ostodes gassiesi* and the species most similar to it, *O. plicatus,* see comparative remarks under the latter species. *Ostodes gassiesi* differs from *O. savaii* in being narrower at a higher whorl count as well as in proportion to

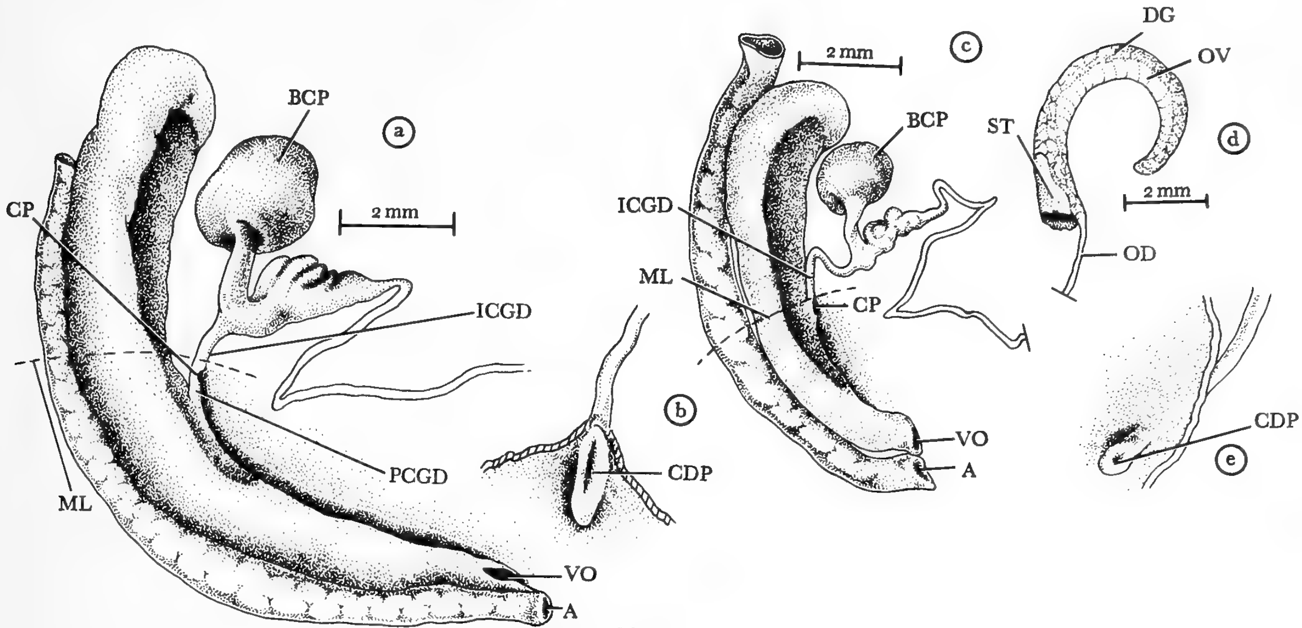

Figure 15

Female reproductive system of *Ostodes gassiesi* and *O. plicatus*
a – *Ostodes gassiesi*; b – *O. gassiesi*, entrance of common genital duct into uterus; c – *O. plicatus*; d – *O. plicatus*, ovary; e – *O. plicatus*, entrance of common genital duct into uterus

[for explanation of abbreviations see Appendix on foldout]

its height, and by its strong radial sculpture, which is lacking in *O. savaii*. *Ostodes gassiesi* is also taller and narrower than *O.* **reticulatus,** and taller than *O. strigatus*, with a more acutely angled spire and a much narrower umbilicus than either of the latter species.

As mentioned under *Ostodes plicatus*, that species and *O. gassiesi* are quite distinct anatomically. *Ostodes gassiesi* is closer anatomically to *O. savaii* than to any other of the middle-sized species, but is still distinct. In the male, both species are short-threaded, but *O. gassiesi* hardly ever has a "safety-valve," while that structure is present in more than ⅓ of the males of *O. savaii*. In the female reproductive system, both sections of the common duct are proportionately shorter in *O. gassiesi* than in *O. savaii;* the anal tip in *O. gassiesi* is a simple tube without hypertrophy, whereas in *O. savaii* there is considerable hypertrophy of the upper margin; and in *O. gassiesi* the upper lip of the vaginal orifice is longer than the lower lip, while the reverse is true in *O. savaii*.

Range: Upolu, southern and northeastern lowlands, western, central and northeastern foothills, central uplands. Altitude range, 15 m – 750 m. Savaii, eastern and southeastern lowlands, southern and southeastern foothills. Altitude range, 75 m – 450 m.

Material: Upolu: Station 2, 1.2 km above Afiamalu seismographic station, right of road, at 720 m elevation, in disturbed upland forest (10 specimens, FMNH 152705); Station 5, 1.6 km N of Tanumalala at 300 m elevation, in a thinned logging area with some bananas (9 specimens, FMNH 152765); Station 6, 1.6 km NW of Mt. Siga'ele, at 555 m – 570 m elevation, in forest patch in gully-pasture area (8 specimens, FMNH 152927); Station 7, foot of SE peak Tafua-Upolu at 450 m elevation, in forest part of transition zone above taro patch and newly cleared land (30 specimens, FMNH 152784, 152912); Station 8, 1.2 km above Afiamalu seismographic station, a wide area on both sides of road, including Station 2, 720 m elevation in disturbed upland forest (2 specimens, FMNH 170545, 152690); Station 9, Tafatafa, at 15 m elevation in heavy lowland forest (1 specimen, FMNH 152938); Station 10, Togitogiga, at 15 m elevation, in heavy lowland forest (1 specimen, FMNH 170535); Station 13, summit of pass to Fagaloa Bay, at 225 m elevation under a large mango tree in mixed foothill forest (1 specimen, FMNH 152666): Station 14, lower slope of SE peak Tafua-Upolu, at 390 m – 420 m elevation in disturbed to good foothill forest (9 specimens, FMNH 152753); Station 16, SE peak Tafua-Upolu at 480 m elevation, in undisturbed foothill forest (8 specimens, FMNH 159175); Station 17, top ridge SE peak Tafua-Upolu at 600 m elevation in disturbed foothill forest (2 specimens, FMNH 152774); Station 18, foot of Mt. Solaua, between 180 m – 240 m elevation, under a large *Ficus* tree in a banana patch at edge of lowland forest (3 specimens, FMNH 170551, 166215); Station 19, rim of Lake Lanuto'o crater at 750 m elevation, in heavy upland forest (18 specimens, FMNH 152809); Station 20, Lake Lanuto'o-Tapatapao trail, at 540 m elevation, in heavy foothill forest (41 specimens, FMNH 152795); Station 23, gully to foot of north side Mt. Siga'ele at 600 m – 645 m elevation in mixed to good foothill forest (8 specimens, FMNH 152606); Station 24, same gully as Station 23, but at 690 m elevation, in good foothill forest (1 specimen, FMNH 152905); Station 26, Afiamalu-Lake Lanuto'o track at 735 m – 750 m elevation, in good to excellent upland forest (36 specimens, FMNH 152670, 152719, 152721).

Savaii: Station 28, Vai'a'ata, near Vailoa, at 270 m elevation, on new road in tall open lowland bush (31 specimens, FMNH 152572, 152649); Station 30, about 8 km NW Vailoa at 180 m elevation, in heavy lowland forest (10 specimens, FMNH 170539); Station 36, about 12.8 km NW Vailoa at 270 m elevation in heavy foothill forest (8 specimens, FMNH 152634, 152642); Station 37, about 6.4 km W of Gatavai in dry stream bed at about 450 m elevation for 9.6 km in heavy foothill forest (6 specimens, FMNH 170541); Station 38, 800 m inland, 8 km E of Vailoa on road to Salelologa wharf, at less than 75 m elevation (1 specimen, FMNH 152631).

Totals: 244 specimens (188 from Upolu, 56 from Savaii); 86 adult females, 71 adult males, 19 juvenile females, 16 juvenile males, 28 not sexed, 24 empty.

c. *Ostodes reticulatus* Girardi, spec. nov.

(Figures 16a; 17a, b; 18a, b)

Diagnosis: Shell turbinate, height of adults 8.0 – 10.8 mm {9.2 mm}, diameter 9.1 – 11.2 mm {10.0 mm} with $5\frac{1}{8}$ – $5\frac{5}{8}$ whorls {$5\frac{3}{8}$}. Whorls with rounded shoulders, dropping to flat, vertical area below periphery. Usually (92%) wider than high: H/D ratio 0.82 – 1.04 {0.93}. Spire angle 90° – 100° {92°}. Umbilicus deep, very wide, often bordered by a rim formed by the innermost cord of spiral sculpture. D/U ratio 2.53 – 3.09 {2.78}. Aperture round, holostomatous, slightly appressed to whorl above. Parietal callus of adults usually not quite as thick as outer lip. Spire smooth; sculpture usually badly worn on early whorls of adults. Body whorl with 4 – 8 {4.5} evenly spaced raised spiral cords on upper palatal surface, 6 – 11 {7.6} spiral cords on lower palatal surface, crossing 19 – 29 {23.0} radial cords on upper surface, of which 18 – 24 {20.6} continue on ventral surface. Both radial and spiral cords are of approximately the same height and width, and their crossing gives a reticulated surface effect, leaving square or oblong hollows, wider and taller than the width of the cords, between them. Color creamy white. Periostracum thin, light amber-brown; wears off raised cords but remains in hollows between them, where it is covered by accumulated environmental debris. Opercular type A-1.

Hypobranchial gland with reduced posterior portion; anterior portion long and dense, but quite slender. Males have long-threaded penes without bulbs. Both prostatic sac and "safety-valve" present. Female internal common duct moderately short – 0.43 times the diameter of the bursa copulatrix. Length of pallial common duct equal to approximately 4 times diameter of copulatory pore, with pore located slightly above mid-point of duct. Common duct enters uterus via an elevated papilla, narrowly heart-shaped with apex up, at right angles to long axis of uterus. Anus shows slight hypertrophy of upper margin. Vaginal orifice an oval hole on ventral aspect of uterus, its horizontal dimension being equal to $\frac{4}{5}$ the uterine diameter at posterior tip of orifice.

Comparative remarks: *Ostodes **reticulatus*** resembles *O. strigatus* more closely than it does any other of the mid-sized species of *Ostodes*. (See comparative remarks under

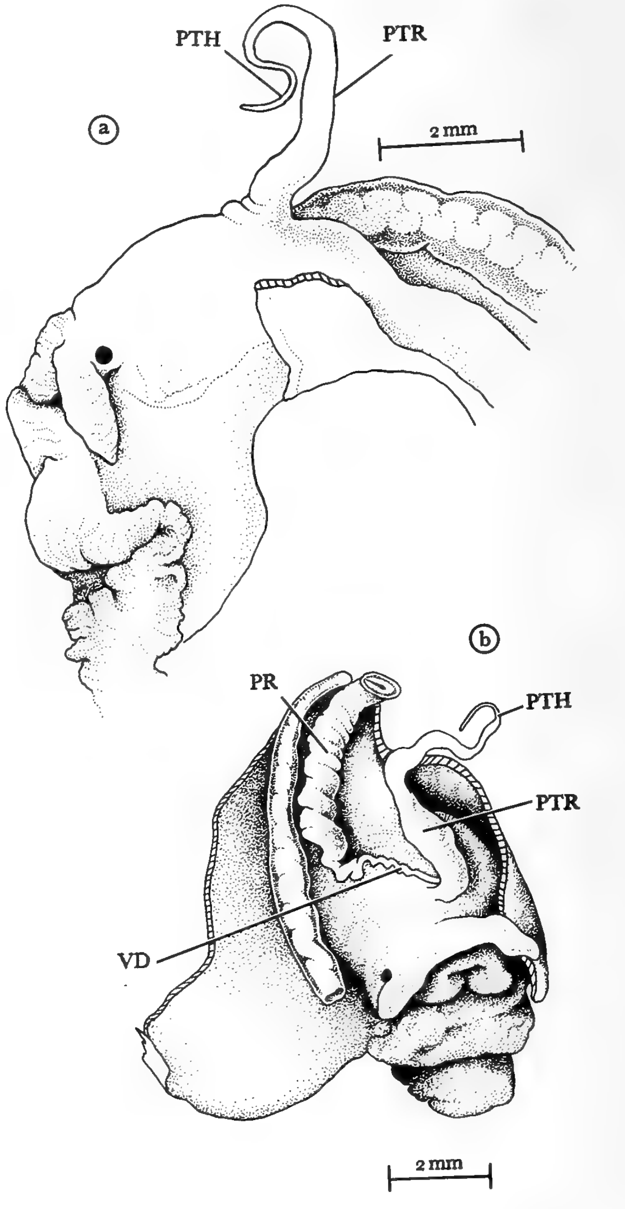

Figure 16

Males of (a) *Ostodes **reticulatus*** and (b) *Ostodes strigatus* [for explanation of abbreviations see Appendix on foldout]

O. strigatus.) As regards the other species in the genus, the reticulated surface and the wide umbilicus are the most notable conchological characters separating *O.* ***reticulatus*** from *O. savaii. Ostodes savaii* lacks the radial threads that contribute to the reticulated surface of *O.* ***reticulatus,*** has a narrower umbilicus, and is in addition a somewhat larger shell, and one that tends to have almost equal vertical and horizontal measurements, instead of being definitely wider than high, as is *O.* ***reticulatus.*** Both *O. gassiesi* and *O. plicatus* are usually taller than they are wide, and have

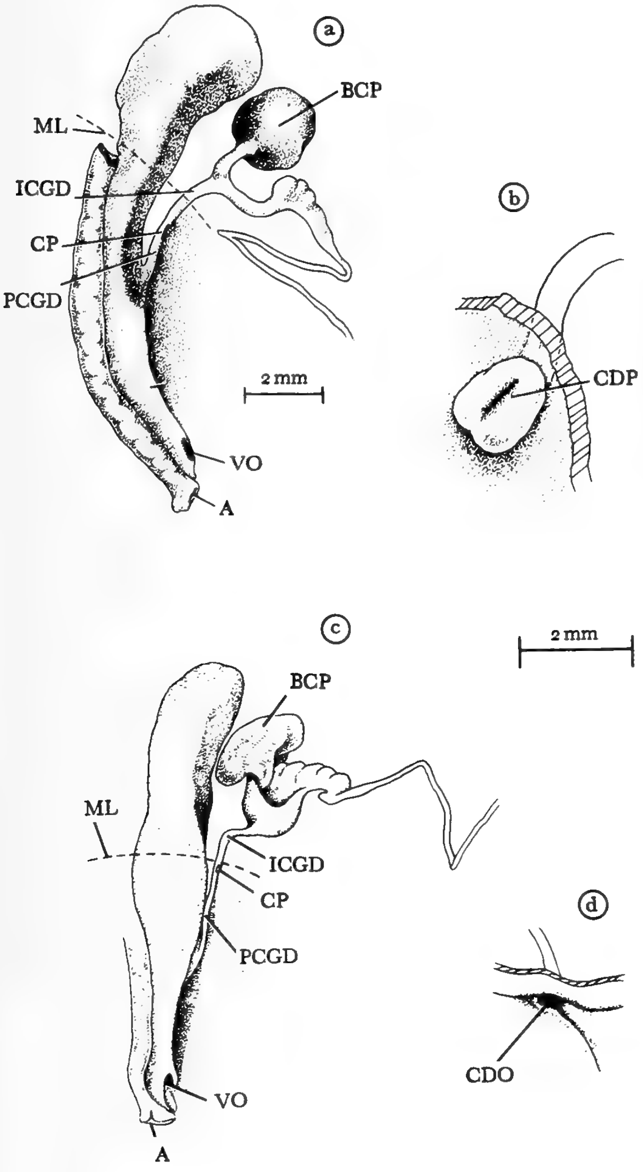

Figure 17

Female reproductive systems of *Ostodes* ***reticulatus*** and *O. strigatus*
a – *O.* ***reticulatus;*** b – *O.* ***reticulatus,*** entrance of common genital duct into uterus; c – *O. strigatus;* d – *O. strigatus,* entrance ot common genital duct into uterus

[for explanation of abbreviations see Appendix on foldout]

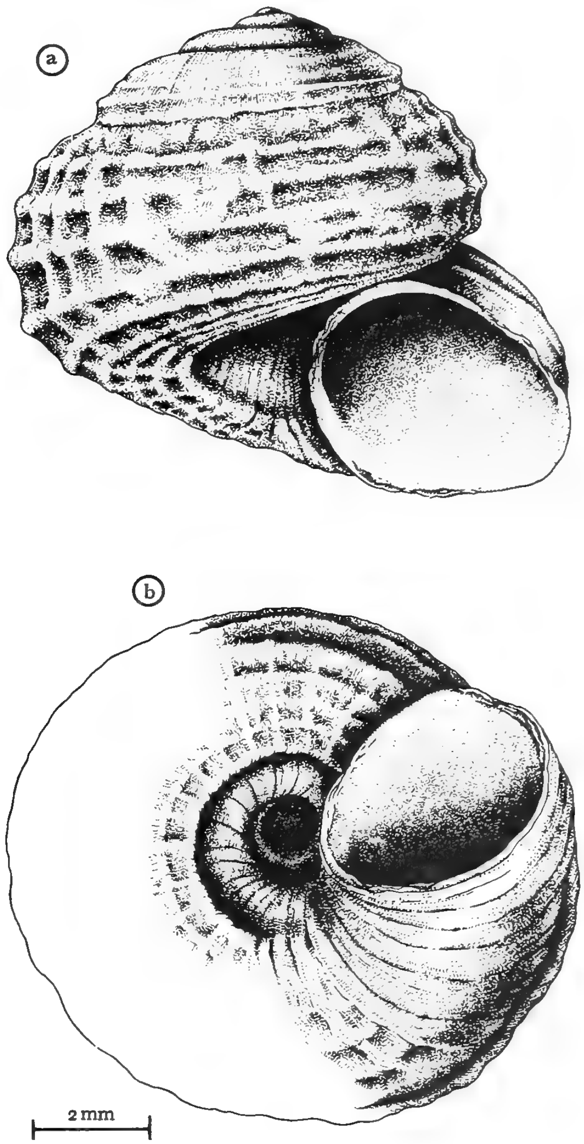

Figure 18

Ostodes ***reticulatus*** (holotype)

a – Shell seen from side b – shell seen from below narrow umbilici. *Ostodes* ***reticulatus*** differs from *O.* ***exasperatus*** and *O.* ***llanero*** not only in its reticulated surface, but also in the shape of its whorls, which descend from the spire almost in a series of steps, whereas in the latter two species, the outline of the shell is a smooth, almost uninterrupted, convex curve.

Anatomically, *Ostodes* ***reticulatus*** seems more closely related to *O. strigatus* and *O. plicatus* than to the other middlesized species, but there should be no difficulty in differentiating among the three. For anatomical differences between *O.* ***reticulatus*** and *O. strigatus,* see under *O. strigatus.* The hypobranchial gland of *O. plicatus* is heavy posteriorly and reduced anteriorly, while that of *O.* ***reticulatus*** is reduced posteriorly but quite prominent anteriorly. Males of both species have similar penes (long threaded, without bulbs), but *O.* ***reticulatus*** is more apt to have a prostatic sac than is *O. plicatus,* and the "safety-valve" of the latter species is much more noticeable. In the female reproductive systems, *O.* ***reticulatus*** never has the downward bend of the terminal portions of rectum and vagina that characterizes *O. plicatus,* and the proportionate lengths of the common ducts are different, the internal duct being the longer in *O. plicatus,* the pallial duct being the longer in *O.* ***reticulatus.***

Description of holotype: An adult female specimen, height, 9.3 mm; diameter, 10.2 mm; spire angle, 90°; H/D ratio, 0.91. Whorls 5⅛, decoiling at even moderate rate until near aperature, when rate increases so last 5 mm of body whorl are indented under periphery of penultimate whorl. Whorls with rounded shoulders but with narrow, flat, vertical area at lower margin of each, between lowest spiral thread and suture below. Nuclear whorl smooth; juvenile whorls somewhat worn. Upper palatal surface of body whorl with 25 radial cords, overlain by 4 spiral cords. Lower palatal surface with 19 radial and 6 spiral cords, of which the innermost forms a rim around the umbilicus. Intersecting radial and spiral cords produce a reticulated surface. Last 5 mm of body whorl with close-set radial lines of gerontic growth replacing major sculpture. Aperture round, holostomatous, diameter 3.9 mm, slightly appressed to whorl above; parietal callus as thick as outer lip. Umbilicus wide, deep, bounded by rim; D/U ratio 2.76. Deepest part of umbilicus filled with environmental debris. Shell white, translucent; periostracum extremely thin, pale amber color, very closely adherent; worn off raised portions of surface, present under organic debris in hollows. Operculum lost.

Collected by A. Solem and L. Price, on November 4, 1965, at Station 16, SE peak Tafua-Upolu, in undisturbed foothill forest at 480 m elevation, Upolu, W. Samoa. FMNH 170532.

Range: Upolu, W. Samoa, central foothills and uplands, northeastern foothills. Altitude range, 180 – 750 m.

Material: Upolu: Station 5, 1.6 km NW of Tanumalala, at 300 m elevation, in thinned logging area with some bananas (2 specimens, FMNH 152897); Station 6, 1.6 km NW Mt. Siga'ele, at 555 – 570 m elevation, in forest patch in gully-pasture area (2 specimens, FMNH 152928, 159186); Station 8, 1.2 km above Afiamalu seismographic station, at 720 m elevation, on both sides of road in mixed to good forest (2 specimens, FMNH 159167, 159182); Station 16, SE peak Tafua-Upolu, at 480 m elevation, in undisturbed forest (7 specimens, FMNH 152757 (paratypes), 170532 (holotype)); Station 17, top ridge of SE peak Tafua-Upolu, at 600 m elevation, in disturbed forest (1 specimen, FMNH 159181); Station 18, foot of Mt. Solaua, at 180 – 240 m elevation, under a *Ficus* tree in banana patch at edge of forest (2 specimens, FMNH 159180, 166213); Station 23, gully to foot of N side Mt. Siga'ele, at 600 – 645 m elevation, in mixed to good forest (2 specimens, FMNH 159169); Station 24, N side Mt. Siga'ele, at 690 m elevation, in good forest (6 specimens, FMNH 159162); Station 26, Afiamalu-Lake Lanuto'o track at 735 – 750 m elevation, in good to excellent forest (1 specimen, FMNH 159178).

Total: 25 specimens; 7 adult males, 6 adult females, 5 juvenile males, 1 juvenile female, 3 not sexed, 3 empty.

d. *Ostodes strigatus* (Gould, 1848)

(Figures 16b, 17c, d)

Cyclostoma strigatum Gould, 1848, Proc. Boston Soc. Nat. Hist., 2: 204 – 205 – Upolu; Gould, 1852, U. S. Expl. Exped., 12: 102 – 103; Pfeiffer, 1853, Conch. Cab. 1 [19(1)]: 302 – 303, plt. 40, figs. 15, 16 – Upolu; Gould, 1860, Atlas of Shells, U. S. Expl. Exped., plt. 8, figs. 117, 117a, 117b.

Cyclophorus strigatus (Gould) Gray, 1852, Cat. Phan. p. 58 – Upolu; Pfeiffer, 1852, Mon. Pneum. 1: 83 – 84 – Upolu; Reeve, 1862, Conch. Icon., 13: sp. 77, plt. 17, fig. 77; Mousson, 1865, Journ. de Conch., 13: 179 – 180 – Upolu and Manua – partly.

Cyclostoma albida Hombron & Jacquinot, 1852 – 1854, Voyage au Pôle Sud, 5 [4(2)]: 50 – 51, plt. 12, figs. 25 – 28 – Samoa.

Cyclophorus (*Ostodes*) *strigatus* (Gould) Mousson, 1896, Journ. de Conch., 17: 350 – 351 – Upolu, Savaii, and Tutuila – partly.

Ostodes albidus (Hombron and Jacquinot) Kobelt, 1902, Das Tierreich, 16: 153 – Samoa.

Ostodes strigatus (Gould) Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 147 – 148 – Upolu, Tutuila, and Savaii – partly; Kobelt, 1902, Das Tierreich 16: 156 – Samoa (Upolu); Clench, 1949, Bull. B. P. Bishop Mus., 196: 13, figs. 4a, 4b – Tutuila: Laulii Valley at 30 – 150 m elevation; Fagatoga at 30 – 270 m elevation; foot of Mt. Tau at 24 m elevation; Logatala Ridge at 60 m elevation; Leone at 45 m elevation; Leone-Aolaoa Trail at 270 – 360 m elevation: Fagasa-Maupasaga Trail at 150 m elevation.

Diagnosis: Shell turbinate, height of adults 7.3 – 10.85 mm {9.32 mm}, diameter 8.6 – 11.6 mm {10.82 mm}, with 4⅝ to 5½ whorls {5⅛}. Sides of upper whorls somewhat flattened; body whorl with rounded shoulder. Suture incised on approximately first 2 whorls; on later whorls, lowest spiral lira tends to overlie suture up to the start of the whorl-inset which marks maturity. Usually (93%) wider than high: H/D ratio 0.73 – 1.10 {0.91}. Spire angle 75° – 100° {86°}. Ventral surface rounded. Umbilicus wide, deep, bordered by a protruding rim which is seen to be hollow in juveniles but becomes solid in adults; D/U ratio of adults 2.38 – 3.52 {2.89}. Aperture circular to (occasionally) sub-ovate with vertical diameter the greater; holostomatous, gently appressed to whorl above. Parietal callus approximately as thick as outer lip. Early whorls smooth. Body whorl with 3 – 7 {4.8} strong spiral cords, with which, in 42% of the shells examined, are interspersed from one to three slender spiral threads. In 37% of the juvenile shells examined, but only 19% of the adults, the spiral threads are beaded in such a way as to give the appearance of radial plicae crossing the spirals. There may be from 19 – 51 {adult: 30.7} such beads on the spiral cords of the body whorl, but only very rarely is there any trace of true raised radial sculptural elements between the spiral cords. In those few shells with true radial sculpture, the radial elements extend only from the suture down through the highest one or two spiral cords; they seldom reach the whorl shoulder, and never extend onto the ventral surface. Ventral surface usually (86%) smooth in adults. Remaining adults and about half the juveniles examined showed from 8 – 12 {8.9} ventral spirals, ranging from moderately prominent threads to barely perceptible lines without any relief at all. Since many more juveniles than adults showed some ventral spiral sculpture, its absence in adults may be due to wear. The absence of radial ventral sculpture, however, is a true shell character, not due to wear. Only one shell of 153 examined showed even the faintest trace of any radial sculptural elements on the ventral surface. Color light tan to cream-color, with an occasional pinkish spire. Periostracum thin, amber-colored; wears off raised spiral cords, but sometimes remains in valleys between cords, where it becomes covered by adherent environmental debris, giving the shell a spiral-striped appearance. Opercular types A-1, A-2, B, C-1, C-2, with half of the type B opercula (20% of the total number) being very concave (see p. 201).

Hypobranchial gland faint, tenuous; begins slightly to left of midline, turns and runs forward only to a point opposite the middle of the kidney. Males have penis with very long thread without bulb. In one male of 43 examined, penis was just to right of cephalic midline; penis on midline in all other specimens. Contrary to previous reports, all specimens seen had a closed vas deferens, not an open sperm groove. Vas deferens seems to be quite a long tube; it can be seen to be very convoluted as it runs beneath the integument from the prostate across to the penis. No "safety-valve" present, no prostatic sac; anterior end of prostate simply squared-off, without any constriction. Anterior medial corner makes a sort of flat flap, under which vas deferens crosses to penial base. Length of female internal common duct approximately equal to diameter of bursa copulatrix. Pallial common duct long; copulatory pore just below mantle line; entry of duct into uterus down 15 pore diameters. Common duct enters uterus via simple hole, partly hidden beneath soft, transverse fold of tissue, and opening into a sort of gutter or channel, which runs forward a short distance before fading into surrounding tissue. Anus with only very slight hypertrophy. Vaginal orifice a broad triangular slit, apex pointing inward, length approximately 1.3 times width of uterus at inner end of orifice.

Comparative remarks: *Ostodes strigatus* resembles *O.* ***reticulatus*** very closely. Although *O. strigatus* tends to have a lower whorl-count for its size than *O.* ***reticulatus,*** and a slightly more acutely-angled spire, shell sizes and proportions in the two species are almost identical. There are, however, considerable differences in sculpture. The spiral cords in *O.* ***reticulatus*** are evenly spaced and of uniform strength, and are crossed by radial cords of the same spacing and strength. Both spiral and radial elements continue strongly on the ventral surface of the shell. In *O. strigatus,* the spiral cords tend to be unevenly spaced and interspersed with much weaker threads. True radial sculpture is seldom found on the upper shell surface, and never on the ventral surface, which is usually entirely smooth.

The anatomical differences between *Ostodes strigatus* and *O.* ***reticulatus*** are much greater than the conchological differences. The hypobranchial gland of *O. strigatus* is much smaller and fainter. In the female, both internal and pallial common ducts are longer in *O. strigatus,* and the vaginal orifice is differently shaped and much larger than it is in *O.* ***reticulatus.*** Males of both species have long-threaded, bulbless penes, but those of *O. strigatus* are longer (mean ratio, thread to trunk, 1/0.60 ± 0.03, compared to 1/0.91 ± 0.15) and a Student's *t* Test of the two ratios yields a *t* of 3.065 with 46 degrees of freedom, which indicates a probability of less than 0.01 that *O. strigatus* and *O.* ***reticulatus*** are the same.

Although GOULD (1848, 1852, 1860) clearly differentiates between *Ostodes strigatus* and *O. plicatus,* later authors, notably MOUSSON (1865, 1869) confuse the two. *Ostodes plicatus* is taller than it is wide, with radial sculpture predominant; *O. strigatus* is wider than it is tall, with almost exclusively spiral sculpture. Students' *t* Tests comparing male and female heights and diameters of *O. strigatus* and *O. plicatus* indicate a probability of less than 0.001 that these two species are the same.

Similar *t* tests of heights and diameters between *Ostodes strigatus* and the 3 other mid-sized species of *Ostodes* indicate that there is less than 0.01 probability of identity between *O. strigatus* and *O. gassiesi*, and less than 0.001 probability of identity between *O. strigatus* and *O. savaii;* in addition, *O. strigatus* has fewer whorls and a wider umbilicus than either *O. gassiesi* or *O. savaii*. The probability of identity between *O. strigatus* and ***O. exasperatus*** is approximately 0.015 as regards shell height and diameter, with *O. strigatus* a smaller shell with fewer whorls, that is much less likely to have spiral sculpture ventrally. Anatomically, both *O. gassiesi* and *O. savaii* usually have short-threaded penes, often with sub-terminal bulbs; *O. strigatus* has a very long-threaded, bulbless penis. The chief anatomical difference between *O. strigatus* and ***O. exasperatus*** is in the female genitalia, with the copulatory pore of *O. strigatus* much closer to the mantle line, and the pallial common duct about 3 times as long as that of ***O. exasperatus***.

Comparison of juvenile shells of *Ostodes strigatus* with the available juveniles of ***O. llanero*** reveals that *O. strigatus* is taller, with a more acute spire angle and a narrower umbilicus. *Ostodes strigatus* is, of course, larger than *O. upolensis, O. adjunctus,* and *O. cookei,* and smaller than *O. tiara* and *O. garretti*.

Range: Tutuila, American Samoa; western portion of island: center and south-east edge of central plateau, extreme southern coast, mountain slope near (just south of) Pago Pago. Altitude range, 60 – 390 m.

Materials: Tutuila. Station AS-6; central plateau above Aolaoufou, 21 km SW Pago Pago, 360 – 390 m elevation (74 specimens, FMNH 181051/N). Station AS-10; middle slopes NE side Matafao Peak, reservoir track, behind Pago Pago, in dense forest (33 specimens, FMNH 181083/N). Station AS-19; upper slopes Olotele Mt., edge of central plateau, at 270 – 330 m elevation, SW of Pago Pago (26 specimens, FMNH 181151/N). Station AS-20; seaward slopes Fagatele Crater, 19 km SW Pago Pago, at 60 m elevation (20 specimens, FMNH 181157/N).

Totals: 153 specimens: 44 adult males, 40 adult females, 20 juvenile males, 17 juvenile females, 32 not sexed.

e. *Ostodes savaii* Clench, 1949

(Figures 19a; 20a, b, c)

Ostodes savaii Clench, 1949, Bull. B. P. Bishop Mus., **196**: 14, 15, figs. 5, 6 – Savaii: Salailua, at 90 – 180 m elevation; Matavanu, ± 900 m; Siuvao-Auala (1.6 – 6.4 km inland) at 150 – 600 m elevation.

Diagnosis: Shell turbinate, height of adults 7.6 – 13.6 mm {10.7 mm}, diameter 8.2 – 13.0 mm {11.0 mm} with 5⅛ – 5⅞ whorls {5½}. Whorls with rounded shoulders, suture well defined. Tends to be approximately equal in height and width, H/D ratio 0.79 – 1.19 {0.98}. Spire angle 70° – 100° {86°}. Umbilicus deep, narrow; inner edge of final whorl often sharply angled at umbilical border, but seldom having a rim. D/U ratio 2.32 – 4.40 {3.18}. Aperture round, holostomatous, slightly appressed to whorl above. Parietal callus not as thick as outer lip of aperture. Early whorls usually smooth. Body whorl with 4 – 12 {5.8} fine but strong spiral threads on upper palatal surface, crossing 11 – 26 {19.9} broad, rather low and poorly-defined radial plicae. Lower palatal surface with 4 – 17 {10.8} spiral threads or lines, usually not as prominent as those on upper surface, often just lines, without any relief. Radial plicae hardly indicated at all on lower surface. Color creamy; periostracum thin, brown, deciduous. Opercular types A-1, B, C-1, C-2.

Hypobranchial gland with quite prominent posterior portion: anterior portion reduced in width and thickness, but runs almost ⅔ of way from mantle line to anterior mantle margin. Males mostly (86.5%) with short-threaded penes; about half have sub-terminal bulbs. Most have prostatic sacs, but only about ⅓ have "safety-valves." Female anterior common duct quite long, being slightly longer than bursa copulatrix is wide. Pallial common duct of moderate length, copulatory pore being anterior to mantle line by its own diameter, with entrance into uterus 4 pore-diameters below pore. Entrance of common duct into uterus via an elevated, round papilla. Anus shows considerable hypertrophy of upper margin, only slight hypertrophy of lower margin. Vaginal orifice a narrow triangular slit, apex in, its length equal to 2.1 X diameter of uterus at inner end of orifice.

Comparative remarks: *Ostodes savaii* resembles ***O. exasperatus*** very closely; the differences and similarities between these two species are discussed under comparative remarks for ***O. exasperatus***. *Ostodes savaii* differs from *O. gassiesi* and *O. plicatus* in proportion, being wider at a lower whorl count as well as in proportion to its height. In addition, both *O. gassiesi* and *O. plicatus* have strong radial sculpture which is lacking in *O. savaii*. *Ostodes savaii* is a larger shell, with more whorls and a narrower umbilicus, than *O. strigatus*. ***Ostodes reticulatus*** is a smaller shell than *O. savaii,* and has a reticulated surface quite unlike that of the larger species.

The anatomical differences between *Ostodes savaii* and ***O. exasperatus***, *O. strigatus* and *O. gassiesi* are discussed under the latter 3 species.

Range: Upolu, Western Samoa: northeastern, southern, and extreme southeastern lowlands; western, west-central, central and north-central foothills; central uplands. Altitude range, 3 – 750 m. Savaii, Western Samoa: eastern, southeastern and southwestern lowlands; western, south-

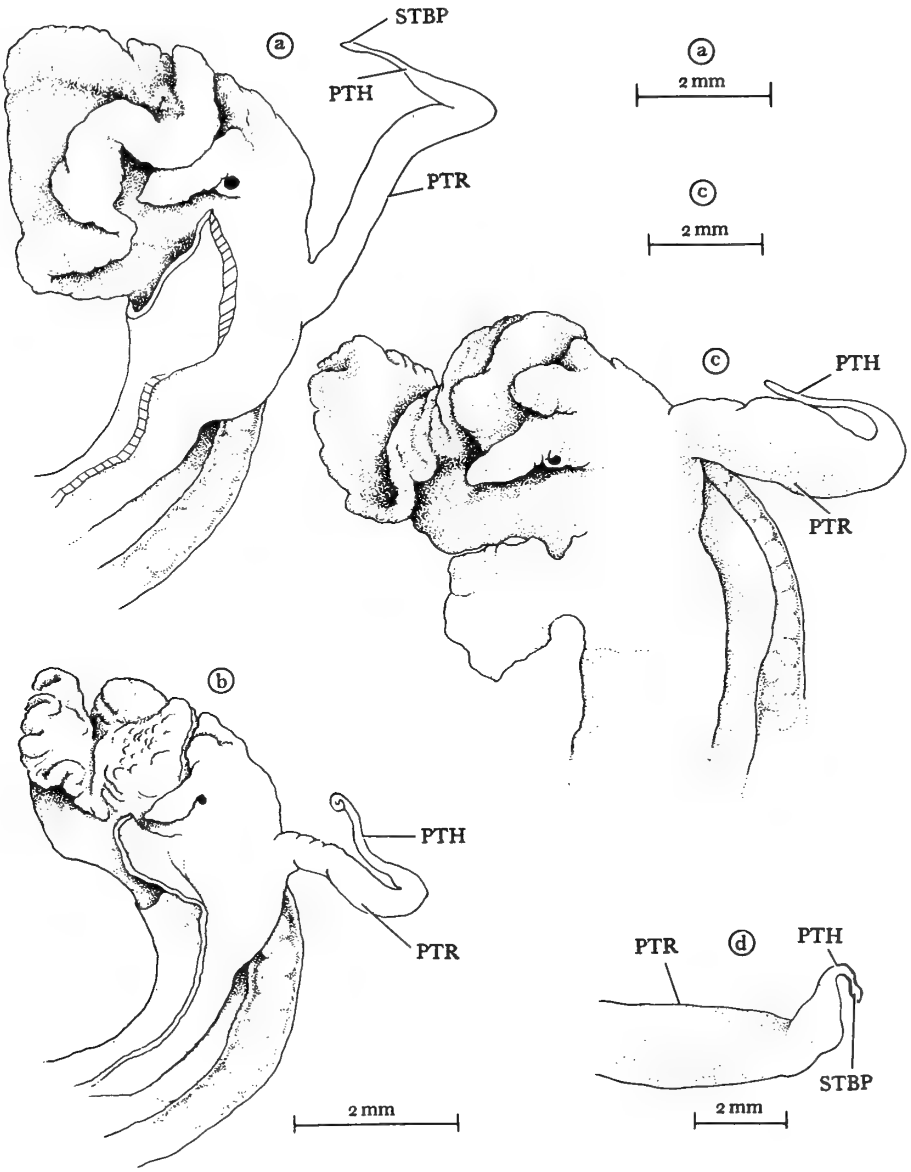

Figure 19

Males of *Ostodes savaii*, *Ostodes* ***llanero*** and *Ostodes* ***exasperatus***
a – *O. savaii*; b – *O.* ***llanero***; c – *O.* ***exasperatus***, male from Upolu; d – O. ***exasperatus***, type of penis found in Savaii population

[for explanation of abbreviations see Appendix on foldout]

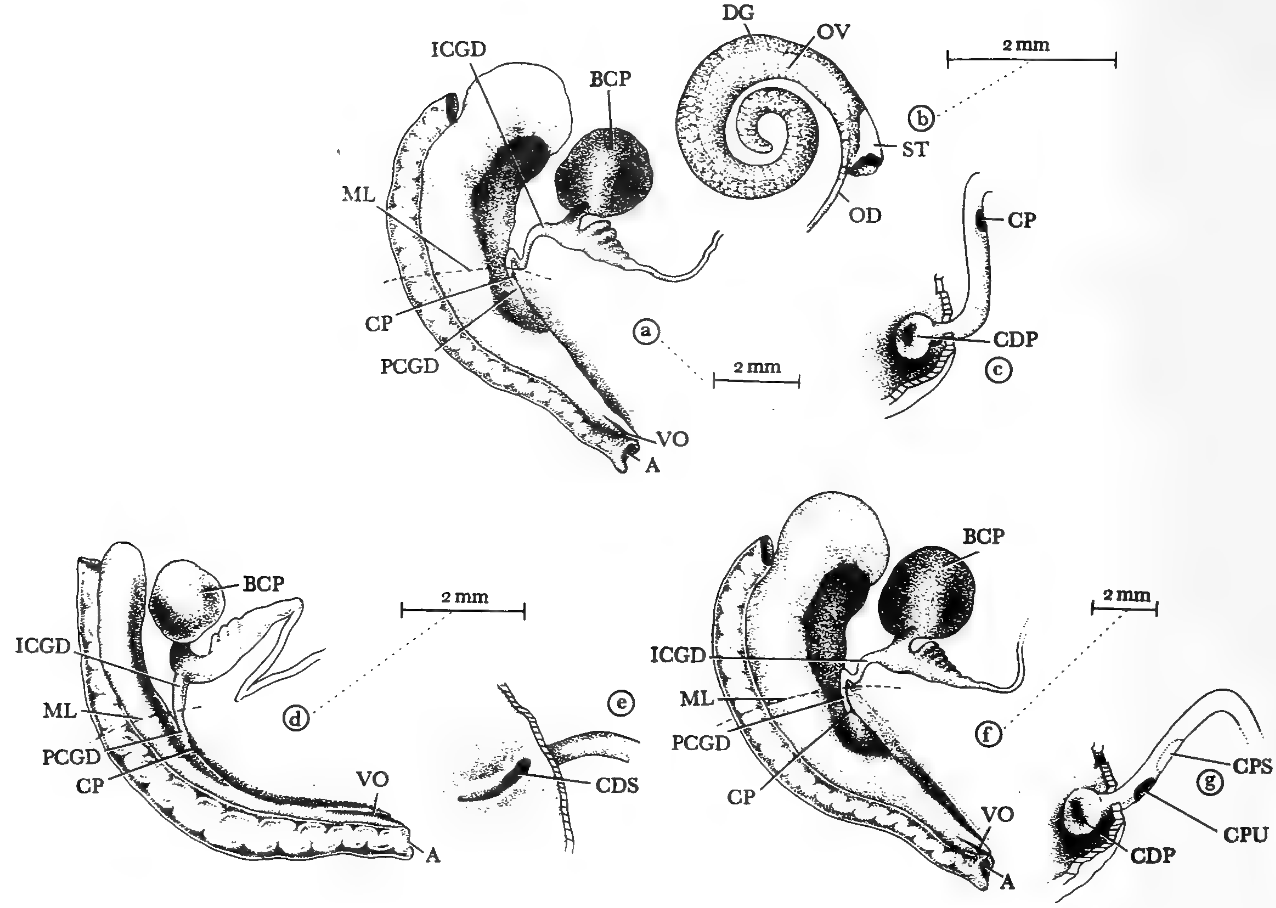

Figure 20

Female reproductive system of *Ostodes savaii*, *Ostodes* ***llanero*** and *Ostodes* ***exasperatus***

a – *O. savaii*; b – *O. savaii*, ovary; c – *O. savaii*, entrance of common genital duct into uterus; d – *O.* ***llanero***; e – *O.* ***llanero***, entrance of common genital duct into uterus; f – *O.* ***exasperatus***; g – *O.* ***exasperatus***, entrance of common genital duct into uterus, and position of copulatory pore in both populations

[for explanation of abbreviations see Appendix on foldout]

Explanation of Figures *43* to *48*

Figure *43*: *Ostodes* ***llanero***, central, lateral, and inner marginal teeth × 736

Figure *44*: *Ostodes* ***llanero***, outer marginal teeth, showing foramina × 786

Figure *45*: *Gonatorhaphe* sp., radula torn, showing base of central tooth and shank of lateral tooth × 235

Figure *46*: *Gonatorhaphe* sp., radula partly closed, showing edge of membrane and foramina in outer marginal teeth × 344

Figure *47*: *Gassiesia* sp., central tooth and tricuspid lateral teeth × 548

Figure *48*: *Gassiesia* sp., radula partly closed, showing outer marginal teeth × 235

[GIRARDI] Figures 43 to 48

43

44

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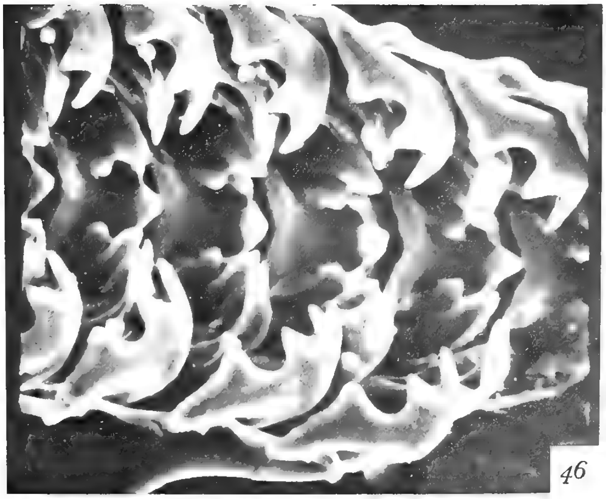

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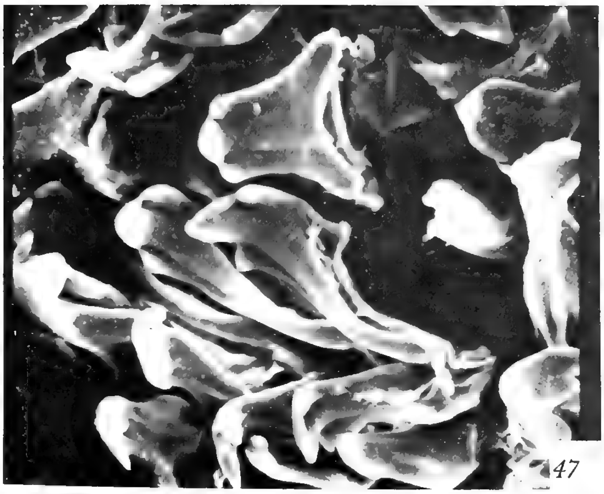

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48

ern and southeastern foothills. Altitude range, 150–450 m.

Material: Upolu: Station 2, 1200 m above Afiamalu seismographic station, on right of road at 750 m elevation in disturbed upland forest (5 specimens, FMNH 159174); Station 6, 1.6 km NW of Mt. Siga'ele at 555 m elevation, in a forest patch in a gully-pasture area (1 specimen, FMNH 159187); Station 7, foot SE peak Tafua-Upolu at 360 m elevation in forest part of transition zone above taro patch and newly cleared land (3 specimens, FMNH 159177); Station 8, 1.2 km above Afiamalu seismographic station, in wide area on both sides of road, including Station 2, at 720 m elevation in mixed to good upland forest (12 specimens, FMNH 170538, 152875, 159168); Station 9, Tafatafa, in heavy lowland forest at 15 m elevation (3 specimens, FMNH 170537, 170533, 159172); Station 10, Togitogiga, two logging roads toward ocean, at 15 m elevation, in thinned lowland forest (1 specimen, FMNH 170543); Station 16, SE peak Tafua-Upolu at 480 m elevation in undisturbed foothill forest (1 specimen, FMNH 159176); Station 18, foot of Mt. Solaua between 180–240 m elevation, under a large *Ficus* tree in banana patch at edge of forest (6 specimens, FMNH 153020, 159164, 159165, 166214); Station 20, Lake Lanuto'o-Tapatapao trail, at 540 m elevation in heavy foothill forest (1 specimen, FMNH 170534); Station 24, N side of Mt. Siga'ele at 690 m elevation, in good foothill forest (1 specimen, FMNH 170542); Station 25, cliffs at Tuiolemu at 3–150 m elevation in mixed to good lowland forest (8 specimens, FMNH 153108, 153432); Station 26, Afiamalu-L. Lanuto'o track at 735–750 m elevation in good to excellent upland forest (9 specimens, FMNH 170544, 170547, 170536, 159178, 159179, 159184, 159185); Station 40, summit of Mt. Vaea, near tomb of Robert Louis Stevenson, at 420 m elevation in much disturbed foothill forest (26 specimens, FMNH 152582).

Savaii: Station 28, Vai'a'ata, near Vailoa, at 270 m elevation, on a new road in tall open lowland bush (19 specimens, FMNH 170548, 170540); Station 30, about 8 km NW of Vailoa at 180 m elevation in heavy lowland forest (17 specimens, FMNH 153001, 153008); Station 31, 2 km in from Salilua, 41.6 km W of Vailoa, at 150 m elevation, in heavy lowland forest (38 specimens, FMNH 152741, 152791); Station 32, up a survey track at 450 m elevation, approximately 8 km inland from Asau in open foothill forest (26 specimens, FMNH 152526); Station 36, about 12.8 km NW of Vailoa, at 270 m elevation, in heavy foothill forest (1 specimen, FMNH 170549); Station 37, about 1.6 km W of Gatavai, at about 450 m elevation, in dry stream bed for 10 km in heavy foothill forest (10 specimens, FMNH 152560).

Totals: 188 specimens (111 from Savaii, 77 from Upolu); 58 adult males, 52 adult females, 11 juvenile males, 16 juvenile females; 22 not sexed, 18 empty.

f. *Ostodes exasperatus* Girardi, spec. nov.

(Figures 19c, d; 20f, g; 21a, b)

Diagnosis: Shell turbinate, height of adults 8.6–12.9 mm {10.4 mm}, diameter 9.8–13.4 mm {11.3 mm}, with 5¼–6⅛ whorls {5¾}. Silhouette smoothly convex, suture not incised. Usually (88%) wider than high; H/D ratio 0.81–1.00 {0.92}. Spire angle 80°–105° {90°}. Umbilicus wide, deep, usually (67%) bounded by a rim formed by innermost spiral cord, D/U ratio 2.36–3.85 {2.98}. Aperture sub-circular, slightly compressed vertically, very slightly appressed to whorl above. Parietal callus not as thick as outer lip. Apex and early whorls usually smooth. Body whorl with 4–7 {5.5} strong spiral cords on upper palatal surface, 6–20 {12.0} spiral cords on lower palatal surface. Only one shell of 24 adults examined showed any trace of radial sculpture except fine growth lines. Color creamy white. Periostracum thin, brown, deciduous. Opercular types A-1, A-2, B, C-1, C-2.

Hypobranchial gland narrow and elongate; runs nearly to front margin of mantle cavity. Males from Upolu have long-threaded penes without bulbs; those from Savaii mostly have short-threaded penes with bulbs. In both populations prostatic sacs and "safety-valves" are unusual. Female internal common duct very long (approximately equal to the diameter of the bursa copulatrix). Pallial common duct also long; copulatory pore anterior to mantle line by 3.5 times its own diameter. In females from Upolu, entrance of common duct into uterus is immediately below copulatory pore; in Savaii females, the entrance is approximately 2 pore diameters below the pore itself. This is the only difference in the female systems between the 2 populations. Entrance of common duct into uterus is via an elevated round papilla. Anus points directly forward, shows considerable hypertrophy of upper margin, slight hypertrophy lower margin. Vaginal orifice a narrowly triangular slit, apex inward, on the medioventral aspect of the uterus. Length of vaginal orifice approximately 1.6 times uterine diameter at inner end of orifice.

Comparative remarks: *Ostodes* ***exasperatus*** is very similar to both *O. savaii* and ***O. llanero.*** For the differences between *O.* ***exasperatus*** and *O.* ***llanero,*** see comparative remarks under the latter species. The principal conchological difference between *O.* ***exasperatus*** and *O. savaii* is the contour of the shell. The spire of *O. savaii* descends with a progressively increasing rate of decoiling; although the early whorls present a fairly even contour, there is a definite "step" effect between the penultimate whorl and the body whorl, with an almost vertical drop from the periphery of the penultimate whorl to the suture below. In ***O. exasperatus,*** the rate of decoiling is slower and more even, with the periphery of each whorl slightly overlying the suture. In addition, *O.* ***exasperatus*** averages very slightly shorter and wider than *O. savaii,* its umbilicus is slightly wider in proportion to the diameter of the shell, and it has a slightly higher whorl count for its size than does *O. savaii.* For differences between *O.* ***exasperatus*** and *O. strigatus,* see under the latter species.

Anatomically, *Ostodes* ***exasperatus*** differs considerably from *O.* ***llanero,*** as discussed under that species. The differences between *O.* ***exasperatus*** and *O. savaii* are smaller, but consistent. In the female, the difference is in the length and proportions of the pallial common duct. In *O.* ***exasperatus,*** the portion of the pallial common duct above the copulatory pore is considerably longer than that below the pore; in *O. savaii,* the reverse is true. In the male, *O. savaii* is much more apt to have a prostatic sac than is *O.* ***exasperatus,*** and slightly more apt to have a "safety-valve." The penial trunk of *O. savaii* is slender

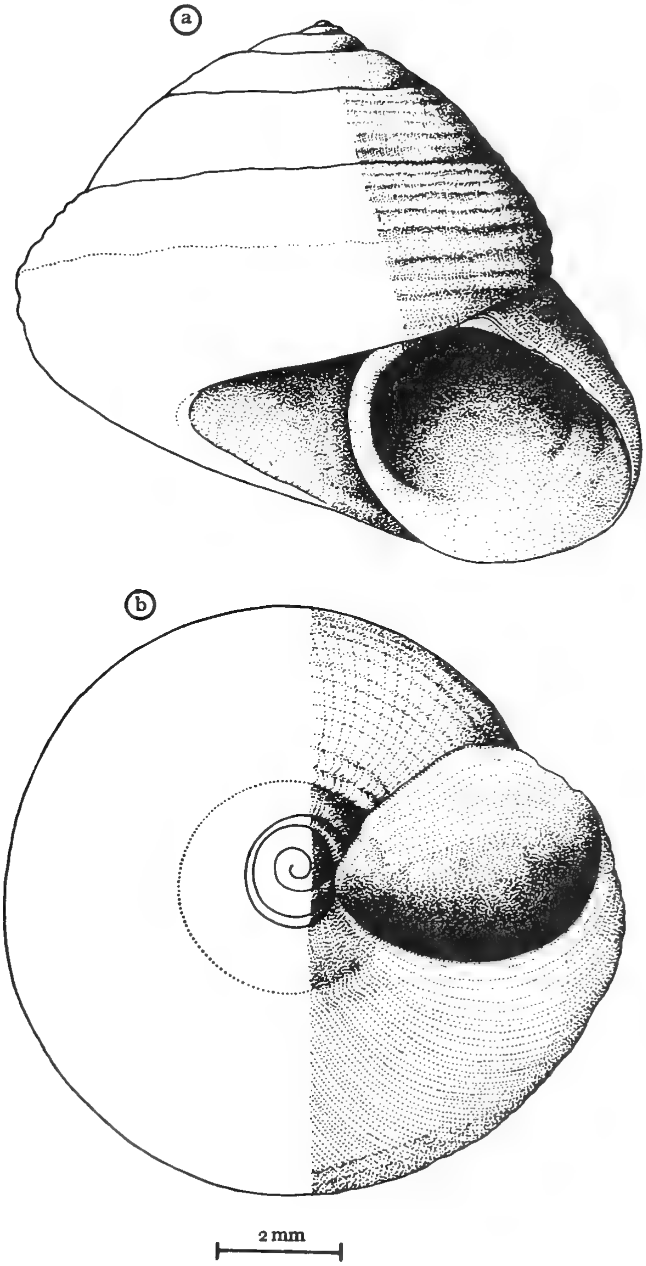


Figure 21

Ostodes ***exasperatus*** (holotype)

a – Shell seen from side b – shell seen from below

in proportion to its length; that of *O.* ***exasperatus*** is thick and heavy. On Upolu, where the 2 species may be sympatric, 86% of *O. savaii* males have short-threaded penes; all *O.* ***exasperatus*** males are long-threaded. On Savaii, where the 2 species are definitely allopatric, they are both mostly short-threaded.

Description of holotype: A young adult male, height 10.2 mm, diameter 11.5 mm, spire angle 85°, H/D ratio 0.88. Whorls $5\frac{7}{8}$, decoiling slowly until the last 4 mm of body whorl, when rate increases so that terminal portion of whorl is slightly inset. Turbinate, with slightly indented suture, for first $2\frac{1}{2}$ whorls. Thereafter suture not indented; periphery of each whorl over-lies whorl below very closely, producing a smoothly convex silhouette. First $2\frac{1}{2}$ whorls smooth; succeeding whorls progressively more sculptured. Body whorl with 6 strong, narrow, raised spiral cords on upper palatal surface, 15 somewhat less emphatic spiral cords on lower palatal surface. Innermost spiral cord of ventral surface forms rim of umbilicus, which is open to nuclear whorl. D/U ratio, 2.74. Major sculpture replaced by fine radial growth lines on last 4 mm of body whorl. Aperture sub-circular, diameter 4.5 mm, vertically compressed and slightly appressed to whorl above. Parietal callus thin. Creamy white with brown, deciduous periostracum. Operculum type C-2.

Collected by L. Price on November 20, 1965 at Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to about 540 m elevation, in light upland forest, Savaii, W. Samoa. FMNH 170530.

Range: Savaii, Western Samoa, northwestern uplands. Upolu, W. Samoa, locality unknown.

Material: Upolu; Station unknown (12 specimens, FMNH 153820). Savaii: Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to about 540 m elevation, in light upland forest (17 specimens, FMNH 170531).

Totals: 29 specimens, (12 from Upolu, 17 from Savaii); 14 adult females, 2 juvenile females, 10 adult males, 3 juvenile males.

Remarks: The 2 populations of this species, from the 2 islands, are not exactly alike. They are definitely closer to each other than either one is to anything else, therefore they are kept together. As has been mentioned above, the Upolu population of *Ostodes* ***exasperatus*** reverses the usual condition of sexual dimorphism in the genus by having males that are bigger than females; the Savaii population conforms to the more normal state of having bigger females.

g. *Ostodes* ***llanero*** Girardi, spec. nov.

(Figures 22a, b; 19b; 20d, e)

Diagnosis: Shell broadly turbinate; height of juveniles 6.6 – 6.9 mm {6.7 mm}, diameter 9.0 – 9.8 mm {9.44 mm}

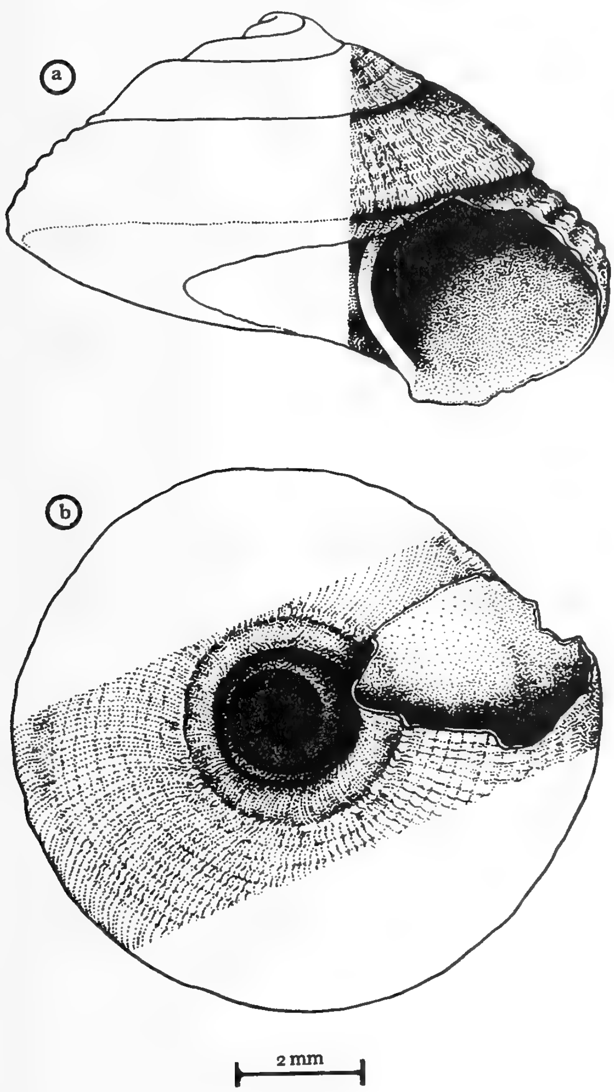


Figure 22

Ostodes ***llanero*** (holotype)

a – Shell seen from side b – shell seen from below

with 5 – 5⅛ whorls. Whorls very slightly convex, almost flat-sided, suture covered by lower margin of whorl above. Body whorl with rounded shoulder. Always wider than high; H/D ratio 0.64 – 0.74 {0.70}. Spire angle 100° – 120° {110°}. Umbilicus very wide, deep, bounded by rim, D/U ratio 1.99 – 2.61 {2.37}. Aperture sub-circular, slightly compressed, appressed to whorl above, and with extension into hollow peri-umbilical rim. Parietal callus very thin. Apex smooth, early whorls usually worn; body whorl with 5 – 7 {6.0} close-set spiral lirae on upper palatal surface, 12 – 15 {13.3} finer spiral traces on lower palatal surface. These strong spirals crossed by numerous exceedingly fine radial threads. Shell thin, fragile, white, almost transparent; periostracum very thin, brown, deciduous. Opercular type C-2.

Hypobranchial gland not well developed in these juvenile specimens. Transverse (posterior) portion begins only slightly to left of midline of mantle; anterior portion also very short. Male has long-threaded penis without bulb; no prostatic sac, no "safety-valve." Female internal common duct moderately short, 0.47 times the diameter of the bursa copulatrix. Pallial common duct very short, with copulatory pore anterior to mantle line by approximately twice its own diameter, and entry of common duct into uterus immediately below copulatory pore, via a vertical slit, slightly wider at top than at bottom, at right angles to long axis of uterus. No papilla, no hypertrophy of edges of slit. Anus shows very slight hypertrophy of both upper and lower edges. Vaginal orifice a very long slit in medial aspect of uterus. Length of slit 4 – 4.5 times diameter of uterus at inner end of slit.

Comparative remarks: *Ostodes* ***llanero*** is a sibling species of *O.* ***exasperatus***. The only differences between juvenile shells of the 2 species (no adults of *O.* ***llanero*** were seen) are the spire angle, which averages 21° wider in *O.* ***llanero***, and the D/U ratio, which averages 0.57 smaller. (Table 6) Otherwise the shells are virtually identical. The anatomy, however, is quite different. Males of *O.* ***exasperatus*** from Savaii tend to have short-threaded penes with sub-terminal bulbs; the single male seen of *O.* ***llanero*** had a long thread without a bulb. The greatest difference

Table 6

Differences between *Ostodes* ***llanero*** and *Ostodes* ***exasperatus*** (juveniles, mixed sex)

	Spire angle			D/U ratio		
	N	Range	Mean	N	Range	Mean
Ostodes ***exasperatus***	5	85° - 90°	89°	5	2.52 - 3.30	2.94
Ostodes ***llanero***	2	100° - 120°	110°	3	1.99 - 2.61	2.37

between the two species is in the female reproductive system. Each section of the common duct in *O.* ***exasperatus*** is approximately twice the length of the corresponding section in *O.* ***llanero,*** each measured in relation to its own bursa copulatrix and copulatory pore. The vaginal orifice in *O.* ***llanero*** is 4 – 4.5 times the width of the uterus at the inner end of the orifice, whereas in *O.* ***exasperatus,*** the vaginal orifice is only 1.6 times the uterine width. Also, in *O.* ***llanero,*** the upper lip of the vagina extends farther forward than does the lower lip, while in *O.* ***exasperatus,*** the lower lip is the longer of the two.

Although its smoothly convex outline, smaller size, and lack of strong radial sculpture set *O.* ***llanero*** apart from the other mid-sized species of *Ostodes,* the most striking difference is the very wide umbilicus. Although there is some overlap of ranges, at 2.37, the mean D/U ratio of *O.* ***llanero*** is considerably lower than that of any other mid-sized species. (Figure 23)

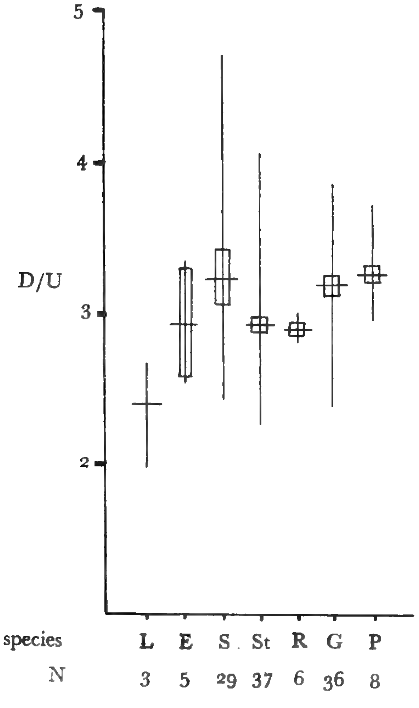


Figure 23

Comparison of D/U ratios of mixed-sex juveniles of 7 mid-sized species of *Ostodes*

E – *O.* ***exasperatus;*** G – *O. garretti;* L – *O.* ***llanero;*** P – *O.* ***plicatus;*** R – *O.* ***reticulatus;*** S – *O. savaii;* St – *O. strigatus*
Vertical line – range of measurements; horizontal line – mean; box – two standard errors on either side of mean

Description of holotype: A juvenile female, height 6.6 mm, diameter 9.78 mm, very broadly turbinate, spire angle 120°, H/D ratio 0.67. Five whorls, decoiling gradually. Almost flat-sided; first 4¼ whorls show very slight rounding of upper portion, then slight concavity, then very sharp periphery which overlies upper portion of lower whorl; sharp periphery changes on body whorl to rounded shoulder at aperture. First 3 whorls smooth. Fourth whorl partly smooth. Upper palatal surface of body whorl with 7 shallow spiral lirae crossing a multitude of very fine radial lines. On lower palatal surface, 13 flat spiral lines, not at all raised, cross many very fine radial lines. Even where shell is badly worn, traces of the spiral lines remain. Sculpture continues unchanged up to aperture. Aperture sub-circular, slightly compressed vertically, slightly appressed to penultimate whorl, slight extension at lower, inner quadrant. Parietal callus very thin. Umbilicus very wide, bounded by rim, open to nuclear whorl. D/U ratio 2.50. Thin, fragile, creamy white, with few remnants of thin, brown, deciduous periostracum. Operculum type C-2.

Collected by L. Price on November 20, 1965, at Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to about 540 m, in light upland forest; Savaii, W. Samoa. FMNH 152991.

Range: Savaii, W. Samoa: northwest foothills and uplands. Altitude range 540 – 600 m.

Material: Station 33, up a survey track at 600 m elevation, approximately 8 km inland from Asau in heavy primary foothill forest (2 specimens, FMNH 152997); Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to 540 m elevation in light upland forest (1 specimen, (holotype) FMNH 152991).

Total: 3 specimens; 2 juvenile females, 1 juvenile male.

h. *Ostodes upolensis* (Mousson, 1865)

(Figures 24a, b; 25a; 26a, b)

Cyclophorus upolensis Mousson, 1865, Journ. de Conch., **13:** 180, 181 – Upolu, Western Samoa.

Cyclophorus (Ostodes) upolensis (Mousson), 1869, Journ. de Conch., **17:** 352 – Upolu.

Ostodes upolensis (Mousson), Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, **1887:** 148 – Upolu; Kobelt, 1902, Das Tierreich, **16:** 157 – Samoa (Upolu); Clench, 1949, Bull. B. P. Bishop Mus., **196:** 12, 13; figs. 3 c, 28 e – Upolu: Latuafara, at 63.8 m elevation; Mt. Vaea; Lake Lanuto'o at 720 m elevation; Maldolelei, at 450 m elevation; Sinaele, at 420 m elevation; Tiavi, at 570 – 660 m elevation. Savaii: Salailua, at 300 – 600 m elevation.

Diagnosis: Shell broadly turbinate, small; height of adults 3.2 – 7.0 mm {4.9 mm}, diameter 2.8 – 8.6 mm {6.2 mm}, with 4⅛ to 5¼ whorls {4⅝}. Some have whorls with rounded shoulders, suture incised; others have smoothly sloping shoulders, very sharp keels, suture not incised. Nearly always wider than high; H/D ratio 0.66 – 1.14 {0.77}. Spire angle, 85° – 110° {98°}. Umbilicus very wide, deep, nearly always sharply margined, but without a bordering rim; D/U ratio 1.62 – 3.77 {2.61}. Aperture round to subcircular, parietal callus not as thick as outer rim. Sculpture of strong spiral lirae and, in about half the adults seen, unobtrusive radial plicae. Body whorl with 5 – 8 {6.3} spiral lirae on upper palatal surface, crossing 15 – 25 {18.0} radial plicae; in about ¼ of adults seen, lower palatal surface showed 2 – 10 {6.0} spiral lirae only, often faint. Cream color, with thin, brown, deciduous periostracum. Opercular type, C-1.

Hypobranchial gland begins at left posterior margin of mantle cavity, runs across to slightly past mid-line, turns and runs forward only a short distance. Both anterior and posterior portions of moderate thickness. Male penis usually long-threaded, without sub-terminal bulb. Usually has both prostatic sac and "safety-valve." Female internal common duct very short, only ⅒ as long as bursa copulatrix is wide. Pallial common duct quite long; copulatory pore down from mantle line 3.5 pore diameters, distance from pore to entry into uterus equal to 6.5 X diameter of copulatory pore. Duct enters uterus via an L-shaped slit, the stem of the L at right-angles to long axis of uterus, the leg of the L pointing forward and having hypertrophied edges. Anus shows considerable hypertrophy of lips, especially on the upper margin. Vaginal orifice a slit on the medio-ventral aspect of uterus, its length approximately equal to uterine width at inner edge of orifice.

Comparative remarks: *Ostodes upolensis* is one of 3 small species in this genus. It occurs in 2 forms, the ordinary, or "stepped" form (Figure 24a) illustrated by Clench (1949: 11; fig. 3c), and a "smooth" form (Figure 24b). The "smooth" form was found only on Upolu, with juveniles at Station 2, and both adults and juveniles at Station 18. No "stepped" shells were found at those stations. Shells of the "smooth" form are slightly smaller than those of the "stepped" form and have a narrower umbilicus. Although males of both forms have long-threaded penes, those of the "smooth" form are very slightly longer, and the vaginal orifice of the females is very slightly smaller. The difference in shape of the 2 forms is caused by a difference in rate of decoiling. The rate is quite slow in the "smooth" form, with each whorl placed well up on the preceding one, and the peripheral carina is extended over the suture, thus producing a smoothly conical silhouette. In the "stepped" form, the rate of decoiling is much faster, each whorl being placed further down the whorl preceding it, and the peripheral carina being almost vertically below the next higher spiral lira, so that the shoulders are rounded. The narrower umbilicus in the smooth form is caused by a very pronounced insetting of the terminal portion of the body whorl under the penultimate whorl (see p. 196). Neither the difference in shape nor the very slight anatomical differences are considered sufficient to warrant separation of the 2 forms.

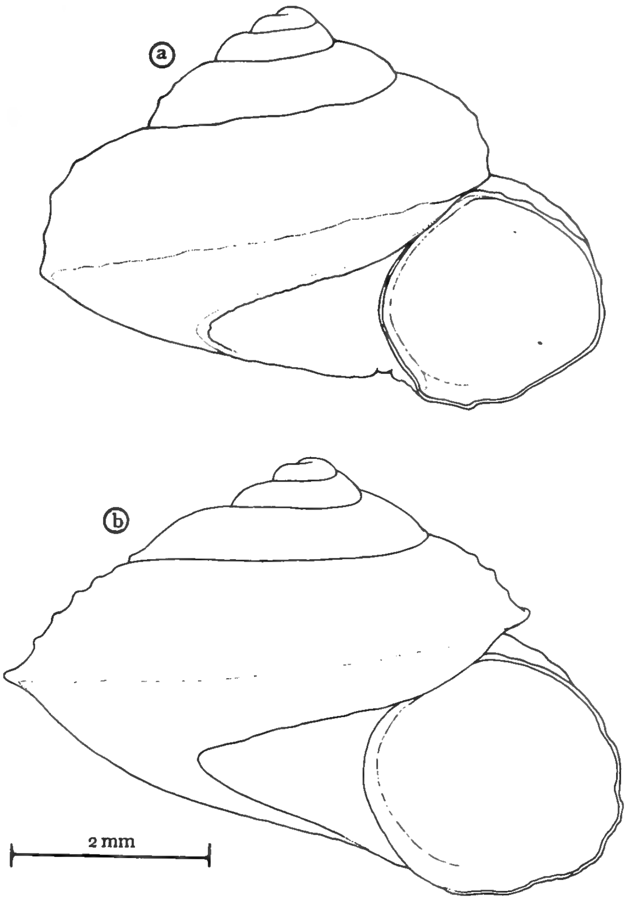


Figure 24

Ostodes upolensis

shell outline: a – "stepped form — b – "smooth" form

Neither form of *Ostodes upolensis* is likely to be confused with another of the small species, *O. cookei. Ostodes upolensis* is quite strongly sculptured, whereas *O. cookei* is the only species in the genus to present a smooth shell surface. The smooth form of *O. upolensis,* however, might be confused with *O. adjunctus,* from Tutuila. Clench's figure of *O. adjunctus* (Clench, 1949: 11, fig. 3b) shows a shell midway in shape between the two forms of *O.*

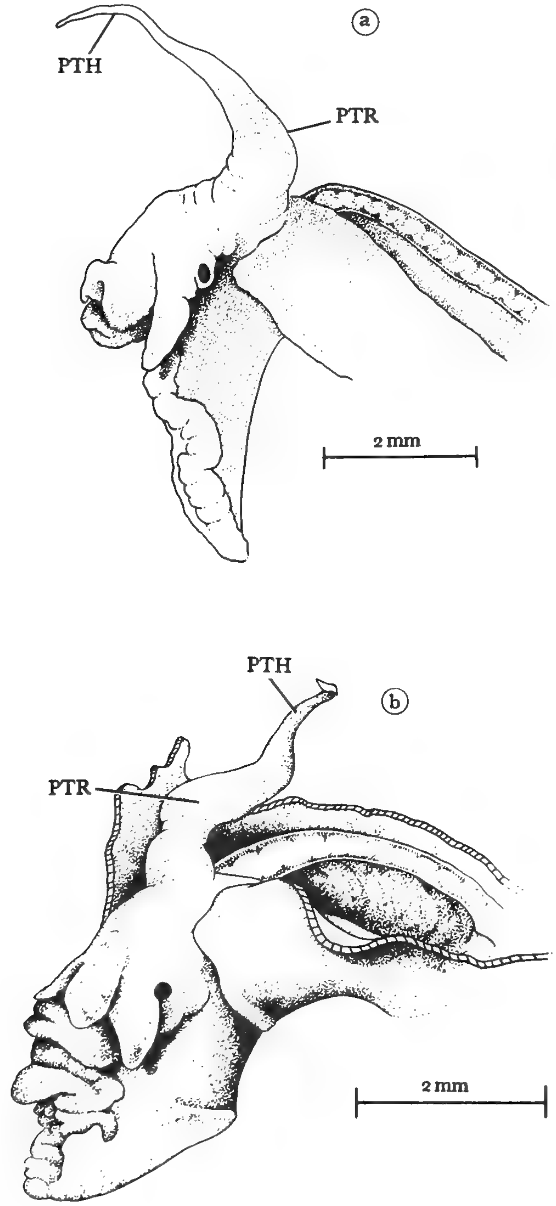


Figure 25

Males of (a) *Ostodes upolensis* and (b) *Ostodes adjunctus*
[for explanation of abbreviations see Appendix on foldout]

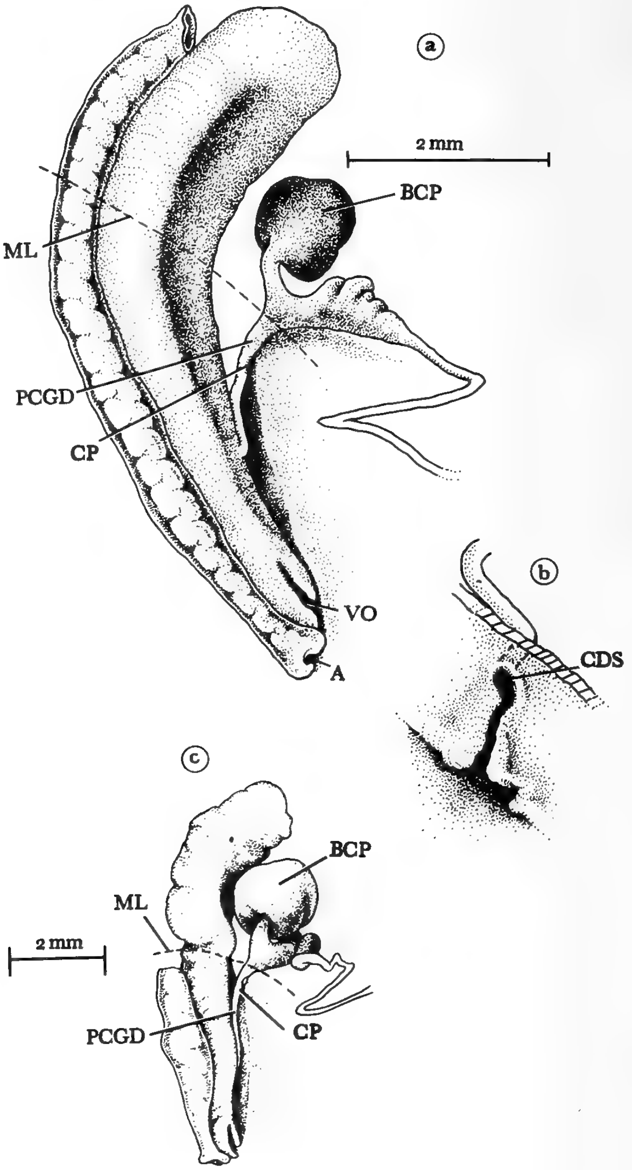


Figure 26

Female reproductive systems of *Ostodes upolensis* and *O. adjunctus*
a – *O. upolensis;* b – *O. upolensis,* entrance of common genital duct into uterus; c – *O. adjunctus*
[for explanation of abbreviations see Appendix on foldout]

upolensis. Mousson's original figure, however (Mousson, 1869: plt. 14, fig. 9) shows a very smoothly conical shell. The 40 shells of *O. adjunctus* available to me are also smoothly conical. Comparison of the "smooth" form of *O. upolensis* with the shells of *O. adjunctus* immediately shows the differences between the two. At the same or a lower whorl count, *O. adjunctus* is larger than *O. upolensis* (Figure 27). The umbilicus of *O. adjunctus* always has a bordering rim, whereas that of *O. upolensis* is rimless. *Ostodes adjunctus* has very strong spiral sculpture on the lower palatal surface, and is entirely lacking in radial sculpture, while in *O. upolensis* ventral sculpture is faint or absent and radials, though unobtrusive, are often present. *Ostodes adjunctus* is the only species of *Ostodes* in which shells that were otherwise clearly adult did not have the terminal portion of the body whorl indented beneath the penultimate whorl; in *O. upolensis,* especially in the smooth form, the indentation is very pronounced. Finally, fully half the shells of *O. adjunctus* examined had a bright red spire, a character never seen in *O. upolensis.*

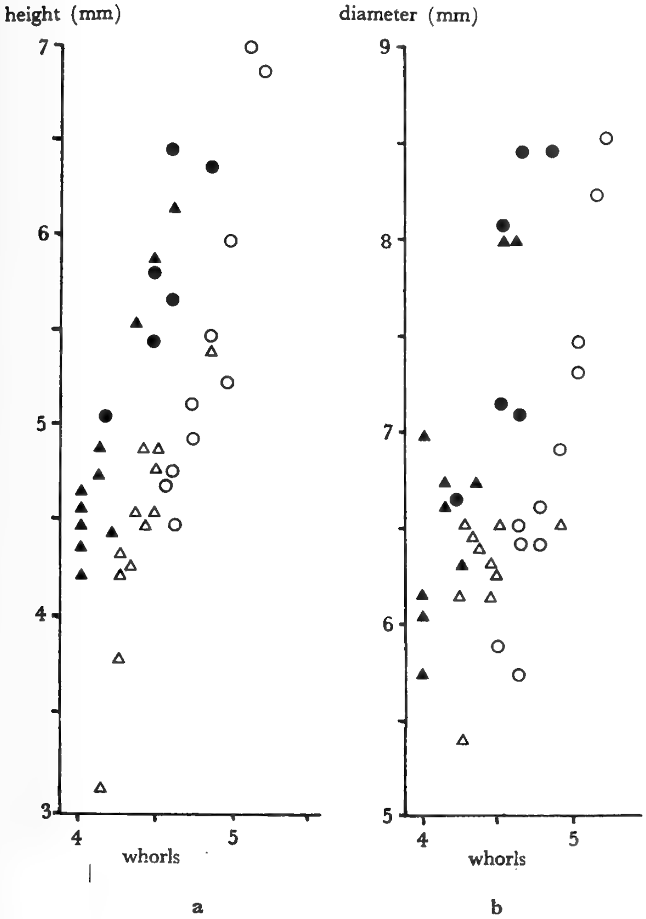


Figure 27

Relationship of whorl-count to size in *Ostodes adjunctus* and *O. upolensis* (both forms together)

a – height/whorls; b – diameter/whorls

▲ – *Ostodes adjunctus,* male ● – *O. adjunctus,* female
△ – *Ostodes upolensis,* male ○ – *O. upolensis,* female

Anatomically, the hypobranchial gland of *Ostodes upolensis* is much larger, especially the posterior portion, than that of *O. adjunctus.* Males of *O. adjunctus* entirely lack the prostatic sac and "safety-valve" so often present in *O. upolensis.* In the female, the pallial portion of the common genital duct is only half as long in *O. upolensis* as it is in *O. adjunctus,* and the vaginal orifice is only ⅔ as long.

Range: Upolu, Western Samoa: southern and northeastern lowlands, central foothills and uplands. Altitude range, 15–750 m.

Savaii, Western Samoa: southwestern lowlands at 150 m elevation.

Material: Savaii: Station 31, 2.2 km in from Salilua, 42 km west of Vailoa, at 150 m elevation, in heavy lowland forest (1 specimen, FMNH 152621); Upolu: Station 2, 1.2 km above Afiamalu seismographic station, on right of road, at 720 m elevation, in disturbed upland forest (4 specimens, FMNH 152710); Station 6, 1.6 km N of Mt. Siga'ele, at 555–570 m elevation, in a forest patch in a gully-pasture area (1 specimen, FMNH 152924); Station 8, 1.2 km above Afiamalu seismographic station, a wide area, including Station 2, on both sides of the road, at 720 m elevation, in mixed to good upland forest (5 specimens, FMNH 152686, 166212); Station 10, Togitogiga, two logging roads toward ocean at 15 m elevation in thinned lowland forest (3 specimens, FMNH 152953); Station 18, foot of Mt. Solaua, between 180–240 m elevation, under a large *Ficus* tree in a banana patch at edge of forest (45 specimens, FMNH 152850, 153026, 153093, 153104, 153169); Station 23, gully to foot of N side of Mt. Siga'ele, at 600–645 m elevation, in mixed to good foothill forest (18 specimens, FMNH 152605, 159170); Station 26, Afiamalu-Lake Lanuto'o track, at 735–750 m elevation, in good to excellent upland forest (1 specimen, FMNH 166211).

Totals: 77 specimens; 11 adult females, 11 adult males, 21 juvenile females, 24 juvenile males, 8 not sexed, 2 empty.

i. *Ostodes adjunctus* (Mousson, 1869)

(Figures 25b, 26c)

Cyclophorus (Ostodes) adjunctus Mousson, 1869, Journ. de Conch., 17: 351–352; plt. 14, fig. 9 – Tutuila.

Ostodes adjunctus (Mousson) Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 148 – Tutuila; Kobelt, 1902, Das Tierreich 16: 153 – Samoa (Tutuila); Clench, 1949, Bull. B. P. Bishop Mus., 196: 11–12; fig.

3b – Tutuila: Fagasa and nearby valley; Pago Pago at 60 – 150 m elevation; Amalau Bay, at 30 m elevation; NW slope on Mt. Pioa, at 180 – 240 m elevation; trail between Olofau and Amouli, at 90 – 120 m elevation; Aua-Afono Trail, at 300 m elevation; Amouli, half-way between Pago Pago and Alofau.

Diagnosis: Shell turbinate; height of adults 4.25 – 6.5 mm {5.25 mm}, diameter 5.75 – 8.5 mm {7.07 mm} with 4 – 4⅞ whorls {4¼}. Upper whorls have rounded shoulder, body whorl has angled shoulder, often with moderate keel. Suture incised. Only 4 adults of 17 examined showed any trace of indentation of terminal portion of body whorl, although the sculptural change marking the onset of maturity was very clear. Always wider than high; H/D ratio 0.67 – 0.83 {0.75}. Spire angle 80° – 110° {92.5°}. Ventral surface flattened. Umbilicus wide and deep, margined with upstanding rim made by innermost ventral spiral lira; D/U ratio 2.50 – 3.89 {3.02}. Aperture almost square in juveniles to round in adults, appressed to whorl above. Parietal wall usually not as thick as outer lip. Early whorls smooth; body whorl with 5 – 6 strong spiral lirae on upper surface, 6 – 8 {6.5} spirals on ventral surface. Ventral spirals nearest umbilicus show the most relief; outer spirals less raised, may be just lines without relief; this may be due to wear. Shell has no radial sculptural elements of any kind except fine, close-set radial growth lines, which dominate shell surface at onset of maturity, when spiral lirae stop very abruptly. Color cream to dirty white except that slightly more than half the specimens seen had intense raspberry red spires for first 1¾ – 3¼ whorls {2¾}. Periostracum deciduous, pale yellow-brown, wears off raised spiral lirae quickly. Operculum types B, C-1.

Hypobranchial gland very small, extending only short distance to left of midline, and running forward hardly at all. Of 11 males examined, 2 had the penis to the right of the cephalic midline; the other 9 had the penis on the cephalic mid-line. Penis of some specimens seems unusually large in proportion to head. Penis usually long-threaded; no sub-terminal bulb, no prostatic sac, no "safety-valve." Prostate squared-off at anterior end, medial corner forming a flap under which vas deferens crosses to penial base. Vas deferens a short, straight tube, not long and convoluted. Female internal common duct very short, only 0.2 times diameter of bursa copulatrix. Pallial common duct quite long: copulatory pore down 2 pore diameters from mantle line, entrance of duct into uterus 16 pore-diameters below pore. Interior aspect of entrance of genital duct into uterus not seen. Anus points straight forward, with considerable hypertrophy all around edges. Vaginal orifice a long, narrow slit on medio-ventral aspect of uterus, its length 1.4 times diameter of uterus at inner end of orifice.

Comparative remarks: *Ostodes adjunctus* resembles *O. upolensis* more closely than it does any other species of *Ostodes;* see comparative remarks under *O. upolensis.* The sculptured shells of *O. adjunctus* could not possibly be confused with the smooth shells of *O. cookei,* and of course all the other species of *Ostodes* are too large to be confused with *O. adjunctus.*

Range: Tutuila, American Samoa: eastern portion of island: south-east coast and ridge of central mountains. Altitude range, 60 – 330 m.

Material: Station AS-1; steep hillside, banks of Visa Stream, 11 km E of Pago Pago at 60 m elevation (6 specimens, FMNH 181005/6). Station AS-2; steep ridge slope, at 90 m elevation, Siliataligalu Point, 11.7 km E of Pago Pago (27 specimens, FMNH 181011/N). Station AS-7; main ridge above Fagaitua, 18.4 km E of Pago Pago, at 210 – 240 m elevation (4 specimens, FMNH 181059/4). Station AS-9; crest of main ridge, left side of Aua-Afono track, 4.8 km E of Pago Pago, at 300 – 330 m elevation (4 specimens, FMNH 181078/4).

Totals: 40 specimens: 11 adult males, 5 adult females, 8 juvenile males, 12 juvenile females, 4 empty.

j. *Ostodes cookei* Clench, 1949

Ostodes cookei Clench, 1949, Bull. B. P. Bishop Mus., **196:** 10 – 11; fig. 3 a – Upolu, Western Samoa: Tiavi, at 630 m elevation.

Diagnosis: Adult shell, turbinate, small, height 5.6 mm, diameter 7.5 mm, with 4⅞ whorls. Whorls with rounded shoulders, suture incised. Last ⅛ of body whorl inset under penultimate whorl. Wider than high, H/D ratio 0.74. Spire angle 110°. Aperture round, holostomatous, parietal wall as thick as outer lip. Umbilicus very wide, deep, open to nuclear whorl, D/U ratio 2.34, bounded by a rim that protrudes over the umbilicus but is not raised from the lower palatal surface of the shell. Shell cream color with very thin yellowish iridescent periostracum which is peeling off in spots and is missing from most of the spire and the last ⅜ of body whorl. Where periostracum is missing, shell shows pitting and wear. Shell appears entirely smooth to naked eye. Magnification of 16X reveals texture of many fine radial growth lines, crossed on upper palatal surface of body whorl only by 7 spiral lines, which are just lines, not raised at all from shell surface. Spiral lines stop and growth lines coarsen for last ⅛ whorl. Operculum not seen.

Anatomy not seen.

Comparative remarks: *Ostodes cookei* approaches the other two small *Ostodes, O. upolensis* and *O. adjunctus* in size and general configuration, but is smooth while the other two species are strongly sculptured. Although *O. tiara* and *O. garretti* may produce a secondarily smooth surface due to wear, the difference in size makes confusion of either with *O. cookei* impossible.

Range: Tiavi, Upolu, Western Samoa, at 630 m elevation.

Material: Tiavi, Upolu, at 630 m elevation (1 specimen, MCZ 140504, paratype).

k. *Ostodes tiara* (Gould, 1848)

(Figures 7a, b; 8a, b)

Cyclostoma tiara, Gould, 1848, Proc. Boston Soc. Nat. Hist., 2: 204 – Upolu, Western Samoa; Gould, 1852, U. S. Explor. Exped., 12: 101; Gould, 1860, U. S. Explor. Exped., Atlas of Shells, plt. 8, figs. 116, 116 a.

Cyclophorus tiara (Gould), Gray, 1852, Cat. Phan., p. 58 – Upolu; Pfeiffer, 1852, Mon. Pneum., 1: 84 – Upolu; Reeve, 1862, Conch. Icon., XIII: sp. 76, plt. 16, fig. 76 – Upolu; Mousson, 1865, Journ. de Conch., 13: 179 – Upolu to 1,000 m elevation.

Cyclophorus (Ostodes) tiara (Gould), Mousson, 1869, Journ. de Conch., 17: 350 – Upolu.

Ostodes tiara (Gould), Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887: 146–147 – Upolu; Kobelt, 1902, Das Tierreich, 16: 156, 157; Clench, 1949, Bull. B. P. Bishop Mus., 196: 17, 18; fig. 7b – Upolu, near Tiavi, at 630 m elevation.

Diagnosis: Shell broadly turbinate, very large; height of adults 12.5–16.2 mm {14.3 mm}, diameter 16.0–22.5 mm {18.2 mm}, with 4⅝–5⅝ whorls {4⅞}. Whorls moderately carinate, suture not incised. Always wider than high; H/D ratio 0.71–0.86 {0.79}. Spire angle 100°–110° {107°}. Umbilicus usually wide, deep, margin smoothly rounded without bordering rim. D/U ratio 2.58–4.13 {3.37}. Aperture round, holostomatous, slightly appressed. to whorl above, parietal callus of adults almost as thick as outer rim of aperture. Sculpture usually worn off early whorls. Body whorl with 9–20 {15.4} spiral lirae on upper palatal surface, 5–11 {8.0} spiral cords on lower palatal surface. On juvenile shells, 14–23 {16.8} radial threads cross the spiral lirae on the upper palatal surface; radial threads may persist in a few adults, but most adults show no radial sculpture except fine growth lines. Color whitish. Periostracum thin, brown, adherent. Opercular types A-2 and C-3.

Hypobranchial gland very thick and heavy posteriorly; anterior portion narrow but dense nearly to front of mantle cavity. Males have two different types of penis, as discussed under anatomy of reproductive system of genus. Of 9 adult males measured, 6 had "smooth" penes – long threaded, without bulb (Figure 7a) while 2 had "bumpy" penes – short threaded, with "knuckle," "collar," and bulb (Figure 7b). (Of juvenile males examined, 4 had "smooth" penes, while 3 had "bumpy" penes.) Both types of penis can be associated with a "safety-valve," but a prostatic sac is rare in an animal with a "smooth" penis. Female internal common duct short, its length equal to only half the diameter of the bursa copulatrix. Pallial common duct very long; copulatory pore anterior to mantle line by twice its own diameter, and distal portion of duct equal to 26 times the diameter of the copulatory pore. Unlike all other species, *Ostodes tiara* has the entrance of the common duct into the uterus on the posterior (ventral) surface of that organ, near the lateral margin (all other species have the entrance on the medial margin of the

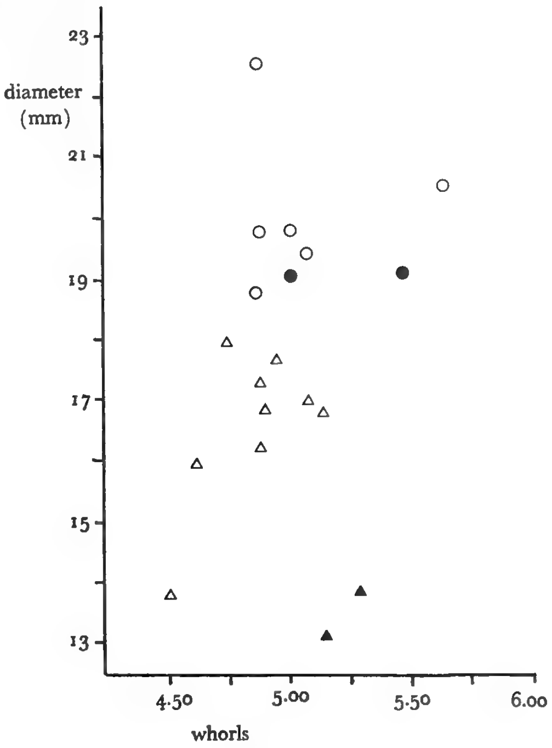


Figure 28

Relationship of whorl-count to diameter in *Ostodes tiara* and *Ostodes garretti*

△ – *Ostodes tiara,* male
○ – *Ostodes tiara,* female
▲ – *Ostodes garretti,* male
● – *Ostodes garretti,* female

uterus). Several attempts to expose the interior papilla of the common duct for drawing failed, and its shape and orientation remain unknown. Anus shows considerable hypertrophy of edges all around. Vaginal orifice a relatively small triangular slit, apex inward, its length only ⅘ the diameter of the uterus at inner end of orifice.

Comparative remarks: *Ostodes tiara* is more similar to *O. garretti* than to any other species. For similarities and differences between the two, see comparative remarks under *O. garretti.*

Range: Upolu, Western Samoa: western, west-central, and north-eastern foothills; central uplands. Altitude range, 180 – 750 m.

Material: Upolu: Station 1, 1.6 km above Afiamalu seismographic station, to left of road, at 720 m elevation, in heavy upland forest to edge of sago-palm swamp (1 specimen, FMNH 152804); Station 2, 1.2 km above Afiamalu seismographic station, to right of road, at 720 m elevation, in disturbed upland forest (4 specimens, FMNH 152700, 153088); Station 8, 1.2 km above Afiamalu seismographic station, wide area on both sides of road, including Station 2, at 720 m elevation, in mixed to good upland forest (19 specimens, FMNH 152663, 152877); Station 16, SE peak Tafua-Upolu, at 480 m elevation, in undisturbed foothill forest (1 specimen, FMNH 152760); Station 18, foot of Mt. Solaua, between 180 – 240 m elevation, under a large *Ficus* tree in banana patch at edge of forest (1 specimen, FMNH 153175); Station 19, rim of Lake Lanuto'o crater, at 750 m elevation, in heavy upland forest (4 specimens, FMNH 152812, 152835); Station 26, Afiamalu-Lake Lanuto'o track, at 735 – 750 m elevation, in good to excellent upland forest (11 specimens, FMNH 152672, 152676, 152718, 166210); no locality given (1 specimen, FMNH 153819).

Totals: 42 specimens; 9 adult males, 10 adult females, 7 juvenile males, 5 juvenile females, 5 not sexed, 6 empty.

1. *Ostodes garretti* Clench, 1949

(Figures 7c; 8c, d)

> *Ostodes garretti* Clench, 1949, Bull. B. P. Bishop Mus., **196**: 18; fig. 7 c – Savaii: Siavao-Auola, at 150 – 600 m elevation; Salailua, from sea level to ± [sic] 780 m.

Diagnosis: Shell broadly turbinate, very large; height of adults 10.8 – 14.8 mm {12.5 mm}, diameter 13.2 – 19.2 mm {16.3 mm} with 5 – 5½ whorls {5½}. Whorls carinate, suture only slightly incised. Always wider than high; H/D ratio 0.69 – 0.82 {0.78}. Spire angle 100° – 115° {108°}. Umbilicus deep, wide; sometimes smoothly rounded, sometimes with bordering rim. D/U ratio 2.9 – 3.5 {3.19}. Aperture round, holostomatous, slightly appressed to whorl above, parietal callus of adults as thick as outer rim of aperture. Sculpture worn off early whorls. Body whorl with 7 – 15 {10.0} raised spiral cords on upper palatal surface, 11 – 13 {12.0} less prominent spiral cords on lower palatal surface. No radial sculpture except fine lines of growth. Color whitish, periostracum very thin, deciduous, brownish-yellow. Opercular types A-1, A-2, C-2.

Hypobranchial gland surprisingly small for so large a snail. Posterior portion very short, extending hardly at all to left of midline. Anterior portion runs well forward but is very narrow. Male penis with long thread without sub-terminal bulb; prostatic sac present; "safety-valve" may or may not be present. Female internal common duct very short, its length equal to only ¼ diameter of bursa copulatrix. Copulatory pore very close to mantle-line, but distal portion of pallial common duct very long – eight times diameter of copulatory pore. Entry of common duct into uterus is via a round elevated papilla inside medial aspect of uterus. Anus a simple tube without hypertrophy of lips, pointing forward. Vaginal orifice a long triangular slit, apex inward, its length equal to 2.6 times diameter of uterus at inner end of orifice.

Comparative remarks: *Ostodes garretti* is closely related to *O. tiara. Ostodes garretti* averages slightly smaller both in absolute measurement and in diameter for a given whorl count (Figure 28). Its umbilicus is very slightly wider in proportion to the diameter of the shell. The anatomical differences are considerably greater than those of the shells. *Ostodes garretti* has a much smaller hypobranchial gland. Its males have long-threaded penes without bulbs, whereas *O. tiara* males either have long-threaded penes without bulbs, or short-threaded, "bumpy" penes with bulbs. The greatest differences between the 2 species are found in the female reproductive system. Although both distal pallial common ducts are long, that of *O. tiara* is proportionately more than 3 times as long as that of *O. garretti,* and terminates on the ventral aspect of the uterus near the lateral margin, while *O. garretti*'s common duct enters the uterus in the usual way on the medial margin. Although *O. garretti* females have far less anal hypertrophy than do females of *O. tiara,* their vaginal orifices are proportionately more than 3 times as large as those of the latter species.

Range: Savaii, Western Samoa; northwest uplands.

Material: Station 34, approximately 8 km SE of Asau along main road, then inland about 8 km along a track to 540 m elevation in light upland forest (8 specimens, FMNH 152986).

Totals: 8 specimens; 2 adult males, 2 adult females, 4 empty shells.

Remarks: *Ostodes garretti* has a more pronounced sexual dimorphism in size than any other member of the genus. At almost exactly the same whorl count, males averaged 21% shorter and 29% narrower than females.

C. The Generic Affinities of *Ostodes*

Tielecke's Poteriidae includes all of the helicoid cyclophorid genera from Central America, South America, the West Indies, and the South Pacific. Of the Pacific genera, *Ostodes* is the only Polynesian taxon, and it is restricted to Western and American Samoa (Clench, 1949: 3, 4). Names and distributions of the other nominate Pacific genera are: *Gassiesia* Clench, 1949 from New Caledonia and the Loyalty Islands; *Dublonia* Clench, 1949, *Paramia* Clench, 1949, and *Kondorhaphe* Clench, 1949 from the Caroline Islands; *Gonatorhaphe* Möllendorff, 1898 from the New Hebrides and Fiji; and *Fijiopoma* Clench, 1949 from Fiji. All of these genera were established on the basis of shell and opercular differences. Except for a few radular notes by Clench (1949: 48) and data in Solem (1959: 182–185; plt. 6, figs. 9, 10) on *Gonatorhaphe* genitalia, no anatomical information has been recorded. During this study, radulae from *Gassiesia* and *Gonatorhaphe* were examined with the aid of a scanning electron microscope (pp. 201-203), and their shells, anatomy, and opercula were examined rather briefly, as presented below. I have not seen any anatomical material from the Caroline Islands or from Fiji.

The Neotropical genera placed by Thompson (1969) in the subfamilies Neocyclotinae and Crocidopominae are included by Tielecke in the Poteriidae. Examples of a representative species from that group, *Mexcyclotus panamensis* (Da Costa, 1903), were dissected so that their reproductive systems could be compared with those of *Ostodes*. The results of those dissections are also presented below, along with a brief discussion of the shell and operculum. The radula of *Mexcyclotus* was not seen.

Specimens of too few genera have been dissected to permit any statements concerning phylogeny within the Poteriidae.

1. *Gonatorhaphe* spp.

Shell broadly turbinate, wider than high. Dorsal surface shows fine, close-set spiral lirae; some individuals also show broad, rounded, radial plicae. The ventral surface is smooth in the specimens from Espiritu Santo, and there is usually no umbilical rim. The spiral lirae are retained on the ventral surface of the specimens from Aoba, and the umbilicus has a rim. Aperture round, lip simple. Operculum with 2 layers. Lower layer smooth, shiny on under (attachment) side, thick centrally, diminishing to the vanishing point toward the edges. Upper layer of thin, transparent corneous material with an iridescent sheen for first 1.5–2.5 volutions, then becomes much thicker and heavily impregnated with calcium, the volutions lying immediately next to each other, their upper surfaces all on same plane. Result is a smooth-surfaced, thick, polygyrous, calcified operculum, with a small, non-calcified, depressed central area.

Radula similar to that of *Ostodes.*

Male reproductive system: Testis occupies entire volume of approximately first whorl; similar to that of *Ostodes* – branched digitiform alveoli, arranged in a single plane, feed into one collecting duct on the columellar side. Collecting duct runs forward as seminal vesicle. Prostatic lumen not seen. Anterior tip of prostate truncated, without sac or "safety-valve." Vas deferens a closed tube.

Penis quite variable. In specimens from Espiritu Santo, penis is standard short-thread type, without sub-terminal bulb; approximate thread-to-trunk ratio, 1/2.8. In specimens from Aoba, thread is shortened into a terminal appendage, triangular in cross-section and with sharp edges, usually found folded back acutely against trunk. Mean ratio, appendage to trunk, 1/3.8. Two specimens were seen in which the appendage was longer, with less acute edges, and looked more like a true thread; both had ratios of appendage to trunk of 1/2. One individual was seen which had both a closed vas deferens and an open groove on the posterior side of the penis. The groove did not run from prostate to penis, but began above penial base, ran up posterior side of penis, and ended just before distal end of penis folded over to become terminal appendage. The groove ran in a straight line, with the loosely coiled vas deferens running along beside it, plainly visible through the integument.

Female reproductive system: Ovary occupies columellar side of visceral mass for approximately first whorl. It is cylindrical in shape, composed of loose white granules, not macroscopically organized, enclosed in an encapsulating membrane which tapers anteriorly and becomes the oviduct.

Oviduct passes down columellar side of body almost to mantle line, then reflexes upon itself, passes upward, and makes another 180° turn into seminal receptacle. Oviduct throughout is thicker than the oviduct of *Ostodes,* and upon entry into seminal receptacle, it appears to be coiled, rather than folded, within the encapsulating membrane. Bursa copulatrix similar to that of *Ostodes,* its duct joining that from seminal receptacle in same way to become common genital duct. Common genital duct heavier than that of *Ostodes;* runs anteriorly along medial margin of uterus. Copulatory pore hidden by a flap of tissue extending from medial margin of uterus to floor of mantle cavity and forming a sort of roof over upper part of infra-uterine channel, which is quite short. Entry of common duct into uterus is via an elevated papilla shaped like an inverted heart. Uterus bi-lobed, as in *Ostodes*. Vaginal orifice a triangular slit on medio-ventral aspect of uterus, just below anus, which shows moderate hypertrophy of upper lip.

Material: Baukaharijitoa above Dunduy, at 450 – 600 m elevation, Aoba, New Hebrides, FMNH 109423; Tasmalune, Espiritu Santo, New Hebrides, FMNH 109424.

2. *Gassiesia* sp.

Shell broadly turbinate, wider than high. Dorsal surface with spiral lirae, larger, wider-spaced, and more prominent than those of *Gonatorhaphe*. No radial plicae. Spirals continue on ventral surface, but umbilicus has no rim. Aperture round, lip simple. Operculum is similar to that of *Ostodes*: corneous, transparent with an iridescent sheen, polygyrous. Radula is enough different from that of *Ostodes* to be useful in differential diagnosis (pp. 202-203).

Male reproductive system: Testis occupies whole volume of approximately first whorl. Composed of branching, digitiform alveoli, arranged along outer aspect of collecting tubule on columellar side of whorl. Alveoli much finer, more closely packed, with fewer branches than in *Ostodes*. Collecting tubule becomes seminal vesicle, runs forward to enter prostate. Whole proximal tip of prostate turned under, with seminal vesicle entering at very tip. Prostatic lumen in turned-under portion is Y-shaped, stem of Y pointing medially, arms pointing laterally. Anterior to the turn in the main part of the prostate, the stem of the Y disappears, and the lumen is U-shaped, as in *Ostodes*. Anterior end of prostate shows small sac, but no "safety-valve." Vas deferens a closed tube. Penis long-threaded, thread/trunk ratio 1/1. In adult specimens, thread appears to have begun as a flattened ribbon which twisted upon itself repeatedly, so that its former edges show as two white lines, spiraling down from beginning of taper to very tip of thread. Thread of juveniles more rounded, lacks the white lines.

Female reproductive system: Ovary as in *Ostodes*: a tapering cylinder filled with loose white granules, enclosed in encapsulating membrane which continues forward as oviduct. Seminal receptacle as in *Ostodes*, with oviduct folded in one plane within encapsulating membrane. Bursa copulatrix very fragile, very thin-walled. Common duct as in *Ostodes*, but hidden for most of its length by a thin membrane running from medial aspect of uterus to mantle cavity floor, turning most of infra-uterine channel into a sort of tunnel. Copulatory pore not located. Uterus with two lobes as in *Ostodes*. Anus shows great hypertrophy of edges, especially of upper edge. Vaginal orifice a fairly large triangular slit, apex in, on medio-ventral aspect of the uterus.

Material: Station N.C. 15, near Thiem, N. E. New Caledonia. (juveniles, FMNH 159215): Station N.C. 28, W side of main range, ⅓ up, 6.4 km E of Ouegoa, N.E. New Caledonia. (adults, FMNH 159358). Both collected by Laurie Price, 1967.

3. *Mexcyclotus panamensis* (Da Costa, 1903)

(Figures 29, 30)

Shell broadly turbinate, wider than high. Surface smooth, showing only very fine radial growth lines. Periostracum adherent, thin, yellow to yellow-brown. Aperture round, lip simple. Operculum with 2 layers, as in *Gonatoraphe*, but of more complicated structure. Under layer smooth, shiny, thick in center, thinning towards rim, from which it protrudes as "cellophane edge." Upper layer corneous, transparent, with iridescent sheen for approximately first three volutions; then become heavily impregnated with calcium. Each subsequent volution is L-shaped, with the central half lying flat, the outer half standing up almost vertically from the surface. Flat half of calcified layer is overlaid by thin layer of iridescent, corneous material, extending upward from the under layer. Result is a small central corneous area, surrounded by upstanding, calcified lamellae, which are separated from each other by flat areas with a layer of calcium under a layer of corneous material. Environmental debris collects in interlamellar areas, where it seems to buttress the very brittle vertical lamellae against breakage.

Radula not seen.

Male reproductive system (Figure 29): Testis fills approximately first whorl of visceral hump. Internal structure not observed. Seminal vesicle runs down columellar side of body, enters prostate directly, without reflexing upon itself as it does in *Ostodes*.

Prostatic lumen approximately L or T shaped, the short arm or arms lying medio-dorsally, and the main part of the lumen running transversely. Prostate terminates in narrow, tapered tip, nearer to the base of the penis than in *Ostodes*. There is neither a prostatic sac nor any "safety-valve." Instead of a closed vas deferens, there is an open seminal groove, running from tip of prostate to base of penis. Penis on cephalic midline, well behind tentacles; short, thick, rugose, tapering abruptly into a slender neck surmounted by a narrowly-ovate, pointed terminal appendage. The seminal groove runs up the posterior sur-

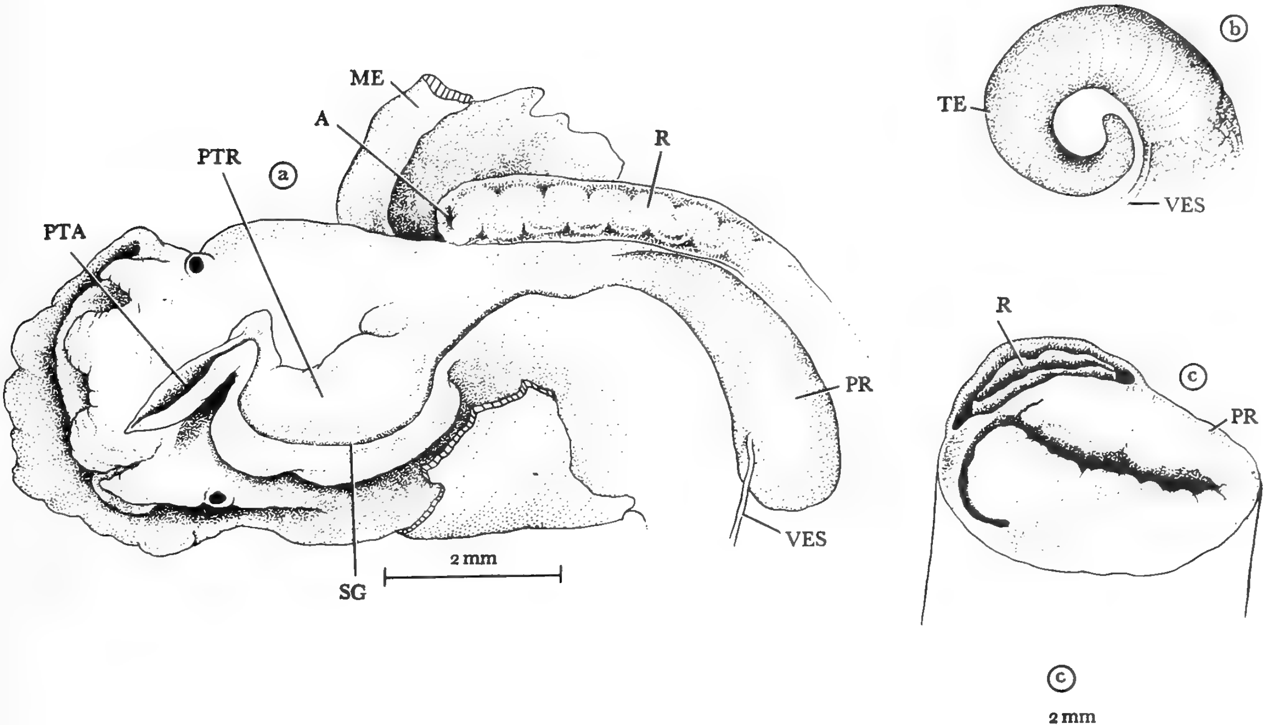


Figure 29

Mexcyclotus panamensis, male

a – viewed from above; b – testis; c – cross-section of prostate
[for explanation of abbreviations see Appendix on foldout]

face of the penis and across the neck, then opens into a deep, narrow, sharp-edged, spoon-like depression on the upper surface of the appendage. No important differences in proportion of terminal appendage to length of trunk were observed in the individuals examined.

Female reproductive system (Figure 30): Two forms of ovary have been observed in this species. One resembles the ovary of *Ostodes*: It occupies the columellar side of the visceral hump for approximately one whorl, and consists of white granular tissue, held together by an encapsulating membrane. It is shaped like a slender sausage, tapering at the ends, with the encapsulating membrane continuing anteriorly as the oviduct. Although ovaries with the second form occupy the same position, they are differently shaped: on the side away from the columella, 4 to 5 short, heavy, clavate alveoli protrude into the tissues of the digestive gland. The alveoli are arranged one behind the other, in a single row. Although one or two may be bifurcated near the outer end, the alveoli are not otherwise branched. This form of ovary seems to be made of the same sort of tissue as the smooth, sausage-like form; if the encapsulating membrane is torn, the white ovarian granules fall out loosely.

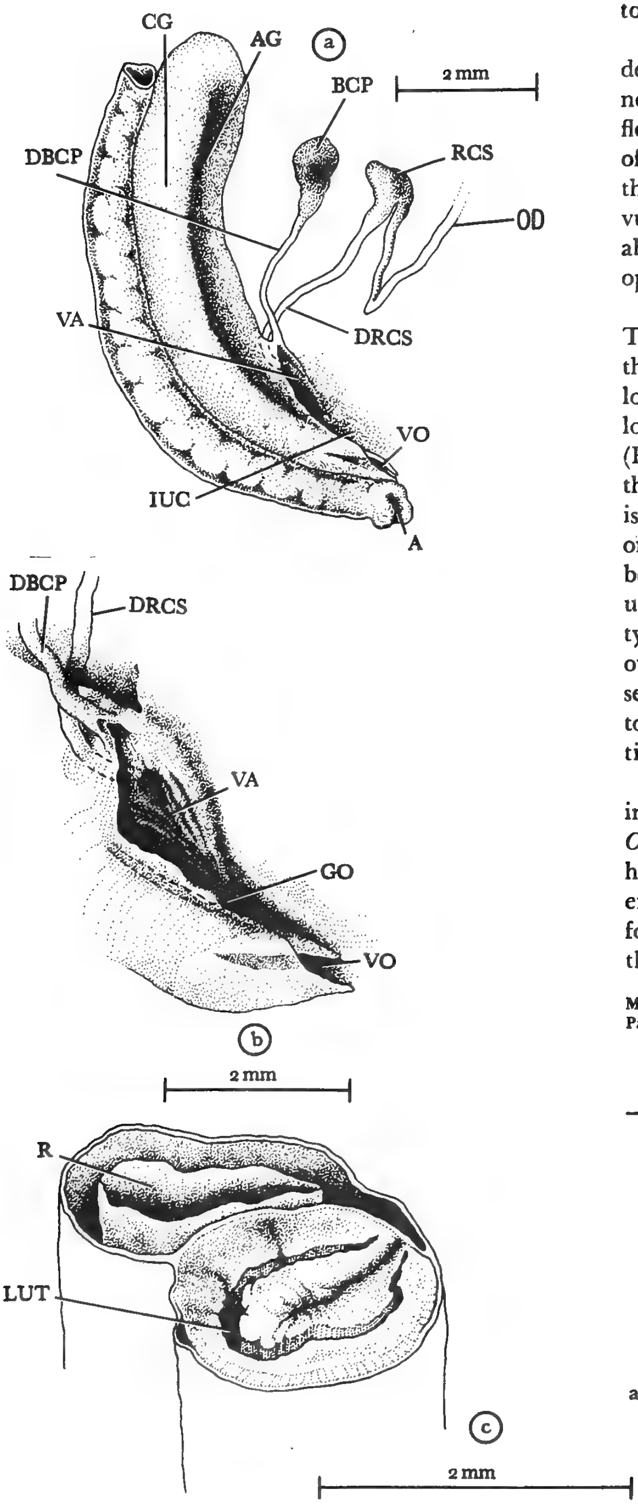
As in *Ostodes,* the oviduct runs down the columellar side of the body, becoming somewhat thickened and convoluted, then forms a seminal receptacle. A small sac-like structure, the bursa copulatrix, lies nearby, but is not directly connected to the seminal receptacle, and there is no common genital duct. Instead, both the receptacle and the bursa have long, slender ducts which open separately into a diamond-shaped vulval area, which is located at the proximal end of a very short infrauterine channel. The duct from the bursa copulatrix opens directly into the upper corner of the vulval area, while the duct from the seminal receptacle crosses behind the bursal duct and makes a right-angled turn before entering the vulva distal to the entrance of the bursal duct.

The floor of the diamond-shaped area is thrown into deep, longitudinal rugae. Its medial margin is a prominent rounded ridge on the right side of the mantle-cavity floor; its lateral margin, and probably roof, is a thin flap of tissue extending medially from the lower portion of the medial aspect of the uterus. At the distal end of the vulvar diamond is a very small hole, hidden in and probably capable of being closed by the vulvar rugae, which opens into the uterus.

Two types of uterine structure have been observed. The first is similar to that seen in *Ostodes* (Figure 9c): there are two lobes, arranged in tandem, with the ventral lobe tan in color and of rather denser tissue than the dorsal lobe, which is creamy white and soft. The second type (Figure 30c) has a U-shaped lumen, which is continuous throughout the length of the organ. No bi-lobed structure is present, nor is there any differentiation in tissue texture or color in different parts of the uterus. There seems to be no correlation between type of ovary and type of uterus, both types of ovary having been found with each type of uterus. Although it is possible that the clavate ovary is a development of advancing age (the smooth types seen were smaller than the clavate examples), it is difficult to see how the uterine type could change during the lifetime of the individual.

The placement of the anal orifice and vaginal opening in *Mexcyclotus* is similar to the general arrangement in *Ostodes,* except that in the Central American snail, the hypertrophy of the anal orifice is horseshoe-shaped, open end up, and the vaginal orifice is partly obscured by a fold of tissue extending posteriorly and downward from the anterior tip of the upper vaginal lip.

Material: La Barca, Finca Lerida, at 1695 m elevation, Boquete, Chiriqui, Panama, FMNH 84611, 84621.



(← adjacent column)

Figure 30

Mexcyclotus panamensis, female

a – reproductive system, with bilobed uterus; b – greatly enlarged view of vulvar area; c – cross-section of uterus with U-shaped lumen

[for explanation of abbreviations see Appendix on foldout]

4. DISCUSSION

Gonatorhaphe and *Gassiesia* are obviously closely related to *Ostodes*. The shells of the 3 genera are very similar, using the same basic sculptural elements in varying combinations and with varying degrees of emphasis to produce shells of different appearance. The method is the same as that used between species in *Ostodes,* but the differences are greater between genera than between species.

In regard to operculum and radula, *Gassiesia* has a transparent, corneous operculum, very like *Ostodes'*. *Gassiesia*'s teeth, however, differ enough from those of *Ostodes* to be a useful diagnostic character. The radula of *Gonatorhaphe* is very similar to that of *Ostodes,* but the operculum, with its upper calcareous layer overlying the corneous under-layer, is quite different from the simple, corneous *Ostodes* operculum.

Although the anatomical differences between the 3 genera are greater than the differences between species of *Ostodes,* the differences all involve small details. In the male, *Gonatorhaphe*'s internal and prostatic arrangements are almost identical to those of *Ostodes,* the only differences being in the thread or terminal appendage of the penis. In *Gassiesia,* the testicular alveoli are smaller, more numerous, and less branched than are those of *Ostodes*. The upper end of the prostate is slightly different, and the penial thread is twisted. The 3 genera are alike, however, in having a closed vas deferens, and all have the penis on the dorsal mid-line of the head, behind the tentacles, the prescribed Poteriid position.

The situation is similar in the female systems. The questions of whether the oviduct folds or coils within the seminal receptacle; whether the wall of the bursa copulatrix is thick or thin; whether the infra-uterine channel is open or roofed-over, long or short – are all essentially minor points. All 3 genera have the oviduct, seminal receptacle, and bursa copulatrix opening into the uterus through a common duct – in accordance with Tielecke's definition of the Poteriidae.

Mexcyclotus is more strongly differentiated from *Ostodes* in shell, operculum, and anatomy, than *Gonatorhaphe* or *Gassiesia*. The shell is smooth and unsculptured; only *O. cookei* of the twelve species of *Ostodes* is smooth. *Mexcyclotus* has a heavily calcified operculum, in contrast to the corneous operculum of *Ostodes*.

In the male, the testis is smaller in *Mexcyclotus* than in *Ostodes;* the prostatic lumen is L- or T-shaped, rather than U-shaped; there is an open seminal groove rather than a closed vas deferens, and a spoon-like penial appendage rather than a smooth thread. Nevertheless, the penis is in the normal midcephalic position for the Poteriidae, and the cited differences do not seem to me to be sufficient cause for removing *Mexcyclotus* from Tielecke's family.

The differences between *Mexcyclotus* and *Ostodes* are much greater in the female reproductive system than in the male system. In *Ostodes,* there is a common duct serving the oviduct, seminal receptacle, and bursa copulatrix; in *Mexcyclotus,* the ovary and seminal receptacle enter the vulval diamond through one duct, while the bursa copulatrix enters through another. Can this be reconciled with Tielecke's definition of the family based on a single common duct? I think so. The basic requirement is that the **products** from the 3 organs enter the **uterus** together, and they do – they meet and mingle among the rugae of the vulval area and drain, together, through the single hole at the bottom of the vulva, into the uterus. This is a larger difference than exists between *Ostodes* and *Gassiesia* or *Gonatorhaphe,* but the functional pattern is the same.

For comparison, let us consider the situation in 2 of the other families. In the CYCLOPHORIDAE, either the oviduct, receptacle and bursa all enter the uterus separately (*Cyclophorus*), or the oviduct enters through the receptacle, and the bursa enters separately (*Spirostoma*). In the male, the penis is located behind the right tentacle, and there is an open sperm groove. In the MAIZANIIDAE, the penis has an open sperm groove and an accessory flagellum, and is located behind and at the same height as the right tentacle. The seminal receptacle drains into the oviduct, and the oviduct and bursa each have a very long, individual duct leading to the uterus. The differences between these families and the POTERIIDAE are much greater than the differences among the genera within the Poteriidae which I have examined. The differences I have seen between *Ostodes, Gonatorhaphe, Gassiesia,* and *Mexcyclotus* are certainly ample to differentiate them as genera, but they are not important enough to warrant separation at the family level.

VII. DESCRIPTIVE GEOGRAPHY

A. Location

Samoa consists of a group of islands at the westernmost extremity of Polynesia, lying between 11° and 15° S latitude, and longitudes 169° to 173° W. In Western Samoa, two small islands, Apolima and Manono, lie between two major islands, Upolu and Savaii. Savaii is the largest of the islands, being 50 km long by 28.8 km wide, with a maximum altitude of 1784 m. Upolu, lying southeast of Savaii, is also 50 km long, but only 17.3 km wide, reaching an altitude of 1170 m. Tutuila, the largest island of American Samoa, lies SE of Upolu. Tutuila is much smaller than Upolu, having an area of only 133.1 km. Matafao Peak, on Tutuila, reaches an elevation of 643 m. Manua lies E of Tutuila, and is smaller; Rose Island lies E of Manua, and is smaller yet. Swain Island lies N and slightly W of Tutuila. The main Samoan islands are the tips of submerged volcanos, and volcanic activity has been observed as recently as 1911 (Schroth, 1971: 291).

B. Climate

The climate of Samoa is hot and wet. The southeast tradewinds flow along both sides of the high central longitudinal axis of the islands, dropping their moisture fairly evenly on the north and south sides. Only the northwest tips of the islands can be said to have an actual dry season. For the rest of the area, the mean annual rainfall ranges from 312½ cm to more than 500 cm. The rainfall increases with increasing altitude, the central uplands receiving more moisture than the coastal lowlands. The temperature falls an average of 1.5° C for every 300 m increase in altitude (Wright, 1963: 30), with the mean annual temperature ranging from 25.5° C in the coastal lowlands to 15.5 in the central highlands of Savaii.

C. Vegetation

The lowlands, from sea-level to about 225 m, used to be covered with a forest whose canopy reached 30 – 39 m high. Scattered remnants of this forest remain at present. The foothill forests, extending from approximately 225 – 540 m elevation, have a canopy height approximately the same as the lowland forests. They have more tree ferns, and the trunks of the canopy trees are adorned with mosses and lichens. The upland forests, from 540 – 1200 m, have still more tree ferns and ground ferns, more mosses and lichens, and an ample representation of monocotyledonous trees and epiphytes, including orchids and perching lilies. There is a 2½ – 7½ cm layer of leaf litter on the ground. An extensive list of the various species of trees, shrubs, and vines found in these classes of forest may be found in Wright (1963: 35 – 38).

VIII. ZOOGEOGRAPHY

A. Spatial

1. DISTRIBUTION ON ISLANDS

During their field work in 1965, Dr. Solem and Mr. Price collected on both major islands of Western Samoa. The material available to me from Savaii came from a wide crescent including the western, southern, and eastern sections of the island. From Upolu, there was material from both north and south coasts, the easternmost tip, and the central and west-central uplands and foothills. The altitude range was from sea-level forest to 750 m. The material from Upolu contained individuals belonging to seven species: *Ostodes gassiesi, O. plicatus, O.* ***reticulatus,*** *O. savaii, O.* ***exasperatus,*** *O. upolensis,* and *O. tiara.* No examples of *O. cookei* were present in this collection. From Savaii came individuals belonging to six species: *O. gassiesi, O. savaii, O.* ***exasperatus,*** *O. garretti, O.* ***llanero,*** and *O. upolensis,* of which only one specimen was found. In 1975, Mr. Price collected on Tutuila, American Samoa, and sent back examples of *O. strigatus* and *O. adjunctus* from almost the whole length of the main central ridge, as well as the southern coast, taken at altitudes of 60 m to 390 m.

Four species of *Ostodes* from Western Samoa occur on both islands: *O. gassiesi, O. savaii, O.* ***exasperatus,*** and *O. upolensis. Ostodes plicatus, O.* ***reticulatus*** and *O. tiara* (as well as *O. cookei*) have been found only on Upolu, while *O. garretti* and *O.* ***llanero*** are known only from Savaii. Although *O. strigatus* has been reported from Western Samoa by older authors, it is now known only from Tutuila, as is *O. adjunctus.*

2. SYMPATRY

Over both islands of Western Samoa, the distributional pattern is one of sympatry. Of 30 collecting stations, only 9 yielded but one species. Of these 9 stations, 4 had only one or two specimens, and hence yield no significant data. In regard to the other 5 single-species stations, the 4 on Upolu yielded from 6 to 26 shells each, while Station 32, Savaii, gave 25 examples of *Ostodes savaii.* Each of the other 21 stations gave at least 2 species; while no station on Savaii had more than 3 species in residence, Stations 2 and 26 on Upolu each had 5 species, and Stations 8 and

18 each had 6 species. Station 18 was the best sampled and most intensively collected of any station visited.

In contrast, the situation on Tutuila seems to be one of complete allopatry. Stations 1, 2, 7, and 9, all on the eastern portion of the island, had only *Ostodes adjunctus*, while Stations 6, 10, 19, and 20, all on the western portion of the island, had only *O. strigatus*.

3. RELATIVE ABUNDANCE

A total of 914 specimens were present in the material available to me. Of these, 526 came from Upolu, 195 were from Savaii, and 193 were from Tutuila. These numbers should not be taken as indicative of the true populations of the islands, however; Savaii is much larger than Upolu, but had less than half as many collecting stations, visited in a much shorter time. Tutuila was quite thoroughly collected. As stated above, 2 species were found on Tutuila, 7 species were found on Upolu, and 6 on Savaii,

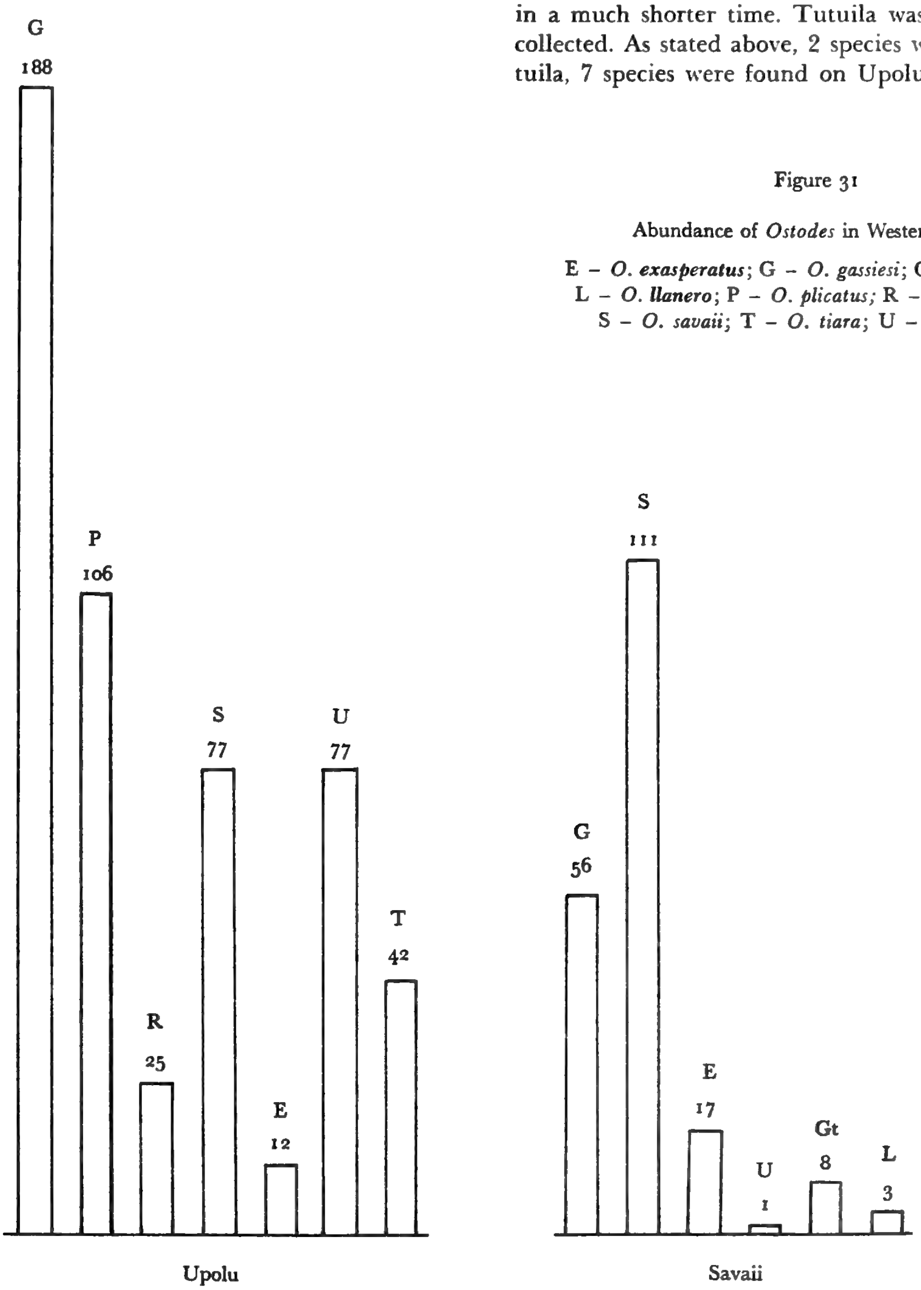


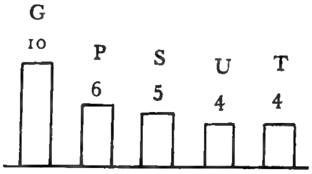
Figure 31

Abundance of *Ostodes* in Western Samoa

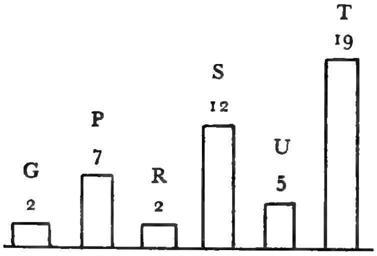
E – *O. exasperatus*; G – *O. gassiesi*; Gt – *O. garretti*; L – *O. llanero*; P – *O. plicatus*; R – *O. reticulatus*; S – *O. savaii*; T – *O. tiara*; U – *O. upolensis* with 4 species being found on both Upolu and Savaii. These species were not collected in equal numbers, however. Taking all islands together, the most abundantly collected species is *Ostodes gassiesi,* with 244 specimens, followed by *O. savaii* (188), *O. strigatus* (153), and *O. plicatus* (106). The 3 species from Western Samoa were taken in different proportions on the two islands. On Upolu. 1.8 times as many specimens of *O. gassiesi* (188) were collected as of the next most abundant species, *O. plicatus* (106); *O. savaii* follows with 77 specimens. On Savaii, there are almost exactly twice as many *O. savaii* (111) as *O. gassiesi* (56), and *O. plicatus* does not occur at all. Figure 31 shows the varying abundance of the several species from both islands.

Within a given species in Western Samoa, the pattern of distribution seems to include both clustering and scattering. Each of the species which was found in any considerable number (more than 25 specimens) showed one to 4 stations having perhaps a dozen or more specimens, with the other individuals of the species divided, singly or in small groups, among a large number of different stations. For example, the 77 specimens of *Ostodes savaii* taken from Upolu came from 13 different stations, only 2 of which yielded 12 or more specimens, and 6 of which gave 3 shells (of this species) or less.

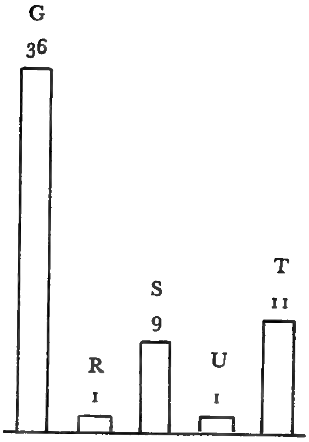
As mentioned above, 4 stations on Upolu had 5 or 6 species living together. The relative abundance of species



Station 2



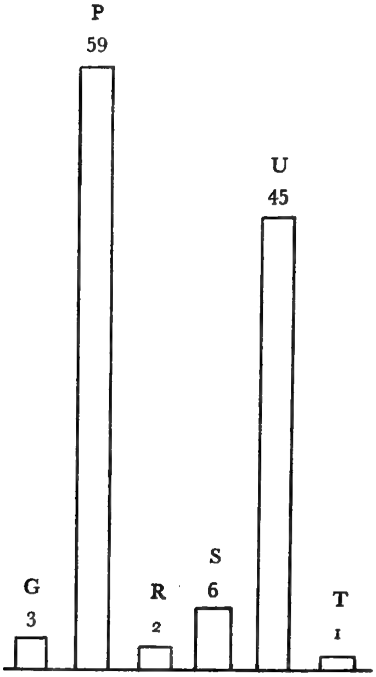
Station 8



Station 26

Figure 32

Composition of sympatric populations of *Ostodes* on Upolu [Species designations as in Figure 31]



Station 18

at these stations is shown in Figure 32. Station 2 (5 species, 29 individuals) is an area on the right side of a road, 1.2 km above Afiamalu seismographic station, at 720 m elevation, in disturbed upland forest. Station 8 (6 species, 47 individuals) includes Station 2 in a wider area of mixed to good upland forest on both sides of the road. The mean annual rainfall for these two stations is 437½ – 500 cm. Station 26 (5 species, 58 individuals) is on the Afiamalu-Lake Lanuto'o track, at 735 – 750 m elevation, in good to excellent upland forest. It receives more than 500 cm of rain annually. Station 18 is at the foot of Mt. Solaua, between 180 and 240 m elevation, under one large *Ficus* tree in a banana patch at the edge of the forest. The mean annual rainfall is 375 – 437½ cm. From this station, 116 individuals were obtained, belonging to 6 species. Dr. Solem has told me that this fig tree was an unusually rich collecting area, and was the only station at which he and Mr. Price made an attempt to "get everything."

It is interesting to note that at Stations 26 and 18, one or 2 species are dominant, with the other 4 represented by only a few individuals. At stations 2 and 8 the species are more evenly represented. The latter 2 stations represent larger sampled areas which probably included more microhabitats than the first 2 stations which were, respectively, a small remnant forest patch and a single huge fig tree.

B. Ecological

1. EFFECTS OF ENVIRONMENTAL DIFFERENCES

The principal environmental influence on land prosobranchs is moisture supply. Rainfall in Samoa is orographic, with higher altitudes receiving greater amounts of rainfall than lower elevations. Degree of moisture retention is controlled primarily by the vegetation cover, with heavy forest retaining moisture at ground level longer than open forest or cleared areas. *Ostodes* was collected only in areas with heavy tree cover (Solem, personal communication). Although specimens were taken in areas having different soil types, these stations also differed in rainfall regimes, and the relative importance of soil type and moisture supply could not be assessed. It is not known whether *Ostodes* obtains calcium through its plant food or by making use of free calcium in the soil.

The influence of a dry season on opercular type has already been mentioned (pp. 200-201). As stated there, specimens of *Ostodes savaii* from Station 32, Savaii (which receives a mean annual rainfall of 312.5 – 375 cm and has a more pronounced dry season than other stations) had thick opercula of a different type than individuals of the same species from areas which receive more rain, more evenly distributed through the year. That correlation did not hold for Upolu. Wet area-dry area differences have also been found in the shells and in the male anatomy, and these latter differences do hold for both Upolu and Savaii.

Specimens of *Ostodes savaii* from Station 32, Savaii, when compared with all other shells of the same species from the same island, prove to be smaller at the same whorl count (Figure 33). They are from 0.6 to 1.7 mm shorter, and up to 0.8 mm narrower. Additionally, although the males still have short-threaded penes, the threads are not quite as short as those of snails from more regularly moist areas. Males from Station 32 have a mean thread-to-trunk ratio of 1/3.2; short-threaded males from wetter areas have a mean ratio of 1/4.6 (Table 7). The

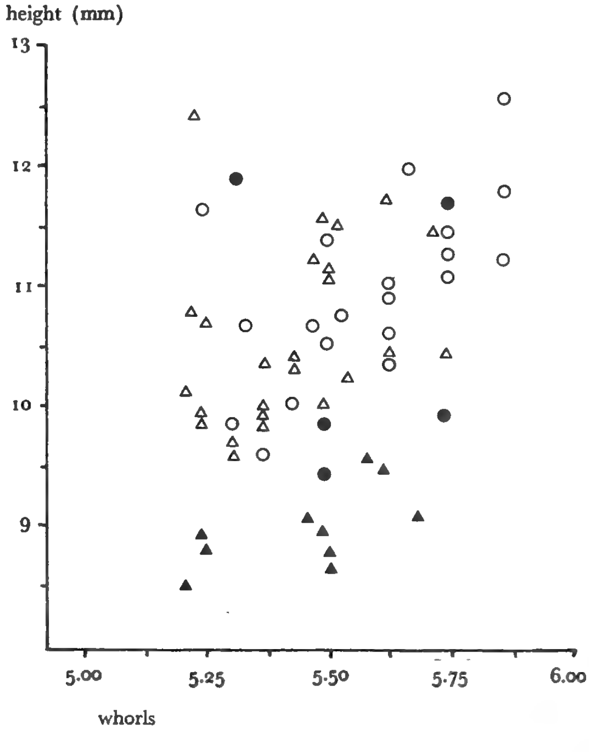


Figure 33

Effect of moisture on size in *Ostodes savaii* on the island of Savaii
▲ – males, Station 32 (dry area) ● – females, Station 32
△ – males, all other stations ○ – females, all other stations

Table 7

Effect of a Dry Season on Penial Thread-to-Trunk Ratio in Short-Threaded Males

Species	Island	Station	N	Range	Mean ± S.E.M.
Ostodes savaii	Savaii	32 (dry)	10	1/1.7 - 1/ 4.5	1/3.18 ± 0.28
		all other	19	1/1.7 - 1/10.0	1/4.38 ± 0.62
Ostodes gassiesi	Upolu	dry cluster	10	1/2.3 - 1/ 4.0	1/3.07 ± 0.17
		all other	26	1/1.7 - 1/10.0	1/4.11 ± 0.39

total length of the penis is the same in both wet and "dry" areas; only the proportion of thread to trunk changes with the climate.

On Upolu, there is a cluster of collection stations (Stations 5, 7, 14, 16, 17) which has the same climate as Station 32 on Savaii. Specimens of *Ostodes gassiesi* from the "dry cluster," when compared with individuals of the same species from areas without a dry season, tend to be smaller at the same whorl count (Figure 34). Males from these stations, like the "dry area" males from Savaii, have less-short penial threads (mean ratio 1/3) than do males from wetter areas (mean ratio 1/4) (Table 7).

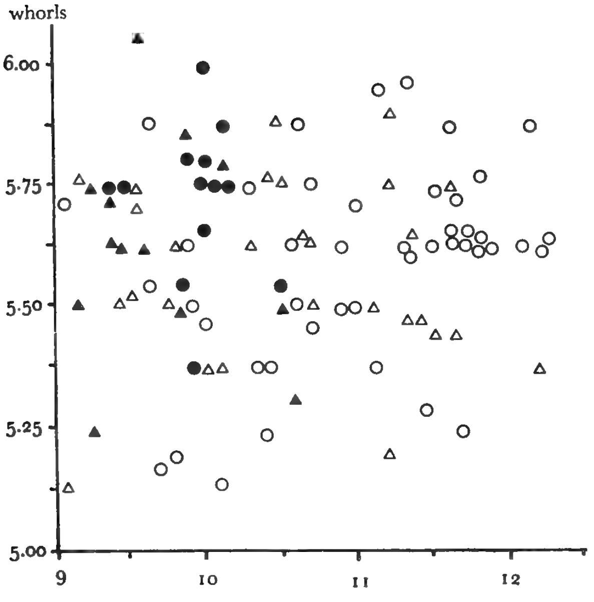


Figure 34

Effect of moisture on size in *Ostodes gassiesi* on Upolu

▲ – males from "dry cluster" ● – females from "dry cluster"
△ – males, all other stations ○ – females, all other stations

As important as the amount and regularity of rainfall, is what happens to the rain after it hits the ground. If a large amount falls, but runs off or evaporates quickly, it has much less value than a retained lesser amount. Therefore, the amount of vegetation – the density of the canopy and understory – is very important; the denser the cover, the more moisture will be retained, and the more favorable conditions will be for snails. This principle can be illustrated by a comparison of adult female *Ostodes gassiesi* from Station 2, Upolu, with adult female *O. gassiesi* from Station 19, Upolu. Both stations are in the upland forest, and both have the same type of climate, receiving from $437\frac{1}{2}-500$ cm of rain per year, with no dry season. They differ, however, in that Station 19 has just average cover, while that of Station 2 is unusually lush. The effect of the increased cover is to make the moisture supply not necessarily more abundant, but less fluctuating in terms of ground-level near-saturation. The results are very apparent; at the same whorl-count, females from Station 2 are 9.3% taller and 8.7% wider than females from Station 19. Table 8 shows the results of a Student's *t* Test, which demonstrates that the size difference is really significant, and not just an artifact of collecting.

2. EFFECTS OF SYMPATRY

Sample size and distribution were such that comparisons of sympatric with allopatric populations were extremely difficult. In species with one good-sized allopatric population, individuals sympatric with other species were usually so scattered that meaningful statistical analysis was impossible. Indeed, there was only one instance in which I had both sympatric and allopatric populations of workable size: *Ostodes plicatus* from Upolu. *Ostodes plicatus* lives by itself at Station 39, and shares Station 18 with 5 other species. Comparison of 5 adults from Station 39 with 32 adults from Station 18 is shown in Figure 35; the

Table 8

Correlation Between Shell Size and Density of Vegetation in Adult Female *Ostodes gassiesi* from Upolu

	Station 2:N=8 dense cover Mean ± S.E.M.	Station 19:N=9 average cover Mean ± S.E.M.	"t" with 15 d.f.	Significance
Height (mm)	12.55 ± 0.338	11.38 ± 0.159	2.283	> .98
Diameter (mm)	11.89 ± 0.093	10.86 ± 0.118	6.764	> .999
Whorls	5.616 ± 0.055	5.619 ± 0.055		

snails from the allopatric population are all larger than those from the sympatric population. Perusal of fragmentary data on other species suggests that "larger when allopatric" may be the general rule in *Ostodes,* but it is impossible to be sure. As to the reason for the larger size of individuals in an allopatric population, it may be that *Ostodes* require a trace element that is in short supply, but no specific information is available.

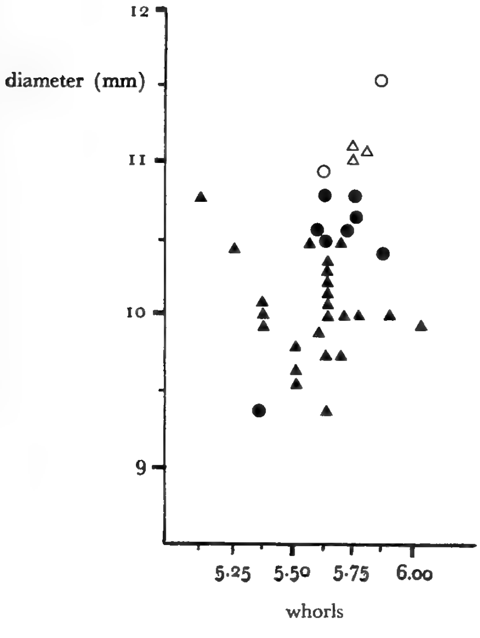


Figure 35

Effect of sympatry on size in *Ostodes plicatus* on Upolu

△ – males from Station 39 (allopatric); ○ – females from Station 39

▲ – males from Station 18 (sympatric); ● – females from Station 18

The only anatomical difference that may be related to sympatry has already been mentioned (on p. 228). The penial thread of *Ostodes* ***exasperatus*** is long in the Upolu population, which may be sympatric with *O. savaii,* a short-threaded species. On Savaii, where the two species are known only from allopatric populations, *O.* ***exasperatus*** has a short penial thread. No other instances of differences in thread length between sympatric and allopatric populations were noted, and no consistent differences in the female reproductive system were found.

3. SPECIES SELF-RECOGNITION MECHANISM

Species-specific recognition features in the terminal genital organs are well-known in pulmonate land-snails. The differences in sympatric European helices have been known for more than a century (Schmidt, 1855), and extensive differences in Pacific Basin endodontids exist (Solem, 1976), but this phenomenon has not, to my knowledge, been reported in terrestrial prosobranchs. Tielecke (1940), Morrison (1955), and Thompson (1967, 1969) studied the reproductive anatomy of Pacific and Middle American cyclophorids, but were concerned with generic and family relationships. Rarely did they deal with sympatric taxa, and they did not mention any possible species-recognition characters.

As has been mentioned previously (p. 242, Figures 31–32), the prevailing distributional pattern of *Ostodes* in Western Samoa is one of sympatry. One of the purposes of this investigation was to discover, if possible, the species isolating mechanism that enables as many as 6 different but closely related species to live together in a small area without losing their identities.While the actual isolating factors are unknown, I believe that the most important factor in species recognition by the snails is the structural differences found in the pallial reproductive organs: the penial thread-to-trunk ratio in the male, and the shape and orientation of the anus and vaginal orifice as well as the location of the copulatory pore in the female. Figure

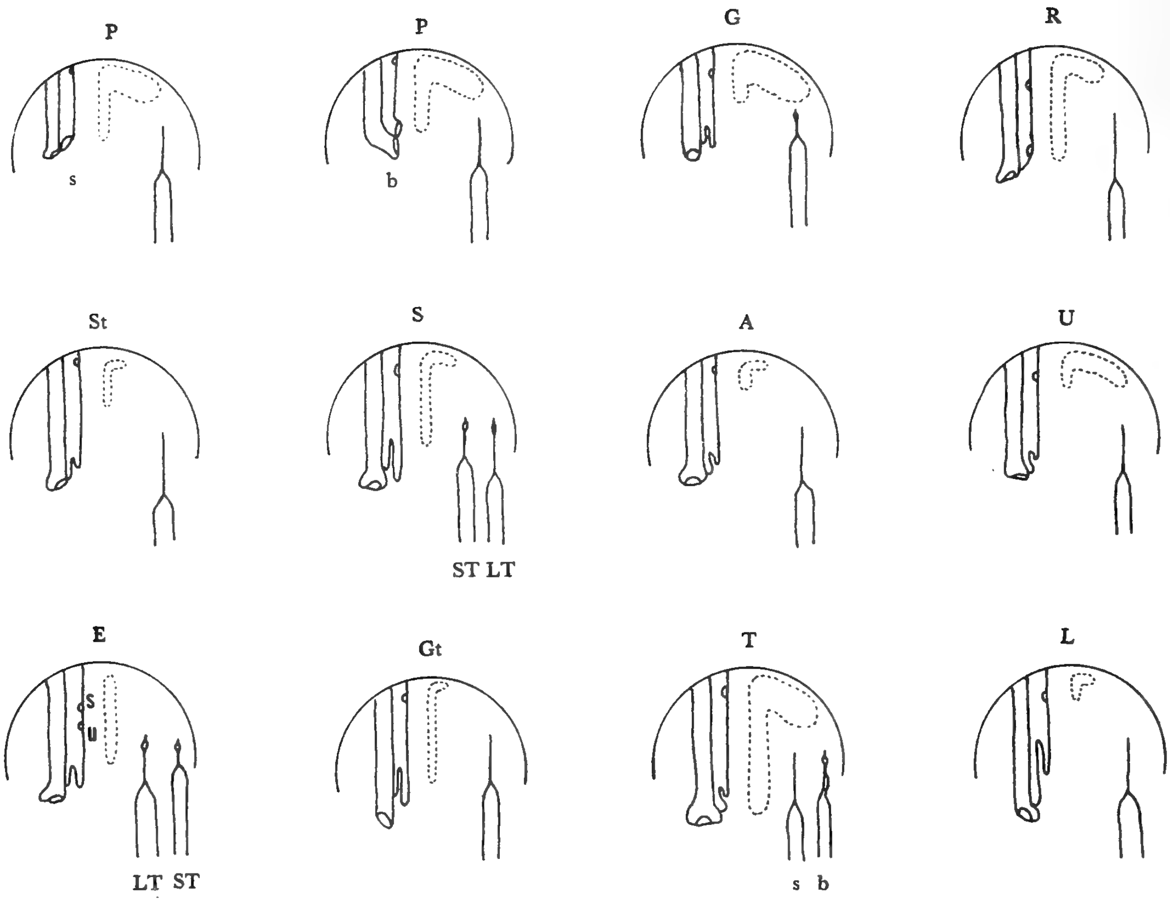


Figure 36

Arrangement of pallial genital organs and hypobranchial gland in female *Ostodes*, with corresponding penis types, by species

A – *Ostodes adjunctus*: penis as shown, 82%; none with bulbs
E – *Ostodes exasperatus*: LT (long thread) penis - 100% Upolu males, 33% Savaii males, 25% with bulbs; ST (short thread) penis - 67% Savaii males, 67% with bulbs
G – *Ostodes gassiesi*: penis shown, 95%; 58% with bulb
Gt – *Ostodes garretti*: as shown, both specimens, no bulbs
L – *Ostodes llanero*: one specimen, no bulb
P – *Ostodes plicatus*: b – vagina and anus bent medially, 80%; s – vagina and anus straight, 20%; penis as shown, 97%, no bulbs
R – *Ostodes reticulatus*: penis as shown, 100%, no bulbs
S – *Ostodes savaii*: ST (short thread) penis, 86%; LT (long thread), 14%; 50% have bulb
St – *Ostodes strigatus*: penis as shown, 100%, no bulbs
T – *Ostodes tiara*: s - "smooth" penis, 67%, none with bulb; b - "bumpy" penis, 33%, all with bulbs
U – *Ostodes upolensis*: penis as shown, 83%, no bulbs

36 shows diagrams of the typical arrangement of the mantle cavity in the female of each species, along with the appropriate penial type. The hypobranchial glands are included in the diagrams; although the secretion of this gland has not been demonstrated to have any sexual significance, its configuration is species-specific, and may possibly be an additional factor in the species-recognition mechanism.

From the diagrams, it can be seen that the onus of recognition falls sometimes on the male, sometimes on the female. A female of *Ostodes plicatus,* for example, could easily distinguish between a male of her own species (long thread without a bulb) and a male of *O. gassiesi* (short thread, probably with a bulb). She might, however, have difficulty in distinguishing a male of *O. plicatus* from a male of ***O. reticulatus*** (both with long, bulbless threads). The male in question, however, could easily distinguish between a female of *O. plicatus* (copulatory pore at extreme rear of mantle cavity, vaginal orifice a largish, round hole, both vagina and rectum probably bent medially at a sharp angle) and a female of ***O. reticulatus*** (copulatory pore well down from rear wall of the mantle cavity, vaginal orifice a smallish oval hole, vagina and rectum pointing straight ahead). Although matings between different species of *Ostodes* are probably physically possible, I doubt that they occur; if they begin, I doubt that they proceed beyond the exploratory stage. The configurations of the terminal genitalia are so distinctively species-specific that mis-mated pairs undoubtedly quickly recognize unlikeness and desist.

C. Patterns of Diversity

Twelve species are now recognized in the genus *Ostodes.* Their recognition was made possible by a correlation of shell characters with anatomical features. Although the snails probably differentiate like from unlike on the basis of the pallial anatomy alone, human observers must consider both shell and anatomy in identifying to the species level. Size, shape and proportions of the shell as well as the occurrence and relative prominence of sculptural elements will serve to identify *O. adjunctus, O. upolensis,* and *O. cookei,* but the identities of the other species are very difficult to establish positively without reference to the anatomy. There are several sets of sibling species in the genus: *O. plicatus* and *O. gassiesi; O. tiara* and *O. garretti; O. strigatus* and ***O. reticulatus;*** *O. savaii* and ***O. exasperatus;*** and ***O. exasperatus*** and ***O. llanero,*** at least as juveniles. In each of these sets, the conchological differences, while present and consistent, are relatively small-scale, and may well be obliterated in an old, worn shell. The differences in the pallial anatomy are of much greater magnitude, and should always be relied on in cases where identification by shell alone is somewhat doubtful. If a shell is empty as well as badly worn, it may well be impossible to decide to which species of a sibling pair it belongs though the pairs may be differentiated on proportions alone.

The material available to me had certain drawbacks. Firstly, I did not collect it myself, it was not collected randomly, and only partial coverage of the islands' area was attempted. Because of these limitations, I am unable to make definitive statements concerning the relative abundance of the various species. The distributional information presented here must be considered partial and tentative until a great deal more field work can be done, planned in such a way as to minimize collecting bias. Secondly, the material was preserved in alcohol, and was not seen by me until it had been so preserved for over a year. I was therefore unable to attempt any histological work or the analysis of the stomach contents. Until I can obtain material properly preserved for histological examination, the designation of certain female structures as "seminal receptacle" or "bursa copulatrix" must be considered tentative. Until I can observe the living snails feeding or examine the stomach contents of fresh specimens, or both, any niche differentiation based on food selection (or indeed any other behavioral characteristic) must remain unknown.

This study of *Ostodes* has uncovered a certain amount of new information about this one genus within the Poteriidae. Only a very limited amount of material from other poterid genera was available to me. Without access to a great deal more material for outgroup comparisons, it would be premature to attempt to make any statements concerning the directions or patterns of evolutionary change in the family.

IX. SUMMARY

The land snail genus *Ostodes* in Samoa contains 12 species: 8 are found on Upolu, 6 on Savaii, and 2 on Tutuila, with 4 species occurring on both Upolu and Savaii. Of the 12 species, 3 were unknown prior to this study. They are ***O. reticulatus,*** from Upolu; ***O. llanero,*** from Savaii; and ***O. exasperatus,*** found on both Upolu and Savaii.

Most species in this genus cannot be identified by study of the shell alone; examination of the pallial anatomy is necessary for the separation of sibling species. Although there are easily observable differences between species in the hypobranchial gland, the chief characters that serve to separate species are found in the pallial reproductive systems of both sexes. In the male, the proportionate lengths of the distal thread and trunk of the penis vary with the species. In the female, the shapes, positions, and relationships of the anus, vaginal orifice, and copulatory pore are species-specific. The species self-recognition mechanism is thought to be based on these differences in genitalia. The anatomical characters confirm Tielecke's placement of *Ostodes* in the Poteriidae.

Opercular characters are useless as a diagnostic tool at the species level, as the 6 types of operculum found in

XI. APPENDIX:

Abbreviations Used in Anatomical Figures

A	anus
AG	albumin gland
BCP	bursa copulatrix
CDO	common duct opening
CDP	common duct papilla
CDS	common duct slit
CG	capsule gland
COL	"collar" of penis
CP	copulatory pore
CPS	copulatory pore, Savaii population
CPU	copulatory pore, Upolu population
DBCP	duct of bursa copulatrix
DG	digestive gland
DRCS	duct of seminal receptacle
ECPM	encapsulating membrane
GO	genital opening
HBG	hypobranchial gland
ICGD	internal common genital duct
IUC	infra-uterine channel
KN	"knuckle" of penis
LUT	lumen of uterus
ME	mantle edge
ML	mantle line
OD	oviduct
OV	ovary
PCGD	pallial common genital duct
PR	prostate
PRS	prostatic sac
PTA	terminal appendage of penis
PTH	penis thread
PTR	penis trunk
R	rectum
RCS	seminal receptacle
SG	seminal groove
ST	stomach
STBP	sub-terminal bulb of penis
SV	"safety valve"
TE	testis
UT	uterus
VA	vulval area
VD	vas deferens
VES	seminal vesicle
VO	vaginal orifice

Ostodes are not species-specific. There are no major differences in radular structure between species, but a number of small differences have come to light through use of a scanning electron microscope.

Sexual dimorphism is confined to size, with females averaging larger than males of equal age. No significant differences between sexes as to shell shape or sculpture were observed. The approximate age of a specimen can be judged by changes in the terminal portion of the body whorl involving sculpture, rate of decoiling, and thickness of the parietal callus. The size of the shell, and in one case the character of the operculum, are influenced by both the amount and regularity of rainfall, and the density of the covering vegetation which serves to retain moisture.

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Spawning and Early Life History of *Murex pomum* Gmelin, 1791

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(2 Plates; 2 Text figures)

INTRODUCTION

The literature on reproduction and larval development of tropical marine prosobranchs has recently been greatly expanded. Of this group, the genus *Murex* has been investigated by Knudsen (1950), Natarajan (1957), Cernohorsky (1965), Fioroni (1966), Gohar & Eisawy (1967), D'Asaro (1970), Spight, Birkeland & Lyons (1974), and Bandel (1976). Observations on the spawning behavior and egg capsules of *M. pomum* have been made by D'Asaro (*op. cit.*) and Bandel (*op. cit.*), but as these formed parts of general surveys of many prosobranchs from the South Florida-Bahamas region and the South Caribbean Sea respectively, detailed accounts, especially of the development of the hatchlings, were not given. This study, inasmuch as it was possible to monitor closely the early development of *M. pomum* from egg masses deposited by adults in the laboratory, will extend existing information on the species. Specifically, the use of two separate sample groups of *M. pomum* differing in size and geographical origin (St. Kitts and St. Vincent, West Indies) served to establish what is the norm for this species, and also helped to provide comparative information on spawning as well as quantitative and qualitative data on the capsules, eggs and young hatchlings.

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We wish to thank Dr. Tom M. Spight and Dr. Jørgen Knudsen for offering relevant and up-to-date material from the literature. We are also very grateful to Dr. Carol Lalli for reading the original manuscript and providing useful criticism. The work was supported jointly by a subvention from the University of the West Indies to the senior author and a grant in aid of research from the National Research Council of Canada to the junior author.

DESCRIPTION, DISTRIBUTION AND HABITAT

Murex pomum is among the larger of the Muricidae. Humphrey (1975) gave measurements of adults of 2 to 4.5 inches (ca. 5 - 11.5 cm), but our largest specimen was just over 12.5 cm long. The shell is heavy and strong with a rough surface, but shell quality varies impressively from one adult to the next and with the age of the newest varix. The colour of the shells is usually a combination of cream, tan, and dark brown, and occasionally tints of purple. The interior aperture is polished, and most often is coloured yellow to ivory, but may be light pink, and least often has all these shades inter-mixed with purple tints. There is usually one dark spot on the upper end of the parietal wall and 2 or 3 on the outer lip.

According to Abbott (1958) and Humphrey (1975), it has a distribution ranging from South Carolina in the southeastern United States to Trinidad in the West Indies. It has been collected from Biscayne Bay in Florida (D'Asaro, 1970), and reported as quite common in Cuba and Puerto Rico (Abbott, *op. cit.*), as common in the Bahamas (Zeiller, 1974) and off the coast of Colombia (Bandel, 1976), and as the most common *Murex* snail in Jamaica (Humphrey, *op. cit.*). It has been found by the junior author to be quite abundant in St. Kitts and St. Vincent and off the coast of Venezuela, but for some reason it is very scarce around Barbados. Only a single specimen was taken from numerous dives over years of shell collecting in Barbados.

For this study *Murex pomum* was obtained from Frigate Bay, St. Kitts, at a depth of approximately 4.5 to 6m. The animals inhabited an area of mixed rubble and sand, in which *Thallassia testudinum* grass flourished, and were invariably seen in groups of 2 - 4 in shallow depressions. In St. Vincent, *M. pomum*, which was generally larger than the average St. Kitts specimens, was collected off Young's Island in 4.5 - 6m of water, also in an area of rubble and sand. However, unlike the St. Kitts specimens, these were always seen buried in the sand with little or no part of the shell protruding above the substratum. Curiously, although HUMPHREY (1975) has described *M. pomum* as located in every imaginable environment, this species was obtained at only one site in St. Vincent and not in numerous other bays of comparable bottom.

The species has been described both as a carnivore (BANDEL, 1976; and others) and a browser (ZEILLER, 1974). The specimens under study exhibited both feeding patterns. They were routinely fed on the flesh of *Strombus pugilis*, alternated with that of the sea urchins, *Tripneustes esculentus* and *Diadema antillarum.*

MATERIALS AND METHODS

Eighteen adult specimens of *Murex pomum*, captured at St. Vincent on the 29th of February, 1976, were transferred to the Bellairs Research Institute, Barbados, where they were kept in a concrete aquarium of 228L[1] capacity with running sea water. Ambient temperatures averaged 27.1 ° C.

Within 4 weeks of arrival a large mass of egg capsules and a few smaller clusters were deposited by some of the animals. Since the major part of this event occurred over a week-end, when they were not under close observation, there was no certainty which of the animals were involved in the process. Just over a week later a specimen was observed to have deposited a few capsules. It was immediately marked with a numbered tag attached by nylon fibre and kept under close watch from 8:00p. m. to 10:00p. m. each day. It was the only specimen seen associated with the increasing egg mass and was not observed to leave the mass until 6:30p. m. on the 3rd day. Thus, not only was the identity of the egg layer certain, but also the time taken for deposition was determined to within minutes. Figure *1* is a photograph of the egg-depositing female and the egg-capsule mass. The latter is hereinafter referred to as sample A.

The egg-capsule mass was removed from the concrete wall of the tank and after careful blotting, was weighed and partitioned. The largest portion was put into a nylon basket of mesh size 0.239mm, which was then suspended in the water table and kept under observation. The second portion was frozen for later biochemical and histological studies, and the third was used for estimation of the total number of egg-capsules, number of eggs per capsule, and for dry weight determinations.

In May, another batch of 20 *Murex pomum* was captured in waters off St. Kitts, labelled, and housed in the same water table. No egg-capsules had been deposited up to 10:00p. m. on June 17th, but by the following morning there was a mass of oothecae on the upright wall of the tank. Five specimens were observed associated with this egg-mass, but 4 of these moved off at various times during that day and only one continued to be associated with the growing mass until 5:00p. m. on the 21st. Thus in both cases a single female was responsible for depositing at least the majority of the egg-capsules. This second capsule mass, now designated sample B, was treated like the first.

Daily samples of 5- 6 capsules were removed from the egg-mass and preserved for later study of development. Almost daily observations were made on the development of the hatchlings. From the 21st day onward, samples of the larvae were transferred to nursery baskets, sometimes still in the capsules and in other instances without capsules. In this way it was possible to determine at what stage they were most likely to survive removal from the egg capsules. The surrounding fluid in the nursery basket was regularly sampled for veligers.

The sizes of egg capsules, larvae and adults were determined and a size factor for the latter was calculated from length and width (L × W).

RESULTS

Adult Sizes

The adult animals from St. Kitts and St. Vincent clearly constituted two distinct size populations. Average length and width for the St. Kitts snails were 6.6cm (5.3 - 7.9cm) and 4.5cm (3.6 - 5.4cm) respectively, while the same measurements for the St. Vincent specimens were 10.4cm (8.5 - 12.5cm) and 6.5cm (5.8 - 7.9 cm). The single female (from St. Vincent) observed in the deposition of sample A egg mass measured 12.3cm in length and 6.95cm in width and weighed 191.50g

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[1] "The Veliger" has adopted the SI metric prefixes and abbreviations exclusively, according to which L stands for liter.

after egg deposition. Of the 5 specimens from St. Kitts associated with capsule mass **B**, average measurements were: length, 7.1 cm; width, 4.8 cm; and weight, 62.70 g. The female that deposited for the longest time was 7.7 cm in length, 5.4 cm in width, and weighed 76.86 g.

Egg Deposition

All the egg-capsule clusters were deposited just on the waterline in the aquarium. Areas free of fouling seemed to have been preferred, but the animals themselves also seemed to do some clearing away of tubiculous worms. The capsules were very firmly cemented to the upright surface of the tank and to each previous layer by their basal points. The time taken for deposition by the first single female was 54 hours. It is not known whether this female had contributed to any of the other clusters deposited earlier or whether it had spawned earlier in the year but did not do so again up to October of that year. The same observations hold for the second set of depositors. In this instance, one female was spawning continuously over a period of approximately 87 hours. The total wet weight of sample A capsule mass was 129.90 g and that of sample B, 53.49 g. The number of capsules estimated from counting an approximate ¼ subsample was 1 862 for sample A and 1 662 for sample **B**. Capsules from sample A contained 45 - 110 eggs and those from B, 25 - 45. The capsules were filled with additional albuminous fluid and lined by a thin albumen membrane.

Description of Egg Cases

The egg cases of *Murex pomum* are roughly tongue-shaped with the convex side uppermost. This side is patterned with striations of variable thickness. The striations are mostly in the vertical plane but those towards the shoulders branch and anastomose to make a network. The pattern is variable. The concave side has striations of much thinner fibres. An exit-window of much more even consistency is located in the apical half of this side (Figure 2). The egg capsules of sample A averaged 7.8 ± 0.5 mm at the base and 7.5 ± 0.5 mm in height. For sample **B**, width and height measurements averaged 5.3 ± 0.4 and 5.4 ± 0.5 mm respectively. There was little difference in thickness, capsules in sample A averaging 2.0 ± 0.2 mm and in sample **B**, 1.8 ± 0.1 mm. The oothecae are leathery in texture and strength and of a creamy off-white colour when deposited, but develop a more yellow colour with age. They retain this colour long after the eggs have hatched. Several times during the late pre- and early-hatching stages, the oo-tests became infested and covered with black fungus. For treatment of this infection, 2 mg of streptomycin and 2 mg of sulphadiazine were dissolved in 1 L of millipore-filtered sea water, and the capsules were immersed therein for 8 hours. But, curiously, after hatching was completed, the portions of egg capsules kept in sea water did not develop any fungal growth or discolorations.

Pre-Hatching Development

Development was not synchronized throughout the egg-mass, nor within the same capsule. This was evidenced by the fact that, although deposition of egg capsules was accomplished within 54 and 87 hours for samples A and **B** respectively, hatching continued over a 12 day period in both instances. Furthermore, individual capsules removed from the mass during any of the hatching days contained

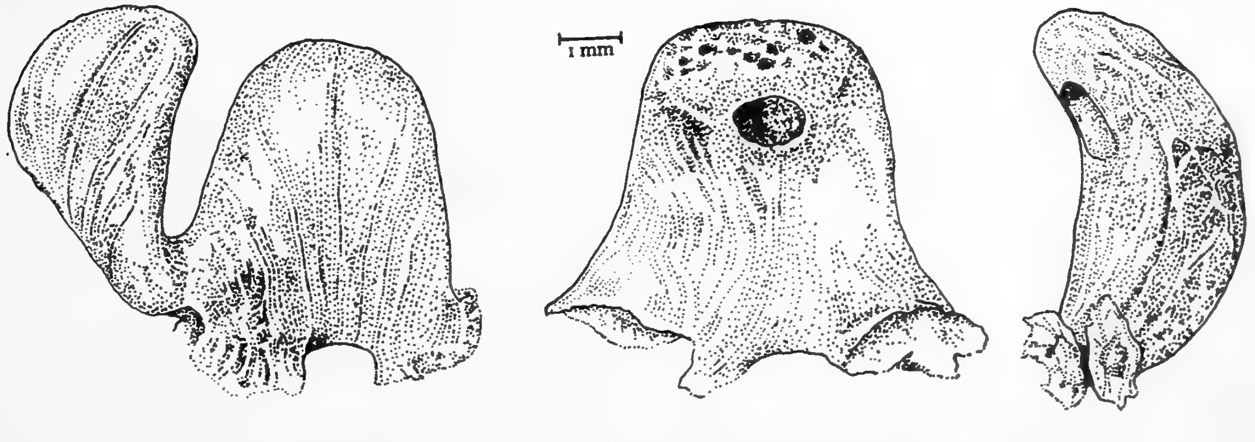

Figure 2

Murex pomum egg capsules taken from an original drawing by the late Dr. Gunnar Thorson, by courtesy of Dr. Jørgen Knudsen young of different sizes and showing different increments of growth. Nevertheless, it was possible to follow the developmental sequence quite easily. The qualitative data on larval stages, hatching times, and later development showed 100% comparability.

In the most advanced larvae, the foot was apparent by the 18th day after spawning had ended. The velum was formed and so was the pulsatile larval heart. The frequency of the heart beat seemed to be related to velar activity, ceasing for several seconds when the velum was withdrawn. Eye-spots were barely visible. The gut was observed extending from the stomodeum, with the gut diverticulum, seen as a coarsely granular mass, jutting towards the posterior end of the larva, which was by then encased in a membrane-like shell. Between the 19th and 21st day torsion took place. New shell material was deposited and the larva then assumed definitive shape. The eyes had been formed, and the gut diverticulum had increased in size.

By the 22nd day the shell had 2½ whorls, was gritty on the outside and quite brittle with a smooth outline on the outer lip. In the St. Kitts specimens, however, the last ½ whorl was marked by a prominent mid-whorl shoulder. At the anterior end of the larva the 4-lobed velum, foot and operculum showed further growth. Orange and brown pigmentation had begun in the foot and operculum. There was also brown pigment in the eyes which were by then supported on short stalks. Tentacles were also formed. The pulsating larval heart could be seen through the still transparent shell just below the outward curvature for the siphon which was not well formed. The gills, however, were present and could be seen coiling backwards from the stomodeum. The mid-gut gland extended into the apical whorl but did not fill it. At this stage the larval velum was very active, and the larvae moved about within the capsules. Some exit-windows of the capsules opened but most of the veligers remained inside. When flushed from the capsules, they swam quite strongly up and down the water column. The foot was by then quite well developed and pigmented, and the larva used it to a limited extent. Larvae, that were transferred to nursery baskets at this stage, did not survive. The causes of death were not known, but were not related to shell damage inflicted during handling as most shells remained intact.

By the 23rd day the shell began to develop colour, and a layer of new material was laid down on the outer lip (Figure *3*). In the St. Vincent specimens the tubercle marking the beginning of the mid-whorl shoulder was then apparent. The eyestalks had grown to extend beyond the shell. The velum had increased in size – when fully extended each lobe on a sample A specimen measured 1.25 mm long. Between the 24th and 26th day the foot became more active and was preferred as a means of locomotion. Pigmentation intensified, particularly in the shell, and so internal structures were less discernible, except for the mid-gut gland which then occupied more of the 2nd whorl. Shell growth continued at the rate of one layer per day, the layers averaging 32 µm in width. Larvae from any capsule showed from 2 - 6 layers on the outer lip. As a result of this variation, their lengths varied in the same way as the lengths of the hatchlings given in Table 1 and shown in Figure *4*. At this stage the highest mortality in nurslings from all causes of death (discussed later in this text) was among the lesser developed specimens.

Table 1

Size variations (in mm) in twenty hatchlings from three connecting egg capsules taken from sample B.
L and W denote length and width respectively.

L	W	L	W
1.4	1.2	1.6	1.2
1.4	1.2	1.6	1.2
1.4	1.2	1.6	1.2
1.4	1.2	1.6	1.2
1.5	1.1	1.6	1.2
1.5	1.2	1.6	1.3
1.5	1.2	1.6	1.3
1.5	1.2	1.7	1.2
1.5	1.2	1.8	1.3
1.5	1.2	1.9	1.4

Explanation of Figures *1*, *3*, *4*

Figure *1*: Egg capsule mass A and depositor

Figure *3*: *Murex pomum* pre-hatching larvae about 24 days after egg deposition showing a day's increment of shell growth and developing foot

Figure *4*: Difference in size of *Murex pomum* hatchlings taken from the same egg-capsule

Figure *1*

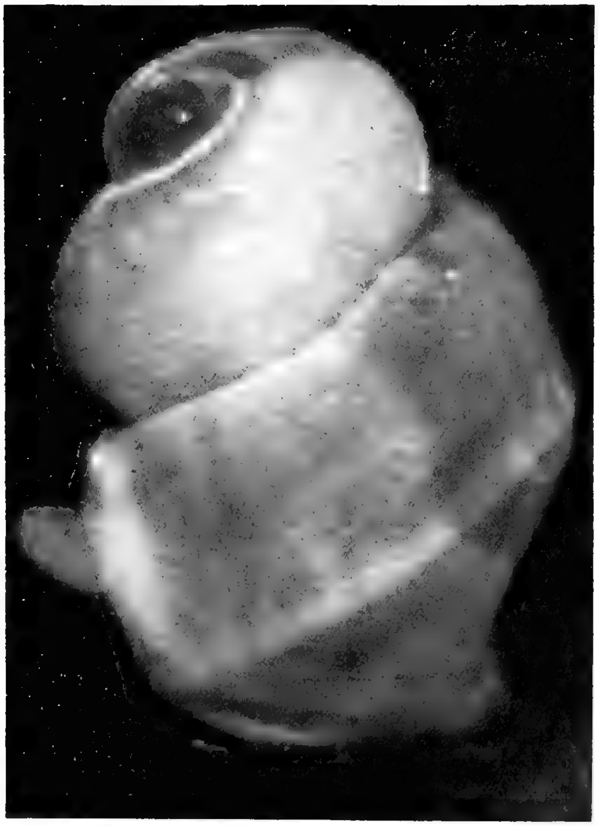

Figure *3*

Figure *4*

There seemed to be a gradual recession in use of the velum, and by the 28th day there was no outward sign of it. When turned over, the protoconchs all righted themselves by extending the foot until contact was made with the surface – none extended the velum although it had not yet degenerated and could still be seen when the shell was broken.

Hatching

From observations on the transfers to nursery baskets and daily sampling of the water from the main hatchery basket, it was determined that successful hatching occurred from the 26th day onwards. None of the transfers made before that day survived, nor did any of the veligers that emerged into the main basket, even though this could be considered a well-protected environment. By then the larvae had 4 - 6 extra layers on the outer lip, the apical whorl was almost filled by the hepatopancreas, and the shell was heavily pigmented. Hatchlings varied in size as shown in Table 1 and Figure *4*. Hatching continued up to the 38th day, the visually-determined peak being between the 32nd and 33rd days. By the 40th day all veligers remaining in capsules, although well developed, showed no sign of life. This happened mainly in the cases where the windows remained closed, but also in instances where the windows were opened. Necrotic larvae were quickly devoured by saprozoic protozoa, leaving only shells.

Most hatching protoconchs crawled out on foot, but many, particularly the early hatchlings, did so when both foot and velum were equally active. Some of them travelled relatively great distances in the first few hours after hatching; many of them crawled up above the water line and perished as a result. Presumably this was an instinctive dispersal response and in their natural environment the problem of desiccation would be of a lesser degree.

Table 2 gives a summary of relevant pre-hatching and hatching data for the 2 samples studied.

Post-Hatching Development

Since hatching continued up to the 38th or 39th day, some later hatchlings undoubtedly were more developed than the earlier ones and so passed some of the so-called post-hatching stages inside the capsule. Early in this period there was marked extension of the eye-stalks and the proboscis became quite prominent. The foot elongated and presumably development and differentiation of internal organs continued – the most obvious of which was the hepatopancreas which continued to extend towards the apical whorl. Colour intensified, further occluding internal structures. Visible growth was by the daily increment of shell material at the outer lip of the aperture (Figure 5).

When 7 - 8 layers had been laid down (*i. e.*, 3 - 5 days after hatching), crenellation of the outer lip began (Figure *6*). At the 9 - 10 layer stage, multiple layers were put down at the same time and same level, somewhat like a set of flounces. This formed the first varix as shown in Figure 7. The lip was continued from the innermost of these at the same rate of one layer per day. The day's increment could always be seen as the thinnest translucent layer at the edge, since older layers were progressively thickened by new material added from the inside.

The second varix was formed similarly to the first at the 12th layer of the new extension, *i. e.*, roughly 18 days after hatching. The third extension involved 14 layers. This possibly marked the real end of the larval stage, since in the 4th growth stage shell deposition was more complicated. The shell material was much thicker and the surface was rougher and corrugated both vertically and transversely, markedly different from the earlier nuclear whorls. Fluting at the lip edge was more pronounced so the number of corrugations at the edge increased gradually (*cf.* Figures *6* and 7). This occurred 30 - 32 days after hatching. Because of the intensity of colour and the difficulty in handling the by then very active protoconchs, it was not certain whether growth continued by the same daily increments, but growth measurements done at wider

Table 2

Summarized data on the respective spawn from the St. Vincent and St. Kitts animals.
H, W and T denote height, width and thickness respectively.

Collection site of samples	Average size measurements of capsules in mm (N = 20)			Calculated average net weights of capsules in g.	Average number of eggs per capsule (N = 20)	Average number of eggs hatching per capsule (N = 40)	Percentage of eggs hatching	Average number of nurse eggs per embryo
	H	W	T					
St. Vincent	7.5	7.8	2.0	0.070	78.7	18.3	23.3	3.3
St. Kitts	5.4	5.3	1.8	0.032	34.4	7.9	23.0	3.3

time intervals on a single individual showed that the 32 μm per day input was closely approximated (Table 3).

Table 3

Growth measurements in mm for a single hatchling from sample B.

Date	Length	Width
20/7/76	1.45	1.20
26/7/76	1.55	1.20
4/8/76	1.80	1.30
10/8/76	1.95	1.35
27/8/76	2.40	1.46
10/9/76	2.90	1.87
14/10/76	3.30	1.90
28/10/76	3.30	1.90
15/11/76	3.30	1.90

By the end of the 10th post-hatching week the snails had each completed one new whorl and were then 3½ whorls big. By far the greater portion of the last whorl was of the thicker corrugated shell type. The 3 last measurements in Table 3 show that no growth took place for a month after this stage had been reached. Presumably the protoconchs had by then adopted the growth pattern of the adults; this involves massive shell growth over a relatively short period of time with increasingly large "resting" intervals. Bandel (1976) has described how older well-fed animals will bury themselves in the sand, and put on a new chamber in about a week. Our experience confirms this and shows further that, if interrupted in the process, the murex will carry around the half-completed chamber for weeks until it finds conditions suitable to resume shell building. This seems to involve some factor other than the availability of sand or mud.

Survival of Young

There was a very high mortality in the hatchlings. Of an estimated 16268 veligers in Sample A, 99% either failed to emerge or died before reaching the age of 3 months, and that in a protected environment. It has already been pointed out that all naturally and artificially hatched veligers died, some from shell damage; many of the veligers and later stages died because their shells were perforated and viscera eaten out by boring worms. Many of the young snails died apparently from dehydration upon crawling above the water level, but others died from no readily discernible cause. The same results were obtained with sample B.

The best rearing results were obtained from those cultures that contained portions of the egg-capsule mass and turtle grass, *Thallasia testudinum*. Coincidentally, relatively large populations of cyclopoid copepods also developed in the same cultures, and the protoconchs, as they crawled over grass and egg capsules, no doubt fed on the crawling nauplius stages as well as nematode worms and bryozoan larvae found on the turtle grass. Later-stage juveniles were fed on the same diet as the adults.

DISCUSSION

High mortality is usually concomitant with high fecundity in animals. Despite the results obtained from rearing in a medium with turtle grass and egg capsules, it is most unlikely that lack of food played an important part in mortality among the young. Spight (1976) has pointed out that few hatchlings starve to death (citing his experience of keeping many young *Thais lamellosa* alive without food for a month or more). Physical stresses and predation are more of a threat to the newly hatched snail than is starvation. Shell damage, dehydration and shell boring by worms naturally qualify as stress factors along with others that would occur in the natural environment. Spight (1975) has calculated that a newly hatched *T. lamellosa* has a 1 - 2% chance to survive its first 3 months. A snail reaching 3 months has a 35% chance to reach age 1, and older snails have a 40 - 60% chance to survive through subsequent years. With this rapid increase in survival rates a 2 mm snail should have much better prospects than a newly hatched 1 mm snail. Our 1% survival of young tallies with Spight's 1 - 2% for *T. lamellosa.*

Explanation of Figures 5 to 7

Figure 5: A ***Murex pomum*** protoconch showing several daily increments of growth and also the mid-whorl ridge

Figure 6: ***Murex pomum*** protoconch showing crenellation of lip as well as pigmented foot, gills and portions of the gut

Figure 7: ***Murex pomum*** shell of 14 week old protoconch showing nuclear whorls and subsequent increments of growth

Figure 6

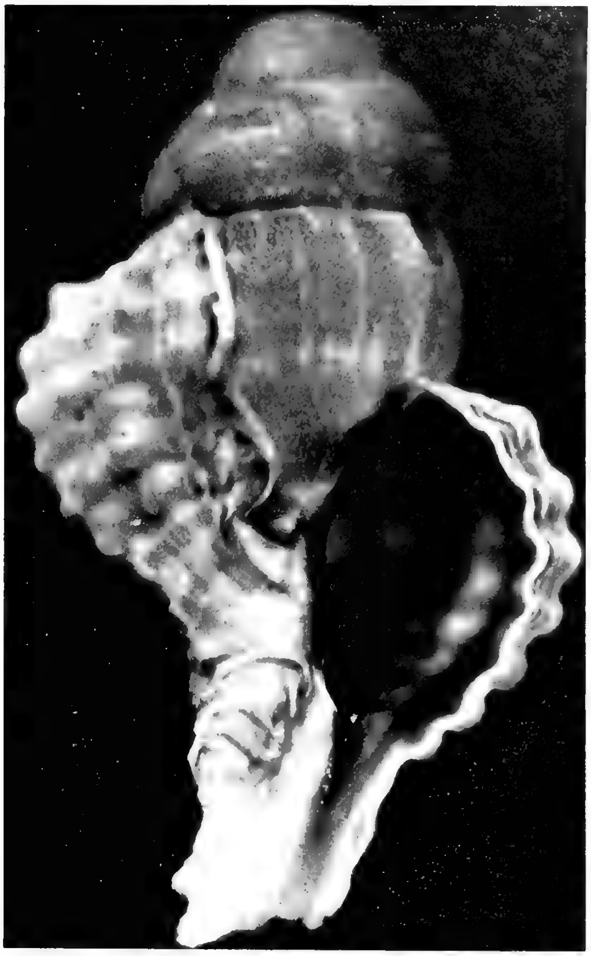

Figure 7

Figure 5

It is noticeable from Table 3 that growth in *Murex pomum* is relatively fast in the early post-hatching stage, that the 2 mm size was reached within one month of hatching, and the 3 mm stage in less than one month thereafter. Considering Spight's calculated increased chances of survival in the open, almost 100% of those reaching the 3 month stage should reach maturity in a protected laboratory environment.

The principal factor upon which depend the early life histories of marine prosobranchs is the type of development. Thorson (1940, 1946) has shown that the percentage of species with a pelagic larval development increases when going from the Arctic seas towards the equator. For example, "in the high Arctic seas (East Greenland) about 95% of all marine species of bottom invertebrates seem to develop without a pelagic phase" (Thorson, 1950), whereas in New Caledonia 57% of the prosobranchs displayed pelagic development, in the Persian Gulf 75%, and off Bermuda about 90% (Thorson, 1940; Lebour, 1945). On the other hand, Knudsen (1950) determined that 69% of 32 species from tropical West Africa depended on non-pelagic development, while D'Asaro (1970) reported that exactly half of the prosobranchs which he studied from South Florida and the Bahamas relied, too, on this direct form of development. In his later studies, Thorson (1950, 1952) also demonstrated the correlation of a relatively small number of eggs with non-pelagic development in marine invertebrates. Most of the species with non-pelagic larval development investigated by Thorson produced less than 1000 eggs per female per breeding season. In contrast, the 2 egg-masses from St. Vincent and St. Kitts were estimated to contain 146 539 and 57 173 eggs respectively. In each instance, at least the majority of the eggs were contributed by a single snail. D'Asaro (1970), though, found far fewer eggs (9 700) per mass for *M. pomum* indicating, thereby, a wide variation in individual fecundity in this species.

It is tempting to offer the explanation that around small Caribbean islands with narrow shelves, such as St. Vincent and St. Kitts, direct development constitutes a means by which snails guarantee that the larval stock is not all dispersed offshore. However, inshore eddy systems acting as retaining mechanisms generally ensure that for such islands at least a portion of the pelagic larvae of benthic invertebrates remain inshore sufficiently long for the planktotrophic larvae to complete development to the crawling stage before settling over a propitious substratum. A species which most likely benefits from such retaining systems is the Rooster Tail Conch, *Strombus gallus*, which in St. Kitts co-exists with *M. pomum* at Frigate Bay, yet is known to have a pelagic development (D'Asaro, 1970). It is, however, more probable that elimination of the pelagic stage is a conservative mechanism adopted in order to lessen the higher mortality rate from predation associated with the temporary planktonic existence. This option possibly allows for the co-existence of *M. pomum* with *S. gallus*, inasmuch as it would reduce competition between the young of *M. pomum* and other benthic snails such as *S. gallus*, especially if the latter also produces large numbers of larvae and breeds throughout the year.

No conclusions regarding spawning season can be drawn from the spawning periods (April and June) of *Murex pomum* from the present study. Although they agree with the results of D'Asaro (1970) who collected spawn from this species from March through May in subtropical Biscayne Bay, Florida, it is likely that this snail is reproductively active all year off the tropical Caribbean islands. In fact, Bandel (1976) has observed spawning activity by *M. pomum* at Santa Marta, Colombia, throughout the year. D'Asaro's observations probably are linked to seasonal climatic changes which are more apparent at higher latitudes.

Judging from all 3 studies, it appears that communal spawning is characteristic of the species, and that individual acts of egg mass deposition precipitate spawning in other ripe animals alerted through chemoreception. It is probable that in instances where spawning appears to be limited to a single snail, no other ripe animals are present. The hatching time of 26 to 38 days observed for both the St. Vincent and St. Kitts samples, and the close agreement with the results of Bandel (1976), who reported a range of 24 to 39 days, probably indicate a norm for the species of the latter range – at least under tropical conditions. D'Asaro (1970) did not give hatching time, but insofar as the accumulated data indicate spawning time to be a latitudinal effect, incubation and hatching times could also be functions of temperature for this species.

Table 2 shows that the larger female(s) from St. Vincent deposited larger capsules than the smaller one(s) from St. Kitts. This agrees with the findings of Hancock (1959) and McKenzie (1961) for the muricids *Urosalpinx cinerea* and *Eupleura caudata* respectively. Also, capsules of the larger snail(s) contained the greater number of eggs – a simple relationship noted long ago when Conklin (1897, 1898), in his now classic studies on the embryology of *Crepidula*, reported that the number of eggs produced was roughly proportional to the size of the body. Average capsule measurements (H, W and T) of samples A and B are comparable to those reported by D'Asaro (1970) (7.5, 6.0 and 2.5 mm) and Bandel (1976) (3 - 4, 3.5 - 4 and 1.5 mm) for *Murex pomum.* Approximately the same degree of variation in number of eggs hatching per capsule exists. D'Asaro listed an average of 13 and Bandel a range of 6 - 15, compared to an average of 18 and 8 for our samples A and B respectively. These findings suggest a rough correlation between capsule size and number of eggs hatching – a relationship previously noted by Gallardo (1973), Spight, Birkeland & Lyons (1974) and Castilla & Cancino (1976) for other muricids.

There is a remarkable agreement in the percentage of eggs hatching in the 2 egg-masses, and, by extrapolation (on the assumption that the remainder constitute such), the average number of nurse eggs per embryo (Table 2). Neither D'Asaro (1970) nor Bandel (1976) reported average number of nurse eggs for *Murex pomum,* but the present finding (3.3) is relatively low when compared to those given for other species of *Murex*, which range from 5.9 for *M. torrefactus* (Cernohorsky, 1965) to 91.4 for *M. quadrifrons* (Knudsen, 1950). However, as is known (Hyman, 1967), albumen is engulfed as food by developing encapsulated prosobranchs and some embryos in a capsule often devour the others. Spight (1976) has pointed out that, in contrast to the standard size reached when an embryo has its entire yolk supply enclosed within its egg membrane (Fioroni, 1966), the prosobranch embryo that feeds on nurse eggs will often reach a hatching size much larger or smaller than the mean for its species. This variable hatching size, which may be disadvantageous if there is an optimum hatching size (Smith & Fretwell, 1974), is demonstrated for a random sample of *M. pomum* hatchlings (Table 1 and Figure *4*) and may, according to Spight (*op. cit.*), be caused by unequal nurse egg supply amongst egg capsules; equal nurse egg supply but unequal embryo numbers amongst egg capsules; and unequal sharing of existing nurse eggs by embryos.

In conclusion, some of the summarized data have been arranged in Table 4 in order to demonstrate the similar numerical ratios between comparable sets of data for A and B. It is apparent that the ratios of slightly more than 2:1 obtained for all the reproductive parameters reflect the same order of difference in size. Hence, larger body size ultimately translated into higher fecundity, agreeing with the results of Spight & Emlen (1977) who noted that clutch size in *Thais lamellosa* and *T. emarginata* was directly proportional to body size. Size differences may be attributed to any one or combination of several intrinsic and extrinsic factors. First, it may be a simple function of age, in which case the value of the reproductive effort increases with age of the adult since the animals are interoparous. It is possible that, at least for this species, growth does take place after initial spawning at maturity although Spight, Birkeland & Lyons (1974) have pointed out that most muricid adults do not grow. Hyman (1967), on the other hand, has stated that while some prosobranchs cease to grow after attaining sexual maturity, most do continue to grow, albeit at a diminishing rate, for several years, spawning annually. Second, it may reflect a difference in nutrient supply at the 2 sites, especially since it is known that size at maturity may vary with availability of food (Spight *et al., op. cit.*). Third, we may be dealing with 2 geographically separated groups, each with its own size potential intrinsically induced. Fourth, the sample groups possibly comprise 2 distinct species. This possibility, however, can be ruled out by visual inspection of the animals. In addition, wet weights and shell dimensions, represented by individual size factors (L × W), are highly correlated, and, although the 2 sets of species characteristics data form separate clusters on a graph (Figure 8), the least squares of regression line fitted to the total data has a high correlation coefficient of 0.99. Statistically, at least, the 2 groups obviously belong to the same universe (species) and size differences are not indicative of any taxonomic differences. To summarize, any one or combination of the first 3 factors may apply since in each case individuals in the 2 groups would describe just such a graph as given in Figure 8.

Table 4

Table of ratios of comparative reproduction data. A and B represent the known major contributors to egg-mass deposition by the St. Vincent and St. Kitts animals respectively. H, W and T denote average height, width at base and thickness respectively (in mm).

	A	B	Ratio
Net weight of animals (g)	191.5	76.86	2.49
Size factor of capsules (H × W × T)	117.0	51.50	2.27
Calculated average wet weight of capsules (g)	0.070	0.032	2.18
Average no. of eggs/capsule	78.7	34.4	2.28
Average no. of hatchlings/capsule	18.3	7.9	2.32

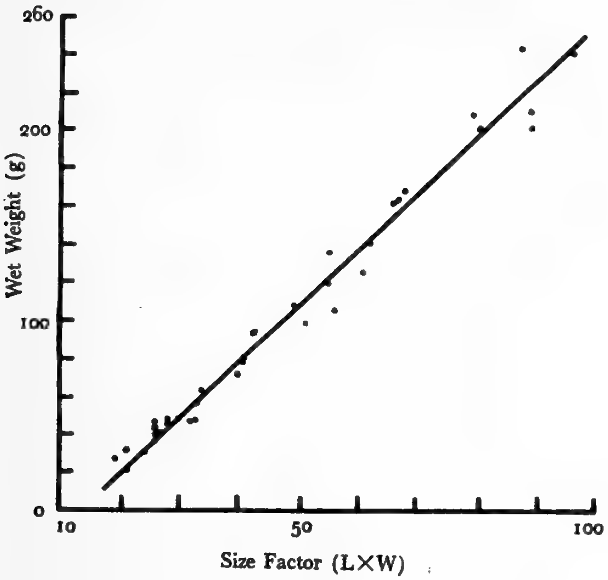

Figure 8

The relationship between wet weight and size of *Murex pomum*

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The Systematic, Adaptive and Physiological Significance of Proteolytic Enzyme Distribution in Bivalves

BY

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INTRODUCTION

THE DISTRIBUTION OF digestive enzymes in animals is believed to be adaptive, and related to the constituents of the diet (YONGE, 1937). Most bivalves have a low protein diet. Consequently, high levels of proteolysis would not be expected, and there has been relatively little interest in protein digestion in this class of molluscs. YONGE (1926) was satisfied that in *Ostrea edulis* Linnaeus, 1758 protein digestion was an intracellular process in the amoebocytes and digestive cells of the digestive diverticula, and he contended that gastric protein digestion would be incompatible with proteinaceous crystalline styles (YONGE, 1930). Therefore some controversy was aroused when MANSOUR (1946) and MANSOUR & ZAKI (1946) argued that the digestive diverticula of bivalves were secretory and that animal food could be digested in the stomach. However, the low levels of protein digestion in the stomachs of *Tridacna elongata* Lamarck, 1819, and *Pinctada vulgaris* Linnaeus, 1758 detected by MANSOUR-BEK (1946) seemed insufficient to justify Mansour's claim. BALLANTINE & MORTON (1956) noted the presence of gastric proteinases in *Lasaea rubra* (Montagu, 1803), and suggested that they were released from "excretory spheres" from the digestive diverticula. OWEN (1956) examined *Nucula sulcata* Bronn, 1831 and found significant gastric protein digestion, but no diverticular activity.

Differences in the distribution of proteolytic enzymes of two herbivorous, suspension-feeding bivalves, *Lima hians* (Gmelin, 1791) and *Mya arenaria* Linnaeus, 1758 indicated an adaptive relationship between enzyme distribution and gastric morphology (REID, 1966). This led to an investigation of animals belonging to different taxa proposed by PURCHON (1963) on the basis of stomach morphology. This study (REID, 1968) provided some support for the original hypothesis concerning the relationship between stomach form and digestion. KOZLOVSKAYA & VASKOVSKY (1970) surveyed a variety of marine invertebrates, including 14 species of bivalves, for alkaline proteases. For the bivalves only the digestive diverticula were assayed. A range of results from zero activity to low activity were obtained for the bivalves, very low in comparison to carnivorous invertebrates. Since the survey dealt only with intracellular conditions it shed no light on the relationship between gastric morphology and digestion. However, a study of 7 species of *Macoma* (Tellinacea) by REID & RAUCHERT (1972) indicated that the suggested relationship between gastric morphology and protein digestion might be spurious. Within the genus *Macoma* a range of proteolytic levels was noted, though all the species have similar stomach structures. This problem was compounded when B. MORTON (1970, 1973) proposed that bivalves undergo rhythmic and possibly endogenous cycles of ingestion, secretion, digestion and absorption. Such cycles might involve proteases, and thus account for differences observed within the genus *Macoma*.

In carnivorous septibranchs there is high proteolytic activity which is related to the high-protein animal food (REID, 1977).

SYNOPSIS OF PREVIOUS OBSERVATIONS

To aid the comprehension of differences and similarities in protein digestion in bivalves, some of the relevant data are summarized below. The animals are grouped by family and gastric morphological type (PURCHON, 1956, 1957, 1958, 1960). Data are given in the following sequence: habit; level of gastric proteolysis; gastric enzymes if known; pH optima of gastric juice level of diverticular proteolysis; pH optima of diverticular extracts; diverticular enzymes if known. The stomach and the digestive diverticula are the main sites of protein digestion (REID, 1966). Gastric proteolytic activity is expressed in units per mL of stomach fluid and diverticular activity in units per mg fat-free dry weight of tissue. These are spectrophotometric units, each equivalent to an absorbance change of 0.001 per minute at 280 nm at 37° C. Absorbance increase is due to the release of amino acids as a result of proteolysis. Free amino acids present in extracts before enzyme assay are measured and deducted from final assay results. Soluble proteins which would also affect absorbance readings are removed by trichloracetic acid precipitation. Fuller technical details may be found in accounts by Reid (1966) and Reid & Rauchert (1970, 1972, 1976). In the following synopsis "low" gastric activity signifies 0 - 100 units per mL; "intermediate" gastric activity signifies 100 - 300 units per mL; "high" gastric activity signifies more than 300 units per mL. "Low" diverticular activity signifies 0 - 50 units per mg; "intermediate" diverticular activity signifies 50 - 150 units per mg; "high" diverticular activity signifies more than 150 units per mg.

Family Nuculidae, Stomach Type I

Acila castrensis (Hinds, 1843): deposit-feeder; intermediate gastric proteolysis; peaks at pH 3, 6, 7.5; diverticular condition unknown. (unpublished observations of author)

Family Nuculanidae, Stomach Type I

Yoldia thraciaeformis Storer, 1838: deposit-feeder, intermediate gastric proteolysis; peaks at pH 3.5, 5.5, 7.5; diverticular condition unknown (Reid, 1977).

Family Cuspidariidae, Stomach Type II

Cardiomya planetica Dall, 1908: carnivorous; high gastric proteolysis; peaks at pH 3, 6, 7.5; enzymes cathepsin B and trypsin; diverticular condition unknown (Reid, 1977).

Family Mytilidae, Stomach Type III

Mytilus californianus Conrad, 1837; suspension-feeder; low gastric proteolysis; peaks at pH 6, 7.5; trypsin; low diverticular proteolysis; peaks at pH 3, 6, 8 trypsin (unpublished observations of author).

Family Ostreidae, Stomach Type III

Crassostrea gigas (Thunberg, 1793): suspension-feeder; low gastric proteolysis; intermediate diverticular proteolysis; peaks at pH 3, 6, 7.5 (unpublished observations of author).

Family Pectinidae, Stomach Type IV

Chlamys hericius (Gould, 1850): suspension-feeder; low gastric proteolysis; trypsin; low diverticular proteolysis; peaks at pH 2.5, 6, 7.5; chymotrypsin (Reid & Rauchert, 1970).

Family Limidae, Stomach Type IV

Lima hians (Gmelin, 1791): suspension-feeder; low gastric and diverticular proteolysis; diverticular peaks at pH 5.5 and 8 (Reid, 1966).

Family Unionidae, Stomach Type IV

Anodonta kennerlyi Lea, 1860: suspension-feeder; tryptic gastric and chymotryptic diverticular enzymes (unpublished observations of author).

Family Veneridae, Stomach Type V

Saxidomus giganteus Deshayes, 1839: suspension-feeder; low gastric proteolysis; peak at pH 5.2; low to intermediate diverticular activity; peaks at pH 3, 6, 8; trypsin (Reid, 1977 and unpublished observations).

Family Mactridae, Stomach Type V

Tresus capax (Gould, 1850): suspension-feeder; low gastric proteolysis; peaks at pH 2, 5, 8; gastric cathepsin B and trypsin; intermediate diverticular proteolysis; peaks at pH 2.5, 6, 8; diverticular cathepsin B and D and chymotrypsin (Reid & Rauchert, 1976).

Family Tellinidae, Stomach Type V

Macoma secta (Conrad, 1837): large particle deposit-feeder; intermediate gastric proteolysis; peak at pH 6; gastric trypsin; intermediate diverticular proteolysis; peaks at 2.5, 5.5, 8; diverticular chymotrypsin (Reid & Rauchert, 1972).

Macoma inquinata (Deshayes, 1854), suspension-feeder; intermediate gastric proteolysis; peaks at pH 5.5, 7; intermediate to high diverticular proteolysis; peaks at pH 3, 5, 7.5 (Reid & Rauchert, 1972).

Macoma lipara Dall, 1916: deposit-feeder; low gastric proteolysis; peaks at pH 7; low to intermediate diverticular proteolysis (Reid & Rauchert, 1972).

Family Myidae, Stomach Type V

Mya arenaria Linnaeus, 1758; suspension-feeder; intermediate gastric proteolysis; peaks at pH 5.5, 7.2; cathepsin B and trypsin; intermediate diverticular activity; peaks at pH 2.5, 3.5, 5.5, 8; diverticular cathepsin B, trypsin (Rosén, 1949; Kozlovskaya & Vaskovsky, 1970; Reid, 1966 and unpublished observations).

Before discussion of these data some qualifications must be noted: in some of the earlier works only qualitative observations were made. In most cases, enzyme assays are incomplete; consequently, the identification of certain enzymes in some examples does not imply that those enzymes are absent from other animals investigated. The studies on *Chlamys hericius* and *Tresus capax* indicated the presence of carboxypeptidases and aminopeptidase in both the acid and alkaline pH range, as well as possible cathepsin A and cathepsin C activity. These exopeptidases are probably of universal distribution. The results of Kozlovskaya & Vaskovsky (1970) are largely excluded from the above due to the different expressions of unit activity employed by them. It is of note that 7 of their 14 bivalve species showed no alkaline endopeptidase activity. *Mya arenaria* showed the most activity. In addition to the data summarized above, I have made observations concerning variations in proteolytic activity within species. In *Macoma secta*, samples taken in May for 2 consecutive years were found to have significantly different proteolytic levels, and gastric protein digestion in *Macoma inquinata* was found to vary significantly (Reid & Rauchert, 1972). Further observations on variations in *Tresus capax* are presented in the following report.

PRELIMINARY OBSERVATIONS ON THE DIGESTIVE PHYSIOLOGY OF *Tresus capax* (Gould, 1850) IN RELATION TO TIDAL RHYTHMS

As noted above in the introduction, considerable interest has been generated in rhythmic physiological activity in bivalve alimentary tracts, by the work of Morton (1970, 1973).

Gastric protein digestion in *Macoma inquinata* was found to vary significantly, and these variations were attributed to feeding behaviour, relative to tidal conditions (Reid & Rauchert, 1972). Proteolytic levels and the relative activities of particular proteases would be direct indicators of rhythmicity. Accordingly a pilot study of *Tresus capax* was carried out, to investigate gastric volume, gastric pH and proteolytic activity, and digestive diverticular activity.

Tresus capax was chosen for its large size and because its proteolytic enzymes are better characterized than those of other bivalves (Reid & Rauchert, 1976). Specimens were obtained from the intertidal region at Cherry Point, in the vicinity of Satellite Channel, British Columbia. This is a locality with a mainly diurnal tide; *i. e.*, where at the spring tidal period the animals in their natural habitat are uncovered once in 24 hours. Specimens of similar shell size were placed in wire baskets and reburied in their natural habitat. The baskets were buoyed, so that they could be collected by boat at high water. After a 48 acclimatization period, during which it was verified that animals were able to use their siphons effectively, sampling began, was carried out at 3 hour intervals for 24 hours. During the 24 hours of sampling the experimental animals were exposed by the tide for 6 hours and submerged for 18 hours.

Gastric pH in the samples was found to range from pH 6.2 to 7.2. Exposed animals were in the lower part of the range, submerged animals in the higher part of the range. Gastric volume was lowest (1 mL) in exposed animals, and highest (up to 8 mL) in animals which had been submerged for 8 hours or more. Gastric proteolysis was low, but constant in all samples. Diverticular proteolysis appeared to be low in exposed animals and intermediate in submerged animals. Sample sizes were too small to provide statistically reliable conclusions beyond the above. There did not appear to be any drop in gastric volume and pH during the 18 hour submergence, which might have corresponded with the minor ebb, which did not expose the specimens. These observations are discussed under the heading "Protein digestion and rhythmic physiological events in bivalves" in the following general discussion.

DISCUSSION

General Features of Protein Digestion in Bivalves

In spite of the cursory nature of some of the observations reviewed above, it may be concluded that all bivalves are capable of digesting protein. Though comprehensive enzymological studies are few it may be inferred that most bivalves have a complement of most of the proteases which are found throughout the animal kingdom. Particular categories of proteases cannot be indentified with particular habits, gastric morphology, nor systematic status. In general, the pH optima of gastric enzymes correspond with the pH of the stomach, *i. e.*, in the pH 6 range (Morton, 1970; Mathers, 1973; Reid, 1977). In the digestive diverticula low pH (2 - 3.5), intermediate pH (4 - 6.5) and high pH (7 - 8) activity peaks occur universally. In *Tresus capax* the enzymes cathepsin D, cathepsin B and chymotrypsin are active in the low, intermediate and high pH regions respectively. This may hold true for other bivalves.

Protein Digestion and Gastric Morphology

It might be generalized that the stomach types such as I and II, which are structurally the simplest, are the ones which have the highest levels of proteolytic activity (*e. g.*, *Cardiomya, Yoldia*). It does not follow that there is an adaptive relationship, since it has been shown that there are significant differences in proteolytic levels within the type V group. The simplicity of the type I and II stomachs is probably more directly related to the triturative process than to the enzymatic process. No definitive adaptive relationship between protein digestion and gastric morphology can be stated at present.

Protein Digestion and Habit

The suspension-feeding bivalves which have been studied exhibit a range of proteolytic activity from low to intermediate in terms of the present study. The question of what constitutes the diet of suspension- and deposit-feeders has been discussed by Pohlo (1969) and Reid (1971). The protein content of the phytoplankton food of suspension feeders is variable, but does not exceed 30% by dry weight (Strickland, 1965). It is generally believed that deposit-feeders depend largely on the microorganisms associated with the detrital and inorganic particulate material of their diet (Newell, 1965). That the protein content of the food of deposit-feeders would warrant different levels of proteolytic enzymes from those found in suspension-feeders is debatable. However, it may be that gastric proteinases in some deposit-feeders play a significant role in separating potential food particles from substrate particles which have no food value, prior to endocytosis, as was suggested for *Macoma secta* (Reid & Rauchert, 1972). While this may also be the case for the deposit-feeding protobranchs it does not apply to other deposit-feeding members of the genus *Macoma*.

Only in the carnivorous septibranchs is there a positive relationship between diet and protein digestion. The family Cuspidariidae is the only group so far investigated which shows high levels of proteolysis. The diet consists of small copepods, ostracods, chaetognaths, polychaetes, etc. (Pelseneer, 1891; Yonge, 1928; Knudsen, 1970; Bernard, 1974), and the food is taken live (Reid & Reid, 1974). The major gastric proteolytic enzymes are trypsin and cathepsin B (Reid, 1977); *i. e.*, the same enzymes which are found in traces of the stomach of other bivalves. Thus, only a minor enzymological adaptation is involved, namely an increase in the synthesis and secretion rates, achievable by a simple gene duplication. In *Cardiomya* and *Cuspidaria* species the crystalline style is truncated, suggesting some attack by the gastric enzymes.

The Systematic Significance of Proteolytic Enzymes

There are a number of ways in which research into proteolytic enzymes might reveal their systematic significance. The first is the study of the primary structure of proteases of a given category. Although this would provide useful phylogenetic information about the bivalves and their affinities with other molluscs this expensive and time-consuming technique has not been applied. The second approach is the comparative study of protease zymograms; *i. e.*, the visualized patterns of electrophoretically separated enzyme extracts. The applicability of electrophoretic data to zoological systematics has been evaluated by Avise (1974). While a number of enzyme categories have been tested for their genetic or general systematic significance in bivalves (*e. g.*, Koehn & Mitton, 1972), and some of these studies have included categories of proteolytic enzyme (Levinton, 1975; Levinton & Fundiller, 1975) the information to date is insufficient to suggest clear systematic relationships. As Avise (*op. cit.*) points out, there are two schools of thought concerning the evolutionary significance of allozymes: the first is the selectionist view that each molecule has been tested by natural selection and is of positive value to the organism or population; the other view being the neutralist one which claims that some allozymatic variations have no particular superiority to others, but, since they are no less valuable, they remain as neutral mutations. Malacologists generally take the traditional selectionist view. However, if there is any truth in the neutralist view, then there is a possibility that some enzymological phenomena have no adaptive significance, but nevertheless have systematic significance. For example, in some members of the Pectinacea there is relatively high activity in the electrophoretically fast-running chymotrypsin. This might be a systematic phenomenon which lacks adaptive significance.

Protein Digestion and Rhythmic Physiological Events in Bivalves

J. E. Morton (1956) outlined phases of alimentary activity in *Lasaea rubra*. These were absorptive, intracellular digestive and excretory phases. The release of gastric proteinases was believed to be part of the excretory phase. B. S. Morton (1970) observed similar phases in *Cardium edule*, and inferred that these were digestive rhythms which correspond to tidal rhythms. He proposed that such rhythmic digestive phenomena were universal among bivalves, even those unaffected by the direct influence of the tide (Morton, 1973). Langton & Gabbott (1974) noted rhythmic changes in style pH, style protein, and amylase activity in *Ostrea edulis*, and concluded that these changes were modulated by the tide. However, they noted that the rhythms were lost following a period of continuous immersion. The pertinent literature has been more extensively reviewed by Owen (1974).

In my study of *Tresus capax* it was observed that gastric volume was at its lowest while animals were exposed and highest about 8 hours after submergence by the rising tide. Gastric pH was lowest in exposed animals and highest in submerged animals. The minor ebb, which did not expose the animals, had no obvious physiological effect.

It is particularly significant that the gastric proteolytic levels remained constant. This indicates an active release of enzymes as the animal feeds and the gastric volume increases. Otherwise the proteolytic activity would decrease with dilution.

The gastric pH changes are similar to those observed by Langton & Gabbott (1974) for oysters. The sequence of events outlined above may accord with Morton's hypotheses concerning rhythmic digestive phenomena in bivalves (Morton, 1973). However, the question of whether these events are endogenous, exogenous and modulated by the tide, or possibly synchronized by experimental artifact, remains open.

The Evolution of Protein Digestion in Bivalves

The range of categories of proteolytic enzymes present in bivalves is no different from that found in other invertebrates. In animals which have been closely examined most of the known invertebrate proteases have been found. The evolution of the endopeptidases is known to have been highly conservative in biochemical terms, and the view that animals, as they undergo adaptive radiation, encounter new diets and consequently evolve "new" digestive enzymes is fallacious with regard to the proteases. The range of peptide groupings in the most primitive protein substrate is the same as in the most highly evolved protein. Consequently, in the course of evolution, the need for a specifically novel category of protease is rarely necessary, though changes in the physiological environment might favour variants of pre-existing categories of enzyme.

While qualitative changes have not occurred in enzyme category, some innovative uses have been made by the bivalves of pre-existing enzymes, particularly in the use of cathepsin B for digestive purposes. In most organisms the lysosomes have a cathepsin complement responsible for autolysis, autophagy and general protein turnover. As indicated by seasonal changes in the relative levels of cathepsin in *Tresus capax* (Reid & Rauchert, 1976), cathepsin B has been turned to a digestive role and in the carnivorous septibranchs is employed for extracellular gastric digestion. A large quantitative change has been made by the septibranchs in response to their high protein diet. If the septibranchs were regarded as a primitive group of bivalves, and considering the protobranch condition, it might be concluded that the relatively high proteolytic capacity of the stomach is characteristic of primitive bivalves. However, considering the relative simplicity of the quantitative evolutionary step and the absence of qualitative differences it is impossible to justify such a conclusion, and, in general, in the absence of information on primary structure, proteases and the process of protein digestion are poor indicators of the direction of bivalve evolution.

SUMMARY

1. There are no systematically significant qualitative differences in the distribution of proteolytic enzymes in bivalves. Members of the Pectinacea have prominent, electrophoretically fast-running chymotryptic enzymes which may be of quantitative systematic significance. Electrophoretic zymograms of proteases may prove to be useful in determining systematic relationships.
2. No definitive adaptive relationships can be traced between protein digestion and gastric morphology. Herbivorous suspension-feeding bivalves have low proteolytic capacities. Carnivorous septibranchs have high proteolytic capacities. Deposit-feeding bivalves range from low to intermediate proteolytic capacities. The adaptive significance of the latter case is not clear.
3. Gastric volume, gastric pH, gastric protease secretion and digestive diverticular proteolytic activity appear to vary in relation to tidal events. It is not known if these are exogenous or endogenous rhythms.
4. The evolution of protein digestion in bivalves has been biochemically conservative. Proteases found in bivalves occur universally in the animal kingdom. Since quantitative changes are relatively simple evolutionary events, and since nothing is known of the primary structure of bivalve proteases, proteases and the process of protein digestion are poor indicators of phylogenetic relationships.

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Reproductive Biology of *Colus stimpsoni*

(Prosobranchia : Buccinidae)

I. Male Genital System [1]

BY

DAVID L. WEST [2]

(5 Plates; 2 Text figures)

INTRODUCTION

THE BUCCINIDAE IS A large family, generally occurring in temperate latitudes, and many of its members undergo larval development within the egg capsules, emerging as juveniles (RADWIN & CHAMBERLIN, 1973; PONDER, 1974). A few studies have dealt with the reproductive biology of this family (DAKIN, 1912; FRETTER, 1941; HOUSTON, 1976) and the larval stages and egg capsules have been described for a few species (PORTMANN, 1926, 1927; THORSON, 1935, 1940; FRETTER & GRAHAM, 1962; WEST, 1973).

Previous studies on the reproductive system have indicated a similarity in the organization of these structures (DAKIN, 1912; FRETTER, 1941; FRETTER & GRAHAM, 1962; HOUSTON, 1976), but these studies mainly concern the female genital system. The male system, particularly in the genus *Colus*, has been neglected. It is of value to study the male genital system in the genus *Colus* for comparative functional and phylogenetic relationships.

The present study concerns the male reproductive system in *Colus stimpsoni* (Mörch, 1867).

MATERIALS AND METHODS

Numbers of *Colus stimpsoni* were collected at Cobscook State Park, Edmunds, Maine, and at Eastport, Maine, and maintained in running seawater aquaria at the Marine Science Institute, Northeastern University, Nahant, Massachusetts. In the laboratory, *C. stimpsoni* was supplied *Littorina littorea* (Linnaeus, 1758) and, occasionally, *Polinices triseriata* (Say, 1826), *Lunatia heros* (Say, 1822), and *Thais lapillus* (Linnaeus, 1758) as food items (RISER, 1969; WEST, 1973).

For light microscope studies, tissues were excised from freshly opened, unrelaxed animals and fixed for 1 - 24 hours in the following: (a) Hollande-Bouin's, (b) Bouin's, (c) alcohol-formalin-acetic acid, (d) buffered formalin (pH 7.4), (e) seawater-Bouin's (WALKER & MACGREGOR, 1968), or (f) buffered glutaraldehyde (pH 7.4). Following fixation, tissues were dehydrated through a graded series of ethanol and embedded in polyester wax (STEEDMAN, 1960). Sections were cut 3 - 10 μm in thickness and mounted on albuminized slides. Sections were stained with the following: (a) Heidenhain's iron hematoxylin, (b) Pollack's rapid trichrome, (c) Heidenhain's azan, or (d) GABE's (1968) modification of Gomori's trichrome. LEHMAN's (1965) polychrome was used for localization of various molecular groups.

For cytochemical tests, tissues were excised from freshly opened, unrelaxed animals and fixed at either 5 - 6° C or room temperature in the following: (a) buffered formalin (pH 7.4), (b) Bouin's or (c) buffered glutaraldehyde (pH 7.4). Following fixation, the tissues were dehydrated in a graded series of ethanol or acetone and embedded in polyester wax or in paraffin (45° C M. P.). Sections were cut 4 - 6 μm in thickness and mounted on unalbuminized slides. The wax was removed from the sections with absolute acetone and the sections were air dried.

The periodic-acid-Schiff (PAS) technique or Best's carmine was used to test for the presence of polysaccharides. The presence of glycogen in PAS positive sections was determined with salivary amylase controls incubated at 37° C for 2 hours. To test for acid mucopolysaccharides, the alcian blue (pH 1.0 and 2.3) or colloidal iron techniques were employed. The acid haematein technique was used to test for the presence of phospholipids. Localization of DNA and RNA was by the Feulgen reaction or by the methyl green-pyronin Y method. Protein groups were stained by LEHMAN's (1965) polychrome method or by mercuric bromphenol blue. Acid and alkaline phosphatases were localized by Gomori's lead nitrate technique (HUMASON, 1967) or by the azo-coupling method (PEARSE,

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1968). Localization of glucose-6-phosphatase was by the azo-coupling method (Pearse, *op. cit.*). No difference in enzyme activity was found between tissues fixed in buffered glutaraldehyde or buffered formalin, nor was enzyme activity inhibited by embedding in polyester wax.

For electron microscopy, tissues were excised from freshly opened, unrelaxed animals, and fixed for 1 hour in cold (5 - 6° C) primary fixative. The primary fixative was prepared just before use and contained: 3% glutaraldehyde, 1% formaldehyde, made from paraformaldehyde (Karnovsky, 1965), 0.1 M phosphate buffer (pH 7.4), 2 - 3% NaCl, and 2 - 4% sucrose. Dimethylsulfoxide (0.2%) was added to aid penetration. Following primary fixation, the tissue was washed for 1 hour in cold 0.1 M phosphate buffer (pH 7.4) which contained 6 - 8% sucrose. The tissue was post-fixed at room temperature with 1% OsO_4 in 0.1 M phosphate buffer (pH 7.4). Following post-fixation, the tissue was washed for ½ hour in cold 0.1 M phosphate buffer (pH 7.4) and dehydrated in a graded series of cold acetone or ethanol. The tissue was allowed to come to room temperature in 95% acetone or ethanol, and final dehydration was at room temperature. The tissue was embedded in Epon or an Epon-Araldite mixture (Burke & Geiselman, 1971; Geiselman & Burke, 1973). Thin sections were double stained with aqueous uranyl acetate (Watson, 1958) and lead citrate (Reynolds, 1963), and examined with a Zeiss EM 9-S electron microscope.

RESULTS

General Morphology

The testis is yellow to orange-yellow in color and spreads over the digestive gland in the ultimate and in part of the penultimate whorls of the shell (Figures 1a, 1b). In large males it may cover as much as ½ of the digestive gland. The seminiferous tubules are generally separated from the digestive gland but they occasionally intrude between the tubules of the latter. The seminiferous tubules join to form a single genital duct which passes along the columellar side of the visceral mass, across the right side of the body and exits through the penis. The penis is flattened laterally and is situated just behind the right tentacle (Figure 1a). It varies from 2 to 5 cm in length and is directed posteriorly when not projected.

The posterior portion of the genital duct, the vas deferens, lies superficially on the visceral mass. It is convoluted and the thin walls contain a few muscle fibers. The posterior ⅔ of the vas deferens are filled with spermatozoa throughout the year and form the seminal vesicle (Figures 1a, 1b). The anterior ⅓ is the renal vas deferens (Figure 1b) which is separated from the seminal vesicle by a small sphincter and straightens at the posterior extremity of the mantle cavity. It opens into the glandular pallial portion

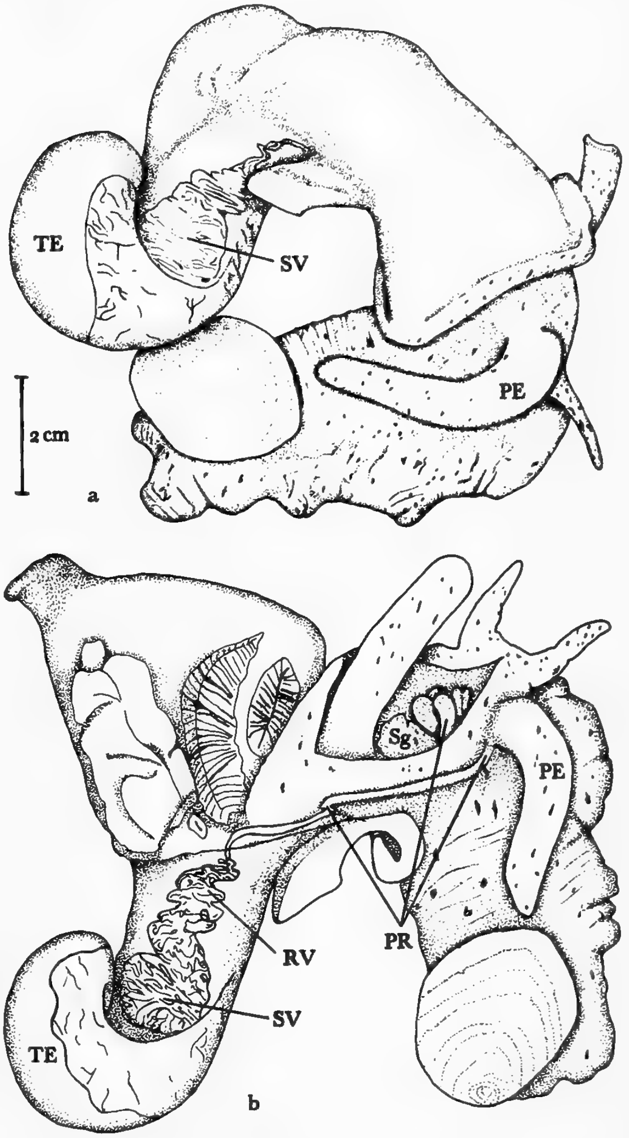


Figure 1

Male *Colus stimpsoni*: a – whole animal with shell removed, b – dissection with mantle cut along right edge and reflected to the left side of the body; proboscis removed from its cavity and the floor of the cavity cut to expose the salivary gland and coiled prostate

PE – penis PR – prostate RV – renal vas deferens
Sg – salivary gland SV – seminal vesicle TE – testis

of the genital duct. At the junction of the renal vas deferens and pallial portion, the duct makes an S-shaped turn and is slightly constricted (Figure 2). Near this constriction, at the posterior limit of the mantle cavity, the renal vas deferens gives off a small diverticulum which passes posteroventrally and opens into the mantle cavity (Figure 2). No functional gonopericardial duct nor any remnant of this duct is found in the male.

The pallial portion of the genital duct, beginning near the posterior limits of the mantle cavity, is muscular and glandular along its entire length and functions as the prostate. The prostate passes just beneath the body wall to the base of the penis where it turns medially and passes into the body. Along the body, the prostate projects as a prominent ridge near the mantle floor (Figure 1b). Within the body, the prostate coils among the lobes of the right salivary gland (Figure 2). It passes outward through the body wall adjacent to its point of entrance and continues through the penis to open at the tip of the penis (Figure 2). Within the penis, the duct is centrally located.

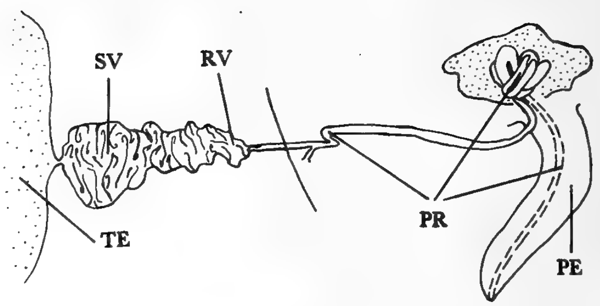


Figure 2

Male reproductive system: line posterior to diverticulum (D) represents the posterior limits of mantle cavity
PE – penis PR – prostate RV – renal vas deferens
Sg – salivary gland SV – seminal vesicle
TE – testis (not drawn to scale)

Histology

Testis: The testis and visceral mass are covered by a single layer of cuboidal epithelium, the pallial epithelium. Subjacent to the pallial epithelium is a thin basal lamina (0.15 - 0.50 μm thick) and a layer of loose connective tissues and muscle fibers. Seminiferous tubules (Figure 3) end blindly at the surface of the testis and are generally oriented perpendicular to the spiral axis of the shell. The seminiferous tubules measure 100 - 800 μm in diameter and are delineated by a layer of connective tissue and a thin basal lamina. The basal lamina is composed of a compact layer of fibers and varies from 0.4 to 0.6 μm in thickness.

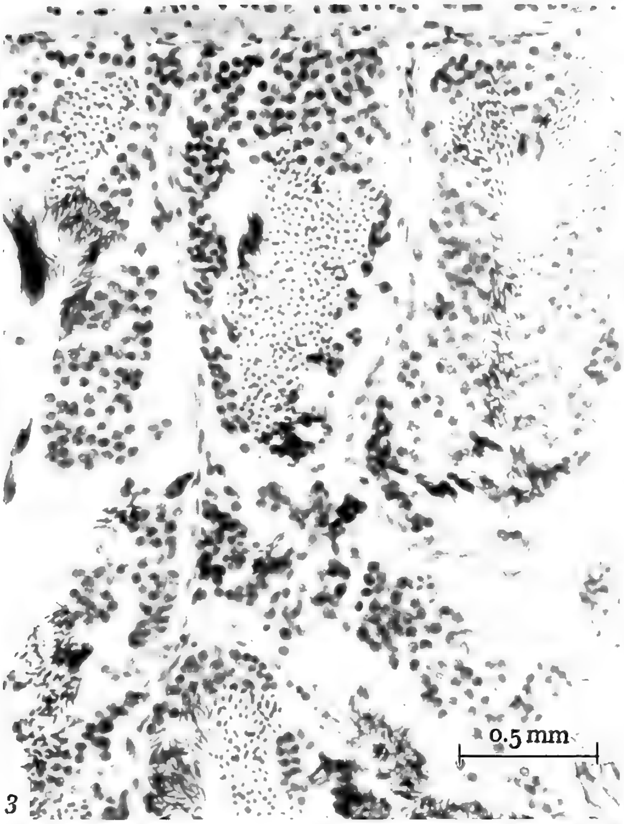
Beneath the connective tissue on the periphery of the seminiferous tubule, a layer of lipid-rich accessory (basal) cells surrounds the spermatogenic cells. These accessory cells are similar to the basal cells in *Goniobasis laqueta* (Say) described by Woodward (1935). The layer of basal cells is irregular in thickness, varying from one small cell in starved animals to one large cell or 2 - 3 smaller cells in well-fed animals, and is occasionally interrupted by spermatogenic cells.

Explanation of Figures 3 to 6

Figure 3: Cross section of testis showing seminiferous tubules
Figure 4: Basal cell within seminiferous tubule.
B – basal lamina; L – lipid; N – nucleus
Figure 5: Type I accessory cell.
I – inclusion; N – nucleus; R – rough endoplasmic reticulum
Figure 6: Type II accessory cell.
D – dense granules within nucleoplasm; I – inclusion; N – nucleus

Explanation of Figures 7 to 11

Figure 7: Type II accessory cell with fields of small tubules (*) and small vesicles with electron-dense granules (arrows).
Figure 8: High magnification of small tubules (arrows) shown in Figure 7.
Figure 9: High magnification of vesicles with electron-dense granules (arrows) shown in Figure 7.
R – rough endoplasmic reticulum
Figure 10: Type II accessory cell with flagella (arrows) and dense inclusion (I).
Figure 11: Cross section through seminal vesicle (S) and renal vas deferens (V).



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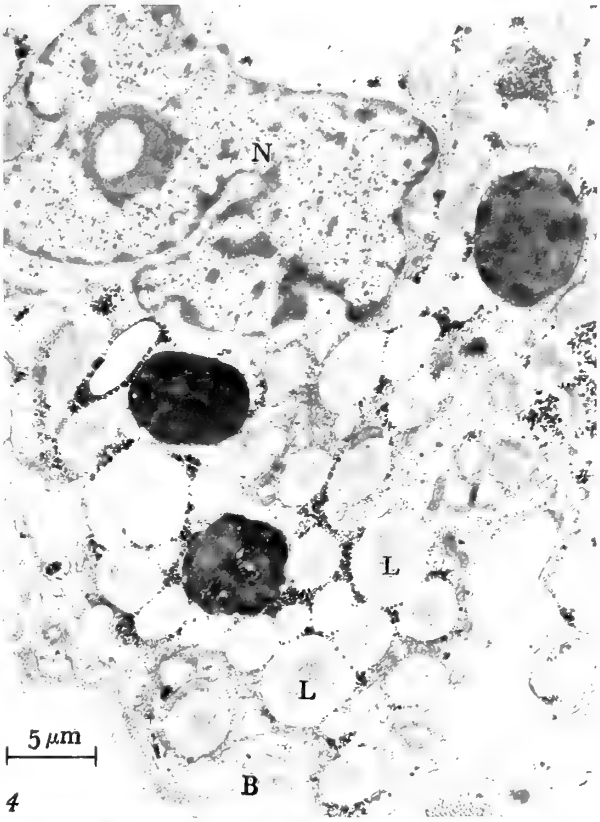

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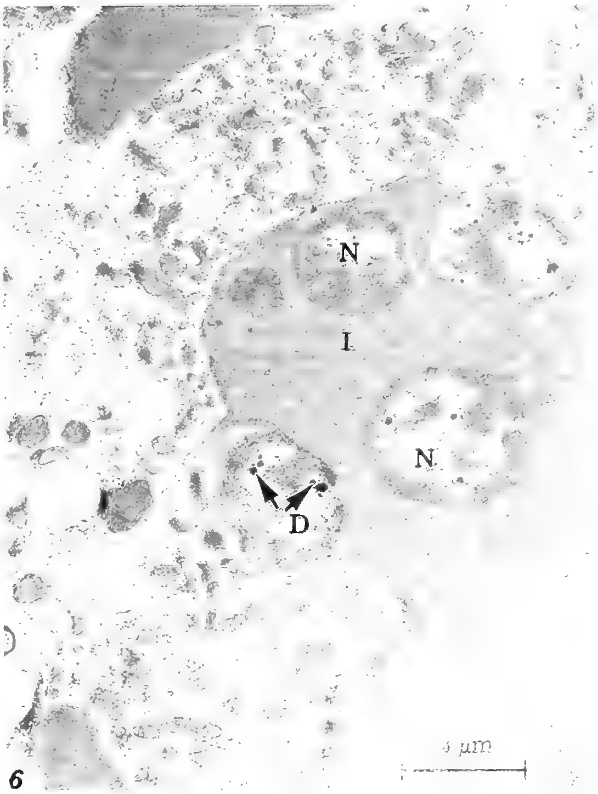

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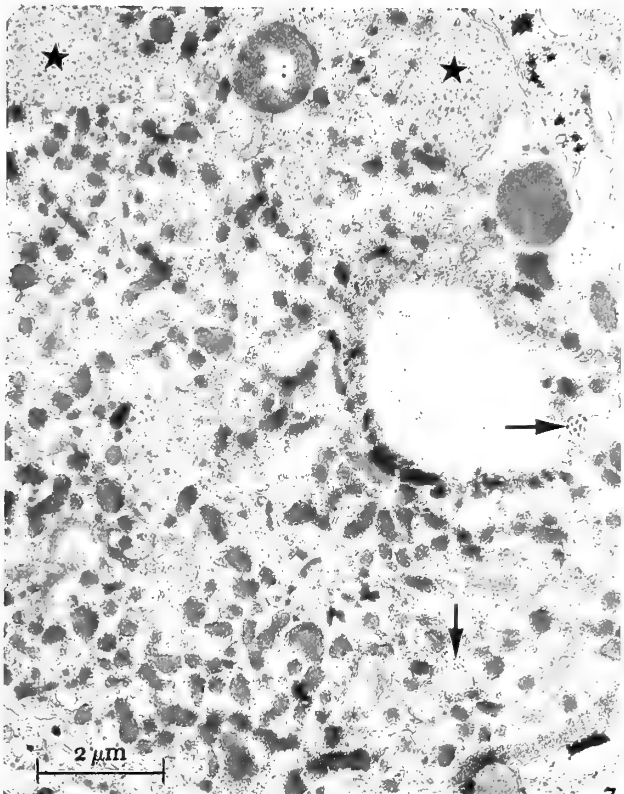

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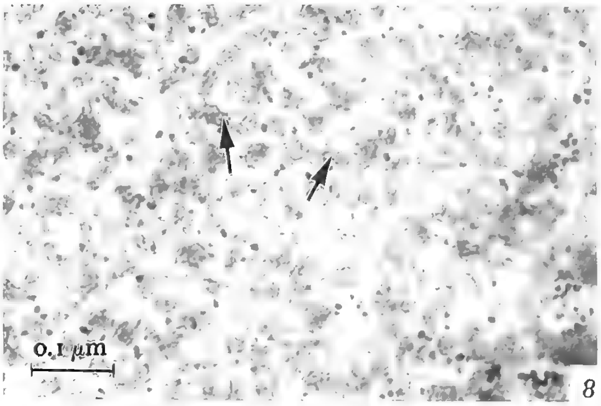

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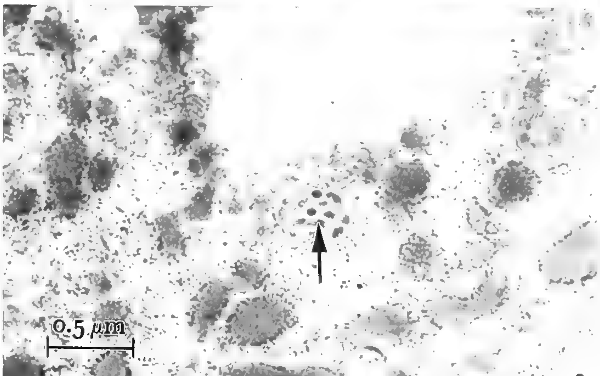

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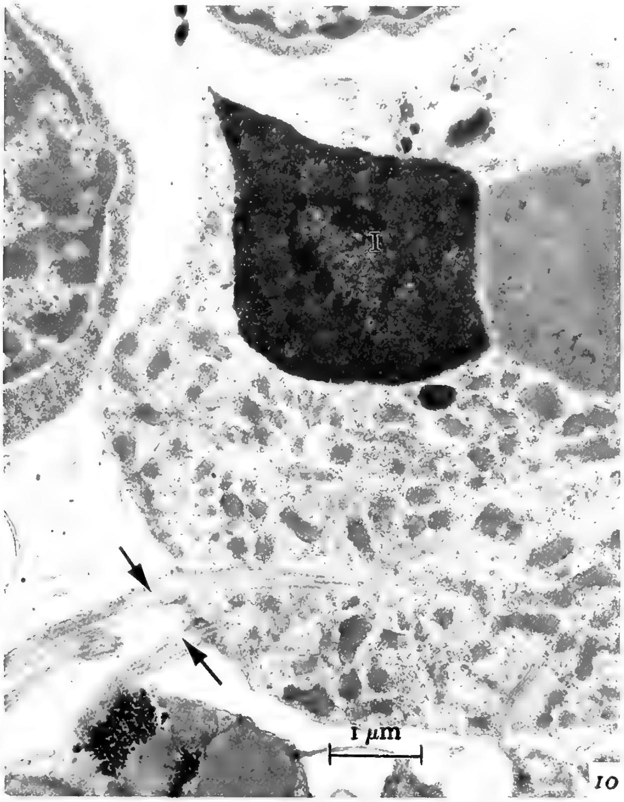

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11

The cytoplasm of the basal cells (Figure *4*) contains glycogen granules and is dominated by lipid droplets which are dissolved during standard histological procedures but are retained with electron microscope techniques. Basal cells are irregular in shape, 10 - 25 µm in length, and contain few organelles. Mitochondria are cylindrical, measuring 2 - 3 µm by 0.2 - 0.4 µm. Occasionally residual bodies are observed in the cytoplasm. The nucleus (7 - 15 µm in length) is lobed and contains 1 or occasionally 2 nucleoli. The chromatin is distributed around the periphery of the nucleus and small clumps of chromatin are scattered throughout the nucleoplasm. The nuclear envelope is perforated by a few pores. The nucleolus is heterogeneous with a light, granular medulla and a dense, granular cortex.

Spermatogenic cells and accessory cells fill the seminiferous tubules subjacent to the layer of basal cells. In sections stained with Heidenhain's azan, accessory cells contain an intensely staining material and are easily distinguished from spermatogenic cells. Two types of accessory cells can be distinguished by their nuclear morphology. They are here designated as type I and type II. The type I accessory cell has a single nucleus (Figure *5*); whereas the type II cell is multinucleated (Figure *6*). From squash preparations and sectioned material, both types of accessory cells appear to be polyploid. Accessory cells occur in groups (4 - 24 cells per group) within the tubules. Each group consists of one type of accessory cell and is usually near the periphery of a tubule. The groups are irregularly distributed along the length of a tubule and are not associated with any particular stage of spermatogenesis. Generally, type II cells are more abundant than type I cells.

The type I cell (Figure *5*) is irregular in shape, measuring 7 - 12 µm in length and is mostly filled with membrane-limited inclusions which stain intensely red with Heidenhain's azan. The nucleus measures 5 - 8 µm in diameter and the chromatin is condensed into large clumps which are distributed around the periphery of the nucleus and within the granular nucleoplasm. The nucleus is lobed and is surrounded by the membrane-bounded inclusion. The small amount of cytoplasm contains numerous free ribosomes and a few small mitochondria. The cisternae of the rough endoplasmic reticulum are enlarged and filled with an electron-dense, homogeneous matrix. The contents of the cisternae accumulate and form a large inclusion which occupies nearly the entire cell volume.

Type II cells contain an intensely staining material. However, the material stains lavender or blue with Heidenhain's azan. The type II cell (Figure *6*) contains 2 relatively large nuclei (4 - 6 µm in diameter) and 3 - 6 smaller nuclei (1 - 3 µm in diameter). The chromatin is condensed into a thick patchwork with small amounts of granular nucleoplasm. The nucleoplasm contains numerous electron-dense granules which vary from 0.05 to 0.3 µm in diameter (Figure *6*). Generally, the nuclei are embedded in the large inclusion. The cytoplasm contains numerous free ribosomes and the Golgi complex. The cisternae of the rough endoplasmic reticulum are discontinuous and are filled with a homogeneous electron-dense substance which is similar in appearance to the material in the inclusion. Localized areas of small tubules which contain a homogeneous material occur within the cytoplasm (Figure *7*). These short tubules measure between 0.06 and 0.15 µm in diameter (Figure *8*). The cytoplasm also contains membrane-bounded vesicles which contain electron-dense, rod-shaped granules (Figure *9*). These vesicles measure 0.2 - 0.4 µm in diameter and the granules measure about 0.05 µm in diameter. Occasionally, type II cells have flagella which vary in number from 1 to 12 and also large, electron-dense inclusions which are similar to large residual bodies or pycnotic nuclei (Figure *10*). These flagella and inclusions may be from ingested germ cells.

Seminal Vesicle and Renal Vas Deferens: The convoluted posterior portion of the single genital duct is embedded in connective tissue and is separated from the digestive gland. The loops of the duct are generally perpendicular to the columellar axis and these loops are separated from one another by loose connective tissue. The duct varies from 100 to 800 µm in diameter and is surrounded by a thin layer of muscle fibers (2 - 5 µm thick) which are generally circularly arranged. The loops of the duct overlap one another such that portions of the renal vas deferens are found in the seminal vesicle region (Figure *11*).

The seminal vesicle and the renal vas deferens are lined with a columnar epithelium of varying height. In the seminal vesicle, the epithelial cells (Figure *12*) rest on a substantial basal lamina (0.6 - 1.1 µm thick). The epithelium varies between 10 and 20 µm in thickness and is composed of 2 cell types. One type (ciliated cell) has long cilia and simple, occasionally branched, microvilli on the apical surface (Figure *12*). The second type (microvillar cell) has only long, anastomosing microvilli on the distal surface (Figure *12*). The cytoplasm of both cell types contains numerous small mitochondria (about 0.3 µm in diameter) and several large residual bodies. Numerous Golgi lamellae are distributed throughout the cytoplasm. The microvillar cell contains numerous small, membrane-bounded vesicles which are filled with fine, electron-dense granules. The rough endoplasmic reticulum of the microvillar cell is more abundant than that of the ciliated cell. These cisternae are discontinuous and filled with a homogeneous matrix.

The epithelium of the renal vas deferens (Figure *13*) is thicker (15 - 30 μm) than that of the seminal vesicle. The undulating basal lamina is also slightly thicker (0.9 to 1.2 μm). Microvillar cells are absent but the ciliated cells are similar to those of the seminal vesicle.

The diverticulum (Figure *14*), which branches from the renal vas deferens, is histologically similar to the renal vas deferens and is about 1 mm long. This short duct is ciliated and opens into the mantle cavity.

Prostate: The anterior portion of the genital duct passes along the body wall just beneath the epidermis and is histologically similar along its entire length. It is yellowish in color and functions as the prostate (Figure *15*). The epithelium is 15 - 50 μm in height and is composed of ciliated columnar and secretory cells which rest on a thin basal lamina. The ciliated cells (Figure *16*) of the epithelium extensively interdigitate with each other and their apical surfaces have numerous cilia and pseudopodial extensions. The cytoplasm contains numerous rod-shaped mitochondria, and is less electron-dense than the neighboring secretory cells. The cytoplasm also contains large clumps of glycogen granules. The nuclei of ciliated cells are lobed and generally elongated in the long axis of the cells.

The secretory cells of the epithelium appear similar in shape to "goblet" cells and are filled with numerous membrane-bounded secretory vesicles (Figure *17*). These vesicles are irregular in outline and are filled with electron-dense granules. Lipid droplets abut against these granules and, generally, are hemispherical in shape. The cytoplasm of secretory cells is dominated by the secretory vesicles, but it also contains rough endoplasmic reticulum and a well developed Golgi complex. The cisternae of the rough endoplasmic reticulum are filled with an electron-dense matrix. The nucleus is irregular in outline and generally contains 2 nucleoli.

A layer of circular muscle (0.8 - 1.2 μm in thickness) lies beneath the epithelium and is interrupted at intervals by secretory cells which are more prominent during periods when males are reproductively active (Figure *15*). The secretory cells are oriented radially within the muscle layer. However, there is no apparent orientation to the secretory cells on the periphery of the duct.

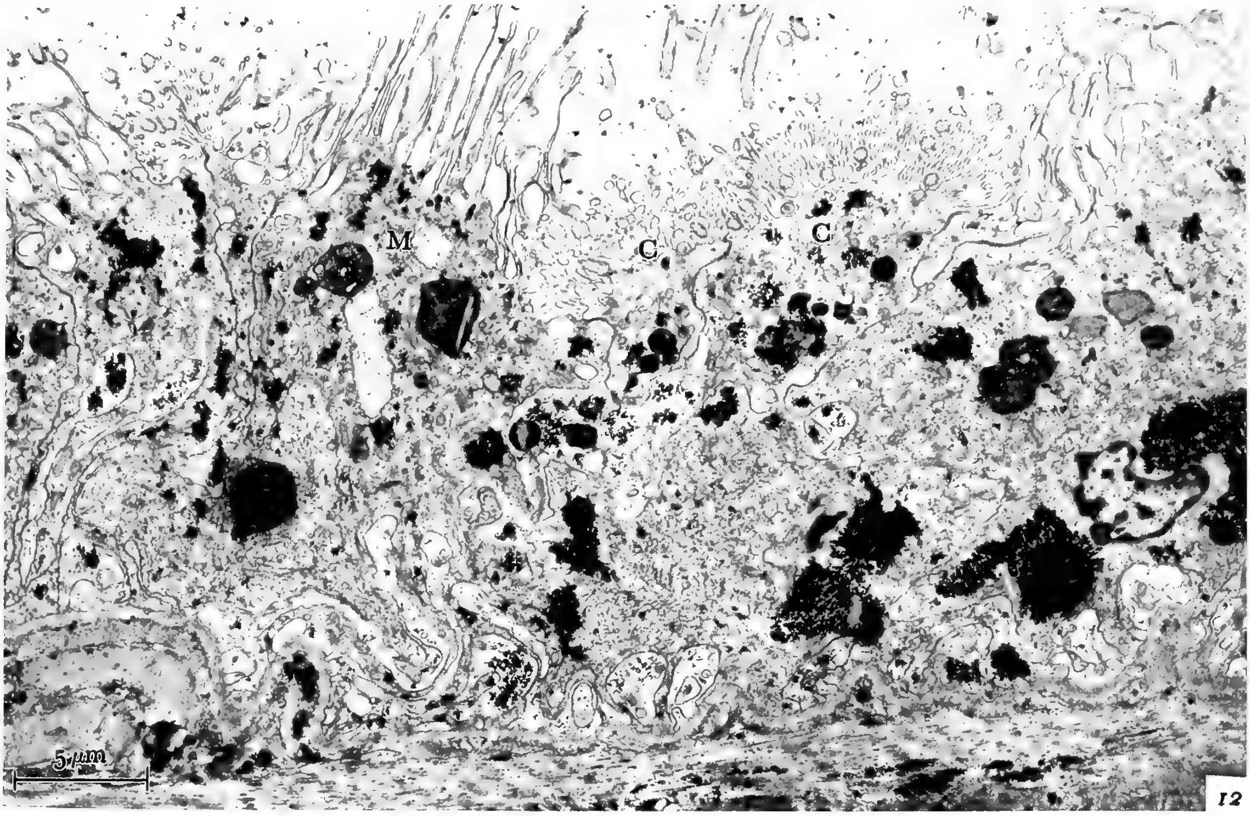
The secretory cells are of 2 types and are here designated as type 1 and type 2. Judging from electron micrographs, type 1 and type 2 secretory cells appear to undergo a maturation sequence. In early type 1 cells (Figure *18*) the cytoplasm is filled with rough endoplasmic reticulum and the Golgi complex. The cisternae of the rough endoplasmic reticulum are discontinuous and dilated. These cisternae are filled with a homogeneous matrix which is slightly less electron-dense than the surrounding cytoplasm. In the middle stage of type 1 cell maturation (Figure *18*) the rough endoplasmic reticulum becomes vesiculated and the cisternae are filled with a dispersed granular material. The lamellae of the Golgi complex are elongated and flattened. Membrane-bounded vesicles which contain an electron-dense material appear in the cytoplasm. The mature type 1 secretory cell (Figure *19*) contains numerous membrane-bounded vesicles. These vesicles contain a heterogeneous, electron-dense matrix which surrounds a small area of electron-dense granules. These small granules are clumped together and this clump is separated from the surrounding matrix by an electron-lucent area. Microtubules occupy much of the remaining cytoplasm of mature type 1 cells and are aligned in the long axis of the cell.

Explanation of Figures *12*, *13*

Figure *12*: Epithelium of seminal vesicle.
C – ciliated cells; M – microvillar cells
Figure *13*: Epithelium of renal vas deferens.

Explanation of Figures *14* to *17*

Figure *14*: Cross section through posterior region of mantle cavity (M) and diverticulum (D) V – renal vas deferens
Figure *15*: Cross section through prostate.
B – body wall; arrows – secretory regions
Figure *16*: Ciliated cell of prostate epithelium.
Figure *17*: Epithelium of prostate.
arrows – interdigitating cells
arrow – lipid droplet; g – clump of glycogen particles within ciliated cell; S – secretory cell



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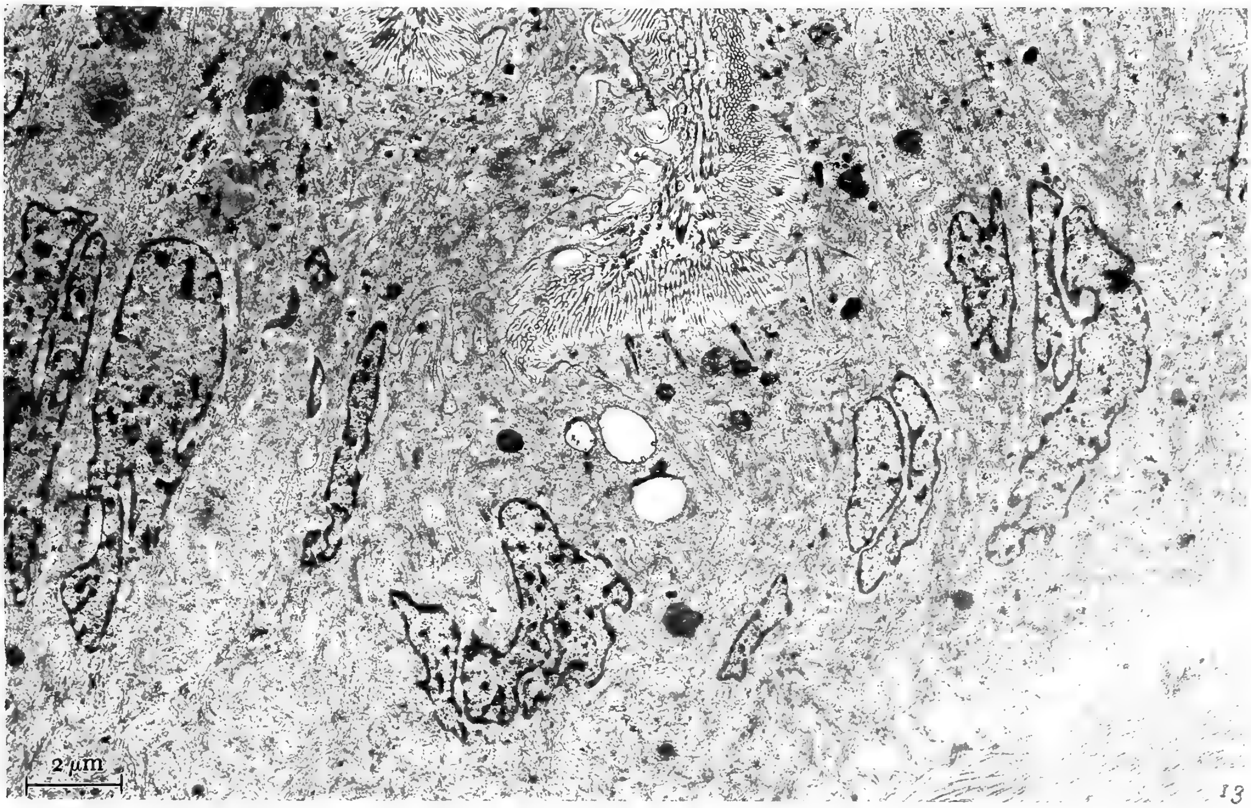

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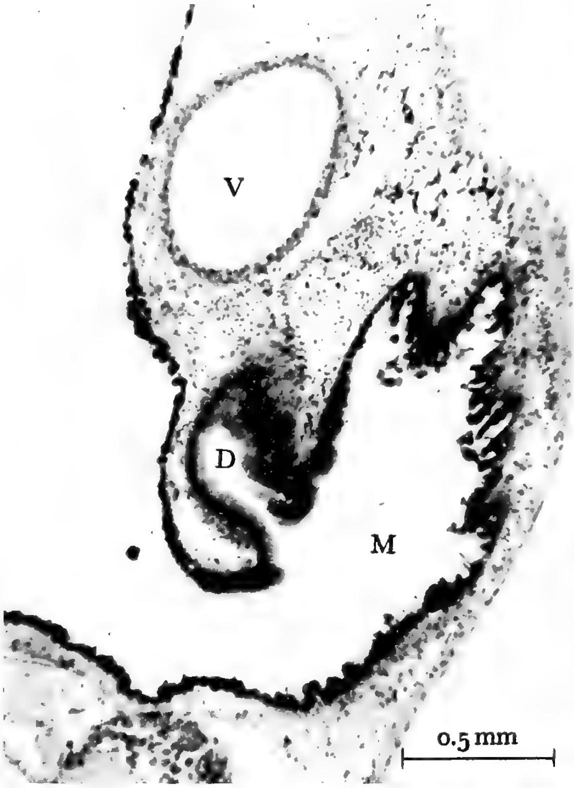

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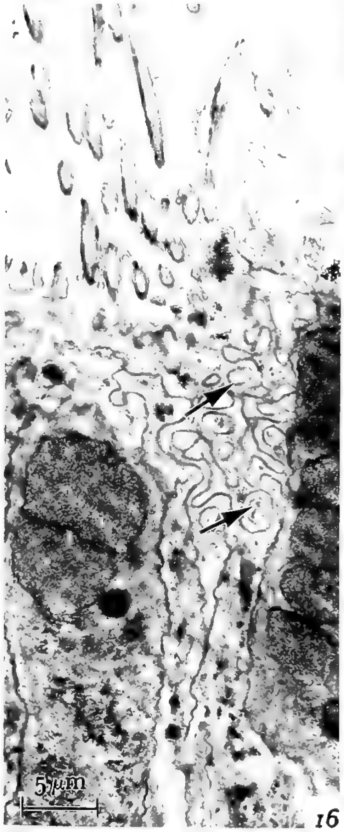

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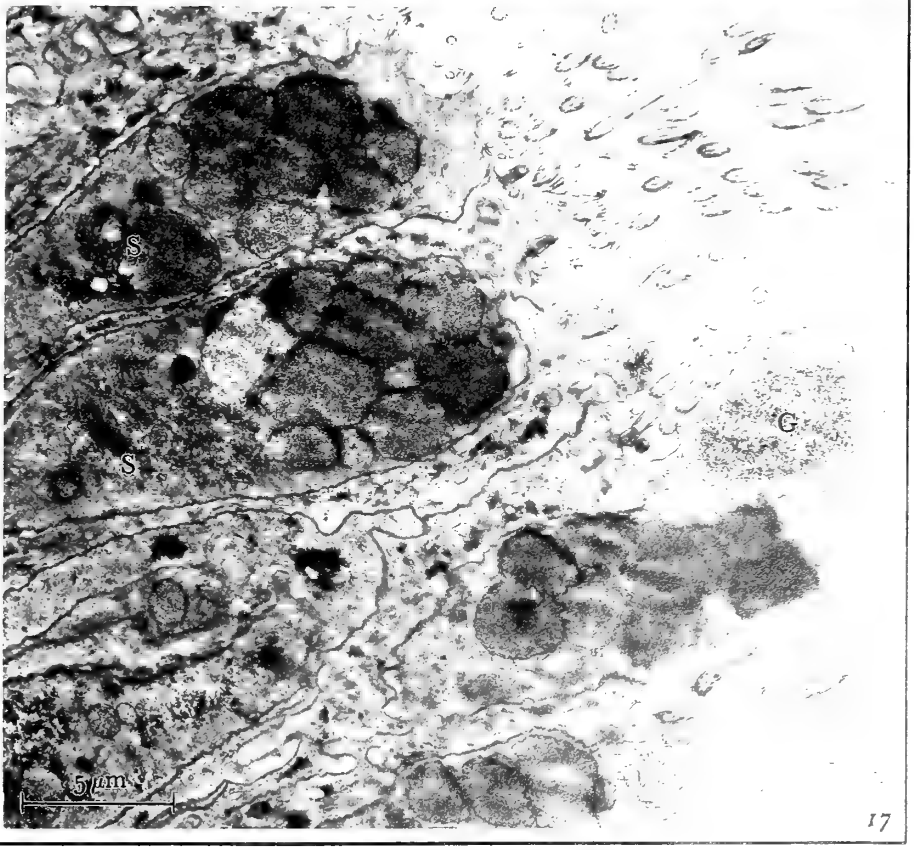

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Type 2 cells also appear to undergo a maturation sequence similar to type 1 cells. Young type 2 cells (Figure *20*) are filled with small membrane-bounded vesicles which contain a granular material. The mitochondria are rod-shaped and small. Elements of the Golgi complex are scattered among the vesicles. Mature type 2 cells (Figure *21*) are filled with larger vesicles which contain a flocculum and a few vesicles containing a heterogeneous material. The Golgi complex of older type 2 cells is composed of flattened lamellae and the cisternae are filled with an electron-dense material and small vesicles are associated with the tips of the Golgi lamellae.

Cytochemistry

Testis: Results from polyester wax sections stained with Lehman's polychrome indicate the specific localization of a number of macromolecular groups. The differential staining suggests the following: spermatogonia and primary spermatocytes are rich in RNA; the vacuoles of type I and type II accessory cells contain an acid or neutral protein; the basal cells contain a polysaccharide.

Basal cells contain granules which stain with PAS and Best's carmine. The basal cells are also positive for glucose-6-phosphatase tests. The inclusions of type I accessory cells stain positively with bromphenol blue. Type I cells with large inclusions retain a reddish color with this dye, suggesting the protein is of an acidic nature. Type I accessory cells concentrate Sudan black, but react negatively for phospholipids. These results suggest that the inclusion contains a lipid moiety and the contents of the inclusion may be a lipoprotein. In young type I cells, a few granules which stain with PAS are present. Type I cells react negatively to both acid and alkaline phosphatase cytochemistry. Type II accessory cells give similar results to type I cells. The inclusion of the type II cell probably contains a lipoprotein which is not a phospholipid and the protein moiety is probably acidic in nature. Type II cells also give a positive reaction for acid phosphatase, but negative for alkaline phosphatase. Type II cells are negative to the PAS technique. Table 1 summarizes the results of cytochemical tests for specific molecular groups.

Seminal Vesicle and Prostate: The results obtained from sections stained with Lehman's polychrome technique suggest the presence of mucopolysaccharides and proteins in the secretory cells of the seminal vesicle and prostate. Specific cytochemical tests suggest that cells of the seminal vesicle contain glycogen and sulfonated, acidic mucopolysaccharides. The type I secretory cells of the prostate contain mucopolysaccharides which are probably sulfonated and acidic in nature. Type 2 secretory cells are rich in sulfonated acidic mucopolysaccharides. Type 1 cells also stain positively for acidic or neutral protein which suggests that the secretory products of the type 1 cells are acidic proteinaceous mucopolysaccharides. Table 1 gives the results of specific cytochemical tests of the seminal vesicle and prostate.

Table 1

Results of cytochemical techniques of the testis, seminal vesicle and prostate

	Testis (Accessory Cells)				
Technique	Basal Cell	Type I	Type II	Seminal Vesicle	Prostate
Alcian Blue (pH 1.0)	−	−	−	++	+++
Alcian Blue (pH 2.3)	−	−	−	++	++
Acid Haematein	−	−	−	−	−
Best's Carmine	+++	±	−	+	+
Bromphenol Blue	±	+	+	+	++
PAS	+++	+	−	++	++
Sudan Black	−	+	+	+	+
Thionin	−	−	−	+	+++
Acid Phosphatase	−	−	+	±	±
Alkaline Phosphatase	−	−	−	±	±
Glucose-6-Phosphatase	+	−	−	−	−

+, ++, +++, increasing degrees of positive staining intensity; −, negative reaction; ± questionable reaction

DISCUSSION

The reproductive system of *Colus stimpsoni* conforms to the fundamental plan described for other neogastropods (Dakin, 1912; Fretter, 1941; Fretter & Graham, 1962; Ponder, 1974; Houston, 1971,1976). In the male genital system of neogastropods, the genital duct may be divided into a posterior thin-walled portion which connects to the gonad, and a glandular, pallial portion which begins at the posterior limits of the mantle cavity. The thin-walled portion generally consists of a coiled, upper vas deferens which may be modified to form a sperm-storing seminal vesicle, and a lower, straight portion, the renal vas deferens (Fretter, *op. cit.*; Ponder, *op. cit.*). In some neogastropod species, areas of the seminal vesicle may also function to ingest sperm (Fretter, *op. cit.*; Smith, 1967). The renal vas deferens opens into the pallial portion which is lined with prostatic tissue. The prostatic tissue may be confined to a localized area (the prostate gland) or may be found along the entire duct.

In *Colus stimpsoni* both upper and lower portions of the vas deferens are convoluted. However, the renal vas deferens is not looped to the extent of the seminal vesicle. Also, sperm-ingesting areas within the seminal vesicle were not observed. Prostatic tissue in *C. stimpsoni* is found along the entire pallial portion of the genital duct and also lines the duct within the penis. The unusual condition of the prostate entering the body and coiling among the lobes of the salivary gland has not been reported for other neogastropods.

In *Colus stimpsoni*, as in most animals, the spermatogenic tissue is confined to compartments which are separated from somatic tissue. These compartments, the seminiferous tubules, contain accessory cells in addition to the germ cells. The accessory cells in *C. stimpsoni* are of 3 types: basal cells, type I and type II cells. Basal cells are generally restricted to the periphery of the seminiferous tubule and evidence from light and electron microscopy suggests that these cells serve a nutritional function. The increases in the number and size of basal cells in relation to an increase in the amount of food available to the snail suggest that these cells may store nutriments, probably in the form of lipids or fatty acids. Basal cells may provide nutriments for the developing germ cells.

The type I and type II accessory cells appear to be endopolyploid. In type I cells, the nuclear material is confined to 1 or occasionally 2 nuclei; in type II cells the chromatin is divided into several nuclei of unequal sizes. Cytochemical and ultrastructural evidence indicates that these accessory cells synthesize proteins and store these products. The type II cell may also ingest abnormal or degenerating germ cells. This function is suggested by the presence of multiple flagella within these cells and the cytoplasmic inclusions which are reminiscent of residual bodies with pycnotic nuclei. The type II cells also show acid phosphatase activity. Type I and type II accessory cells in *Colus stimpsoni* may function in providing large amounts of proteins for gamete development.

Endopolyploid cells have been reported in various tissues of gastropods and in the ovotestis of pulmonates (Babrakzai & Miller, 1974). Babrakzai & Miller postulated that endopolyploid cells provide high rates of protein synthesis for rapid use by developing gametes in the ovotestis of pulmonates. Results from the present study are consistent with this postulation.

SUMMARY

The male genital duct in *Colus stimpsoni* consists of a thin-walled posterior portion and a glandular, pallial portion. The posterior portion is convoluted and consists of the seminal vesicle and the renal vas deferens. In *C. stimpsoni*, the renal vas deferens is convoluted, unlike some other neogastropods. The pallial portion of the genital duct is lined with prostatic tissue along its entire length and functions as the prostate. The prostate passes into the body at the base of the penis and coils among the lobes of the right salivary gland. It then passes back out of the body near its point of entrance and enters the penis. The prostate is centrally located within the penis. At the junction of the renal vas deferens and prostate, a short diverticulum arises from the renal vas deferens and

Explanation of Figures *18* to *21*

Figure *18*: Early stage (1) and middle stage (2) of maturation of type 1 secretory cell.

R – rough endoplasmic reticulum; V – vesicle

Figure *19*: Mature type 1 secretory cells of prostate.

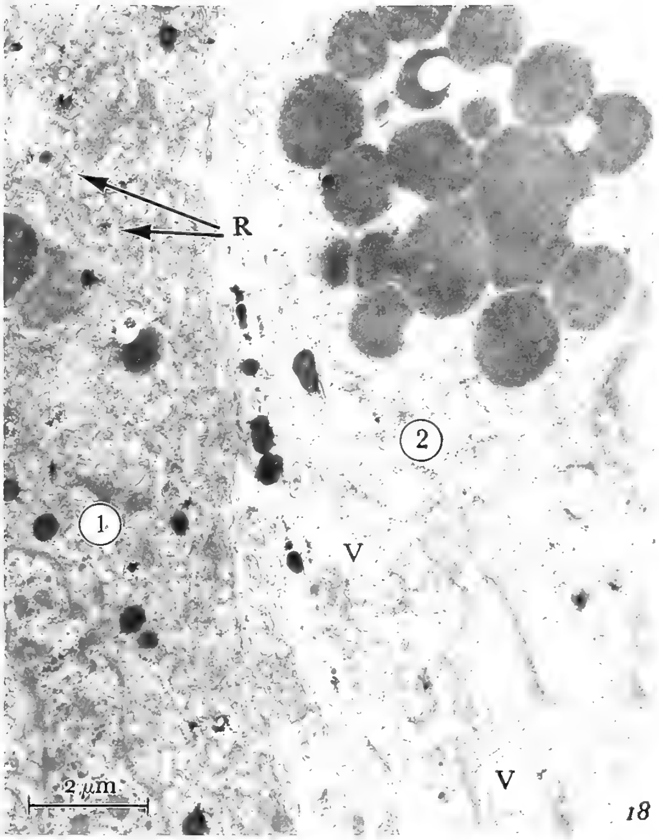
Arrow – microtubules; M – muscle; S – secretory cell

Figure *20*: Early maturation stage of type 2 secretory cell (2) with heterogeneous inclusion (*).

(1) – type 1 secretory cell

Figure *21*: Mature type 2 secretory cell.

Arrows – Golgi complex; * – heterogeneous inclusion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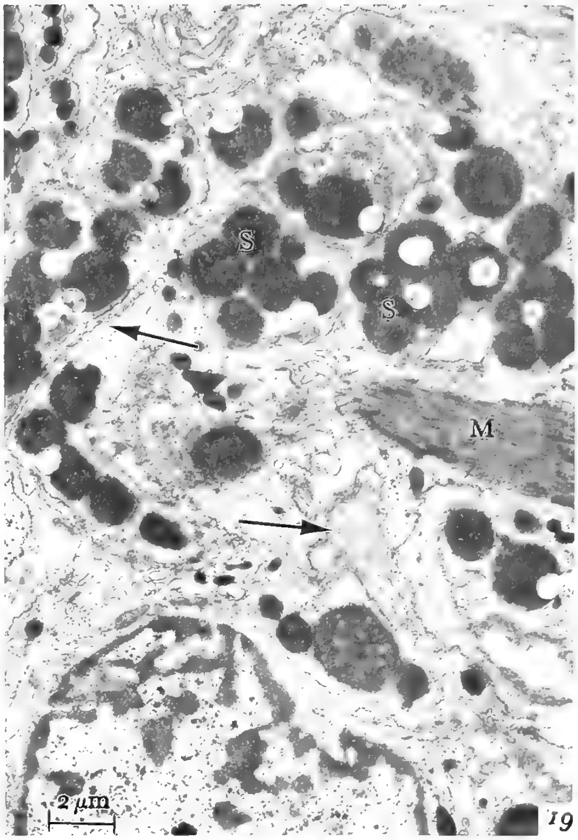
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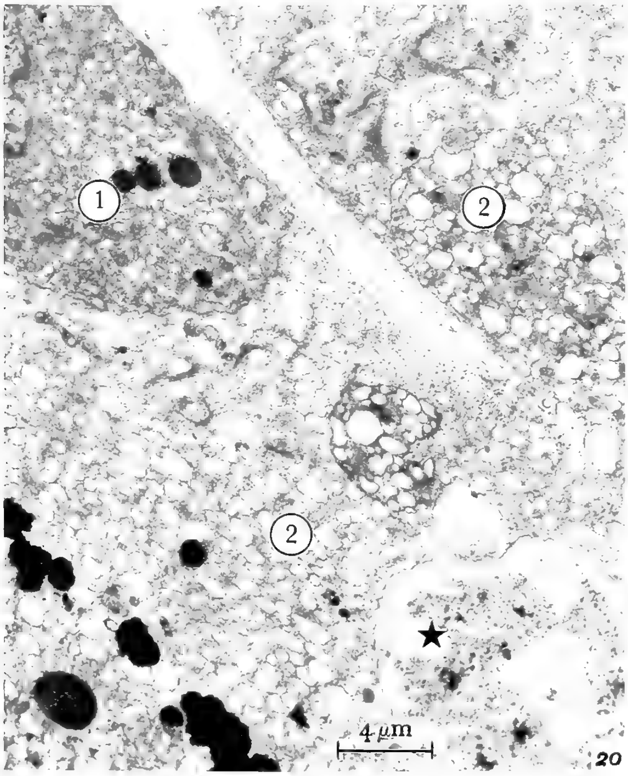
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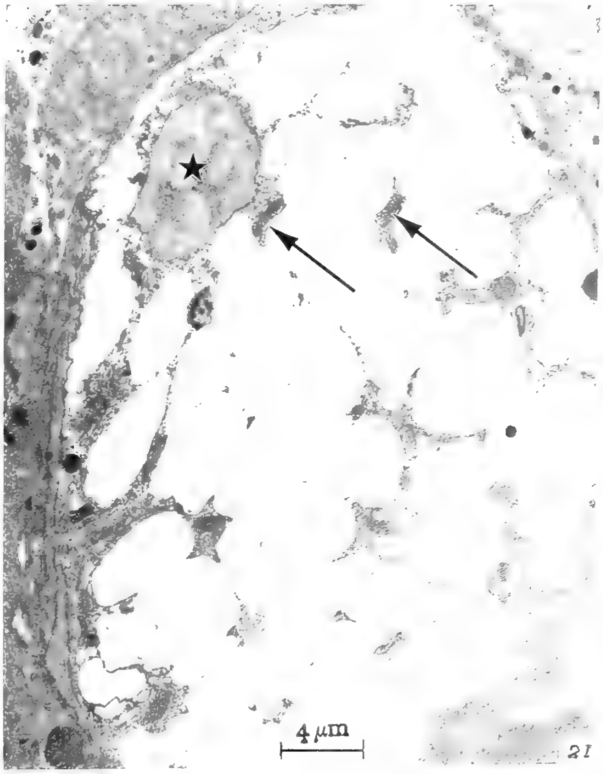
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passes posteroventrally, opening into the posterior limits of the mantle cavity.

The testis of *Colus stimpsoni* consists of numerous seminiferous tubules which end blindly at the surface of the testis and are perpendicular to the spiral axis of the shell. The seminiferous tubules are filled with accessory cells and spermatogenic cells. Basal cells occur on the periphery of the seminiferous tubules and are filled with lipid droplets. It is suggested that these cells function in a nutritive manner. Type I and type II accessory cells occur in groups of 4 - 24 cells and these groups of cells are irregularly scattered within the seminiferous tubules. These accessory cells are endopolyploid and contain large amounts of protein. It is suggested that these cells function to provide large amounts of proteins for gamete development and phagocytose abnormally developing gametes.

ACKNOWLEDGMENTS

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Hiatella solida (Sowerby, 1834)

(Mollusca : Hiatellidae)

on *Concholepas concholepas* (Bruguière, 1789) and other Substrates

BY

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(3 Text figures)

INTRODUCTION

THE ABILITY TO PERFORATE hard substrates has evolved independently in different groups of bivalves. In species of the genus *Hiatella* this specialization was probably assumed after initial life as byssally attached nestlers (YONGE, 1964). The primitive byssiferous nestler characteristic is still present in *Hiatella gallicana* (Lamarck, 1818) and in *H. arctica* (Linnaeus, 1767), according to HUNTER (1949). Members of a single species may reveal other fixation behavior determined by the substrate. On a hard but creviced rock surface, the spat nestle, using the byssus, and those settling on a smooth rock surface of a soft, homogenous rock will move about until they find a crevice wherein to bore. HUNTER (*op. cit.*) points out that the byssus is absent in boring individuals.

According to NARCHI (1973) and to data compiled by CARCELLES (1944), *Hiatella solida* uses both behavioral patterns to place itself securely in the substrate. In Brazil, NARCHI (1973) reports that individuals use the byssus to fix themselves to the sea-squirt *Polyandrocarpa zorritensis*, among tubes of the polychaete *Phragmatopoma lapidosa*, or under clusters of the bryozoan *Zoobotryon pellucidum*. They have also been found boring or nestling in the intertidal zone. According to CARCELLES (*op. cit.*), in Argentina the species lives on rocky sea-beds in inter- or subtidal zones, boring the sandstone or incrusted in bivalve or gastropod shells.

There is very little in Chilean literature on habitat or relationship of the different substrates. SOOT-RYEN (1959) states that *Hiatella* occurs on hard sea-beds from the intertidal zone to depths of 70 m. MARINCOVICH (1973) found it nestling in crevices of intertidal rocks as well as on holdfasts of the kelp *Lessonia nigrescens* Bory, 1825. Its geographic range is rather extensive, from South Ecuador to Cape Horn,and in the Atlantic its northern limit is the southern part of Brazil. This paper provides information on occurrence in southern Chile, especially the association with the gastropod *Concholepas*.

MATERIAL AND METHODS

Two collections of adult *Concholepas concholepas* (Bruguière, 1789) (Table 1) as well as sporadic samplings of *Fissurella nigra* (Lesson, 1830) and the tunicate *Pyura chilensis* (Molina, 1782) were made. Samples were obtained by scuba-diving in the south bank of the entrance to Corral Bay (39°51'S; 73°27'W).

Specimens of *Concholepas* were kept in aquaria, where the presence of *Hiatella solida* was revealed by their projecting siphons. To remove the bivalve, the shells of the *Concholepas* were gradually broken up. Notes were taken on the size of the bivalves, their location, and their relation with the accompanying epibiontic community. Macroscopic sections of *Concholepas* shells showed the shape of the excavations and the position of the *Hiatella* within.

Other substrates on which *Hiatella solida* occurs were also studied: *Megabalanus psittacus* (Molina, 1782), bought at the market in Valdivia on October 26, 1975; intertidal samples of *Phragmatopoma virginii* Kinberg, 1867, and holdfasts of the kelp *Lessonia nigrescens* obtained in Mehuin Bay (39°25′S; 73°10′W) on April 15, 1976.

Descriptions by Olsson (1961) and Dell (1964) were used for the identification of the *Hiatella*, the identification being later confirmed by Dr. Myra Keen.

RESULTS

Hiatella solida was found as an incrustive epibiont in the calcareous shells of *Concholepas concholepas* from Corral Bay (Table 1); on *Fissurella nigra* from among the kelp *Durvillaea antarctica* (Chamisso) (obtained with scuba-diving by Col. C. Moreno on May 5, 1975), and on *Megabalanus psittacus.*

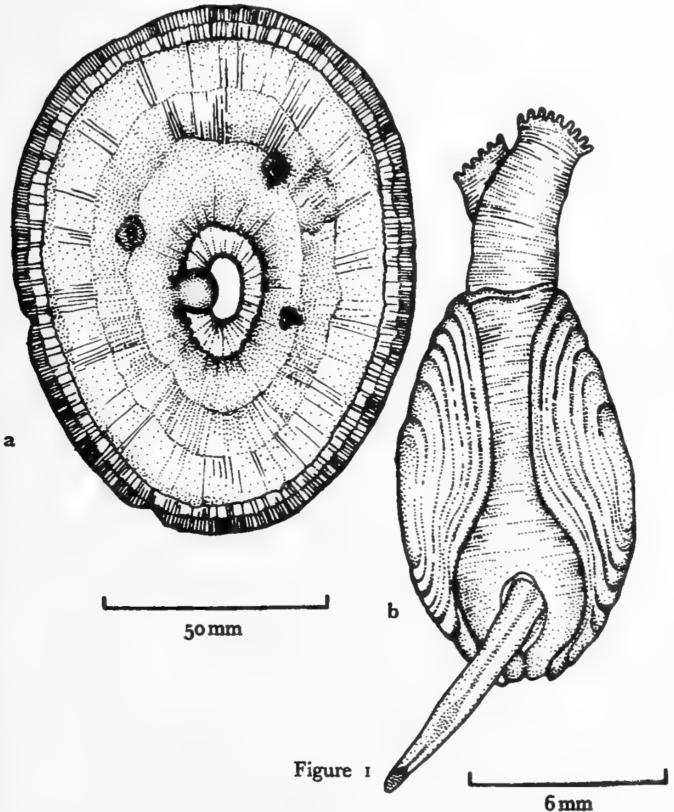

Figure 1

Hiatella solida

A. – Incrustive manifestations of the bivalve as seen from the inside of a *Fissurella nigra* shell
B – Ventral view of *Hiatella solida*

On a *Fissurella nigra* specimen measuring 11.6 cm in length, 9 cm in width, 4 *Hiatella* specimens occurred. Three of them were on different parts of the shell, with an oblique orientation to the surface. Their lengths were 11.5, 6.4, and 6.2 mm, respectively. The 4th specimen was 9 mm long and was next to the apical foramen in a mound formed by the internal layers of the shell (Figure 1A). Both the periostracum and the middle layers of the *Fissurella* were seriously damaged by several tubiculous polychaete tunnels. A specimen of *Hiatella* measuring 27× 14 mm was found to have incrusted the base of a *Megabalanus* shell.

In sublittoral samples of the colonial tunicate *Pyura chilensis* in Corral Bay, the *Hiatella* nestled in the interstices between individuals. It forms part of the *Pyura* community, along with other bivalves such as *Hormomya granulata* (Hanley, 1843), *Lyonsia fretalis* Dall, 1915, *Aulacomya ater* (Molina, 1782), and *Mytilus chilensis* Hupe, 1854, cited by Zamorano & Moreno (1975). However, *Hiatella* was absent in intertidal samples of *Pyura chilensis, Phragmatopoma virginii,* and *Lessonia nigrescens* from Mehuin Bay.

EPIBIOSIS on *Concholepas*

The frequency with which *Hiatella solida* acts as an incrustive epibiont on *Concholepas* is variable, as can be seen in Table 1. It may also be noted that on a single shell both juveniles – the smallest measuring just over 2 mm – and adults of different sizes may occur. The largest adult specimen studied was 17 mm long. The bivalves lie in their burrows approximately perpendicular to the surface, with the posterior end directed toward the external opening (Figure 2A). Some individuals assume a more oblique position, thus attaining greater length without perforating the inner layer (Figure 2B). However, no matter which is the orientation, larger specimens may reach the inner layer. At such points, the shell material takes on a yellowish-brown color and is fibrous and brittle. In high density areas individuals are very close together and 2 or more burrows may come to communicate with each other as individuals grow. In a 9 cm² area, 10 medium and large sized individuals were counted. One specimen was byssally attached to its excavation by a single thread. Hunter (1949) observed in *Hiatella gallicana* and *H. arctica*, a single byssus thread is used, but rarely by borers, to alter their position in the burrow.

There seems to be no direct relationship between the frequency of bivalve occurrence on *Concholepas* and the size of the gastropod shell. Mostly, presence on the shell is closely related to the developmental stage of the epi-

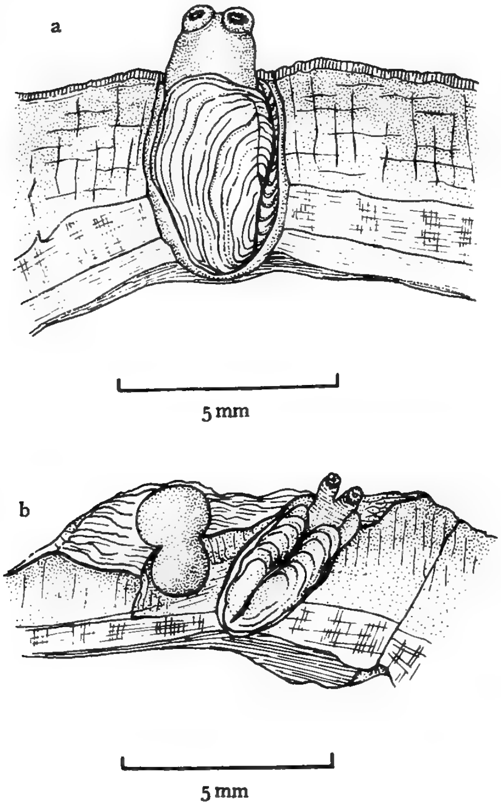

Figure 2

Hiatella solida

A – *Concholepas concholepas* shell section showing an adult bivalve incrusted perpendicularly
B – Section showing the bivalve in an oblique orientation

biontic community (see Table 1). Specimens of *Hiatella solida* are frequently found on shells with large numbers of tubicolous epibiontic polychaetes, calcareous seaweeds, and empty dead barnacle shells, or among abundant phoronids. These seem to be the most important in helping the *Hiatella* to bore successfuly, especially on the less protected faces of the substrate. Several juvenile and medium sized bivalves with siphons projected were found inside empty shells of *Balanus flosculus* Darwin, 1854, and *B. laevis* Bruguière, 1789 (Figure 3). This indicates that the bivalve first entered the shell, then became a burrower. Being small, it had been capable of going through the narrow opening. A similar habitat was reported for *Hiatella* by Hunter (1949) – non-boring adults byssally attached inside empty shells of large barnacles. Some parts of the gastropod shell were eroded either by mechanical or by abrasive agents, leaving the *Hiatella* partially exposed or even completely dislodging it from the shelter (Figure 3). Incrustive juvenile bivalves may often be found at the umbo or in adjacent areas eroded by tubiculous polychaetes of the family Spionidae or by abundant *Phoronis ovalis* Wright, 1856, as epibionts. The incrustive worms therefore play an important part in preparing an adequate substrate for *Hiatella* to bore in.

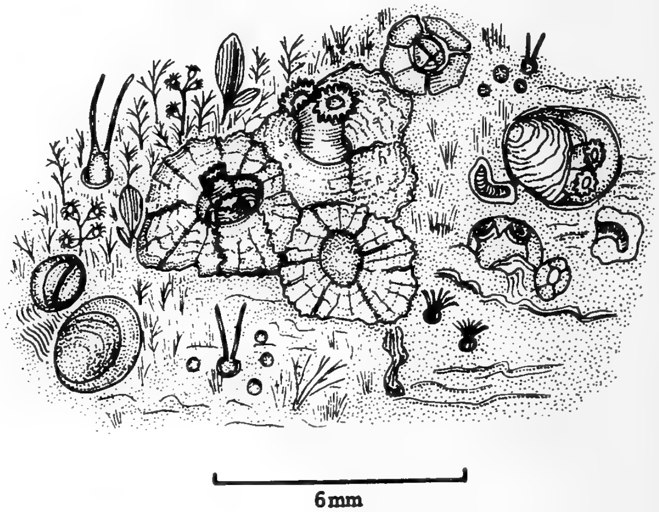

Figure 3

Hiatella solida

Surface view of *Concholepas concholepas* shell with *Hiatella solida* and other incrustive epibionts. Young specimens of *Hiatella solida* are observed inside empty dead barnacle shells

Gastropod shells with only a few epibionts do not afford the bivalves adequate conditions for quick penetration. Then the Hiatellas are restricted to the crevice on the left side of the *Concholepas* shell, under the umbo, where attachment is usually by a byssus. Hiatellas using this shelter, especially large individuals, bore deep burrows, possibly to avoid exposure as they grow. The corrosion carried on by other burrowers greatly aids *Hiatella* with its boring. Some other filtering epibionts also colonize the area, the most important being *Verruca laevigata* (Sowerby, 1827), bryozoans, and some sea-squirts.

Table 1

Incidence of *Hiatella solida* and other epibionts on *Concholepas concholepas* shells from Corral Bay (11/10/74 - 1/4/76)

	Epibionts									
Diameter of *Concholepas concholepas*	*Hiatella solida*	Polychaete tunnels	*Spirorbis* sp.	*Phoronis ovalis*	Bryozoa	*Balanus flosculus*	*Verruca laevigata*	*Balanus laevis*	*Chthamalus scabrosus*	Calcareous algae
63 mm	3	++	–	–	++	–	++	–	–	–
96	–	–	×	–	×	–	–	–	–	–
98	3	++	×	–	–	–	–	–	–	–
99	3	++	–	–	–	+	–	–	–	–
100	–	×	×	–	×	–	–	–	–	–
102	–	+	–	–	–	+	–	+	–	–
102	–	–	–	–	–	++	–	–	–	×
103	–	×	–	–	–	+	–	–	–	–
103	3	+	+	–	–	+	–	–	–	–
104	16	++	++	–	–	++	–	–	–	++
105	4	++	–	–	–	++	–	–	++	++
105	–	+	–	–	–	–	–	–	–	–
107	5	–	–	++	–	++	–	–	–	–
108	–	–	+	–	–	+	–	–	–	–
110	9	++	–	–	–	–	++	–	–	–
110	–	–	–	–	++	–	++	–	–	–
112	1	++	–	++	–	–	–	–	–	–
112	–	+	–	–	–	–	×	×	–	–
120	1	++	–	–	–	++	–	++	–	–
123	4	–	–	++	–	–	–	–	–	–
125	28	++	–	–	–	++	–	–	–	++

++ = abundant; + = scarce; × = presence.

DISCUSSION

Hiatella solida is a nestler, using the byssus to fix itself among colonies of the tunicate *Pyura chilensis*, in intertidal crevices, in *Lessonia nigrescens* holdfasts in northern Chile (Marincovich, 1971), or in the sea-squirts *Polyandrocarpa zorritensis* and *Phragmatopoma lapidosa* on the coasts of Brazil (Narchi, 1973). The ability to perforate certain substrates and gastropod shells, mentioned briefly by Carcelles (1944), is confirmed here by observations on *Concholepas concholepas* and *Fissurella nigra*. It can bore not only in the calcareous shells of mollusks but also in those of other invertebrates, such as *Megabalanus psittacus*.

The nestling or boring behavior is determined not only by the hardness of the substrate but also by whether there are adequate shelters – cracks or crevices – in which to nestle. These shelters seem to be required for attachment on hard, impenetrable substrates or in intertidal rocks (Marincovich, 1973). Thus, the species never prospers in impenetrable hard substrates with homogeneous areas lacking shelters. These conclusions also seem to apply for *Hiatella gallicana* and *H. arctica*. Substrates with plenty of safe shelters for permanent nestling would be those offered by such sea-squirt colonies as *Phragmatopoma*, *Lessonia nigrescens* holdfasts, and probably some others. *Concholepas* affords *Hiatella solida* shelter and crevices on a transitory basis. Neither the chink under the umbo of the *Concholepas* or the empty cirriped shells attached on it offer *Hiatella* a safe shelter on which it can grow without becoming exposed. However, these shelters are vital in helping the bivalve to bore into the shell successfully. Empty barnacle shells play an essential role. Moreover, abrasion and burrows of other incrustive epibionts such as polychaetes and *Phoronis ovalis* seem to be prerequisites for successful boring into the substrate.

The calcareous shells of *Megabalanus psittacus* apparently offer the *Hiatella* an unsafe substrate for byssal fixation alone. Besides being easy prey for possible predators while so attached, the bivalves must also undergo the same abrasion as the *Concholepas*, especially when the gastropod enters into cracks and crevices of the hard substrate. The fact that the valves of *Hiatella solida* close partially, leaving the ventral side exposed, seems to indicate that the species is adapted to life only inside shelters in the substrate.

As Yonge (1962, 1964) postulated, the boring habit of *Hiatella* in calcareous shells as well as in other substrates can be considered to have developed subsequently to the nestling habit and byssal fixation in benthonic shelters. Adopting the boring habit seems to be an important step toward the colonization of penetrable substrates that are open and homogeneous and therefore not suitable for long-time nestling.

Assessment of the damage that incrustive epibionts cause on *Concholepas* shells is scanty. Only Arenas (1972) gives information on the effect that *Phoronis ovalis* has on the gastropod. It has been observed that large specimens of *Hiatella solida* can penetrate even the inner layer. However, no manifestations of layer thickening were apparent at the affected points, though this occurs with massive incrustations of *Ph. ovalis*. The effect of *H. solida*, though damaging, is local and secondary, almost always following incrustations of polychaetes and *Phoronis*. A similar situation seems to occur in *Fissurella nigra*. In one specimen, shown in Figure 1A, the mound around the incrustive bivalve may possibly be a defense used when the penetrator endangers vital functions. No such response was apparent in other areas of the shells that were affected by *H. solida*.

In systematic studies of *Hiatella solida* Soot-Ryen (1959) distinguishes two forms and Dell (1964) observed variability in form and shape in specimens from the East Coast of South America and the Magallanes region. This variability, which has probably led to the series of names for the species, could be caused by the types of surface on which they settle.

In studies carried out on epibionts in *Concholepas concholepas* from Caleta Leandro (36°39′S; 73°05′W) *Hiatella solida* was not found (Lozada *et al.*, 1976).

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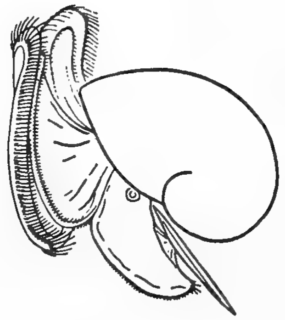

Zonation of Marine Gastropods on a Rocky Intertidal Shore in the Admiralty Gulf, Western Australia, with Emphasis on the Genus *Nerita*

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(3 Text figures)

INTRODUCTION

THE ZONATION OF MARINE MOLLUSCS along the intertidal shorelines of the world has been intensively investigated in many areas since the broad perspectives of the Stephensons were published (STEPHENSON & STEPHENSON, 1949). A number of more recent studies have investigated the zonation of marine molluscs on the eastern and southern coasts of Australia (ENDEAN *et al.*, 1956; UNDERWOOD, 1972) or have examined particular features of the biology of intertidal molluscs occurring on those shores (COLEMAN, 1976; UNDERWOOD, 1975, 1976). Development of our understanding of the marine intertidal communities of Western Australia has been severely handicapped by the size of the coastline, about 6500 km, and the small number of marine biologists in the state. The marine intertidal communities of the Perth area have been examined (HODGKIN, MARSH & SMITH, 1955; MARSH & HODGKIN, 1962; PRIDEAUX, 1976) but there is almost no published information available on any aspect of the molluscan communities of the north coast of Western Australia east of Derby. The coastline of that area has been largely inaccessible from land because of a lack of roads and access from the sea has been prevented by the lack of available ship-time. Over the last several years the Western Australian Museum has conducted several field programs in the northeastern corner of the state and it was felt that sufficient information was now available to pinpoint a number of areas of particular interest which could be examined on a major expedition. The Western Australian Museum in conjunction with the Field Museum of Natural History, Chicago, USA, conducted an intensive survey of the land, freshwater and marine fauna of the Admiralty Gulf and adjacent Mitchell Plateau from 16 October to 6 November 1976. The teams had a variety of interests: mammals, birds and reptiles, fish, insects, mites, and molluscs. This paper is the first report on the work done on molluscs during the expedition.

THE STUDY AREA

The Admiralty Gulf (Figure 1) is a large marine embayment with an area of approximately 1700 km^2 on the extreme northeast coast of Western Australia about 300 km W of the Northern Territory border. The waters of the Gulf are essentially marine but minor freshwater inflows are received from the Mitchell and Lawley Rivers; limited estuarine areas are associated with each river. The complex system of tides which occurs in the Gulf makes the area an interesting one for the examination of the patterns of zonation of marine intertidal mollusc species. The tidal range is extensive, with a maximum range of as much as 8.8 m on spring tides, from −1.7 m on the shore to +7.1 m. The average tidal amplitude is 4.4 m. The tides are predominantly semidiurnal, but diurnal tides occur during the changeover between neap and spring tide periods. When the changeover occurs the tidal levels remain static for several hours at a level of about +2.6 m.

Two major intertidal habitats occur in the Admiralty Gulf. A myriad of small bays is found, each with extensive mangrove development at the midtide levels. In many of the bays well developed mudflats occur landward of the

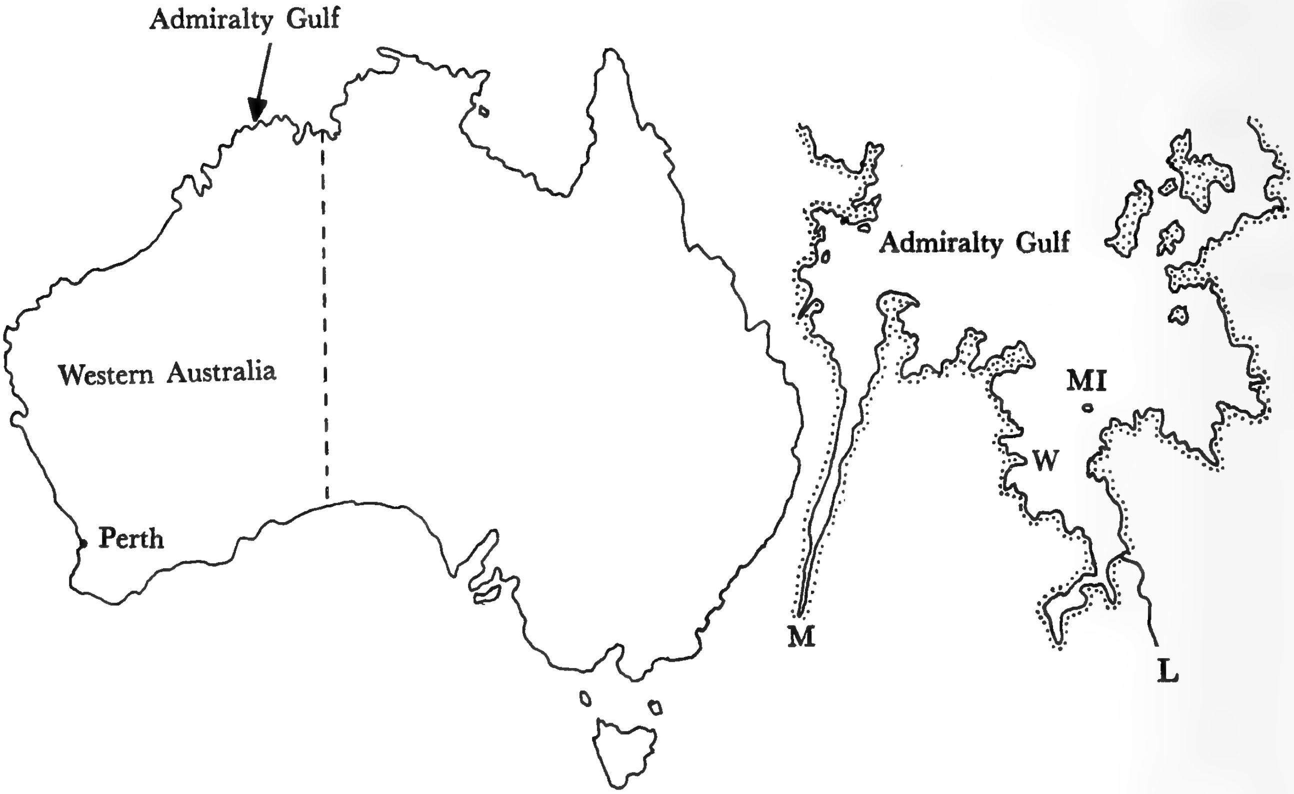

Figure 1

Map of Australia Showing the Position of the Admiralty Gulf. The Insert shows the Admiralty Gulf itself and the Location of Walsh Point in the Gulf.

L, Lawley River; M, Mitchell River; MI, Malcolm Island
W, Walsh Point

mangroves. These areas are baked dry by the tropical sun during the neap tides but are submerged intermittently during spring tides. Few molluscs occur on or in the landward mudflats. Extensive mudflats which project seaward of the mangroves for as much as a kilometer are exposed by low spring tides. A variety of molluscs is found on the surface and in the mud of these flats. The headlands between the bays are rocky shores in the intertidal zones; the rock is of either sandstone or basalt, depending on the particular location in the Admiralty Gulf. Three marine programs were conducted in the Admiralty Gulf by the WAM Mollusc Department. The results of a faunal survey of the Gulf and the nearby Institut Islands and an intensive examination of the molluscs of the mangrove swamp at Port Warrender in the Gulf will be published elsewhere. The present paper examines the zonation of epifaunal marine gastropods at Walsh Point in the Admiralty Gulf.

Walsh Point is a small basaltic peninsula 2.7 km long (Figure 1) located at latitude 14°35′S and a longitude of 125°50′E. The seaward tip of Walsh Point, where the samples reported here were collected, is almost completely rocky in the intertidal areas. The shore of the high intertidal zone is composed of small rocks 5 to 13 cm in diameter which are several layers deep. These rocks are easily moved about by even moderate wave action. The rocks are larger at the midtide level, about 10 to 30 cm in diameter, and are only 2 or 3 deep. Base rock is exposed in some areas of the midtide zone. At the lower intertidal areas the basalt rocks are 30 cm or larger in diameter and are separated from each other by up to 30 cm of sand; very few rocks adjoin each other in the low intertidal zone. At a level of about 0.5 m the shore changes rapidly into a sandy beach in which rocks are rare.

Walsh Point is located well within the Admiralty Gulf and is thus protected from the wave action of the open sea. The water is extremely turbid at low tide even on calm days, with a visibility of 15 cm or less. As the tide rises, visibility increases to about 90 cm.

MATERIALS AND METHODS

Four transects approximately 10 m apart were made along the rocky shore of Walsh Point from the 0.5 m tide level to the 7.0 m level. The tide level was determined by comparison of the water levels at Walsh Point with tide charts for nearby Malcolm Island. A 1 m × 1 m quadrat was searched at every other meter along the transect and all gastropods found were removed and preserved in 10% formalin. All specimens were returned to the museum laboratories where they were identified and counted. Shell length of all individuals of *Nerita* was measured with vernier calipers. The resulting data were grouped into 0.5 m shore levels. Voucher specimens of all species collected have been deposited in the Western Australian Museum where they have catalogue numbrs WAM 1256-76 to 1274-76.

RESULTS

A total of 3375 individuals belonging to 18 species of gastropod molluscs was collected in the study. The density of each species and the standard deviation in each zone is given in Table 1. Three zones were demonstrated by the species: species which had their maximum level of abundance at the lowest tide level, then tapered off as the height on the shore increased; species with a maximum density near the midtide level whose densities decreased both above and below the midtide region; and species most abundant in the upper tidal levels whose density decreased below the hightide zone. The species comprising each zone will be discussed in turn.

Of the 18 species collected 10 had their maximum abundance in or near the lowest zone studied. Although a majority of species was restricted to this lowest tidal area, the numbers of individuals of each species were generally very low. The entire group was represented by 507 individuals, which was 15.0% of all gastropods collected. Included in this group is a number of minor species which were represented by 25 or fewer individuals: *Cantharus erythrostoma*, *Cantharidus strigatus*, *Columbella duclosiana*, *Haliotis varia*, *Onchidium daemelli*, *Pattelloida saccharina*, *Montfortula variegata*, and *Trochus lineatus*. The most abundant species in the low intertidal zone was *Morula margariticola*. This species had its maximum density in the lowest two zones (Figure 2), from 0.5 to 1.5 m on the shore, where it had an average density of 13.7/m². The density of *M. margariticola* decreased rapidly above this level, with only 3 individuals being found above the 2.5 m mark. The other abundant species in the lowest group, *Thais kieneri* (Figure 2), had a wider distribution which ranged from 0.5 to 4.5 m. This species was much less abundant than *M. margariticola* and had a maximum density of only 3.5/m² in the 1.5 to 2.0 m zone.

The second group of 6 species had their highest densities in the middle tidal ranges and were less abundant at both higher and lower levels on the shore. The midtide group was numerically dominant on the shore and accounted for 76.0% of all specimens collected. Four minor species are included in this group: *Monodonta labio*, *Morula granulata*, a species tentatively identified as *Cuma gradata*, and an unidentified thaiad species. The most interesting feature of the midtide group was the dominance of 2 species of the genus *Nerita*: *N. reticulata* and *N. undata*. *Nerita reticulata* (Figure 2) was the most abundant species collected in the study, being represented by 1300 individuals or 38.9% of all gastropods collected. *Nerita undata* (Figure 2) was second with 1090 individuals (32.3% of the total). Both species had a wide vertical range on the shore that encompassed virtually all of the zones studied. *Nerita reticulata* had low numbers of individuals below the 1.5 m mark and increased gradually in density to the 3.0 m level, after which the numbers dropped steadily. While it had essentially the same vertical range as *N. reticulata*, the zonation pattern of *N. undata* was very different (Figure 2). Low numbers of 4.8 and less per m² were encountered both below 2.5 m and above 5.5 m. Instead of a gradual increase toward the midtide level as was observed in *N. reticulata*, the number of individuals of *N. undata* was relatively constant at high levels of 16.0 to 20.3/m² between the 2.5 and 5.5 m levels. The maximum abundance of *N. reticulata* occurred in the 2.5 to 3.0 m level, one step below the highest density of *N. undata*. While the mean heights of the populations of the 2 species were different, *N. reticulata* had a mean of 3.0 ± 2.5 m and *N. undata* was 3.9 ± 2.6 m, the differences were not statistically significant (t-test, 0.05 level).

Only 2 species had their maximum abundances in the upper intertidal levels and together they constituted only

Table 1

Density (No./m²) of Marine Gastropods in the Intertidal Zone of Walsh Point, Admiralty Gulf, Western Australia, With one Standard Deviation from the Mean Indicated for all Zones in which more than Four Individuals of a Species were Found. The Level of Maximum Density of a Species is enclosed by a Square

	Height above datum (m)												
Species	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0	6.0-6.5	6.5-7.0
						Lower intertidal species							
Cantharidus strigatus	$\boxed{0.3}$	0.1	0.1	0.1	0.1								
Cantharus erythrostoma Linnaeus, 1758	$\boxed{1.3}$ $\boxed{\pm1.0}$	0.6 ±1.3	0.1										
Columbella duclosiana		$\boxed{0.3}$											
Haliotis varia Linnaeus, 1758	$\boxed{0.2}$	0.1	0.1	0.1	0.1								
Montfortula variegata Adams, 1852	0.1	0.1	0.2	$\boxed{0.4}$	0.3								
Morula margariticola Broderip, 1832	$\boxed{14.6}$ $\boxed{\pm5.5}$	12.9 ±8.5	3.4 ±3.5	2.4 ±1.1	0.3	0.1							
Onchidium daemelli Semper, 1882	0.2	0.3	$\boxed{0.6}$	0.5									
Patelloida saccharina (Linnaeus, 1758)		0.1	0.1	0.1	0.1								
Thais kieneri Deshayes, 1844	0.9 ±1.2	1.7 ±1.6	$\boxed{3.5}$ $\boxed{\pm2.3}$	1.5 ±1.1	1.4 ±1.3	1.4 ±0.7	0.1	0.3					
Trochus lineatus Lamarck, 1822			$\boxed{0.1}$										
						Middle intertidal species							
cf. *Cuma gradata*	0.3	0.1	0.5 ±0.6	0.8 ±0.4	0.8 ±1.1	0.4	$\boxed{2.3}$ $\boxed{\pm2.3}$	1.0 ±2.7					
Monodonta labio Linnaeus, 1758	0.1		0.3	0.4	1.8 ±1.5	$\boxed{3.0}$ $\boxed{\pm1.4}$	2.5 ±1.7	0.8 ±1.4	0.3				
Morula granulata Duclos, 1832								$\boxed{0.1}$					
Nerita reticulata Karsten, 1789	5.0 ±14.4	7.6 ±9.4	12.8 ±14.3	13.4 ±9.6	$\boxed{35.9}$ $\boxed{\pm10.2}$	32.5 ±14.3	20.8 ±13.2	11.7 ±9.0	3.8 ±5.0	0.4 ±0.4	0.3		
Nerita undata Linnaeus, 1758		0.5 ±0.6	1.3 ±1.8	4.8 ±5.0	17.9 ±7.3	$\boxed{20.3}$ $\boxed{\pm9.7}$	19.5 ±6.1	19.3 ±6.0	17.6 ±9.2	16.3 ±8.9	3.4 ±3.0	1.5 ±1.9	
Thaiad Species 1		0.3	0.6 ±0.6	0.4 ±0.5	$\boxed{2.4}$ $\boxed{\pm2.6}$	1.0 ±1.0	1.0 ±0.9	0.3					
						Upper intertidal species							
Nerita polita Linnaeus, 1758							0.3	1.1 ±0.5	0.6 ±0.4	$\boxed{2.3}$ $\boxed{\pm1.9}$	1.5 ±2.2	0.6 ±0.5	
Planaxis sulcatus (Born, 1780)	0.3						1.1 ±2.6	3.5 ±3.6	3.3 ±5.4	$\boxed{10.5}$ $\boxed{\pm6.4}$	5.8 ±8.4	1.4 ±3.0	
Total density	23.3 ±11.7	24.7 ±10.8	23.7 ±17.5	24.9 ±10.1	$\boxed{61.1}$ $\boxed{\pm11.3}$	58.7 ±25.8	47.6 ±1.8	38.1 ±18.4	25.6 ±18.4	29.5 ±18.5	11.0 ±10.9	3.5 ±3.8	

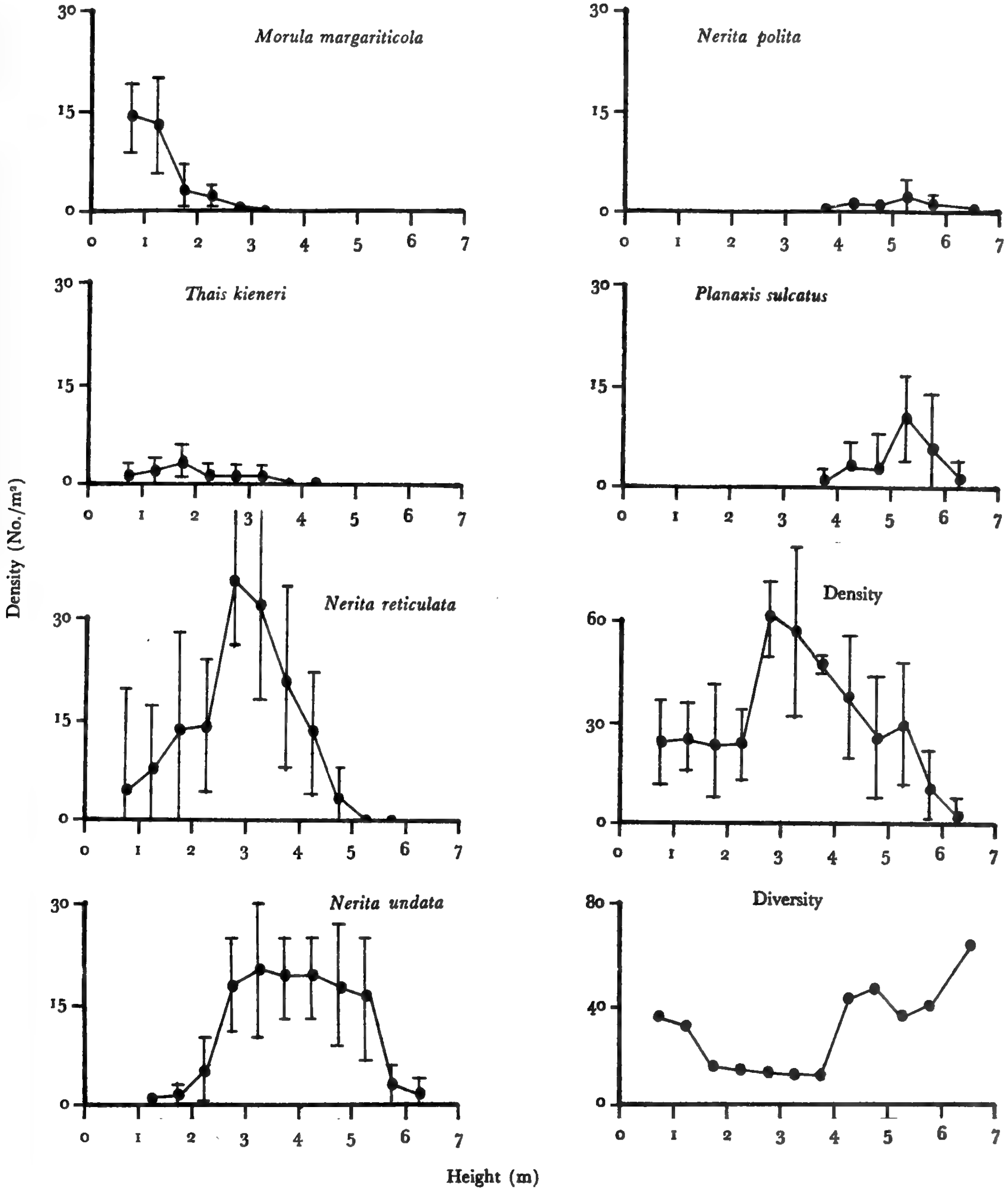

Figure 2

Zonation of Marine Gastropod Species at Walsh Point, Admiralty Gulf, Western Australia, Showing the Density of Each Species at the Various Tidal Heights. Densities Shown are Means and the Standard Deviation for Each Mean is Indicated

9.0% of all gastropods collected. Both *Nerita polita* (Figure 2) and *Planaxis sulcatus* (Figure 2) were found from 3.5 to 6.5m on the shore and had their maximum concentrations in the zone of 5.0 to 5.5m. *Planaxis sulcatus* was the dominant member of this group, being 4 times as abundant as *N. polita*.

The total density of gastropods (Figure 2) was moderate in the lower intertidal levels, ranging from 24.3/m² at the 0.5 to 1.0m level to 24.9/m² at the 2.0 to 2.5m interval. Density in the next shore zone more than doubled to 61.1/m², largely due to increases in the densities of *Nerita undata* and *N. reticulata*. The fact that the total abundance of gastropods declined steadily above the 3.0m mark is a further indication of the numerical dominance of these 2 midtide species. A Simpson's (1949) index of diversity was calculated for each of the intertidal zones. Maximum diversity, where each individual belongs to a different species, is indicated by a value of 0 on the Simpson index; minimum diversity, where all individuals are of the same species, has a value of 1. The diversity index closely paralleled the total gastropod density (Figure 2). The midtide region of highest density was also the area of highest diversity. Diversity was lower both above and below the midtide region, as was the total density. The index is designed to prevent the total number of individuals studied from influencing the index of diversity. Thus the higher diversity in the midtide region is real and is not simply an artifact of the higher number of individuals which occurred there.

One of the most interesting features that can be examined with a study of this type is the partitioning of the environment by groups of closely related species in a sympatric association with each other. Two such groups were identified in this investigation. Four species of thaiad: *Cuma gradata* (tentative identification), *Morula granulata, M. margariticola,* and an unidentified species, occurred in the middle and lower intertidal regions. Despite the fact that they are all carnivorous species in the same subfamily, the thaiads belong to 3 different genera and are not closely related taxonomically. Together they comprised only 16.1% of all gastropods collected. More interesting are the 3 species of the herbivorous genus *Nerita* which feed by rasping algal material off the surfaces of the rocks on which they live. In contrast to the thaiads the nerites all belong to the same genus and numerically dominated the study, accounting for 72.9% of all gastropods collected.

A number of studies (*e. g.* Edwards, 1969) of intertidal gastropods have demonstrated that smaller individuals of a species tend to be concentrated on the lower shore areas and larger specimens tend to be located higher in the intertidal zone. Lower intertidal areas are covered by seawater for a greater length of time during each tidal cycle than the areas higher up, providing a more gentle environment for a marine species. Juvenile individuals are generally more susceptible to variations in condi-

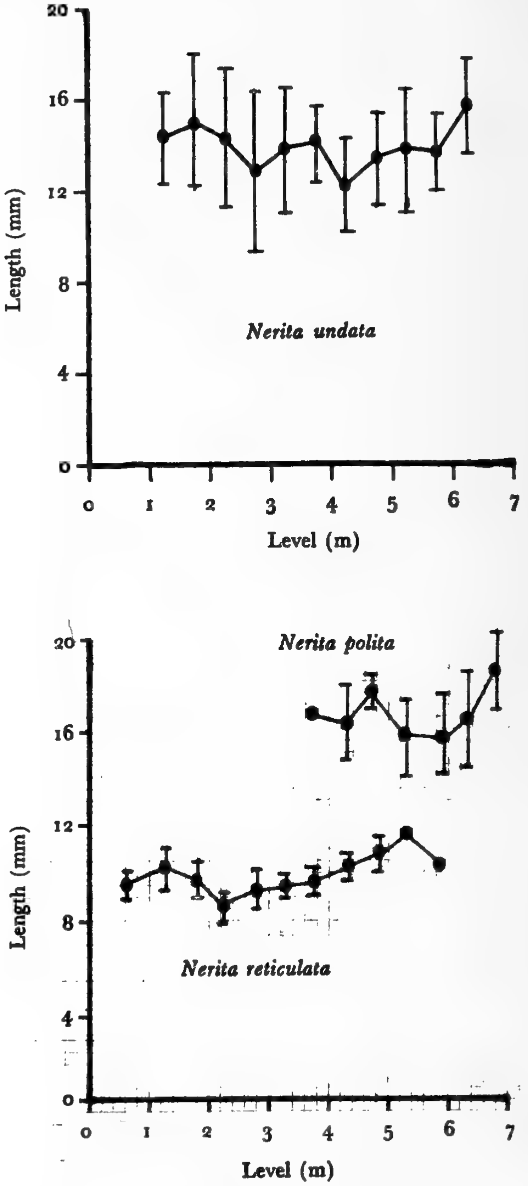

Figure 3

Mean Lengths of the Three *Nerita* Species Collected at Walsh Point, Admiralty Gulf, Western Australia. For Each Tidal height a Standard Deviation of the Mean is Indicated for Every Sample of More than Five Individuals tions than are the adults, which usually have greater environmental tolerances. Thus the mean sizes of each of the 3 *Nerita* species would be expected to increase as the area sampled moved up the shoreline, but this was not the case (Figure 3). The mean sizes of each species were stable throughout the tide levels and no demonstrable trends were evident, indicating that juveniles were not in fact found lower on the shore than adults, but there was a distinct tendency for very large individuals of each species to be concentrated in the upper meter of the species' range. The species themselves demonstrated a clear increase in size with tidal height (Table 2). The average length of all *N. reticulata* measured was 9.4±0.7mm. This species was the lowest on the shore with a mean tidal height of 3.0±2.5m. The intermediate *N. undata* at 3.9 ±2.6m averaged 13.0±2.1mm, 1.4 times as large as *N. reticulata*. *Nerita polita*, which was highest on the shore at 5.2±0.2m, averaged 16.1±1.6mm, 1.2 times as large as *N. undata*.

The index of diversity devised by Simpson (1949) was modified by Morisita (1959) as the basis of an index of overlap; the appropriateness of the overlap index has been discussed by Horn (1966). The overlap index developed by Morisita (*op. cit.*) has been used to determine the degrees of overlap between the populations of the 3 *Nerita* species on the shore of Walsh Point (Table 2). The 2 species which occur at opposite ends of the shore, *N. reticulata* and *N. polita*, had the lowest overlap, 0.07. *Nerita undata* occupied an intermediate position on the shore and had a high overlap with both *N. reticulata* below and *N. polita* above.

DISCUSSION

The diversity of gastropods was highest in the midtide areas and tapered off towards both the higher and lower portions of the shore. One would expect diversity to be highest in the lowest intertidal areas which are covered by seawater for the longest periods during each tidal cycle. Reimer (1976), for example, studied the intertidal fauna on rocky shores on the Pacific coast of Panama. Of 220 species identified, 42% were found exclusively in the lower intertidal zone, 17% were limited to the midlittoral and only 6% were exclusive to the upper shore. The remaining species had distributions that overlapped at least 2 zones. The lower intertidal zone had the highest diversity and the splash zone the lowest. The unexpectedly low diversity in the lower intertidal zone of the Admiralty Gulf can be easily explained in terms of the beach structure. The rocks of the midtide region are large enough that they are not rolled about by waves except during storms. With one rock lying on another there is an abundance of crevices and nooks and crannies for the snails to retreat into during the emersion at low tide. In the lower portion of the intertidal zone the rocks are spaced about 30cm apart, eliminating the availability of refuges in the gaps between adjacent rocks. The index of diversity is based on the quantitative samples in which only 18 of the most common gastropod species were found. Intense collection in the area for the report on the molluscan fauna of the Admiralty Gulf has shown that at least 75 gastropod species occur at Walsh Point.

The dominance of the 3 *Nerita* species was overwhelming: *N. reticulata* constituted 38.9% of all gastropods collected and *N. undata* 32.3%. *Nerita polita* was a minor species at 1.8%. The dominance of the 3 congeneric species raises the question of how they partition the available resources and which factors are potentially limiting. The population of *N. polita* is partially segregated spatially from the other 2 species. *Nerita polita* is an upper intertidal species with a mean population level of 5.2±0.2m, above the levels of *N. reticulata* and *N. undata*.

Table 2

Characteristics of the Populations of *Nerita* at Walsh Point, Admiralty Gulf, Western Australia

	Shell length			Shore height			Niche overlap	
	Minimum (mm)	Maximum (mm)	Mean ± 1 SD (mm)	Minimum (m)	Maximum (m)	Mean ± 1 SD	Index	Species
Nerita reticulata	4	12	9.4±0.7	0.5	6.0	3.0±2.5	0.07	*Nerita reticulata—Nerita polita*
Nerita undata	3	22	13.0±2.1	1.0	6.5	3.9±2.6	0.29	*Nerita undata—Nerita polita*
Nerita polita	11	22	16.1±1.6	3.5	7.0	5.2±0.2	0.35	*Nerita reticulata—Nerita undata*

The index of overlap between *Nerita polita* and *N. reticulata* was very low, only 0.07. The overlap between *N. polita* and *N. undata*, which occupies the intermediate position on the shore is much higher, 0.29, indicating a considerable overlap. Populations of the 2 dominant nerites, *N. reticulata* and *N. undata*, are also somewhat segregated vertically, with *N. undata* being higher on the shore (3.9 ± 2.6m) than *N. reticulata* (3.0±2.5m), but the overlap between populations was substantial. Both occurred at virtually every tide level sampled. The maximum density of *N. undata* was in the 3.0 to 3.5m tide level, one zone above the maximum abundance of *N. reticulata*. The index of niche overlap was high, 0.35, reflecting the substantial mixing of the populations.

Most studies of density regulation of intertidal gastropods have been done on limpets. FRANK (1965) showed that the density of the limpet *Acmaea digitalis* Rathke, 1833, was limited by an interaction of space and food resources. This appears to be a general condition in limpets. UNDERWOOD (1975; 1976) found density regulation in *Nerita atramentosa* Reeve, 1855, to be a function of food competition. Significant natural mortality was only found in the adults of the population. Underwood suggested that if the density of *N. atramentosa* was increased above the critical level by excessive numbers of juveniles settling on the shore the growth rates of the juveniles would be slowed and adult mortality would increase until the population had returned to normal levels. *Nerita atramentosa* feeds on diatoms and algal spores which are thought to be replenished on each high tide (UNDERWOOD, 1975; 1976). The exact food of the 3 *Nerita* species of the Admiralty Gulf is unknown, but their radular structure is similar to that of *N. atramentosa* and it is reasonable to suggest that food could also be a limiting factor for the Admiralty Gulf species. Food competition would be lessened by the differences in mean tidal height of the 3 species, which means that each is concentrating its feeding on a different shore level. Another possible factor in reducing competition is differences in the behavior of the species. This possibility has not been examined in the present study. COLEMAN (1976) reported on the activity patterns of 3 species of *Nerita*: *N. albicilla* Linnaeus, 1758; *N. plicata* Linnaeus, 1758, and *N. polita*. All 3 actively move about while immersed at high tide and during the initial stages of emersion as the tide falls. When the rocks dry during low tide, the snails retreat into sheltered areas and become quiescent. While the pattern of behavior of the 3 species is similar, the selection of sheltered areas varies between species: *N. plicata* congregates in crevices and hollows; *N. albicilla* remains in damp, shaded crevices; and *N. polita* tends to burrow into the sand. If similar behavioral differences are operating in the species found in the Admiralty Gulf they could influence the areas grazed by each species.

A number of nerite species occurs along the rocky shores of the Western Australian coastline (WILSON & GILLETT, 1974). *Nerita atramentosa* is a cold water species which is widely distributed along the south coast and extends northward along the west coast as far as Point Cloates. *Nerita albicilla, N. plicata, N. polita, N. reticulata,* and *N. undata* are all tropical species which have a range extending across the entire tropical north coast of the state and range southwards on the west coast. The numerous possible interactions between these 6 species offer a wide range of interesting avenues of investigation. Possible behavioral differences and mechanisms of density regulation have already been mentioned. Varying combinations of the nerites occur at various localities along the northwestern coasts of the state. It would be interesting to investigate the populations of several species for evidence of character displacement. FENCHEL (1975) has shown that character displacement occurs in the gastropod genus *Hydrobia* where mean individual sizes of the species change when 2 or more species are present. A similar factor could be operating in *Nerita*: *N. undata* averaged 1.4 times the mean shell length of *N. reticulata*, and the average *N. polita* was 1.2 times as large as *N. undata*. The sizes of all 3 species in the Admiralty Gulf were well below the maximum sizes reported by both CERNOHORSKY (1972) and WILSON & GILLETT (1974). A second possible mechanism of character displacement is a change in the mean shore level of a nerite species when it occurs with one or more other nerites. Particularly interesting in this regard is *N. atramentosa* which is the only nerite on most shores, where the population is centered in the low intertidal zone (PRIDEAUX, 1976). It would be interesting to see if the population of *N. atramentosa* is forced to lower shore levels by competitive interaction with other nerites in areas where it is sympatric with other species of *Nerita*.

ACKNOWLEDGMENTS

An expedition such as this cannot succeed without assistance of all kinds from a wide variety of people too numerous to mention here. The Western Australian Museum participation was made possible by a special grant from the Treasury Department of the State of Western Australia to the Western Australian Museum. The area studied by the expedition is on a mining lease owned by the ALUMAX Mining Company. ALUMAX provided invaluable assistance to the expedition, particularly through

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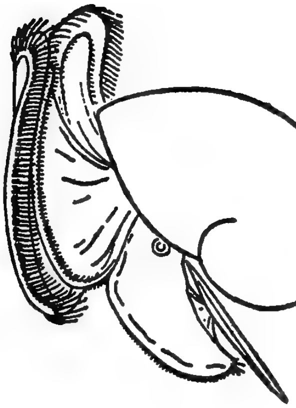

A New Species of *Serpulorbis*

(Gastropoda : Vermetidae)

from South Africa

BY

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(4 Text figures)

INTRODUCTION

In December 1975, a new species of *Serpulorbis* was discovered living on stones within the mouth of the Umngazana estuary near Port St. Johns, Transkei and in large rock pools on the open coast outside the estuary. The species is named *Serpulorbis (Serpulorbis)* ***aureus*** after the golden yellow colour of the exposed parts of the living animal. The taxonomy is based on Keen (1961).

DESCRIPTION

Taxonomy

Genus *Serpulorbis* Sassi, 1827
 Subgenus *(Serpulorbis)* Keen, 1961
Serpulorbis (Serpulorbis) ***aureus*** Hughes, spec. nov.

Morphology

SHELL

The adult shell (teleoconch) is cemented to the substratum forming a dextral spiral with loose concentric whorls. The whorls are approximately triangular in cross-section with the flat base cemented to the substratum. Their surface is textured with low axial ridges which are sigmoid in lateral aspect (Figure 1a). A few individuals possess faint longitudinal ridges. The outer whorl is extended into a vertical feeding tube circular in cross-section. Scars of old feeding tubes are evident at every quarter or half whorl. The holotype is 2.5 cm across its outer whorl, the feeding tube is 1.5 cm long with an internal diameter of 4 mm. Most adults are approximately of this size.

The protoconch is about 1 mm long, mostly clear but with a brown tinge to the dorsal lip or hood of the aperture. The apical whorl is almost as large as the basal whorl (Figure 2a).

ADULT BODY

The animal reaches a length of about 4 cm. The shapes and relative proportions of the various organs are shown in Figure 3a. Brooding females have a deep dorsal cleft in the mantle (Figure 3b) to accommodate the egg capsules which hang from the roof of the shell. The head, foot and exposed part of the mantle have a golden yellow background colour which fades after fixation. The mantle edge is coloured with alternate bands of golden yellow and dark brown. In many individuals the foot and dorsal parts of the head are dark brown.

EGG CAPSULES AND EMBRYOS

A brooding female contained 20 egg capsules attached to the roof of the shell in 2 staggered ranks (Figure 2c) from the base of the feeding tube to half way along the outer whorl. Older capsules each contained about 30 advanced embryos. Younger capsules contained eggs with a distinctive pale green yolk. The green colour is lost on fixation. The advanced embryos had well developed protoconchs and were clearly destined for benthic life after hatching.

RADULA

The radula, shown in Figure 4a, has a row formula of 2 · 1 · 1 · 1 · 2. The rachidian tooth has convex sides while the inner marginal tooth has 2 or 3 well developed lateral cusps on its outer edge and 2 lateral cusps on its inner edge.

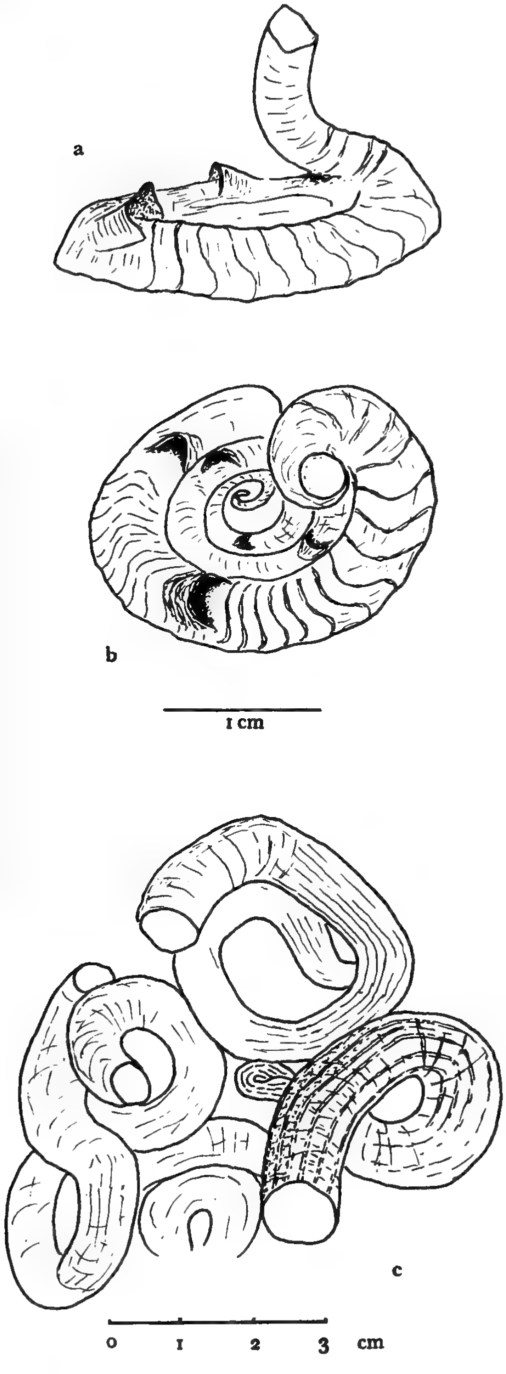

Figure 1

(a) *Serpulorbis aureus* holotype from lateral aspect
(b) Holotype from above
(c) *Serpulorbis natalensis*

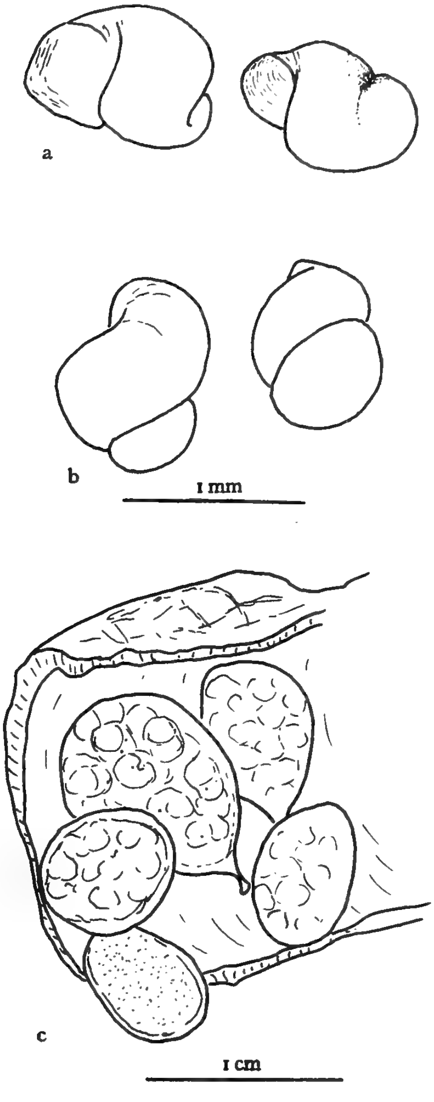

Figure 2

(a) Protoconchs from left lateral aspect
(b) Protoconchs from dorsal aspect
In both figures the larger protoconch is of *Serpulorbis natalensis* and the smaller protoconch is of *Serpulorbis aureus*
(c) *Serpulorbis aureus* egg cases attached to the roof of the adult shell

DIAGNOSIS

Genus *Serpulorbis*: lack of operculum in adult; bright pigmentation of exposed body.

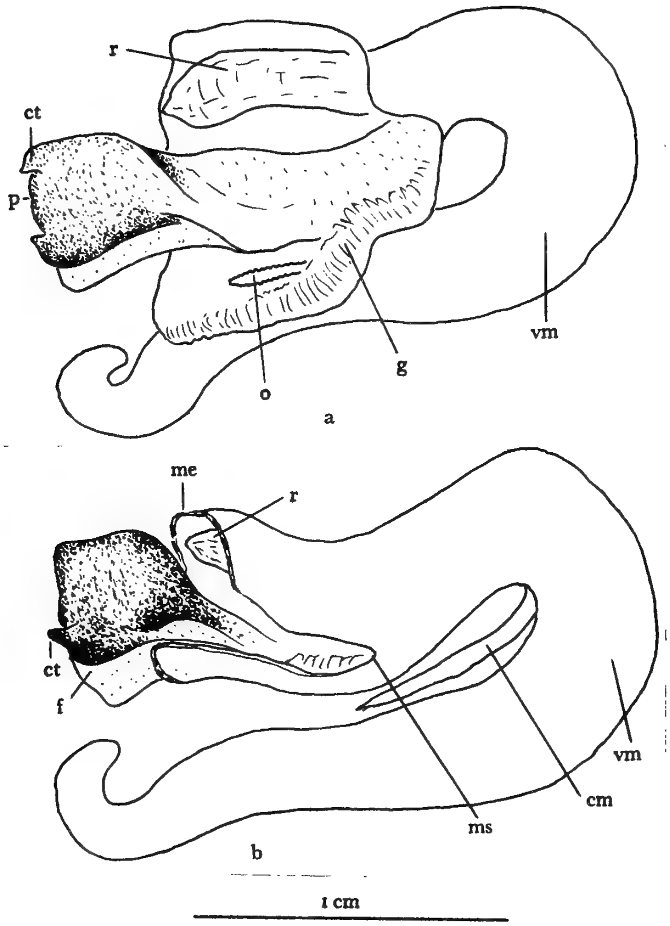

Figure 3

Serpulorbis aureus

(a) The mantle slit has been opened further to expose the contents of the mantle cavity

(b) The intact female showing the dorsal slit in the mantle through which the egg capsules hang

cm – columellar muscle ct – cephalic tentacle f – foot
g – gill me – mantle edge ms – mantle slit
o – osphradium p – proboscis r – rectum
vm – visceral mass

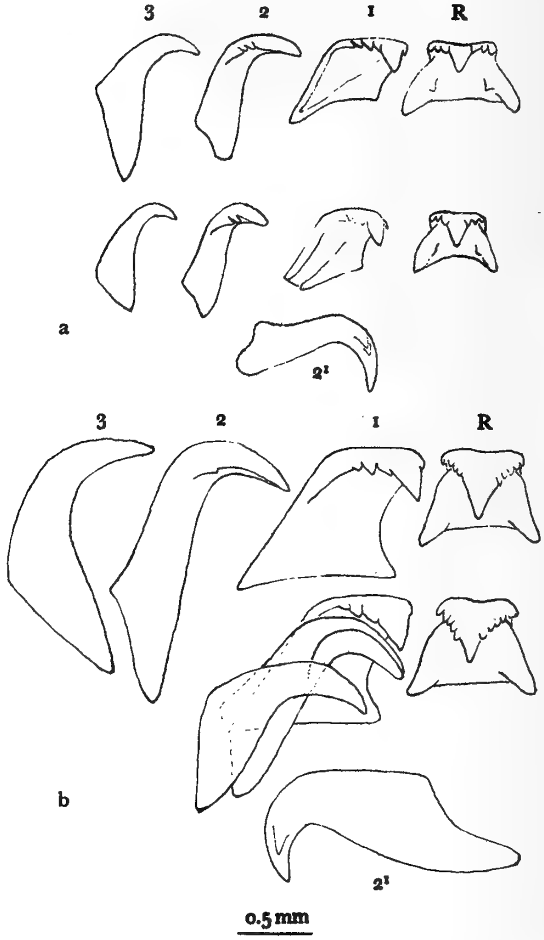

Figure 4

Radular teeth of

(a) *Serpulorbis aureus* (b) *Serpulorbis natalensis*

R – rachidian 1 – lateral 2 – inner marginal (marginal 1)
3 – outer marginal (marginal 2)
2¹ – lateral aspect of inner marginal showing cusps

Subgenus *(Serpulorbis)*: shell not tightly planorboid throughout life.

Species *aureus*: adult shell with concentric whorls and vertical feeding tube; protoconch clear, apical whorl almost as large as basal whorl; rachidian tooth with convex sides, inner marginal tooth with at least 2 lateral cusps on each side; exposed body with golden yellow background colour; embryos with pale green yolk.

TYPE MATERIAL

British Museum [Natural History], Department of Zoology. Holotype 1976/W/1. Embryos 1976/W/2. Late embryos 1976/W/3.

TYPE LOCALITY

On stones at side of main channel, southern shore, mouth

Table 1

Serpulorbis ***aureus***	*Serpulorbis natalensis*
Body up to 4 cm long.	Body up to 6 cm long.
Foot, head and mantle with golden yellow background colour.	Background colour orange.
Yolk pale green.	Yolk pale yellow.
Sides of rachidian tooth convex.	Sides of rachidian tooth concave.
Inner marginal tooth with more than one cusp on each edge.	Inner marginal tooth with one or no cusp on each edge.
Protoconch mostly clear, apical whorl almost as large as basal whorl.	Protoconch pale brown, apical whorl much smaller than basal whorl.
Teleoconch with dextral, usually concentric spirals triangular in cross-section, vertical feeding tube circular in cross-section. Feeding tube scars evident. Sculptured with axial ridges sigmoid in lateral aspect.	Teleoconch vermiform or with loose laterally displaced spirals circular in cross-section. No feeding tube. Sculptured with longitudinal ridges and fine axial striae.

of Umngazana estuary near Port St. Johns, Transkei, South Africa, 32° S; 29½° E.

HABITAT

Serpulorbis ***aureus*** forms loose aggregations on the tops of large silt-covered stones (HUGHES, in press a, fig. 2) at the edge of the main tidal current in the Umngazana estuary. They are not uncovered at low tide. Isolated individuals were also found in large tide pools at mid to high tide level outside the estuary. The feeding tube raises the head away from the silty substratum and thus avoids excessive clogging of the mucous net which is used for feeding. The shell whorls of the estuarine individuals were covered with short algae matted with silt.

DISCUSSION

It is possible that *Serpulorbis* ***aureus*** has been confused previously with *S. natalensis* (Mörch, 1862) which is an abundant species in more southerly waters of the Cape Province (HUGHES, in press b). Anatomical differences between the two species are summarized in Table 1, Figures 1a, 1b, 2a, 2b and 4a, 4b. The anatomy of the soft parts shows little variation within the genus (MORTON, 1951). *Serpulorbis* ***aureus*** and *S. natalensis* differ in microhabitat, *S.* ***aureus*** colonising the upper surfaces of stones in turbid water whereas *S. natalensis* usually colonises the under surfaces of stones where silting is less heavy. Feeding tubes raising the head away from the substratum are not found in *S. natalensis* (personal observations).

Serpulorbis ***aureus*** probably replaces *S. natalensis* as an ecological equivalent in the warmer waters of the South African Indian Ocean just as *Dendropoma tholia* Keen & MORTON, 1960 replaces *D. corallinaceum* (Tomlin, 1939) (HUGHES, in press b).

The coiled shell with vertical feeding tube of *Serpulorbis* ***aureus*** closely resembles that of *S. squamigerus* (Carpenter, 1857) of Californian waters, but the latter is distinguished by its geographical range and by its predominantly black colour with orange pigmentation around the foot and lateral regions of the head (HADFIELD, 1970).

ACKNOWLEDGMENTS

I thank George Branch for inviting me on the expedition to Umngazana and for pointing out the colony of *Serpulorbis* ***aureus*** in front of our camp site.

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A New Species of *Coryphella*

(Nudibranchia : Flabellinidae)

from Santa Barbara, California

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(2 Plates)

On March 25, 1973, 2 nudibranch specimens were collected by David Laur while diving in 20m of water, 1.6 km off Arroyo Burro County Beach, Santa Barbara, California. At first they appeared to be color varieties of *Coryphella iodinea* (Cooper, 1863); however, upon closer examination they were found to have many unique traits. During the ensuing 2 years, several more individuals were found. Preliminary investigations carried out by Robert Cowen yielded promising results, thereby initiating the following study.

On April 16, 1975, 25 specimens were collected in 18 to 24m of water, 1.3 to 1.7km offshore Arroyo Burro County Beach by Craig Fusaro, Shane Anderson and the the senior author. Comparison of these specimens with *Coryphella iodinea* were made using starch-gel electrophoresis, scanning electron micrographs of the radula, and morphometric counts. From our results (given in the discussion) we propose the following taxon.

Flabellinidae Bergh, 1890

Coryphella Gray, 1850

Coryphella sabulicola Cowen & Laur, spec. nov.

Description: Body typical flabellinid shape, laterally compressed, elongate, tapering posteriorly. Body length, excluding oral tentacles, 46 to 55mm, average length 50.5 mm. Length of oral tentacles 17 to 23mm, average length 19.25mm.

Body pale bluish-purple in color, foot bordered with white (Figure *1*). Basal third of oral tentacles same color as body, distal two-thirds white. Base of cerata same as body color, remainder pale orange. Rhinophores red-brown in color.

Cerata in 8 to 10 groups per side, each arising from single ridge-like processes. Anterior-most group separated

Explanation of Figures *1*, *6*

Figure *1*: *Coryphella sabulicola* Cowen & Laur, spec. nov.; photograph by Dave Laur

Figure *6*: Example of starch-gel electrophoresis results. Starting point indicated by arrow. Cathode-attracted proteins (*e. g.*, present in *Coryphella iodinea*), are below the starting point. Odd numbered bands are *C. iodinea*, even numbered bands are *C. sabulicola*.

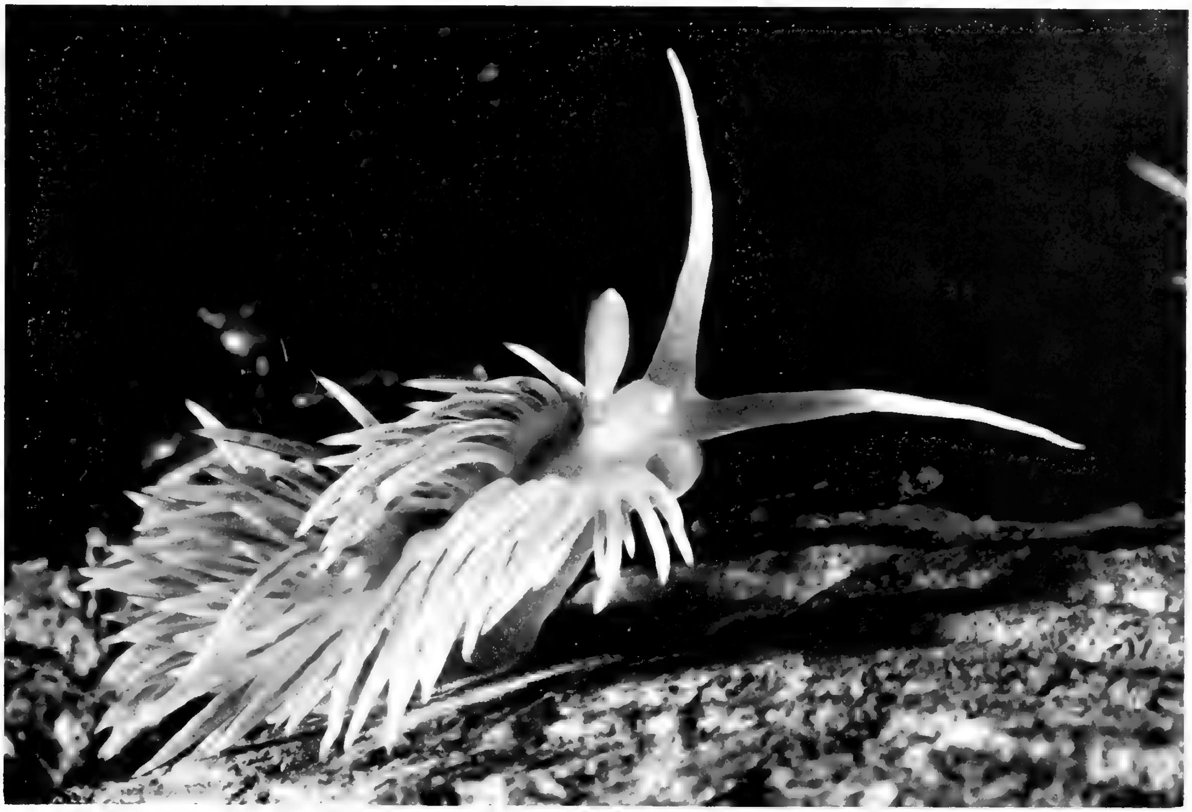

Figure *1*

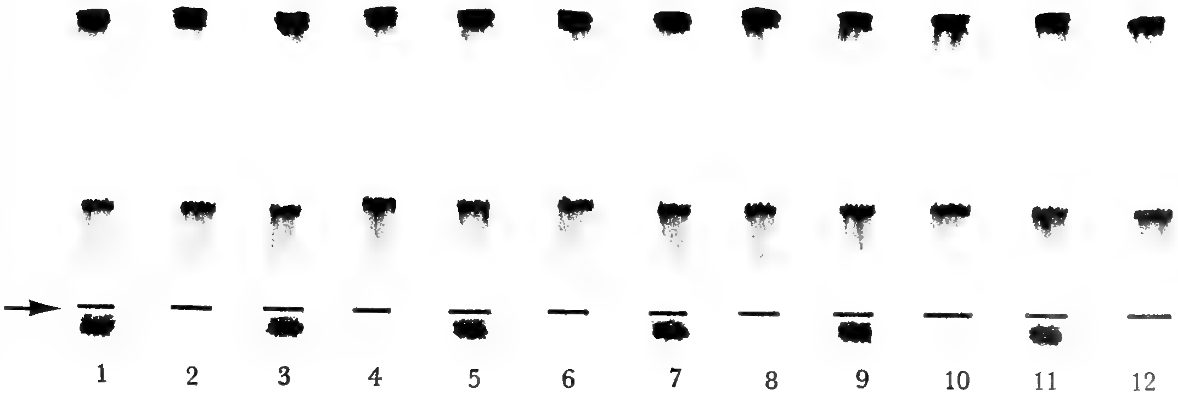

Figure *6*

from remainder by cardiac projection. Number of cerata per group decreases from anterior to posterior. Total number of cerata per side 67 to 82, mode 75. Rhinophores perfoliate with mode of 50 plates.

Radular formula 16 (1 · 1 · 1). Rachidians triangular in shape with deep U-shaped base, bearing 11 to 13 denticles per side (Figure *2*). Median denticles about twice width of side denticles. Laterals roughly triangular in shape with strong central cusp and 13 to 16 equal denticles on inner margin; inner margin ⅔ length of outer margin (Figures *3*, *4*). Laterals set at angle to rachidians; laterals of rows 10 to 16 folded over rachidians and within sheath.

Type Locality: 24 m depth, approximately 1.4 km SSW of Arroyo Burro County Beach, Santa Barbara, California (34°24′N; 119°44′W).

Type Disposition: Holotype - Invertebrate Zoology Type Collection No. 700, California Academy of Sciences, San Francisco, California.

Paratypes: submitted to the California Academy of Sciences for distribution to other institutions.

Habitat: Known from sand and silt bottom with no rock relief, in 15 to 29 m of water, off Arroyo Burro County Beach. Several specimens also have been dredged 3.2 to 4.8 km off Santa Barbara Harbor from a depth of 50 m.

Discussion: ***Coryphella sabulicola*** differs from *C. iodinea* by its paler colors and white foot border and its habitat preference of deep sand and silt bottom rather than shallower rocky relief or pier piling preference of *C. iodinea*. Our study yielded further differences.

A morphometric comparison of 8 specimens of each species was made. The cerata were counted on the left side, and additional counts and measurements were taken which included: total length, oral tentacle length, number of cerata groups, length of longest and shortest cerata. Means and variances were calculated and a Student's t-test was applied (Table 1). The difference in cerata number between the 2 species, relative to length, was significant at the 0.001 level. None of the other morphometric measurements proved significant.

The heads of starved animals were used to test protein differences by starch-gel electrophoresis. Twelve animals of each species were tested, utilizing a general protein stain. In 11 *Coryphella iodinea* tested, there was a cathode attracted protein which was absent in all 12 ***C. sabulicola*** (Figure *6*).

A study of the radulae of 3 animals of each species by scanning electron microscope did not reveal any obvious differences, yet some trends are evident. In ***Coryphella sabulicola*** the rachidians have 11 to 13 denticles per side, while in ***C. iodinea*** the number of denticles ranges from 12 to 14 per side. The range of denticles on the lateral teeth, though more variable, again was smaller in ***C. sabulicola*** than in ***C. iodinea***, 13 to 16 and 13 to 18, respectively (Figures *2* to *5*).

The results of the above study, in conjunction with the color and habitat differences, strongly support the designation of ***Coryphella sabulicola*** as a species distinct and

Table 1

Cerata count results. Cerata counted on left side only.

Animal Number	Body length (mm)		Number of Cerata	
	Coryphella **sabulicola**	*Coryphella iodinea*	*Coryphella* **sabulicola**	*Coryphella iodinea*
1	52	53	81	110
2	50	55	74	96
3	46	50	81	91
4	46	46	67	94
5	55	49	73	78
6	53	51	82	102
7	52	51	71	103
8	50	56	74	106
$\bar{X}$	50.5	51.4	75.4	97.5
S^2			29.4	102.3

$t = 11.82$ p 0.001

separate from *C. iodinea*. Additional work on the ecological differences between these 2 species of *Coryphella* should yield further support for this contention.

Coryphella sabulicola is named with reference to its sand-dwelling habit.

ACKNOWLEDGMENTS

We would like to thank Dr. Demorest Davenport and Dr. F. G. Hochberg for critically reading this manuscript; Lou Haldorson and Dr. Jack King for their help with the electrophoresis; Dr. Preston Cloud for the use of his laboratory's scanning electron microscope and David Pierce for operating it. Chris Kitting helped with the preliminary study. Cathy Engle's help and interest is also appreciated.

Explanation of Figures 2 to 5

Figures 2 to 4: The radula of *Coryphella sabulicola* Cowen & Laur, spec. nov.; scanning electron micrographs by David Pierce

Figure 2: First and second rachidians showing base and denticles × 400

Figure 3: Center of radula showing position of laterals relative to rachidians × 260

Figure 4: Rachidians and laterals showing denticles × 260

Figure 5: The radula of *Coryphella iodinea* (Cooper, 1863). Center of radula showing denticles on laterals and rachidians × 260

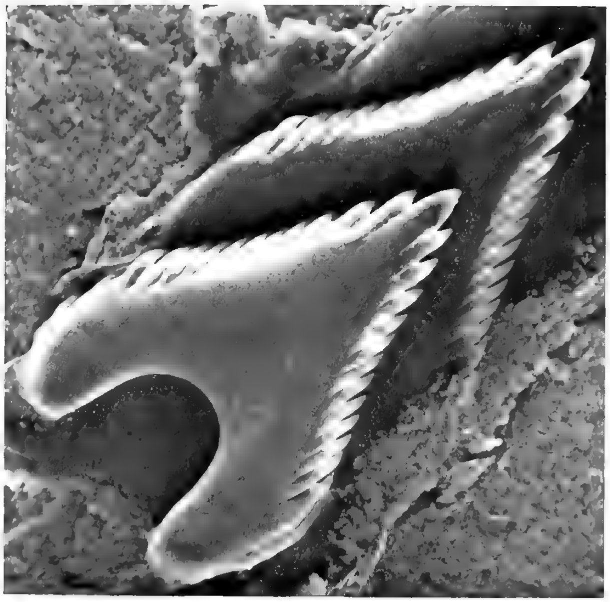

Figure 2

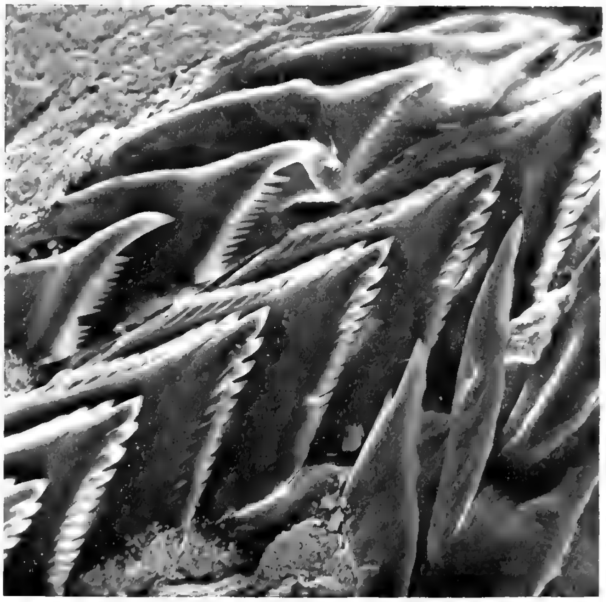

Figure 3

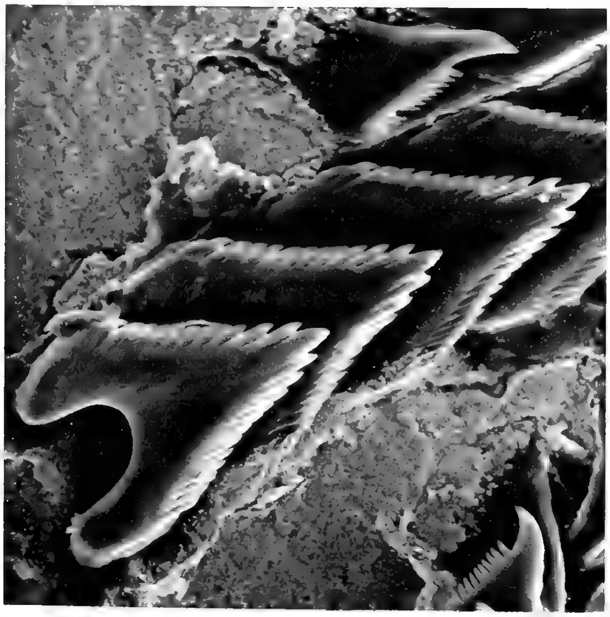

Figure 4

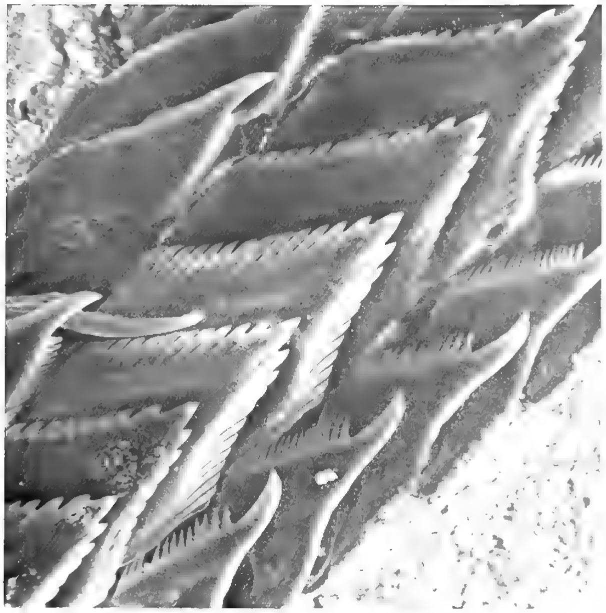

Figure 5

A New Species of *Anachis*

(Gastropoda : Columbellidae)

from the Eastern Pacific

BY

R. A. WHITNEY

2140 North Main Street, Decatur, Illinois 62526

(2 Text figures)

I HAVE EXAMINED numerous specimens of *Anachis* over the past year, and have encountered a species of *Anachis* from the Eastern Pacific region which has not been previously described. This species is seen with some frequency in several of the larger institutional collections as well as in private collections.

Through the interest and generosity of the Los Angeles County Museum of Natural History, I have been able to examine a number of this *Anachis* species, and locality records as well as geographical range can be reported here. These are recorded here immediately following the listing of paratypes. I have assigned the new species to the genus *Anachis,* and, in order not to add confusion to the taxonomic problems in the family Columbellidae, I have avoided the use of other supraspecific taxa, leaving this to a future investigator who might make the necessary anatomical studies to complete a monograph on the Columbellidae of the Eastern Pacific.

Anachis ***lillianae*** Whitney, spec. nov.

(Figures 1, 2)

Description: Size small; color white with light to deep brown markings; whorls somewhat convex with body whorl inflated; axial sculpture predominant over entire shell; nucleus of 2½ glassy whorls; 6 post-nuclear whorls; axial ribs wider than interspaces with ribs on penultimate and earlier whorls having keel-like ridge running down center of each rib; keeled appearance not so much in evidence on body whorl as ribs become less pronounced and more rounded; intercostal striae between ribs impinging on ribs but not crossing center of ribs; 15 ribs on body whorl; basal portion of body whorl has spiral cording; parietal wall of aperture smooth; outer lip of aperture with 6 weak denticles inside lip; deep-brown band anterior to suture forms white subsutural band; deep-brown band broken, giving irregular zig-zag appearance; base of shell marked with irregular cloudings, blotches, and streaks of light brown; anterior canal short; length 7 mm; diameter 3 mm; 6 whorls plus nucleus.

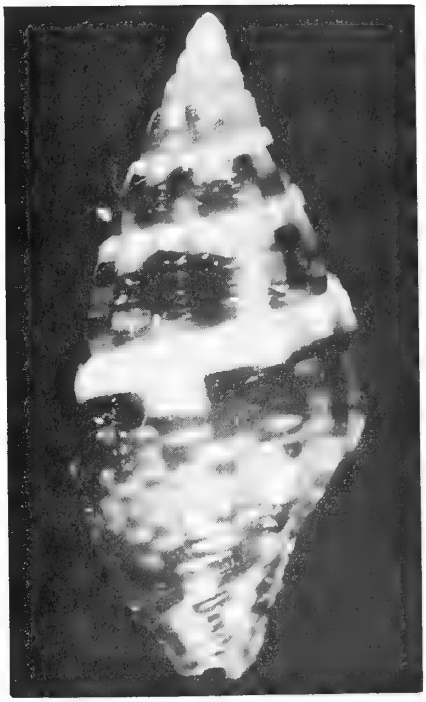

Figure 1

Holotype, Los Angeles County Museum of Natural History Type No. 1852. Dorsal view × 13

Holotype: Los Angeles County Museum of Natural History, Type Collection No. 1852.

Type Locality: All specimens of the type material were collected at Playa Alicia near San Felipe, Baja California, Mexico, under rocks at low tide, March 1976.

Paratypes: Los Angeles County Museum of Natural History Type collection no. 1847; Academy of Natural Sciences, Philadelphia, Type Collection no. 344375; Douglas and Sherry Welker collection no. 6; R. A. Whitney collection no. 37.

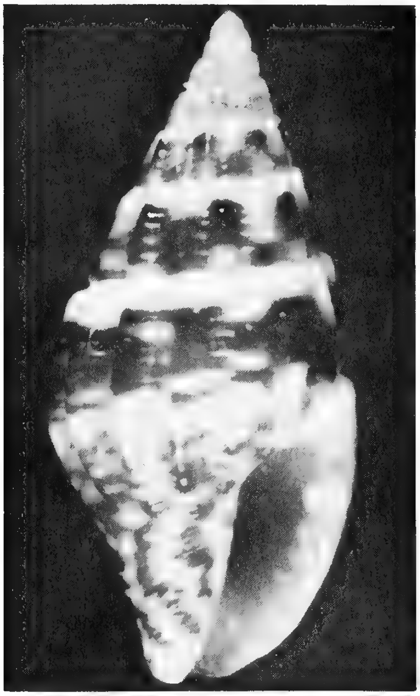

Figure 2

Holotype, Los Angeles County Museum of Natural History Type No. 1852. Ventral view × 13

Other Material Examined: In addition to the type lot – Los Angeles County Museum of Natural History no. 67-17 - Libertad, Sonora, Mexico; no. 11833 - San Blas, Nayarit, Mexico; no. 11834 - Bahía Adair, Sonora, Mexico; no. 63-56 - Puerto Peñasco, Sonora, Mexico; no. 30-74 - Mazatlán, Mexico; no. 59-9 - Topolobampo Bay, Mexico; all intertidal. Also no. 72-58 - 30-75 ft. (9 - 22.5 m), rocky, small islets off Punta Quepos, Puntarenas Province, Costa Rica, 9°52′43″N; 84°09′41″W.

Discussion: There is little variation among the specimens examined of this species. The shell has a striking color pattern and varies in the number and intensity of brown blotches that comprise the subsutural bands. The variation in color markings is especially marked at the base of the body whorl, where the brown markings may appear as streaks, dots, or cloudings. The number of axial ribs on the body whorl varies from 14 to 17.

Anachis lillianae bears some superficial resemblance to other species which should be considered in making identifications. A very closely related species is *A. adelinae* (Tryon, 1883). This species differs from ***A. lillianae*** in having a distinct checkerboard pattern of brown spots on the base of the body whorl, and in the spire being more attenuated. ***Anachis albonodosa*** (Carpenter, 1857) is light brown with white spots showing at the ends of the axial ribs; it is a somewhat smaller shell, with the body whorl being less inflated than ***A. lillianae***. ***Anachis dalli*** Bartsch, 1931 is pale yellow with 2 zones of interrupted brown spots and 1 of white; *A. pygmaea* (Sowerby, 1832) has a distinct pattern of 2 or 3 rows of brown spots; *A. diminuta* (C. B. Adams, 1852) could possibly be mistaken for an immature ***A. lillianae***, but the brown shell of *A. diminuta* is 4 mm or less in size.

The new species is named in honor of Mrs. Lillian Whitney of Decatur, Illinois, in appreciation of her encouragement of, and assistance in, the author's study of Columbellidae.

ACKNOWLEDGMENT

I am sincerely grateful for the generous cooperation given me over a period of many months by the individuals who have contributed so much of their time towards the completion of this paper. I wish to express my thanks to Dr. James H. McLean of the Los Angeles County Museum of Natural History for his advice, and to Mr. Gale Sphon, also of the Los Angeles County Museum, for arranging a loan of museum specimens for comparative studies. I also wish to acknowledge the excellent photographs of the holotype by Mr. Bertram C. Draper, Museum Associate, Los Angeles County Museum of Natural History.

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NOTES & NEWS

Nomenclatural Notes on *Hinnites giganteus* (Gray)

BY

BARRY ROTH[1] AND EUGENE V. COAN

The common rock scallop, or "purple-hinged scallop," of the Pacific Coast appears in recent literature under two names: *Hinnites giganteus* (Gray, 1825) and *Hinnites multirugosus* (Gale, 1928). Gale (1928: 92) introduced the latter because he believed that Gray's name and other possible substitutes were homonyms and therefore unavailable. Other authors (Adam, 1960; Hertlein & Grant, 1972) have given reasons for preferring use of the older name, *H. giganteus*. The valid name of this taxon depends on two related factors: (a) the availability, or not, of Gray's name, and (b) the nature and validity of Gale's rejection of it — both points to be evaluated in light of the ICZN rules governing such cases.

From a review of the relevant literature, we have come to the following conclusions:

1. Gale's (1928) stated reasons for proposing "*Pecten (Chlamys) multirugosus*" — a new taxon, not a simple renaming — and his remark that *Lima gigantea* Gray was "stillborn" are erroneous. *Lima gigantea* Gray (1825: 139), as the species was first named, is the earliest use of this combination of generic and specific names. It is not a primary homonym of *Plagiostoma giganteum* J. Sowerby, 1814, whether or not *Lima* Bruguière, 1797, and *Plagiostoma* J. Sowerby, 1814, are considered synonymous genera of the Limidae. Grau's (1959) claim that *Plagiostoma* was proposed as a subgenus of *Lima* is incorrect. Moreover, Gray (1826) removed his *gigantea* from *Lima* and placed it in "*Hinnita*" (an invalid emendation of *Hinnites* Defrance, 1821), and the species has not been reallocated to *Lima* since that time. We have located no citation of Sowerby's *giganteum* in the genus *Lima* prior to those by Deshayes (1831, 1832), although the possible synonymy of *Lima* and *Plagiostoma* was being debated as early as 1823 (G. B. Sowerby, 1823). Modern workers consider the two genera separable.

As Adam (1960) noted, Gray's and Sowerby's names were not secondary homonyms at the time of Gale's (1928) publication. It is evident that Gale himself did not believe the two species to be congeneric, since he cited Sowerby's *giganteum* as a *Lima* but described *multirugosus* as a species of *Pecten*. Under ICZN rules [Art. 59(b)(2)], Gray's name required no replacement then and requires none today.

2. Jay (1835) and many subsequent authors placed Gray's *gigantea* in the genus *Pecten* Müller, 1776. While several other pectinid taxa share the specific epithet "*giganteus*," the earliest of these is *Pecten giganteus* Münster *in* Goldfuss, 1833. The *gigantea* of Gray (1825) is therefore not a junior secondary homonym in *Pecten*.

3. Gale (1928) specifically stated that his *Pecten (Chlamys) multirugosus* was proposed as a new species, and not the simple renaming of a homonym: "*Pecten multirugosus* **is virtually** a new name for the common Pliocene to Recent West Coast species formerly known as *Pecten (Hinnites) giganteus* (Gray); but in order to avoid any questions about the location or identity of the original types, **the species is described as new and a new type is cited**" (Gale, 1928: 92; emphasis supplied). In contrast, "*Pecten (Chlamys) multirugosus* var. *crassiplicatus*," a renaming of the homonymous *Hinnites crassa* Conrad, 1857, by Gale in the same paper, was unequivocally proposed as a replacement name.

4. In summary, Gray's (1825) name *gigantea* was available when proposed and has remained available throughout its nomenclatural history. Gale's (1928) rejection of it was invalid because he did not contend that the two species-group taxa, "*Lima*" *gigantea* Gray and *Plagiostoma giganteum* Sowerby, were congeneric. *Pecten (Chlamys) multirugosus* Gale, 1928, is therefore a junior synonym of *Hinnites giganteus* (Gray, 1825), and the latter is the valid name for the Pacific Coast rock scallop.

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[1] Department of Geology, California Academy of Sciences, San Francisco, California 94118

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1823 (1821-1834). The genera of Recent and fossil shells. 2 vols. London. 262 plts. & accompanying text (unpag.)[Part 17, incl. genus *Lima*, publ. about 20 August 1823, *fide* Sherborn, C. D., 1894, Ann. Mag. Nat. Hist. (6) 13 (76): 371]

Sowerby, James de Carle
1814 (1812-1815). The mineral conchology of Great Britain ... Vol. 1. London. 236 pp., 102 plts. [Part 14, pp. 169-178, plts. 74-78, publ. 1 December 1814, *fide* Sykes, E. R., 1906, Proc. Malacol. Soc. London 7 (3): 191]

Publication Dates of Bergh's 1879 Papers Describing American Chromodorids

BY

ROBERT BURN

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Melbourne, Victoria, Australia 3000

Three papers containing descriptions of American chromodorid opisthobranchs were published by Rudolph Bergh in the year 1879. In an attempt to establish an order of priority for original descriptions, synonymies and future revisions, the publication dates of the 3 papers have been determined.

According to internal evidence, *i. e.*, the numbering in the lists of *Chromodoris* species in the papers, Bergh wrote his papers in the sequence (1) Neue Nacktschnecken der Südsee, (2) On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska, and (3) Neue Chromodoriden. The papers are treated here in this order.

(1) The 4th and last part of Bergh's series "Neue Nacktschnecken der Südsee" was published in part 14 of volume 5 of *Journal des Museum Godeffroy.* In reply to an enquiry to the Zoological Library, British Museum (Natural History), Miss A. Lucas informed me that their copy has "a list of other publications of the publisher (L. Friederichsen & Co.), on the back cover, at the end of which are the words 'Hamburg, im Februar 1879'. The other piece of evidence is the words 'Zool. Dept. 28/3/79' written faintly in pencil on the front cover – presumably the date of receipt here" (*in litt.* 19 June 1970).

Thus it can be shown that the date of publication was probably not earlier than the printer's date of February 1879, and certainly prior to 28 March 1879, the date of receipt at the B. M. (N. H.). In the absence of evidence to the contrary, it is possible to stipulate the last day of February, *i. e.*, 28 February 1879, as the date of publication.

(2) Bergh's "On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. Part I" appeared in 2 simultaneously published journals (W. H. Dall, *in* Bergh, 1879d: 125); Russell, 1968: 141). A printer's date, 10 May 1879, appears at the foot of the first page of Part I. In the certification notice in the title pages for the *Proceedings of the Academy of Natural Sciences of Philadelphia, 1879,* the then editor and recording secretary, Edward J. Nolan, reports that the pages containing Bergh's article were presented at the meeting of the Academy on 13 May 1879.

The closeness of these 2 dates, plus the certification notice, suggests that it is reasonable to accept 10 May 1879 as the publication date.

(3) There being no internal evidence to qualify the date of publication for Bergh's "Neue Chromodoriden" more specifically than 1879, under I. C. Z. N. Article 21(b) the publication date would be 31 December 1879. However, external evidence indicates a much earlier date.

In the 'Literaturbericht' of *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft 1879,* the '*Malakozoologische Blätter*, herausgegeben von S. Clessin, Neue Folge, Bd. 1, Lfg. 1, Mit 3 Tafeln' is reviewed article by article on pages 41 - 42. Page 42 has the following entry: 'p. 77. Bergh, Dr. R., Notizen über *Pleurophyllidia lovéni*.' The last lines of Bergh's *Pleurophyllidia* paper are printed on the same page (p. 87) as the title and first paragraphs of his "Neue Chromodoriden" (yet for some reason there is no entry in the 'Literaturbericht' for this latter paper). Plate 3, which belongs to "Neue Chromodoriden", is the 3rd plate of the 'Mit 3 Tafeln' mentioned in the 'Literaturbericht.'

It is thus demonstrable that these 2 papers by Bergh were published at the same time.

Dates of publication of the parts of *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft 1879* are found in the printer's notices at the end of each part. Page 48, the last page of 'No. 2 & 3 Februar - März

1879', is dated 'März 1879'. Under combination of I. C. Z. N. Articles 21(b)(i) and 21(f), the date of publication for "Neue Chromodoriden" must be regarded as 31 March 1879.

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1879c. Neue Chromodoriden. Malakozool. Blätt., N. F. 1: 87 - 116; plt. 3 (31 March 1879)

1879d. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. Part I. Proc. Acad. Nat Sci. Philadelphia 31: 71 - 132; plts. 1 - 8 (10 May 1879)

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The Date of Publication of Anton's "Verzeichniss der Conchylien"

BY

WALTER O. CERNOHORSKY

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ANTON'S IMPORTANT CONCHOLOGICAL work "Verzeichniß der Conchylien ...", which besides descriptions of new taxa also contains generic type-species designations, has always been deemed to have been published in 1839, despite the note on page 110 "Im Druck beendigt den 9. Oktober 1838", meaning that by that date the printing was completed.

Irrefutable proof that Anton's work already appeared in 1838 can be found in TROSCHEL (1839) who states:

"Unter dem Titel: Verzeichniß der Conchylien, welche sich in der Sammlung von Hermann Eduard Anton befinden, herausgegeben von dem Besitzer, Halle b. Eduard Anton 1839, erschien in der Mitte des Jahres 1838 ein Buch, das schon bei seiner Geburt sich um ein Jahr jünger machte."

TROSCHEL (*op. cit.*), who every year reviewed molluscan literature published during the previous year for the "Archiv für Naturgeschichte", clearly states that Anton's work appeared already in the middle of 1838 and that the book "made itself one year younger at the time of its birth". The date 1839 on the title page is thus certainly an error and the date of 9. Oktober 1838 on page 110 a probable error which does not coincide with a middle of the year publication date. Both these dates may represent tentative completion dates.

The acceptance of 1838 as the publication date for Anton's "Verzeichniß der Conchylien ..." will change only a few specific name priorities and no major taxonomic changes are expected.

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TROSCHEL, FRANZ HERMANN

1839. V. Mollusca. Arch. f. Naturgesch. 5 (2): 201 - 241

Another Cephalopod from Northern California

(Mollusca : Cephalopoda)

BY

ROBERT R. TALMADGE[1]

Eureka, California 95501

LATE IN JANUARY 1977, the crew and Captain James Riley of the drag boat *Ina* noted a rather unusual "squid" on the deck of the vessel after making a daylight tow in 330 fathoms (603m) on a soft (green) mud substrate. The tow was made at approximately 40°15′N, north of Eureka, California. The specimen was salvaged from amid the fish on deck and preserved on shipboard in a 10% solution of formalin. The specimen came to my hands and I deposited it in the "wet collection", Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California.

Although this squid appeared to represent a species new to this part of the northern California coast, a possibly related species or variety has been taken a few times

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previously. Both species belong to the genus *Calliteuthis*. One species with an elongate body has been called *C. hoylei* (Pfeiffer, 1900), while the short-bodied form has been referred to *C. meleagroteuthis* Chun, 1910. Voss (1963) places the two taxa in synonymy.

This note is presented in order to alert students of the Cephalopoda as to the whereabouts of this specimen. Based on my own observations, both species are uncommon in collections.

Literature Cited

VOSS, GILBERT LINCOLN
1963. Cephalopods of the Philippine Islands. Bull. U. S. Nat. Mus. 234: i-v+1-180; 35 text figs.

W. S. M.

THE 1978 MEETING of the Western Society of Malacologists will be held at the University of Santa Clara, near San Jose, California, June 28 through July 1. Presentation of papers concerning mollusks and other invertebrates will be complemented by field trips, work shops, and displays. A symposium concerning current studies of American land mollusks is also scheduled. A second symposium of research dealing with freshwater mollusks is probable. Information about the meeting is available from Dr. Peter Neal D'Eliscu, President, W. S. M., Department of Biology, University of Santa Clara, Santa Clara, CA 95053.

A. S. Z.

THE AMERICAN SOCIETY of Zoologists, Society of Systematic Zoology and the American Microscopical Society will meet Wednesday, December 27 through Saturday, December 30, 1978 at the Hotel John Marshall in Richmond, Virginia. A call for contributed papers will be issued in April, 1978. For more information write to: Ms. Mary Wiley, American Society of Zoologists, Box 2739 California Lutheran College, Thousand Oaks, CA 91360.

Late News

Rate Increases:

Because of continued inflationary pressures, it has become necessary to increase subcription rate and membership dues effective with volume 21. The subscription rate will be U. S. $30.00 plus postage, while membership dues will be U. S. $15.00 plus postage charges. For the time being, that is, until the U. S. Postal Service further increases postal rates, our charges will remain as follows: $1.00 for all domestic addresses, $2.50 for addresses in the so-called P. U. A. S. countries, and $3.50 in all other countries, including Canada. A more detailed announcement will be included with the invoices sent to subscribers. Subscription agencies have already been informed, those in foreign countries by air mail.

Sale of C. M. S. Publications:

Effective January 1, 1978, all back volumes still in print, both paper covered and cloth bound, will be available only from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644, at the prices indicated in our Notes and News section, plus postage and, where applicable, California State Sales Tax. The same will apply to the Supplements that are still in print, except for supplements to vol. 7 (Glossary) and 15 (Ovulidae), which are sold by The Shell Cabinet, P. O. Box 29, Falls Church, VI(rginia) 22046; and supplement to volume 18 (Chitons) which is available from Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

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We are pleased to announce that Dr. George V. Shkurkin has assumed the duties of Manager. Correspondence may be addressed to him at 1332 Spruce Street, Berkeley, CA(lifornia) 94709.

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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 will be presented in a forthcoming issue in the Notes and News section.

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We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US$12.- to US$24.-, depending on the cost to us.
Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

The Veliger is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

A Glossary of A Thousand-and-One Terms Used in Conchology
by Winifred H. Arnold

originally published as a supplement to volume 7 of the Veliger has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US$ 3.50 postpaid if remittance is sent with the order.

We are pleased to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. 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:

Volume 1: $1.50
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Volume 4: $4.50
Volume 5: $4.50
Volume 6: $4.50
Volume 7: $6.00
Volume 8: $6.00
Volume 10: $9.00
Volume 11: $9.00
Volume 12: $9.00
Supplement to Volume 6: $1.50; to Volume 18: $3.00

California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, P. O. Box 243, Santa Maria, CA 93454.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644. Orders should be sent directly to Mr. West.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of $1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $4.25 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to Dr. George V. Shkurkin, *Manager*, 1332 Spruce Street, California 94709
However, until further notice, we are suspending the publication of supplements until it will be reasonably certain that we will not be forced to spend many hours in tracing of lost insured or registered parcels and entering claims for indemnification. The special mailing list of members and subscribers who have entered an "including all supplements" will be preserved because of our innate optimism that sometime within our lifetime the postal services throughout the world will return to the former excellent and reliable performance.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims of missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues. This refusal is necessary as we have received an increasing number of "claims" as much as 6 months before the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address – $1.-

change of address and re-mailing of a returned issue – $2.75 minimus, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of $12.50 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 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); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of $1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of $5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is $25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

REGARDING POSTAL SERVICE

Complaints regarding late arrival of our journal are increasing in number, steadily, continually. However, we very conscientiously dispatch our journal on the printed publication dates. What happens after deposition at the Post Office is, of course, beyond our control. From some of our members we have been able to construct a sort of probable delivery schedule. In general, within California, 8 days is usual; outside of California, the time lapse increases with the distance; the East Coast can consider a lapse of "only" two weeks as rapid service; 4 to 5 weeks are not uncommon. Foreign countries may count on a minimum of one month, six weeks being the more usual time requirement and over two months not rare!

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address).

New Postage Rates

The U. S. Postal Service has increased second class mail rates, effective on July 6, 1977. We will, however, not increase our charges for mailing The Veliger, but must insist that we are reimbursed in all cases for returned copies and for the expenses involved in remailing such copies to a new address. It is very important for our members to realize: a) the postal service will not forward any mail other than first class for more than 90 days, even though forwarding postage may be guaranteed by the addressee; and b) it is totally impossible for us to make changes in addresses in less than 6 weeks.

We must make an address change even if only one digit in the ZIP code is changed, and the cost to us is the same as for a completely new address.

Under no circumstances are we able to supply free replacement copies of issues that fail to reach their proper destination. However, we will ship by insured mail replacement copies at half the announced single copy rate of the particular issue plus postage. We have developed a triple check system so that, if we say that a copy has been mailed, we are absolutely certain that we delivered that copy to the post office in Berkeley and on the date we indicate. From our experience with the loss of insured mail, we are tempted to suggest that subscribers figure on a 10% reserve fund for the purchase of replacement copies. The only alternative remaining would be for us to increase subscription rates and membership dues by at least 10%. This, however, does not seem quite fair to us as some of our subscribers in almost 20 years have never failed to receive their copies.

On July 6 the rates for book parcels and the library rate have been increased. This necessitates that we must increase the postage charges on back volumes, supplements and individual back numbers. The charges stated must be increased by 20¢ for one item and by 8¢ for each additional item.

It has been announced by the Postal Service that no increase in postage rates would be asked during the current year; it was not stressed sufficiently that this applies only to the so-called first class mail. Second class mail rates are "phased," that is, they are scheduled to be increased each year until the rates are sufficiently high to pay the actual cost of handling that type of mail. While it is true that the rates have been very low, it should be borne in mind that the original intent of the special low rates was to aid in the dissemination of knowledge. This philosophy has, seemingly, been abandoned.

The regulations pertaining to second class mailing require "pre-sorting" of the mail which involves a large amount of time, especially if the total number of pieces is too small to warrant the employment of computerization. This requirement seems justified as long as the rates for second class matter remain substantially below those for first class matter. However, our members should be aware of the fact that postal regulations rule that second class matter can not be forwarded three months after an address change, even though the addressee guarantees forwarding postage (in contrast, first class mail, at least for the time being, is forwarded for one year and that without charge!). Thus, issues mailed to the "old" address will be returned to the publisher if return postage is guaranteed at a rate that is considerably higher; we have been charged as much as $1.45 for such returned copies. There is also a charge of 25¢ for a postal notification of the new address. It must be obvious that we cannot keep absorbing such extra expenses and keep membership dues and subscription rate at the current low rate. We must ask for the wholehearted cooperation of all concerned to help us to hold the line against increases. Also, if a copy is returned we will, as in the past, advise the member of this fact and indicate the total costs incurred for which we must seek reimbursement. If this reimbursement is not made, we cannot continue to send future issues to the delinquent member. Membership will have to be considered as terminated and can be re-instated only upon payment of all arrears. We regret that this apparently hard rule is necessary, but we wish to continue publishing the Veliger – which will not be possible if these rules are not observed.

Although the Postal Service continues to deteriorate consistently, the postal rates are increased by 30 to 100%. We are, therefore, forced to increase the handling charges as well as the postage charges on the subscription. The following rates will be in effect on all new subscriptions and subscription renewals as of December 28, 1975:

$1.- on subscriptions and memberships in the U. S. A.; $2.50 on memberships and subscriptions to PUAS countries (Mexico, Central and South America and Spain); $3.50 to all other foreign countries, including Canada. We wish to stress that we are NOT INCREASING either membership dues or subscription rates, in spite of increased printing costs. But at the same time, we wish to call the attention to our Endowment Fund, the income from which enables us, in part, to keep these charges at the established levels. Contributions (tax deductible in the U. S. A.) are always welcome.

Publication Date of THE VELIGER

The publication date of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed $200.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, $200.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U.S.A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office, in other words, it is destroyed.

BOOKS, PERIODICALS, PAMPHLETS

Shells of New Zealand

by A. W. B. Powell. Fifth revised edition. Whitcoulls Publisher, Christchurch, New Zealand. 154 pp., 45 plts. (2 in color) $12.00. April 1977

This latest edition of a classic work lists a total of 2 256 molluscan species, both marine and non-marine, that have been reported in New Zealand, and it illustrates 555 of them. Except for updating, the general format of the work is unchanged; papers cited in the bibliography again are cross-referenced into the body of the list, and this has been completed up through 1974. Some new illustrations are added, as well as new paragraphs in the introductory text, which includes useful notes on collecting, on classification, and on the significance of molluscan studies in understanding both the geologic past and present-day distribution patterns of marine life. The bibliography runs to 14 pages; the check list, with its mine of references, to 56.

The book is hardbound, and the dust-jacket carries a small portrait of Dr. Powell, who has been on the staff of the Auckland Museum for more than 56 years. Although he formally retired in 1968 as Director, he continues work as Honorary Research Associate. This book is yet another in a long list of significant contributions to malacology that have come from his pen.

A. Myra Keen

Sea Shells from Cape Verde Islands

by Luís P. Burnay & António A. Monteiro. Lisbon, 88 pp., 2 text figures, 2 maps, 54 photographs on coated paper. January 1977
Available from Seashell Treasures, P. O. Box 730, Oakhurst, CA 93644 at US$5.00

This paperback book, rather charmingly written though not without an occasional grammatical or spelling error (the authors deserve commendation for their erudite use of the English language which is far better than that of some American writers!) is organized into two parts, the first of which contains chapters on collecting and preserving techniques; but of special interest are the introductory remarks on the collecting area. The second part contains a systematically arranged account of the species found by the authors during 2 successive collecting trips in 1975 and 1976. A bibliography of 122 titles and a 2-page index complete the volume.

As can be expected when collecting is extended to an area that has not been readily accessible in the past, specimens are obtained that do not completely agree in every detail with the otherwise well-known representatives of a particular taxon. Such differing forms are too frequently described as new species with little supporting or comparative material being adduced. It is therefore extremely refreshing to find that these authors, while acknowledging having found such different forms, have specifically refrained from describing and naming them and thus they have avoided joining the ranks of the extreme splitters. We congratulate them on this very wise choice.

R. Stohler

Wonders of Starfish

by Morris K. Jacobson & William K. Emerson. Dodd, Mead & Company. New York, N. Y. 10016. 80 pp., numerous, though unnumbered, photographs and drawings. $4.95 5 July 1977

Although the hardbound booklet is intended for the juvenile reader (from 10 years up), it is nevertheless scientifically accurate. It is a reliable introduction to a very interesting and highly specialized group of marine animals that even the most unobservant casual visitor to the sea shore cannot fail to notice. And young children with their unsatiable curiosity will find almost all the answers in this book.

R. Stohler

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. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

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 specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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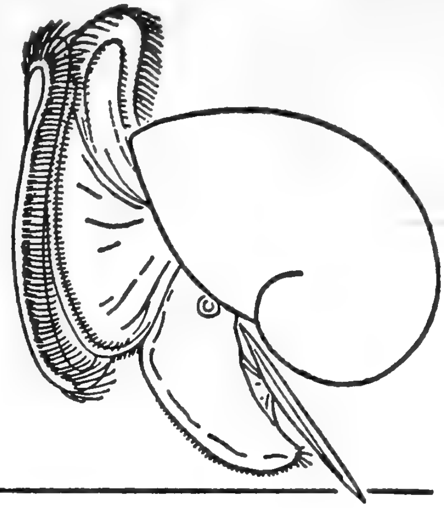

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[Continued on Inside Front Cover]

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, *(Subgenus)*
New Taxa

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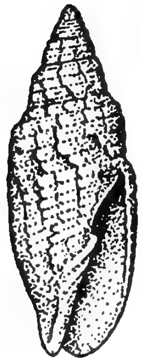

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1584 Milvia Street, Berkeley, CA 94709, U. S. A.
Address all other correspondence to Dr. R. STOHLER, *Editor*, Department of Zoology
University of California, Berkeley, CA 94720

The Chromodoridinae Nudibranchs from the Pacific Coast of America. - Part II. The Genus *Chromodoris*

BY

HANS BERTSCH[1]

Donner Laboratory and Department of Zoology, University of California, Berkeley, California 94720

(3 Plates; Text figures 4 - 15)

THIS IS THE SECOND article in a 4-part series monographing the Chromodoridinae from the Eastern Pacific. Figures and tables are numbered consecutively through all 4 articles.

Part I (BERTSCH, 1977) consisted of Materials and Methods and supra-specific chromodorid taxonomy. In Materials and Methods, I examined the use of the radula in opisthobranch taxonomy by: 1) analyzing both the contribution of scanning electron microscopy (SEM) to radular studies (cf. also a recent paper by HICKMAN, 1977, which appeared too late for inclusion in Part I) and methods of specimen preparation for successive viewing by SEM and light microscopy; 2) discussing the numerical analysis of radular variation (see also BERTSCH, 1976a); and, 3) defining the structural terms applicable to radular teeth. The taxonomic coverage of Part I was at the levels of the family, subfamily and genus.

Chromodoris Alder & Hancock, 1855

Chromodoris baumanni Bertsch, 1970

(Figures 3-A, 4, and 10 - 12)

References and Synonymy:

Chromodoris norrisi (not Farmer, 1963). MARCUS & MARCUS, 1967: 170 - 173; fig. 24; Material 3
Chromodoris sp. BERTSCH, 1971: 16
Chromodoris baumanni Bertsch, 1970: 8 - 12; figs. 3 - 13 SPHON & MULLINER, 1972: 150 - 151. SPHON, 1972b: 59. BERTSCH, FERREIRA, FARMER & HAYES, 1973: 289, 292. BERTSCH, 1973: 108, 110. KEEN & COAN, 1975: 43. BERTSCH, 1976b: 157

Material Examined and Distribution:

Baja California, Mexico:

1) 1 specimen, Isla Carmen; *leg.* C. Gage, April 1974 (identified from a color transparency)
2) 3 specimens, 1 km north of Isla Monserrate; *leg.* A. J. Ferreira, 16 June 1974 (HB 377 A - C)
3) 1 specimen, La Paz area; *leg.* E. Janss, Jr., April 1972 (HB 398; LACM A-9555)
4) 1 specimen, 2 - 3 m subtidal, Bahía Carisalito, 4 km N of Bahía Las Cruces; *leg.* H. Bertsch, 23 July 1972 (HB 5)
5) 1 specimen. Isla Espíritu Santo; *leg.* W. M. Farmer, 29 June 1964 (identified from a color transparency)
6) 1 specimen, Isla Espíritu Santo; *leg.* E. Janss, Jr., April 1974 (HB 401; LACM A-9555)
7) 1 specimen, Isla Cerralvo; *leg.* W. M. Farmer, May 1962 (identified from a color transparency)
8) 2 specimens, intertidal to 6 m subtidal, Cabo Pulmo; *leg.* C. Gage *et al.*, 25-26 May 1971 (HB 386 A-B; LACM)

Mainland Mexico:

9) 1 specimen, 20 m subtidal Guaymas, Sonora; *leg.* A. Kerstitch, 12 March 1966 (HB 321; USNM 753559)
10) 2 specimens, intertidal, Sayulita, Nayarit; *leg.* G. G. Sphon, January 1970 (HB 397 A-B; LACM 70-4)
11) 3 specimens, intertidal, Punta Mita, Nayarit; *leg.* F. & R. Poorman, 2 January 1976 (HB 416 A-C; LACM A-8477)

South America:

12) 1 specimen, Academy Bay, Santa Cruz Island, Galápagos Islands; *leg.* A. G. Smith, February 1964 (identified from a color transparency)
13) 1 specimen, intertidal, Academy Bay, Santa Cruz Island, Galápagos Islands, *leg.* Ameripagos Expedition, March 1971 (HB 400; LACM 71-44)

Type Locality:

The type locality of *Chromodoris baumanni* is Isla San Francisco, Baja California; previous collecting records of this species include the Gulf of California, southern Mexi-

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[1] Present address: Biological Sciences, Chaminade University of Honolulu, Honolulu, Hawaii 96816

Editor's Note: For Figures 3-A, 3-B, etc. see The Veliger 20 (2): 115

co, Central America, and the Galápagos Islands. Its northernmost reported occurrence is Bahía San Carlos, Sonora, Mexico (Bertsch *et al.*, 1973).

External Morphology and Coloration:

Chromodoris baumanni reaches at least 62 mm in total length. Notal and foot background color is white; in the notal dorso-median region this background color is light yellow. Numerous small red-purple dots cover the notum and the posterior and lateral surfaces of the foot. An interrupted band of orange (or light red) dots and streaks surrounds the lateral edges of the notum and foot. The rhinophores are white, with a red-purple coloration distally; the extreme tip is white. The gills are white, with a purplish hue on the distal portion (cf. the color illustrations in Bertsch, 1970: figs. 3 - 6).

Radula:

Sizes of each radula examined, the respective width: length ratio, number of tooth rows and maximum number of teeth per half-row are given in Table 1. The combined radular formula (including literature references) is 47 - 84 rows with 29 - 68 teeth per half-row; rachidian tooth absent.

Least squares regression line analysis shows that the number of rows of teeth and the maximum number of teeth per half-row are positively correlated (Figure 10-A). The coefficient of correlation (r) is 0.949 ($n = 16$, $P < 0.001$). The regression line is described by the equation $Y = -11.09 + 0.922\ X$.

The number of rows is positively correlated with the length of the radula (Figure 11-A). The regression line formula is $Y = 37.96 + 11.228\ X$; $r = 0.922$, $n = 14$, and $P < 0.001$.

The maximum number of teeth per half-row is dependent upon the width of the radula (Figure 12-A). The equation, $Y = 24.52 + 19.674\ X$, describes the regression line and the coefficient of correlation equals 0.8808, $n = 14$, $P < 0.001$.

Figure 4-A presents an outline sketch of a flat-mounted radula. The innermost lateral tooth (Figure 4-B) has 3 - 4 denticles on the inner face, and 2 - 6 (usually 3 - 5) denticles on the outer face. The inner lateral teeth (approximately the first 5 - 10) are short, with a strongly recurved shaft and a proportionately long base; the cusp is much longer than the succeeding denticles (Figures 4-C - 4-G). Throughout the middle of the half-row, the teeth (Figures 4-H, 4-I) have a longer, straighter shaft, with 6 - 9 denticles on the posterior surface. The denticles are larger in size relative to the cusp.

The length of the cusps (measured on a straight line, from the notch joining the first denticle with the cusp,

Table 1

Radular variation in *Chromodoris baumanni*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
[1]	—	—	—	82	65
[2]	—	—	—	84	64
5	1.99	1.13	1:1.77	53	41
321	3.33	1.82	1:1.83	85	68
377 A	2.99	1.66	1:1.8	74	55
377 B	2.81	1.58	1:1.78	70	55
377 C	3.29	1.86	1:1.77	67	54
386 A	3.76	1.58	1:2.38	80	67
386 B	3.64	1.92	1:1.89	78	55
397 A	1.27	0.57	1:2.23	59	34
397 B	0.85	0.46	1:1.85	47	31
398	2.26	1.13	1:2	64	55
401	1.52	0.75	1:2.03	49	37
416 A	1.18	0.53	1:2.23	55	42
416 B	0.92	0.36	1:2.56	48	29
416 C	1.58	0.85	1:1.86	55	39
$\overline{X}$	2.24	1.16	1:1.99	65.625	49.438
s	1.045	0.572	0.254	13.657	13.261

[1] Marcus & Marcus, 1967; [2] Bertsch, 1970

to the tip of the cusp) averaged 0.0086 mm (range, 0.005 - 0.013 mm, n = 26) for the inner 15 lateral teeth and random teeth from the middle of the half-row. The mean ratio of the length of the first denticle to the length of the cusp is 1:1.79 (range, 1.2 - 3.25; s = 0.457; n = 27). The outermost lateral teeth (Figures 4-J, 4-K) become smaller, with cusp and denticles greatly reduced in size.

Developing teeth (Figures 4-L - 4-O) show earliest development of the base and shaft, with minute denticles. Denticles begin growth as small points on the future posterior surface of the tooth. After initial formation, growth

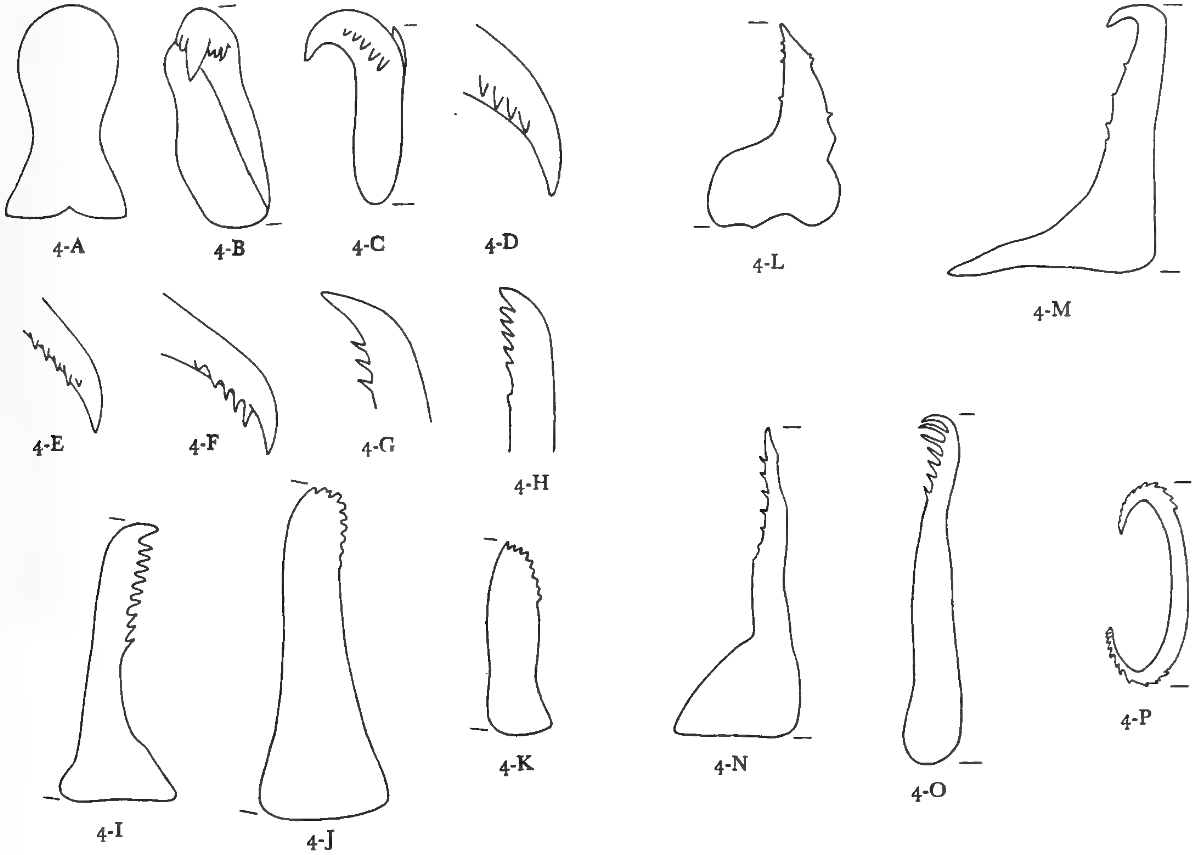


Figure 4

Radular teeth of *Chromodoris baumanni*

A – HB 398; outline sketch of entire radula

B – HB 5; innermost lateral tooth, approximately row 17, right side of radula (RSR); length between marks (LBM) 0.059 mm

C – HB 5; postero-lateral view of 2nd lateral tooth, row 40, RSR; LBM, 0.053 mm

D – HB 398; distal portion of shaft, 2nd lateral tooth, row 55, left side of radula (LSR)

E – HB 398; distal portion of shaft, 3rd lateral tooth, row 55, LSR

F – HB 398; distal portion of shaft, 7th lateral tooth, row 55, LSR

G – HB 386 A; distal portion of shaft, 11th lateral tooth, row 37, RSR

H – HB 398; distal portion of shaft, 26th lateral tooth, row 21, RSR

I – HB 5; tooth from middle of half-row, approximately row 42, LSR; LBM, 0.081 mm

J – HB 5; second outermost tooth, approximately row 42, LSR; LBM, 0.079 mm

K – HB 5; outermost tooth, approximately row 40, LSR; LBM 0.055 mm

L – HB 398; developing 1st lateral tooth, row 64, RSR; LBM 0.03 mm

M – HB 398; developing 5th lateral tooth, row 64, RSR; LBM, 0.039 mm

N – HB 398; developing 10th lateral tooth, row 64, RSR; LBM, 0.071 mm

O – HB 398; developing 36th lateral tooth, row 64, RSR; LBM, approximately 0.12 mm

P – Monaxon sponge spicule (with recurved ends) found under the shafts of lateral teeth in *Chromodoris baumanni* (HB 377-C) radula; LBM, approximately 0.24 mm proceeds by thickening and enlarging of the various tooth parts.

In the original description of this species, Bertsch (1970: figs. 7 - 10) presented scanning electron micrographs of the radular teeth.

Discussion:

Chromodoris baumanni is closely related to *C. norrisi.* Differences between the 2 species will be analyzed under *C. norrisi. Chromodoris baumanni* also shows similarities with the Hawaiian *C. lilacina* (Gould, 1852), but the colorations and radular morphologies of these species fall outside each other's range of variation. The rhinophores and gills of *C. lilacina* are orange-yellow or straw-colored (Kay & Young, 1969: 202), distinct from the reddish-purple hues of *C. baumanni*; *C. lilacina* has proportionately fewer teeth per half-row (relative to the number of tooth rows) than does *C. baumanni.*

Feeding habits of *Chromodoris baumanni* are not known; a sponge spicule (Figure 4-P) was lodged beneath the tooth shafts of one radula. The cusp and denticle morphology of the radular teeth are primarily adapted for scraping across sponge tissue, but the teeth can also hook the curved ends of such C-shaped spicules and extract more tissue adjacent to the spicule.

Chromodoris ***galexorum*** Bertsch, spec. nov.

(Figures 3-B, 5, 10 - 12, *33 - 36*)

Material Examined and Distribution:

Gulf of California, Mexico:

1) Holotype. 17m subtidal, under a ledge, Isla San Pedro Martir, Sonora, Mexico (approximately 28°22′N; 112° 20′W); *leg.* A. Kerstitch, 16 June 1976 (HB 467 B). This dissected specimen and its mounted radula have been deposited in the collections of the Los Angeles County Museum of Natural History, LACM Type Series, No. 1848.

2) Paratypes. 2 specimens, 17m subtidal, under a ledge, Isla San Pedro Martir; *leg.* A. Kerstitch, 16 June 1976 (HB 467 A, D). Water temperature at depth collected, 22.3°C

3) 1 specimen, 12m subtidal, in a dark cave, Isla San Pedro Nolasco, Sonora, Mexico (approximately 27°58′N; 111° 22′W); *leg.* A. Kerstitch, 22 June 1976 (HB 467 C)

4) 2 specimens, subtidal, Guaymas, Sonora, Mexico; seen by A. Kerstitch, April 1972 (identified from a color transparency)

5) 1 specimen, La Paz area, Baja California; *leg.* E. Janss, Jr., April 1974 (HB 256)

The known occurrence of this new species is from subtidal localities in the central and southern Gulf of California. Isla San Pedro Martir is the type locality. Mr. A. Kerstitch (personal communication) states it is fairly common subtidally around Guaymas in the springtime. He collected an additional specimen of *Chromodoris galexorum* at Isla San Pedro Nolasco, in 15m of water, on 16 March 1977.

External Morphology and Coloration:

The lengths of 5 preserved specimens were 15, 16, 17, 22, and 24mm. The number of gills (usually more numerous in larger specimens) were 7, 10, and 16 in 3 specimens; rhinophore lamellae varied from 18 - 24.

The body background color is white. Scarlet spots occur on the dorsum, many of them being immediately surrounded by a chrome yellow ring. At times the yellow coloration is present also as small splotches within the scarlet. The scarlet spots are largest down the midline of the dorsum. One specimen also had a transverse series of 3 larger spots (with overlapping edges) halfway between the rhinophores and the gills. The notal border is rimmed dorsally with a solid chrome yellow band. The lateral and posterior surfaces of the foot are white, with small scarlet dots scattered throughout; the sides of the foot can have 4 - 5 loose rows of these scarlet maculations. Except for yellow rings surrounding 2 or 3 scarlet spots on the midline of the postero-dorsal foot surface, there is no yellow coloration on the foot. The rhinophores and gills are scarlet, darker distally.

Whitish glands occur on the underside of the notal overhang. There are 6 - 7 per side of the body, and each consists of an ovalish structure that has 4 - 5 finger-like extensions protruding towards the animal's body.

Radula:

Meristic data of 5 radulae are found in Table 2. The range of variation of the radular formula is 56-59 (47-57 · 1 · 47-57). The number of teeth per half-row is only slightly less than the number of rows. There were too few specimens available to perform regression analyses on radular characteristics; the points of the radular parameters are graphed in Figures 10 - 12.

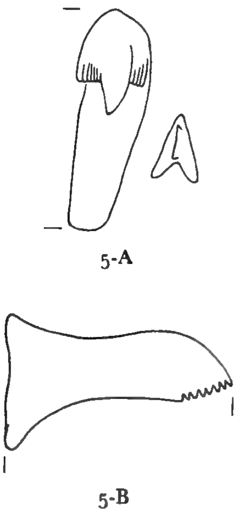
The radular teeth have the typical unicuspid *Chromodoris* shape: inner laterals have shorter shafts with denticles on the outer face (Figure *34*), followed by longer shafted teeth in the middle of the half-row that show denticulation on the posterior surface (Figures *35*, *36*).

A triangular rachidian tooth is present (Figures 5-A, *33*), with an elevated central cusp. The innermost lateral tooth (Figures 5-A, *33*) has 3 - 4 denticles on the inner face, 5 - 6 on the outer face. Denticles increase in number on each tooth towards the middle of the half-row, where there are usually 15 - 18 denticles on the posterior surface. Scanning electron micrographs cannot be used to count

Table 2

Radular variation in *Chromodoris galexorum*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
256	–	1.37	–	–	53
467 A	3.21	1.64	1:1.96	57	52
467 B	2.87	1.56	1:1.84	56	47
467 C	3.11	1.92	1:1.62	59	49
467 D	3.88	2.24	1:1.73	59	57
$\bar{X}$	3.27	1.75	1:1.79	57.75	51.6
s	0.433	0.34	0.146	1.5	3.847


5-A

5-B

Figure 5

Radular teeth of *Chromodoris galexorum* Bertsch, spec. nov.

A – HB 256; rachidian tooth and 1st lateral tooth drawn in relative position to each other, row 11, LSR; LBM, 0.071 mm; rachidian 0.028 mm long

B – HB 256; lateral tooth 52, row 11, LSR; LBM, 0.071 mm

denticles routinely, since overlapping teeth in the field of view obscure parts of teeth behind them. Denticular counts must be verified with the light microscope.

Lengths of tooth cusps ranged from 0.012 - 0.024 mm, with a mean of 0.019 mm (n = 21). The cusp of each tooth averages 5.05 times as long as the first denticle (n = 21; range is 3 - 7; s = 1.073). The outermost 4 - 5 teeth approach the first denticle length : cusp length ratio of 1 : 1; the cusp, denticles, and shaft length become markedly shorter (Figure 5-B).

It is of special note (with reference to the later discussion of *Chromodoris sphoni*) that in the last 8 radular rows of specimen HB 467 D, the inner 3 - 6 lateral teeth have a slight denticulation or ridging of 1 - 5 denticles on the inner face of the distal shaft area. These are in addition to the normal positioning of denticles on the outer face of the tooth shaft.

Discussion:

Chromodoris ***galexorum*** needs to be compared with Panamic chromodorids that exhibit a white notal background. It is immediately distinguishable from those species with dominant blue coloration. *Chromodoris baumanni* does not have a solid yellow band bordering the notum edge, but it has a broken orange or red band; moreover, it does not have bright yellow enclosing its red-violet spots. The spots of *C. baumanni* are also smaller and more regularly circular than the big, irregular red blotches of *C. galexorum*. *Chromodoris marislae* has yellow-orange circlets (some with open centers, others solid), with white surrounding the larger markings. *Chromodoris norrisi* has evenly circular markings of red and yellow, with a broken orange band around the notum. *Chromolaichma dalli* has black dots on its notum, and *Chromolaichma sedna* has a completely white notum with solid yellow and red bands around the periphery of the mantle.

Two Australian species appear similar to *Chromodoris galexorum*, but can be readily separated on the basis of coloration and radular morphology. The ranges of variation of the 3 species do not overlap. *Chromodoris daphne* (Angas, 1864) lacks yellow borders to the scarlet maculations, and has both yellow and red color bands surrounding the notum; it has proportionately shorter teeth cusps and fewer denticles on the shafts of the teeth than *C. galexorum* (the teeth of *C. daphne* are illustrated in Thompson, 1972: figs. 3i, 3j, 3k). *Chromodoris splendida* (Angas, 1864) also lacks yellow rimming the scarlet maculations; in large specimens, the scarlet spots are highly irregular blotches, often fusing into a thick reticulating pattern. The teeth of *C. splendida* have fewer denticles (cf. Thompson, *op. cit.*: plt. 2d, figs. 2k - 20) than *C. galexorum*; the outer teeth, not reduced in size, have thin erect shafts devoid of denticles (Thompson, *op. cit.*: plt. 2 c). Thompson also presents color drawings of living *C. daphne* and *C. splendida.*

Etymology:

The specific name ***galexorum*** is chosen as an acronym of Gale and Alex, to honor Mr. Gale Sphon (Los Angeles County Museum of Natural History) and Mr. Alex Kerstitch (Tucson, Arizona), who provided me with specimens of this new species.

Chromodoris marislae Bertsch, *in* Bertsch, Ferreira, Farmer & Hayes, 1973

(Figures 3-C, 6, 13 - 15)

References:

Bertsch, Ferreira, Farmer & Hayes, 1973: 289 - 292; figs. 1 - 11. Bertsch & Ferreira, 1974: 344. Keen & Coan, 1975: 45

Material Examined and Distribution:

Baja California, Mexico:

1) 1 specimen, Guaymas, Sonora; *leg.* A. Kerstitch, April 1972 (identified from a color transparency)
2) 1 specimen, Los Islotes; *leg.* A. J. Ferreira, September 1971 (HB 370)
3) 5 specimens, La Paz area; *leg.* E. Janss, Jr., April 1972 (HB 34 A-E)

The known distribution of *Chromodoris marislae* had been limited previously to localities along the Baja California Gulf coast, between Isla Santa Catalina (type locality) and La Paz. The Guaymas record is the first report from the coast of mainland Mexico, and constitutes a northward range extension of over 230 km. The specimens from La Paz are part of Lot 4 of the original description.

External Morphology and Coloration:

Living *Chromodoris marislae* reach 80 mm in total length (Bertsch *et al.*, 1973). Body color is an off-white, with 2 or 3 irregular rows of orange spots encircling the periphery of the notum; centrad to these rows is a roughly circular arrangement of larger orange ringlets, which are often surrounded or marked centrally with a pure white coloration. The bases of the rhinophores have almost a translucent quality, and the distal end is light brown; there is a prominent median white longitudinal septum on both its anterior and posterior faces. The gills are also light brown, with pure white on the center of each branching of the gills (color photographs of *C. marislae* are in Bertsch *et al.*, *op. cit.*: figs. 1, 2).

Radula:

The radular formula varies from 59-82 (53-70·1·53-70). Meristic data for 8 radulae are presented in Table 3.

The number of rows and the maximum number of teeth per half-row are positively correlated (Figure 13); $Y = 20.56 + 0.6039\,X$; $r = 0.9005$, $n = 8$, $P < 0.01$.

Table 3

Radular variation in *Chromodoris marislae*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
34 A	5.07	2.99	1:1.69	76	70
34 B	4.14	2.26	1:1.83	60	57
34 C	3.9	2.3	1:1.7	58	54
34 D	3.66	2.02	1:1.81	60	59
34 E	4.71	2.16	1:2.18	82	68
370	4.59	2.3	1:1.99	77	67
Holotype[3]	–	–	–	59	59
Paratype 2[3]	–	–	–	62	53
$\overline{X}$	4.35	2.34	1:1.87	66.75	60.875
s	0.535	0.3366	0.188	9.8	6.578

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[3] Bertsch *et al.*, 1973

A positive correlation exists between the length of the radula and the number of rows (Figure 14). The regression line formula is $Y = -6.27 + 17.28\ X$, $r = 0.8691$ ($n = 6$, $P < 0.01$).

Because of the small sample size, no correlation could be proven statistically between the radular width and the maximum number of teeth per half-row ($r = 0.5001$, $P > 0.1$). The parameters are simply plotted in Figure 15.

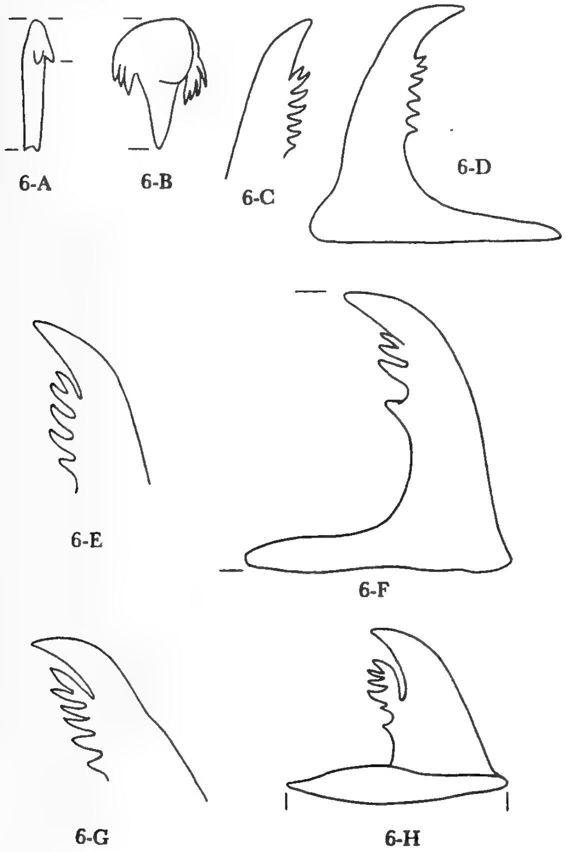


Figure 6

Radular teeth of *Chromodoris marislae*

A – HB 34 C; rachidian tooth, row 13; LBM, left side 0.04 mm, right side, 0.014 mm
B – HB 370; dorsal view of cusp of innermost lateral tooth, posterior portion of radula; LBM, 0.032 mm
C – HB 34 A; distal portion of shaft of lateral tooth 19, row 17
D – HB 34 B; lateral tooth 28, row 21, LSR
E – HB 370; distal portion, shaft of 8th lateral tooth from outer edge, row 30, RSR
F – HB 370; 6th tooth from outer edge, row 30, RSR; LBM 0.053 mm
G – HB 370; 4th tooth from outer edge, row 30, RSR
H – HB 370; 3rd tooth from outer edge, row 30, RSR; tooth is tilted, and foreshortened shaft is not parallel with plane of focus; LBM, 0.057 mm

The rachidian tooth (Figure 6-A) has a long base, and a bifurcated, erect cusp. There are 3 - 4 denticles on both the inner and outer faces of the innermost lateral tooth (Figure 6-B). The denticles increase in number from the center of the radula to the middle of each row, and then decrease towards the outermost teeth. For example, row 41 (left side of radula, HB 34 B) has 3 denticles on the outer face of each of the first 13 lateral teeth, 4 - 5 denticles on the posterior surfaces of the next 10 teeth, 5 - 7 on each of the succeeding 20, and 5 - 3 denticles on each of the outermost 14 teeth. The innermost laterals are not smooth (contrary to the statement in Bertsch *et al.*, 1973: 290), but are denticled on the outer face. Figure 8 of Bertsch *et al.* is a view of the inner face of an innermost lateral, and denticles are not visible because of the non-transparency of teeth in scanning electron micrographs.

The teeth of *Chromodoris marislae* are large, with solid cusps and fairly large denticles. The cusp lengths of the inner 36 teeth of row 20 (HB 34 B) varied from 0.02 - 0.032 mm ($\overline{X} = 0.027$ mm). The reduced size of the outermost lateral teeth is accompanied by reduced cusp and denticle size. The outer 10 teeth had cusp lengths of 0.02 - 0.01 mm ($\overline{X} = 0.016$ mm). In this same row, the cusps averaged 2.26 times longer than the denticles (range, 1.25 - 3.2, $s = 0.449$, $n = 46$).

Quite a few of the lateral teeth show a unique specific denticulation pattern (Figures 6-C to 6-H). The first 2 denticles below the cusp are united from a common base, giving the appearance of bifurcating. Although this is not universal, it appeared often enough on each of the radulae examined to be considered diagnostic. This condition was illustrated by Bertsch *et al.* (1973: figs. 5 A, B, D, E) but they did not comment upon its occurrence.

Scanning electron micrographs of *Chromodoris marislae* radular teeth are in Bertsch *et al.*, 1973.

Discussion:

The current records of *Chromodoris marislae* are all from subtidal locations; increased SCUBA research in the Gulf of California should yield more specimens.

Chromodoris mcfarlandi Cockerell, 1901

(Figures 3-D, 7, 13 - 15, *37 - 40*)

References and Synonymy:

Chromodoris mcfarlandi Cockerell, 1901: 79 - 80. Cockerell, 1902: 20 - 21. Bertsch, 1976b: 157 - 158

Glossodoris macfarlandi (Cockerell). O'Donoghue, 1926: 212. O'Donoghue, 1927: 89 - 90, 116; plt. 2, figs. 33 - 37. Pruvot-Fol, 1951a: 120. Pruvot-Fol, 1951b: 152. Lance, 1961: 66. Paine, 1963: 4, 7, 8. Farmer & Collier, 1963: 62. Steinberg, 1963: 69. MacFarland, 1966: 153 - 157; plt. 22, figs. 1 - 5; plt. 34, figs. 1 - 11. Sphon & Lance, 1968: 79. Ricketts & Calvin, 1968: 119, 514. McBeth, 1970 (not seen; *fide* Bloom, 1976). Abbott, 1974: 354, fig. 4239. Bloom, 1976: 292 - 294

Chromodoris macfarlandi Cockerell. Cockerell & Eliot, 1905: 36. MacFarland, 1906: 129. Cockerell, 1908: 106. Johnson & Snook, 1927: 494; plt. 11, fig. 2. Marcus & Marcus, 1967: 178. Roller & Long, 1969: 425, 429. Lance, 1969: 37. Roller, 1970a: 371. Roller, 1970b: 482. Long, 1970: 19. McBeth, 1971a: 28. Keen, 1971: 822; Schmekel, 1972: 194. Sphon, 1972: 59. Bertsch *et. al.*, 1973: 287. Smith & Carlton, 1975: 528, 538; plt. 121, fig. 6. Keen & Coan, 1975: 43 (# 2330)

The correct date of authorship, as O'Donoghue (1927: 89) showed, is 1901. The description published 28 November 1901 has priority over Cockerell's intended new species description published June 1902.

The spelling of the specific name requires comment. Cockerell's original spelling was a misspelling of MacFarland's name. The species name occurs once in his 1901 paper and once in his 1902 article, both times as *Chromodoris mcfarlandi.* In acknowledging the patronym, Cockerell (1902: 21) wrote, "Named after Prof. F. M. McFarland [sic] of Stanford University, who has done some excellent work on the nudibranchs of Pacific Grove, California." Cockerell was clearly in error on the proper spelling of Dr. MacFarland's name.

The rules of zoological nomenclature provide that the original spelling of a species name is to be retained as the correct spelling unless it contravenes certain mandatory provisions or there is clear evidence in the original publication that an inadvertent error (*lapsus calami*, copyist's or printer's error) has occurred (Mayr, 1969: 312 to 313; 355 to 356). The evidence is to the contrary. Both of Cockerell's papers misspelled MacFarland (including the patronymic designation), and there are no multiple spellings in the original 1901 paper (nor in the 1902 paper). Repetition of the error in 2 different papers submitted to 2 separate journals, makes it highly unlikely that a slip of the pen or a printer's error occurred. There is no clear evidence of an inadvertent error (in the sense of the Code), and no contravention of mandatory provisions. Therefore, the spelling of *C. macfarlandi* is an unjustified emendation and a junior objective synonym of the original *C. mcfarlandi.*

Material Examined and Distribution:

California and Offshore Islands:

1) 1 specimen, subtidal, off Monterey breakwater; *leg.* R. Ames, January 1963 (HB 458; CAS)

2) 2 specimens, Monterey Bay; *leg.* F. M. MacFarland, December 1908-January 1909 (HB 453 A-B; CAS)

3) 1 specimen, 22 m subtidal, off Del Monte, Monterey Bay; *leg.* S. S. Berry (no date) (CAS)

4) 2 specimens, Pacific Grove; *leg.* F. M. MacFarland, June 1908 (HB 454 A-B; CAS)

5) 1 specimen, Point Pinos, Monterey; *leg.* R. Page, 12 July 1941 (HB 455; CAS)

6) 1 specimen, 24 m subtidal, north end San Jose Creek Beach (36°32'N; 121°56'W); *leg.* J. McLean, 9 July 1971 (HB 393; LACM 60-24)

7) 1 specimen, intertidal, White's Point, Palos Verdes Peninsula (33°43'N; 118°18'W); *leg.* G. G. Sphon, 9 December 1969 (HB 396; LACM 69-37)

8) 2 specimens, Newport Bay; *leg.* G. E. MacGinitie, June 1948 (HB 457 A-B; CAS). These are the specimens drawn on plt. 22, figs. 1 - 5, of MacFarland, 1966

9) 2 specimens, Corona del Mar; *leg.* G. E. MacGinitie, 25 June 1948 (HB 456; CAS)

10) 1 specimen, La Jolla; *leg.* T. D. A. Cockerell, 1902 (HB 452; CAS)

11) 1 specimen, Isthmus, Santa Catalina Island; *leg.* A. J. Ferreira, 9 July 1975 (HB 361)

12) 1 specimen, intertidal, Catalina Harbor, Santa Catalina Island; *leg.* G. G. Sphon, 7 March 1970 (HB 392; LACM 70-8)

13) 1 specimen, 23 - 29 m subtidal, upper reef of Farnsworth Bank, Santa Catalina Island (33°21'N; 118°31'W); *leg.* C. Turner, 1-2 June 1970 (HB 394; LACM 70-74)

14) 1 specimen, 27 - 34 m subtidal, northwest of Pyramid Head, San Clemente Island; *leg.* C. Swift, 1 July 1971 (HB 395; LACM A 9325)

Mexico:

15) 3 specimens, 21 - 24 m subtidal, Isla Coronado (31°48' N; 116°48'W); *leg.* A. J. Ferreira, 28 September 1973 (HB 253)

16) 1 specimen, intertidal to 11 m subtidal, Man-of-War Cove, Bahía Magdalena (24°37.5'N; 112°7.5'W); *leg.* J. McLean and P. LaFollette, 31 October 1971

The original material used by Cockerell was collected from La Jolla and San Pedro.

The reported range of *Chromodoris mcfarlandi* has been from Monterey to the Isla Cedros area, Baja California (Keen, 1971: 822). The specimen collected at Bahía Magdalena represents a southern range extension of over 480 km. Despite this new record at the northern boundary of the Panamic faunal province (tropical West America), Keen & Coan (1975: 43) were correct in considering *C. mcfarlandi* a member of the temperate and cooler water Californian and southern Oregonian marine provinces (*sensu* VALENTINE, 1966, and 1973: 351 - 356). This new record of *C. mcfarlandi*, while representing a true "range extension," is not indicative of the normal occurrence of this species. It is a thermally anomalous record (ZINSMEISTER, 1974) on the extreme periphery of the species' range.

Chromodoris mcfarlandi has also been reported from San Luis Obispo County, Santa Barbara County, Laguna Beach, Santa Catalina Island (California), and Isla Coronado (Mexico).

Lot 14 represents a new subtidal bathymetric range.

External Morphology and Coloration:

Living *Chromodoris mcfarlandi* are reported to reach 50 - 60 mm in length (JOHNSON & SNOOK, 1927: 494), but more commonly will vary in length up to 35 mm (MACFARLAND, 1966: 156).

Overall body color a brilliant reddish-violet. A yellow line runs down the center of the notum, from just anterior to the rhinophores to the forward edge of the gill pocket; an additional yellow line begins postero-laterally to each rhinophore, runs lengthwise along the animal's body, and joins behind the gills. A longitudinal yellow line is on the dorso-posterior foot surface. The notum is rimmed by narrow yellow and white bands (color photograph in LANCE, 1969: 37). MACFARLAND (1966: 155) also described slight yellow markings on the posterior surface of the foot and on the notum posterior to the gills.

Radula:

Although *Chromodoris mcfarlandi* was named over 75 years ago, there are published descriptions of only 2 radulae. O'DONOGHUE (1927: 90) reported about 62 rows of teeth, with about 50 teeth per half-row, and MACFARLAND (1966: 155) gave a radular formula of 62 (47-50 · 1 · 47-50). These reports indicate little of the vari-

Table 4

Radular variation in *Chromodoris mcfarlandi*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
[4]	—	—	—	62	50
[5]	—	—	—	62	50
253 A	1.51	0.48	1:3.15	46	32
253 B	1.43	0.51	1:2.8	41	27
253 C	1.11	0.69	1:1.61	41	32
361	1.66	0.63	1:2.63	41	30
392	0.87	0.32	1:2.72	41	23
393	2.95	1.56	1:1.89	76	49
394	2.55	1.03	1:2.48	57	50
395	1.76	0.73	1:2.41	44	32
396	0.78	0.32	1:2.44	36	16
452	1.72	0.83	1:2.07	50	34
453 A	1.818	0.808	1:2.25	51	38
453 B	1.66	0.67	1:2.48	56	—
454 A	1.39	0.65	1:2.14	46	32
454 B	1.68	0.73	1:2.3	48	31
456 A	2.1	1.01	1:2.08	52	36
456 B	1.94	1.05	1:1.85	51	34
457 A	1.66	1.01	1:1.64	43	36
457 B	1.64	0.909	1:1.8	60	35
458	2.1	1.05	1:2	52	43
$\overline{X}$	1.7	0.789	1:2.249	50.286	33.89
s	0.515	0.297	0.412	9.482	8.123

[4] O'DONOGHUE, 1927; [5] MACFARLAND, 1966

ability of the radular teeth counts. Table 4 gives the sizes, rows and teeth counts for 21 radulae. The combined radular formula is 36-76 (16-50 · 1 · 16-50). MacFarland and O'Donoghue examined specimens at the upper size range of the species. Their data were used by Bloom (1976: 292) in his significant study correlating predator-prey morphology of dorid nudibranchs and sponges. His "radular mean" column, however, should not be used uncritically. The mean of *C. mcfarlandi* is given as 62 (49 · 0 · 49). The 49 is based on only the numbers (47, 50, 50) given by O'Donoghue and MacFarland, and contrasts sharply with the mean number of maximum teeth per half-row (33.89) that I calculated based on many more specimens. *Chromodoris mcfarlandi* possesses a rachidian tooth.

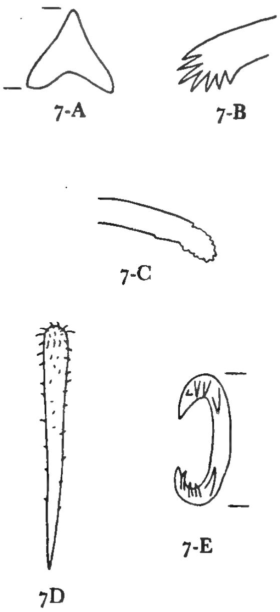


Figure 7

Chromodoris mcfarlandi

radular teeth and sponge spicules found among the teeth

A – HB 393; rachidian tooth; LBM, 0.02 mm

B – HB 394; lateral view of distal portion of 5th tooth from outer edge of radula (prominent cusp does not occur on the outermost teeth); approximately row 31, RSR

C – HB 394; 3rd tooth from outer edge of radula; row 25, LSR

D – HB 414 A; sponge spicule (0.071 mm long) found on radula

E – HB 455; sponge spicule (monaxon, recurved ends with accessory points) found on radula; LBM, 0.04 mm

The expected positive correlation exists between the number of tooth rows and the maximum number of teeth per half-row (Figure 13). The regression line formula is $Y = -4.47 + 0.799X$; $r = 0.8421$, $n = 20$, $P < 0.001$.

The number of tooth rows is dependent on radular length (Figure 14). The regression line formula is $Y = 24.12 + 14.65\,X$; $r = 0.8283$, $n = 19$, $P < 0.001$.

The maximum number of teeth per half-row is dependent on the radular width (Figure 15). The regression line formula is $Y = 15.51 + 23.11\,X$; $r = 0.8664$, $n = 18$, $P < 0.001$.

O'Donoghue (1927: 90) and MacFarland (1966: 154 - 155) have described the morphology of the teeth. The rachidian is small and triangular-shaped (Figure 7-A). The innermost lateral teeth have 3 - 4 main denticles on the inner face of the shaft, 3 - 6 small ridge-like denticles on the inner side of the cusp, and 4 - 5 denticles on the outer face of the shaft (Figure *37*). Lateral teeth in the middle of each half-row have a prominent cusp and numerous denticles (10 - 16) on the posterior surface of the shaft (Figure *38*). The outer lateral teeth (Figures 7-B, 7-C, *39*) become smaller, with a greatly reduced cusp.

Developing lateral teeth (Figure *40*) are thin and narrow, with weak cusps and needle-like denticles.

Discussion:

Sponge spicules (Figures 7-D, 7-E) were found under the teeth in 2 radulae. Bloom (1976: 294) reports that

Explanation of Figures *33* to *38*

Scanning Electron Micrographs of the Radular Teeth
of *Chromodoris* ***galexorum*** and *Chromodoris mcfarlandi*

Figure *33*: *Chromodoris* ***galexorum***; rachidian and innermost lateral teeth (specimen HB 256) × 775

Figure *34*: *Chromodoris* ***galexorum***; inner lateral teeth (HB 256) × 1300

Figure *35*: *Chromodoris* ***galexorum***; lateral teeth from middle and outer portions of half-row (HB 256) × 275

Figure *36*: *Chromodoris* ***galexorum***; cusps and distal portion of teeth from middle of half-row (HB 256) × 800

Figure *37*: *Chromodoris mcfarlandi*; innermost lateral teeth (HB 253 C) × 1975

Figure *38*: *Chromodoris mcfarlandi*; lateral teeth from middle of half-row (HB 253 C) × 1650

Figure 33

Figure 34

Figure 35

Figure 36

Figure 37

Figure 38

Chromodoris mcfarlandi feeds on sponges from the genera *Gellius* and *Haliclona*.

Chromodoris mcfarlandi is a beautiful nudibranch, immediately identifiable by its coloration and the large numbers of denticles on the lateral teeth in the middle of the half-rows. It is a fitting tribute (even though the name is misspelled) to Prof. MacFarland and his magnificent detailed work on Californian nudibranchs.

Chromodoris norrisi Farmer, 1963

(Figures 3-E, 8, 13 - 15, *41 - 46*)

References and Synonymy:

Chromodoris norrisi Farmer, 1963: 81 - 84; plt. 1 a; text figs. 1 a-e. Marcus & Marcus, 1967: 170 - 173; figs. 21 - 23 (Material 1 only); 237 - 238. Farmer, 1968: 24 - 25, VII. Ev. Marcus & Er. Marcus, 1970: 198. Bertsch, 1970: 8, 12; fig. 3. Bertsch, 1971: 16. Keen, 1971: 822, fig. 2331; plt. 20, fig. 4. Farmer, 1971: 19. Sphon, 1972b: 59. Bertsch *et al.*, 1973: 292 - 293. Bertsch, 1973: 108. Brusca, 1973: 174. Bertsch, 1975: 105. Bertsch, 1976b: 157

Glossodoris norrisi (Farmer). Abbott, 1974: 355; fig. 4246

Material Examined and Distribution:

Baja California, Gulf Coast:

1) 1 specimen, Bahía de Los Angeles; *leg*. J. Lance, April 1968 (identified from a color transparency)

2) 1 specimen, subtidal, Notri (13 km S of Loreto); *leg*. H. Bertsch, M. Ghiselin, & J. Allen, 4 July 1974 (HB 95)

3) 2 specimens, intertidal, Juncalito (19 km S of Loreto); *leg*. H. Bertsch and B. Rose, 24 December 1973 (HB 40 A-B)

4) 5 specimens, subtidal 2 - 3 m, Nopolo and Juncalito; *leg*. H. Bertsch, M. Ghiselin, & J. Allen, 27 June 1974 (HB 85 A-E)

5) 1 specimen, subtidal 1.5 - 3 m, N end of Isla Santa Cruz; *leg*. D. Chivers, 26 June 1964 (HB 448; CAS)

6) 3 specimens, 14 m subtidal, S end of Isla San Diego; *leg*. E. Janss, Jr., April 1974 (LACM)

7) 5 specimens, intertidal on mangrove roots, Isla San Jose; *leg*. G. G. Sphon, 2 April 1974 (LACM)

8) 1 specimen, Caleta San Evaristo, Isla de San Francisco; *leg*. G. G. Sphon, 1 April 1974 (LACM)

9) 1 specimen, 6 m subtidal, Piedra del Saltito, 6 km S of Puerto Mejía, La Paz; *leg*. A. J. Ferreira, 12 June 1974 (HB 376)

10) 7 specimens, 1 - 3 m subtidal, Bahía Carisalito (4 km N of Las Cruces); *leg*. H. Bertsch, T. Cooke, & G. Stellern, 26 July 1972 (HB 15 A-G)

11) 4 specimens, Las Cruces; *leg*. H. Bertsch, 1 - 18 July 1969 (HB 68 - 71)

12) 4 specimens, Las Cruces; *leg*. H. Bertsch, 1 July 1974 (HB 92 A-B, 93, 94)

13) 6 specimens, 1.5 - 10 m subtidal, N of Punta Gorda, 8 km S of Las Cruces; *leg*. H. Bertsch, 22 July 1972 (HB 14 A-F)

14) 1 specimen, N end of Isla Cerralvo; *leg*. H. Bertsch, 29 July 1969 (HB 72)

15) 1 specimen, subtidal, SW Isla Cerralvo; *leg*. H. Bertsch, 25 July 1972 (HB 19)

Mainland Mexico, Gulf Coast:

16) 1 specimen, intertidal, Puerto Peñasco, Sonora; *leg*. H. Bertsch, 24 December 1975 (HB 344)

17) 2 specimens, intertidal, Puerto Peñasco, Sonora; *leg*. H. Bertsch, 26 and 29 December 1975 (HB 350 A-B)

18) 3 specimens, rocky intertidal, Guaymas, Sonora; *leg*. A. Kerstitch, 30 July 1966 (HB 323 A-C; USNM 753561)

19) 2 specimens, Puerto Peñasco and Guaymas, Sonora; *leg*. P. Pickens & M. A. Hill, 7 August 1964 and 28 June 1965 (HB 322 A-B; USNM)

The type locality of *Chromodoris norrisi* is Isla Cerralvo, The animal has been collected from the outer coast of Baja California and numerous localities within the Gulf of California (summarized in Bertsch *et al.*, 1973: 292 to 293); the known range along the Gulf coast of Baja California is from Bahía San Luis Gonzaga to SW Isla Cerralvo; it has been reported from Puerto Peñasco to Guaymas along Mainland Mexico.

Lot 6 represents a new bathymetric range for this species.

External Morphology and Coloration:

Large specimens of living *Chromodoris norrisi* will reach 61 mm (Farmer, 1963: 83). Between 1 - 19 July 1969, 22 - 26 July 1972, and 27 June - 4 July 1974, 28 specimens collected near Loreto and Las Cruces varied from 21 - 50 mm long alive ($\overline{X} = 33.5$, $s = 8.66$). Six specimens collected during winter and early spring (24 December 1973, Loreto area; 24 December 1975, Puerto Peñasco; April 1968, Bahía de Los Angeles) varied from 4 - 12 mm total length alive ($\overline{X} = 8.7$, $s = 2.66$). There is a significant difference ($t = 6.867$, $P < 0.001$) between these 2 seasonal groups, that hints at possible population cycles within the Gulf of California. As water warms in spring and summer, the animals grow to reproductive size, copulate and lay eggs. Settling of larvae may occur twice (in early summer and early autumn), with rapid summer growth and F_1 reproducing late summer. Those hatching in autumn metamorphose and are the smaller individuals found during winter. A year-round study (with biweekly or monthly sampling) is needed to test this hypothesis.

Body background color is white. Some specimens show a violet coloration in the middle of the dorsum that is sub-epidermal in origin (Farmer, 1963: 81). The notum and lateral and posterior surfaces of the foot have numer-

Table 5

Radular variation in *Chromodoris norrisi*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
[6]	—	—	—	65	44
[7]	—	—	—	68	48
14 A	3.39	1.74	1:1.95	68	58
14 B	3.29	1.58	1:2.08	69	52
14 C	3.84	1.86	1:2.06	71	58
14 E	3.58	1.88	1:1.9	74	63
14 F	3.696	1.96	1:1.89	71	60
15 A	3.11	1.62	1:1.92	76	58
15 B	3.8	1.8	1:2.1	75	64
15 C	3.15	1.76	1:1.79	70	56
15 D	4.02	2.22	1:1.81	80	62
15 E	2.83	1.82	1:1.55	67	62
15 F	3.37	2.0	1:1.69	68	59
15 G	3.47	1.74	1:1.99	68	56
19	—	—	—	65	54
40 A	0.76	0.299	1:2.54	36	25
40 B	1.13	0.57	1:1.98	50	40
68	3.92	2.08	1:1.88	71	55
69	4.1	2.1	1:1.95	73	61
70	4.55	2.32	1:1.96	85	67
71	3.66	1.76	1:2.08	65	62
72	3.9	1.9	1:2.05	76	62
85 A	4.6	2.16	1:2.13	86	71
85 B	3.72	1.96	1:1.9	67	52
85 C	3.96	2.2	1:1.8	79	63
85 D	3.7	2.08	1:1.78	69	55
85 E	2.95	1.53	1:2.06	64	51
92 A	4.06	2.22	1:1.83	79	67
92 B	4.24	2.3	1:1.84	76	69
93	3.9	2.02	1:1.93	68	58
94	3.76	2.22	1:1.69	74	56
95	4.44	1.94	1:2.29	83	56
322 A	2.08	1.35	1:1.54	69	55
322 B	1.15	0.77	1:1.49	49	38
323 A	3.37	1.9	1:1.77	80	66
323 B	3.64	2.08	1:1.75	97	72
323 C	3.01	1.86	1:1.62	77	58
344	1.07	0.57	1:1.88	48	39
350 A	2.02	0.87	1:2.32	51	37
350 B	1.74	1.01	1:1.72	53	40
$\overline{X}$	3.26	1.73	1:1.905	69.5	55.725
s	1.015	0.525	0.217	11.59	10.233

[6] MARCUS & MARCUS, 1967; [7] FARMER, 1963

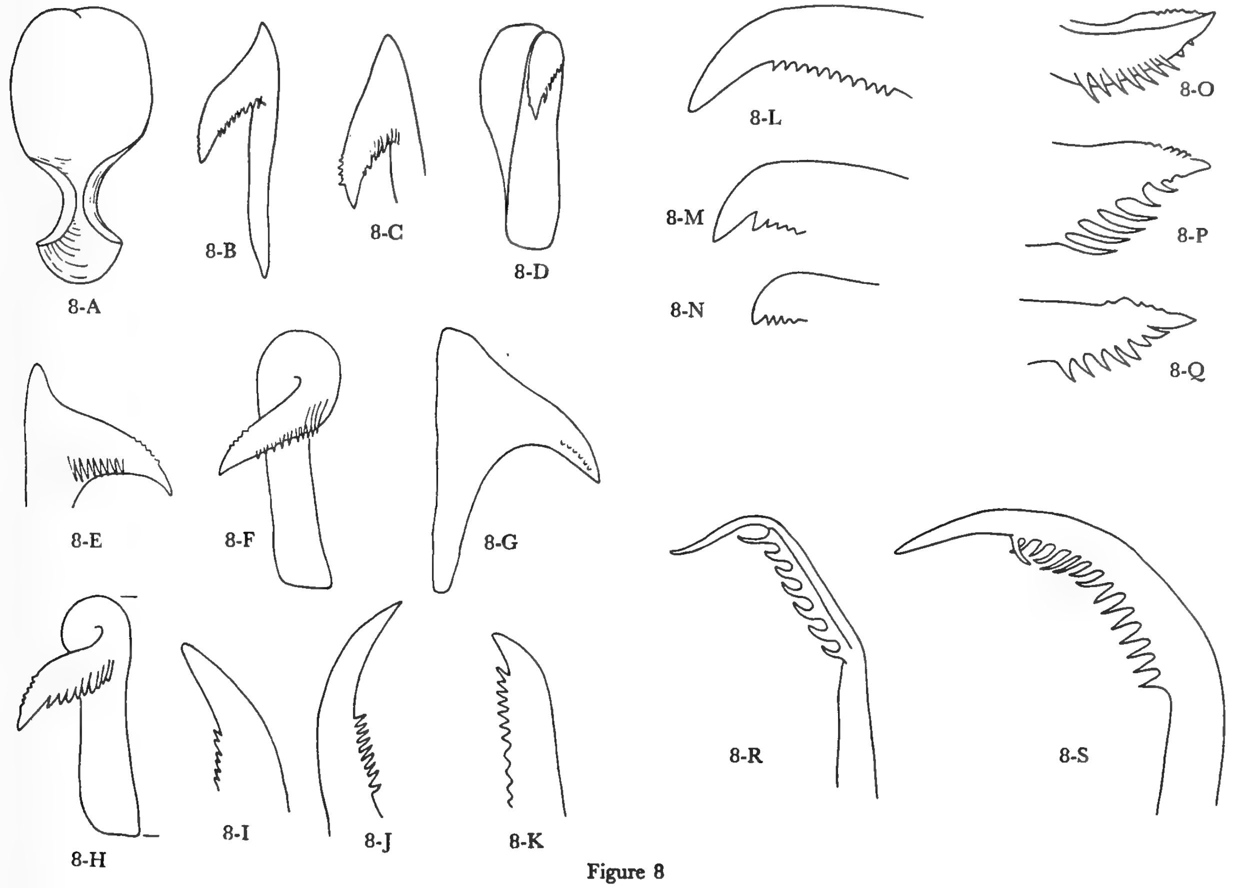


Figure 8

Radular teeth of *Chromodoris norrisi*

A – HB 40 B; outline sketch of entire radula prior to flat-mounting
B – HB 14 A; dorso-lateral view of 2nd tooth, row 55, RSR
C – HB 14 A; 3rd lateral tooth, row 55, RSR
D – HB 14 A; 5th lateral tooth, row 55, RSR; adjacent inner tooth overlaps the lateral basal flange
E – HB 14 A; outer face of 4th lateral tooth, row 60, LSR
F – HB 14 F; 2nd tooth, row 64, RSR
G – HB 69; inner face of 5th tooth, row 66, RSR
H – HB 15 B; dorso-lateral view of 5th lateral tooth, row 74, RSR; LBM, 0.057 mm
I – HB 323 B; distal portion of shaft, tooth 28, approximately row 30
J – HB 15 B; distal portion of shaft, tooth 26, row 69, LSR
K – HB 323 B; distal portion of shaft, 5th tooth from outer edge of radula, approximately row 32
L – HB 323 C; approximately tooth 13, row 28
M – HB 323 C; 10th tooth from outer edge of radula, row 28
N – HB 323 C; 5th tooth from outer edge of radula, row 28
O – HB 14 A; distal shaft of developing 1st lateral tooth, last row, LSR (outer face with heavier denticulation)
P – HB 14 A; distal shaft of developing 3rd lateral tooth, last row, LSR
Q – HB 14 A; distal shaft of developing 4th lateral tooth, last row, LSR
R – HB 14 A; shaft of developing lateral tooth, approximately ¼ the distance from radular outer edge to center of radula; last row, RSR
S – HB 14 B; shaft of developing 27th lateral tooth, drawn to same scale as Figure 8 R; last row, RSR

ous small red dots; the notum also has about ½ as many yellow dots. A bright orange broken band encircles the edge of the notum. There is a wide range of variation in the number and size of the dots from very many small ones to fewer, larger spots (Bertsch *et al.*, 1973: 293). Color photographs appear in Farmer (1963; plt. 1a) and Keen (1971: plt. 20, fig. 4).

Radula:

Farmer (1963) and Marcus & Marcus (1967) have published radular formulae of *Chromodoris norrisi.* Although Farmer gives a range of variation for 6 specimens, he only gives the holotype formula separately. This is the only count from Farmer's paper that can be analyzed statistically. Table 5 presents the individual radular sizes and counts of the 2 published radular formulae and the 38 radulae I examined. The new combined radular formula is 36-111 (25-72 · 1 · 25-72).

Least squares regression analysis shows that the number of tooth rows and maximum number of teeth per half-row are positively correlated (Figure 13). The equation, $Y = -0.147 + 0.804\,X$, describes the regression line. The coefficient of correlation is 0.9106 ($P < 0.001$, $n = 40$).

The number of tooth rows is positively correlated with the radular length (Figure 14). The regression line formula is $Y = 36.84 + 10.07X$, and $r = 0.8513$ ($P < 0.001$, $n = 37$).

The radular width and maximum number of teeth per half-row (Figure 15) are positively correlated, with $r = 0.8965$. The formula describing the regression line is $Y = 25.7 + 17.7\,X$ ($P < 0.001$, $n = 37$).

Figure 8-A is an outline sketch of the entire radula; the smaller posterior portion has not been flattened. The innermost lateral tooth has approximately 5 inner and 5 outer denticles. Inner lateral teeth have a thick, squat shaft, with 4 - 9 denticles on the outer face (Figures *41* and *42*). Toward the middle region of the half-row, the teeth become longer with more erect shafts. The denticles change from thick lateral structures to pointed prongs (7 - 14 in number) on the posterior surface of each tooth, and the cusp becomes quite prominent (Figures 8I - 8L). Towards the outer margin the teeth are reduced in size, and cusps and denticles become smaller (Figures 8M, 8N, *43*). Denticles on the outer and posterior surfaces averaged 8.19 across a half-row ($n = 32$; of the 66 teeth in the half-row, only half were lying in such a way as to allow denticle counts).

The length of the cusps across a half-row averaged 0.0154 mm (range, 0.006 - 0.022 mm, $n = 53$). The mean ratio of the length of the first denticle to the length of the cusp is 1:4.517 (range from 1.17 on the extreme ends of the half-row to 11 in the central region of the half-row; $s = 2.42$, $n = 53$).

The radulae of 18 specimens (47% of the *Chromodoris norrisi* radulae dissected for this study) had a double-denticulation pattern on the first 2 - 9 innermost teeth (Figures 8B - 8H). In addition to denticles on the outer face of the shaft, these teeth had 2 - 8 denticles on the inner face of the cusp ($\overline{X} = 5.1$, $n = 45$). This is the same as the double-denticulation pattern described for the first 4 lateral teeth of *C. sphoni. Chromodoris norrisi* specimens 14 A, E, F, 15 B, had an average of 6.7 double-denticled teeth ($n = 39$) on each half-row in the posterior 16, 6, 7, and 6 rows respectively. This pattern was not visible in the anterior half of the radulae.

Patterns of tooth growth are shown in Figures *44* and 8-O to 8-S (progressing from the innermost laterals to teeth nearer the middle of the half-row). The early development of the central lateral teeth is from thin shafts with just the hint of posterior denticulation (Figure *45*) to stronger shafts with needle-like denticles (Figure *46*). The scanning electron micrographs (Figures *41* - *46*) offer an immediate visual comparison of developing and fully-formed teeth.

Discussion:

Chromodoris norrisi is readily separated from the related *C. baumanni.* Visual examination of their radulae reveals immediate perceptual differences. The cusps of the middle lateral teeth of *C. norrisi* are longer and more pronounced than the *C. baumanni* cusps (compare Figures 8-I to 8-K with Figures 4-H, 4-I). This gestalt impression can be proved statistically. The length ratio of the first denticle:cusp is significantly different (longer) for *C. norrisi* than *C. baumanni* ($t = 5.78$, $P < 0.001$, D.f. = 78). The absolute cusp lengths of *C. norrisi* teeth are significantly different from (longer than) *C. baumanni* ($t = 7.042$, $P < 0.001$, D.f. = 77). Other radular differences are treated in Discussion of *Chromodoris*; color differences are summarized in BERTSCH, 1970: 12; fig. 3).

Explanation of Figures *39* to *44*

Scanning Electron Micrographs of the Radular Teeth
of *Chromodoris mcfarlandi* and *Chromodoris norrisi*

Figure *39*: *Chromodoris mcfarlandi*; outermost lateral teeth (HB 253 C) × 2475

Figure *40*: *Chromodoris mcfarlandi*; developing lateral teeth, innermost teeth at upper left (HB 253 C) × 825

Figure *41*: *Chromodoris norrisi*; rachidian area and innermost lateral teeth (HB 376) × 825

Figure *42*: *Chromodoris norrisi*; 3 innermost lateral teeth (enlargement of Figure *41*) (HB 376) × 2300

Figure *43*: *Chromodoris norrisi*; outermost lateral teeth (HB 376) × 825

Figure *44*: *Chromodoris norrisi*; developing rachidian and innermost lateral teeth (HB 376) × 825

Figure 39

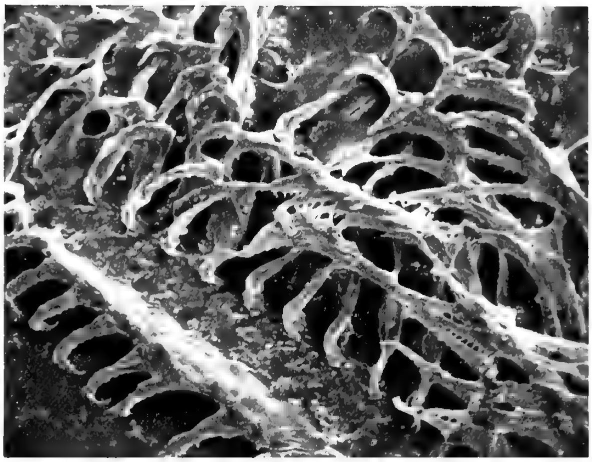


Figure 40

Figure 41

Figure 42

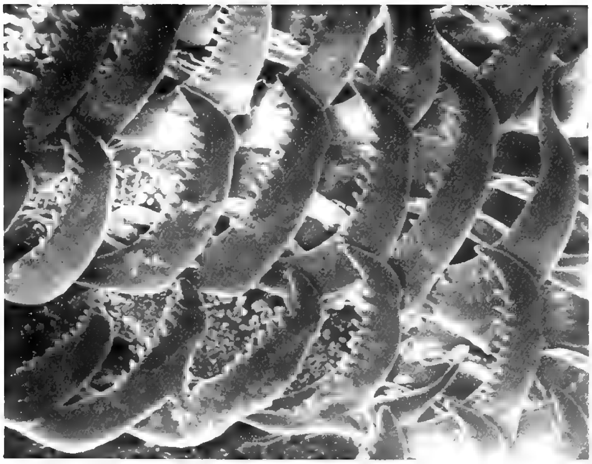


Figure 43

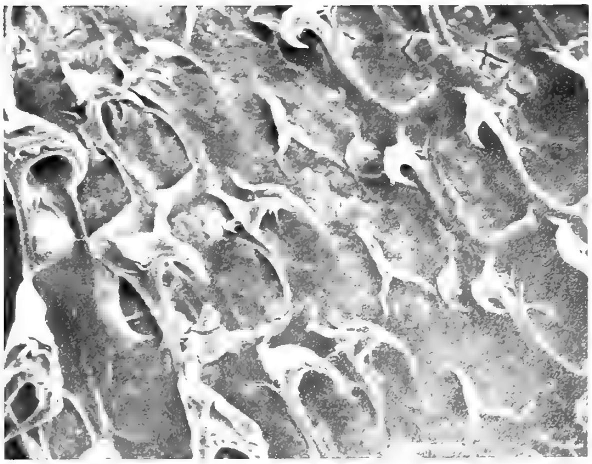


Figure 44

Thompson (1972: 401) suggests that *Chromodoris norrisi* is merely a subspecies of *C. amoena* Cheeseman, 1886. I cannot agree with this; *C. norrisi* is similar to *C. amoena*, but shows important characteristics that warrant full specific status. The coloration of *C. amoena* has many irregular orange blotches with a few irregular purple blotches. This is the opposite pattern of *C. norrisi*, where purple dots (quite regularly circular, not irregular) are at least twice as numerous as the yellow (not orange) dots. Under the mantle of *C. norrisi* are purple spots, not orange. The gills of *C. norrisi* are orange distally, not completely red. Rudman (1973) has commented on the usage of color patterns. The differences between *C. amoena* and *C. norrisi* are not just subtle color tints, but entire pattern differences. Marcus & Marcus (1967: 173) summarized radular differences (absolute numbers of teeth per half-row and tooth denticles) between the 2 species. The proportion between the numbers of tooth rows and maximum number of teeth per half-row is also important. *Chromodoris amoena* has a greater number of teeth per half-row than of tooth rows; the opposite characterizes *C. norrisi*. Although these 2 species show similarities, they are separate species, each with its own distinctly different range of variation.

Chromodoris sphoni (Marcus, 1971), *comb. nov.*

(Figures 3-F, 9, 10 - 12)

References and Synonymy:

Felimida sphoni Marcus, 1971: 355 - 357; figs. 1 - 3. Anonymous, 1972: 11; color photograph. Sphon, 1972b: 64. Bertsch *et al.*, 1973: 292, 293. Marcus & Hughes, 1974: 520. Keen & Coan, 1975: 43. Bertsch, 1976b: 158

Chromodoris sphoni (Marcus). Bertsch & Meyer, in prep.

Material Examined and Distribution:

Mainland Mexico and Central America:

1) 1 specimen, 3 m subtidal, SE Isla Venado, Mazatlán, Mexico; *leg.* A. J. Ferreira, March 1971 (HB 420; LACM)
2) 3 specimens, intertidal, Punta Mita, Nayarit, Mexico; *leg.* F. & R. Poorman, 2 January 1976 (HB 422 A-C; LACM)
3) 1 specimen, 2 m subtidal, Puerto Angel, Oaxaca, Mexico; *leg.* A. J. Ferreira, December 1971 (HB 421; LACM)
4) 1 specimen, Islas Tortugas, Costa Rica; R/V *Searcher*, 440 (no additional data) (HB 419; LACM)
5) 2 specimens, Taboguilla Island, Panamá Bay, Panamá; *leg.* G. Hendler, 11 September 1974 (HB 217, 218)
6) 1 specimen, Taboguilla Island, Panamá; *leg.* G. Hendler, 1 October 1974 (HB 266)

All the records of *Chromodoris sphoni* are from the mainland Pacific coast of Mexico and Central America, from the Mazatlán area to Panamá Bay. The type locality was never designated; the original material came from 2 localities about 300 km apart in the Mexican states of Nayarit and Colima.

External Morphology and Coloration:

Living *Chromodoris sphoni* from Panamá were 11 and 7 mm in total length; their preserved lengths were 4.5 and 3 mm long, respectively. Marcus (1971: 357) described preserved specimens 18, 16, 15, 15, and 8 mm long. The other 7 specimens I dissected ranged in length from 4 to 15 mm preserved ($\overline{X} = 6.7$ mm). Average-sized living animals are probably 10 - 20 mm long, with a maximum size of 30 - 40 mm.

Characteristic of *Chromodoris sphoni* is a red-cross pattern on its notum (color photograph in Anonymous, 1972). The overall coloring is described by Marcus (1971: 356 - 357). Small specimens from Panamá (HB 217, 218) had the prominent longitudinal red band between the rhinophores and gills, and the lateral red bar from edge to edge of the notum. The rest of the animal was cream-yellow, with a bar of red running lengthwise on each side of the notum; a red band surrounded the mantle edge. The red markings were punctuated and rimmed by rows of small whitish dots. The smaller specimen (7 mm; HB217) had only a partial lengthwise red band on each side of the notum; the small markings were strongest adjacent to the lateral red bar, fading out anteriorly and posteriorly. This marking develops into a longer line with increased growth of the animal. Both of these specimens had only faint greenish markings, and an overall light coloration. Gills and rhinophores were white basally and pink-red distally.

Radula:

The radular formula from only one specimen has been described in the literature (Marcus, 1971), and it is aberrant from the radular counts obtained from 9 specimens (Table 6). The combined radular formula is 40-59 (26-60 · 1 · 26-60).

The numbers of tooth rows and maximum teeth per half-row are positively correlated (Figure 10). The regression line formula is $Y = -20.19 + 1.131\ X$; ($r = 0.5688$, $P < 0.01$, $n = 10$).

The number of tooth rows is dependent on the radular length (Figure 11); $Y = 26.23 + 16.896\ X$; $r = 0.921$, $P < 0.001$, $n = 9$.

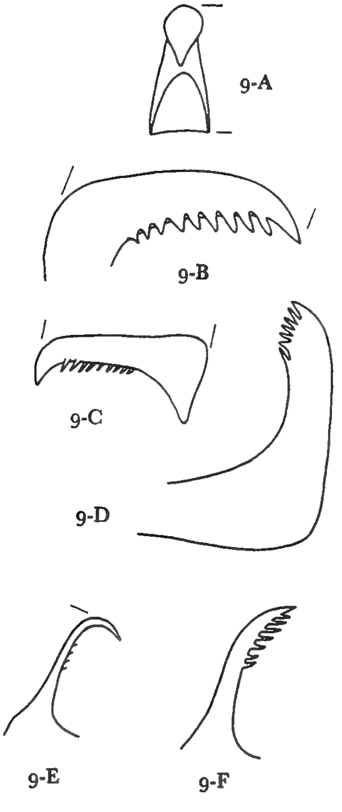
The radular width and maximum number of teeth per half-row are positively correlated (Figure 12). The formula is $Y = 16.99 + 24.58\ X$; $r = 0.907$, $P < 0.001$, $n = 9$.

Table 6

Radular variation in *Chromodoris sphoni*

Specimen (HB numbers)	Length (in mm)	Width (in mm)	Width: length ratio	Number of tooth rows	Maximum number of teeth per half-row
[8]	–	–	–	58	60
217	0.776	0.307	1:2.53	40	26
218	0.929	0.404	1:2.3	42	26
266	1.09	0.48	1:2.27	40	27
419	1.551	0.808	1:1.92	54	36
420	1.058	0.566	1:1.87	45	33
421	1.172	0.654	1:1.79	42	28
422 A	1.58	0.91	1:1.74	54	41
422 B	1.92	0.71	1:2.7	59	37
422 C	0.865	0.331	1:2.61	45	26
$\overline{X}$	1.216	0.57	1:2.19	47.9	34
s	0.384	0.212	0.372	7.535	10.625

[8] MARCUS, 1971



Rachidian tooth is present (Figure 9-A). At times it may be a triangular plate with a slightly raised median cusp and without the basal flanges. Innermost laterals are standard *Chromodoris*-shape, but with small denticles on the inner face of the cusps of lateral teeth 1 - 4. These denticles may not always be obvious in the anterior portion of the radula. Lateral teeth (Figures 9-B, 9-C) have prominent cusps and are greatly denticulated (MARCUS, 1971, reported up to 17 - 19 denticles). Outermost laterals become smaller, with greatly reduced cusps.

Two stages in the development of lateral teeth are shown in Figures 9-E, 9-F.

Scanning electron micrographs of the radula and drawings of the reproductive system are in **BERTSCH & MEYER** (in preparation).

Discussion:

MARCUS (1971) erected a new genus for this species, because of the unique double-denticulation pattern. How-

---

(← adjacent column)

Figure 9

Radular teeth of *Chromodoris sphoni*

A – HB 217; rachidian tooth; LBM, 0.024 mm
B – HB 266; 12th lateral tooth, row 26, LSR
C – HB 217; 14th lateral tooth, row 32, RSR; LBM, 0.026 mm
D – HB 266; outer lateral tooth, row 11, LSR
E – HB 266; newly forming tooth, row 40; thin shaft with minute, sharply-pointed denticles; LBM, 0.032 mm
F – HB 266; shaft of developing tooth, 0.034 mm long, row 40

ever, examination of a large number of radulae indicates that this characteristic is present at times in other species (*i. e., Chromodoris galexorum* and *C. norrisi*). The strength and size of these inner-face denticles vary, as does also the number of laterals exhibiting the pattern. Because the double-denticulation can be present or absent in other species, and (perhaps more importantly) because it is a relatively minor morphological character trait that does not affect major portions of the radula nor indicate a major functional (nor evolutionary) divergence, and because it is an inconsistent structure, justification is lacking for the retention of a separate genus to encompass *C. sphoni.*

Therefore, *Felimida* is a junior synonym of *Chromodoris* and the species should be referred to as *Chromodoris sphoni.* Double-denticulation on the first 8 lateral teeth (usually less than 10 - 15% of the total teeth per half-row) is part of the variation that may occur in the genus *Chromodoris.*

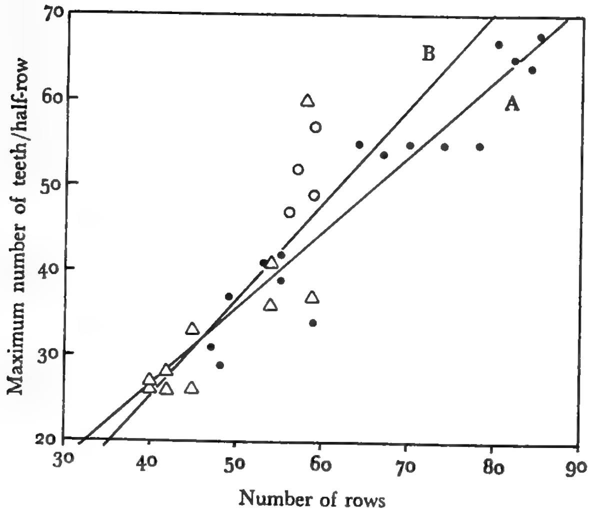


Figure 10

Relation between maximum number of teeth per half-row and the number of tooth rows

A – *Chromodoris baumanni* regression line

B – *Chromodoris sphoni* regression line

●: *C. baumanni*; △: *C. sphoni*; ○: *C. galexorum*

Regression formulae for the plots of all graphs are given in the text

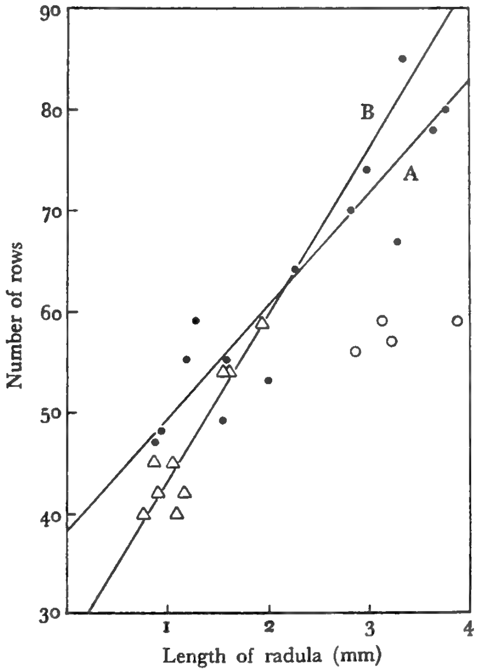


Figure 11

Correlation between number of rows and length of radula *Chromodoris baumanni, Chromodoris sphoni* and *Chromodoris galexorum.* Same symbol explanations as in Figure 10

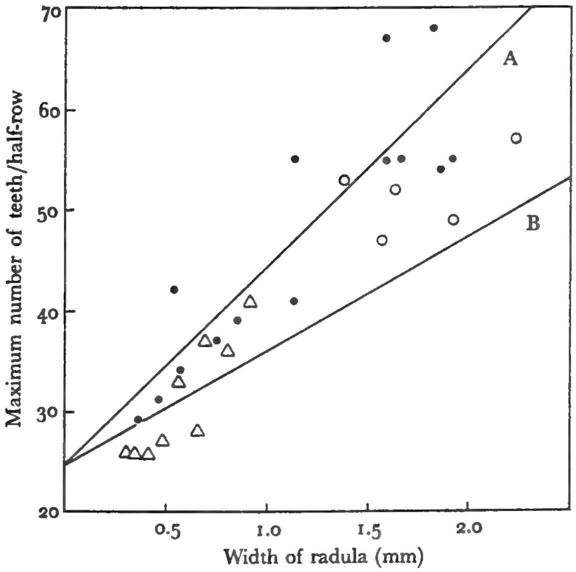


Figure 12

Relation between maximum number of teeth per half-row and width of radula, *Chromodoris baumanni, C. sphoni,* and *C. galexorum.* Same symbol explanations as in Figure 10

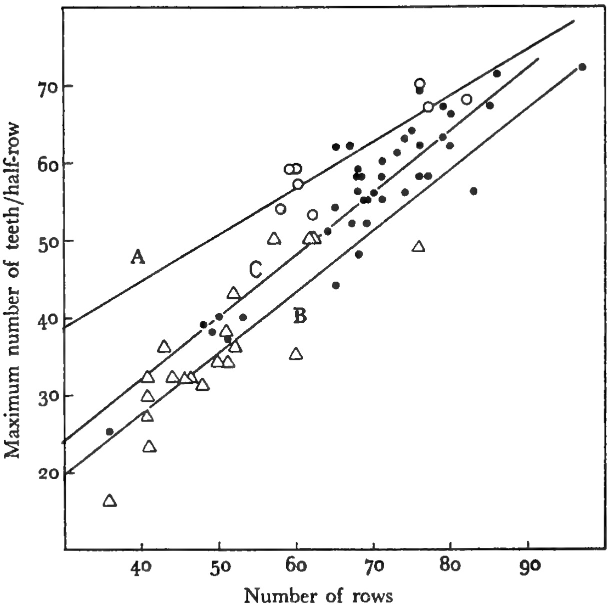


Figure 13

Correlation between maximum number of teeth per half-row and the number of tooth rows
A – *Chromodoris marislae* (○); B – *Chromodoris mcfarlandi* (△); C – *Chromodoris norrisi* (●)

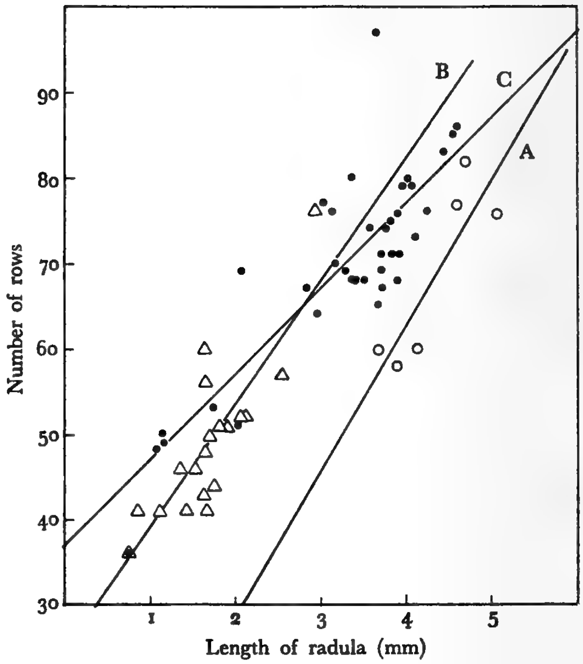


Figure 14

Relation between number of tooth rows and length of radula
Chromodoris marislae, C. mcfarlandi, and *C. norrisi*
Explanation of symbols the same as in Figure 13

DISCUSSION OF *Chromodoris*

The 6 known species of *Chromodoris* from the Pacific coast of America share common radular morphological characteristics with each other and with valid *Chromodoris* from other regions of the world. The radular characteristics of the genus *Chromodoris* can be defined: Radula with unicuspid lateral teeth; innermost lateral tooth usually with denticles on the inner and outer faces; following inner laterals (approximately 2 - 10) with denticles on outer face; remaining teeth throughout the major portion of the half-row usually have denticles on the posterior surface (at times they may be on the postero-lateral surface). Majority of teeth (in the functional central region of each half-row) with a prominent cusp larger than any of the denticles; outermost laterals (approximately 10) reduced in total size, cusp also becoming progressively smaller.

Explanation of Figures 45 to 50

Scanning Electron Micrographs of the Radular Teeth
of *Chromodoris norrisi* and *Chromolaichma sedna*

Figure 45: *Chromodoris norrisi*; youngest developing lateral teeth from middle of half-row (HB 376) × 825

Figure 46: *Chromodoris norrisi*; developing lateral teeth from middle of half-row (older than Figure 45) (HB 376) × 825

Figure 47: *Chromolaichma sedna*; innermost lateral teeth (HB 371 A) × 800

Figure 48: *Chromolaichma sedna*; teeth from middle of half-row (HB 371 A) × 800

Figure 49: *Chromolaichma sedna*; outer denticled lateral teeth (HB 371 A) × 800

Figure 50: *Chromolaichma sedna*; smooth outermost lateral teeth (HB 371 A) × 800

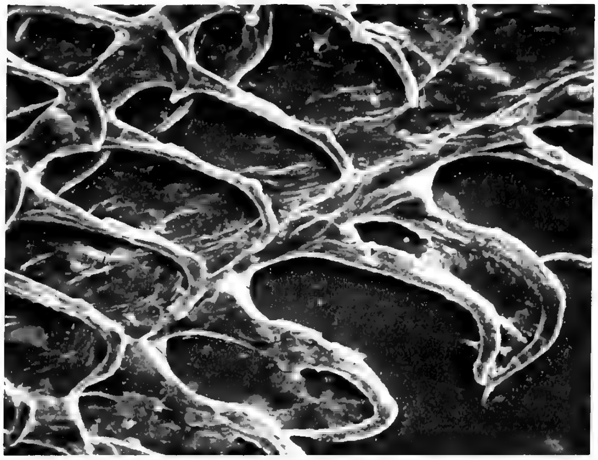


Figure 45

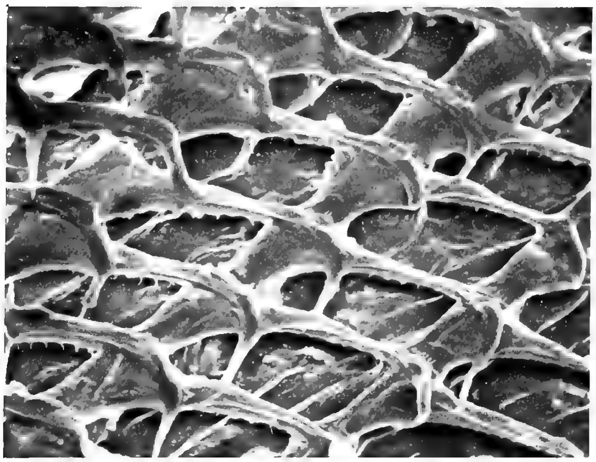


Figure 46

Figure 47

Figure 48

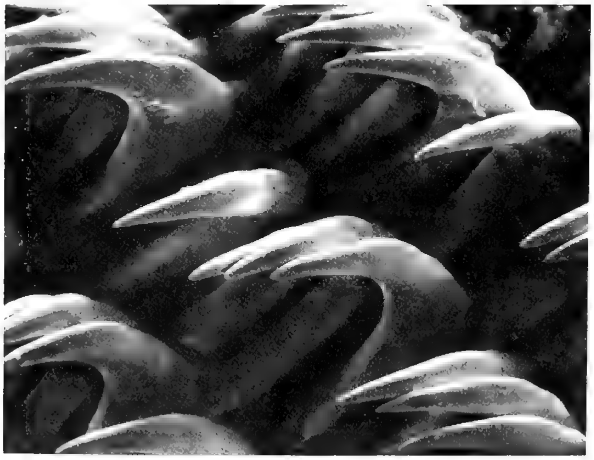


Figure 49

Figure 50

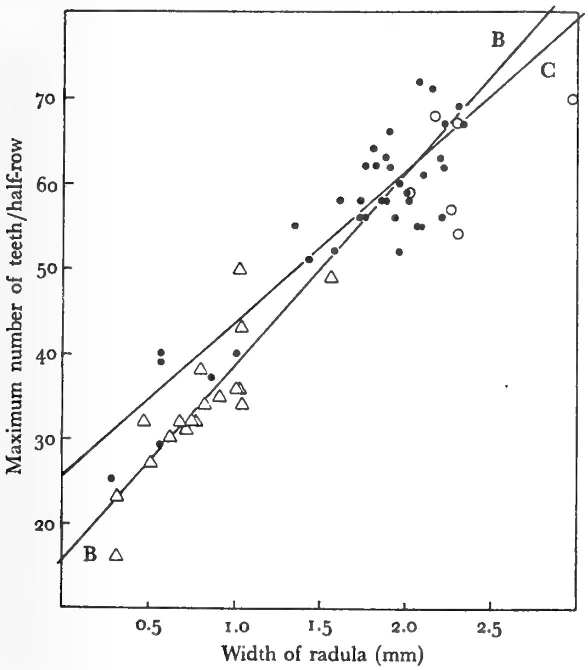


Figure 15

Correlation between maximum number of teeth per half-row and width of radula
Chromodoris marislae, *C. mcfarlandi*, and *C. norrisi*
Explanation of symbols the same as in Figure 13

Within the pattern of similarity, the 6 species show statistically significant differences from each other (Table 7). The means used to calculate the t-tests are given in each species' respective Table (1 - 6), or in the text. At a glance, one can translate subjective impressions of radular differences into statistical statements. Based on these data calculated from many radulae and the P values in Table 7, the following statements can be made regarding species-level separations:

1. The radula of *Chromodoris baumanni* is wider than that of *C. mcfarlandi* and *C. sphoni*, and is narrower than the radulae of the other 3 species; but there is no difference between the width: length ratio of *C. baumanni* and the other 4 species. *Chromodoris baumanni* has the same number of tooth rows as *C. norrisi*, but less teeth per half-row.

2. The radula of *Chromodoris galexorum* shows great similarity with those of *C. norrisi* and *C. baumanni*; *C. marislae* approximates the meristic characters of *C. norrisi*.

3. Numerous other correlations can be made from these tables, but they all can be summarized under 2 statements. First, all of the species can be separated from any other species either by direct significant differences from each other or indirectly through their direct relationships with a third species. Second, there are 2 species groups that share greater radular similarity among themselves than across the groups. *Chromodoris baumanni, C. galexorum, C. marislae,* and *C. norrisi* comprise one group, and *C. mcfarlandi* and *C. sphoni* comprise the other (the latter group also shares having a large number of denticles, between 10 and 20, on the lateral teeth). Correlation of a large number of factors (including body shape, color, and radular tooth morphology) indicates that these relationships may well be phylogenetic. An equally rigorous examination of all the worldwide species of *Chromodoris* is needed before a definitive statement of relationships can be made. The similarity of certain Hawaiian and Indo-Pacific species to Pacific American species has already been noted.

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Table 7

Results of t-tests conducted between all species pairs of American Pacific coast *Chromodoris*. Numbers are significance probabilities (P). N.S.: not significant, no difference between the species for the particular measurement or count; — : insufficient specimens.

Chromodoris:	***galexorum***	*marislae*	*mcfarlandi*	*norrisi*	*sphoni*
baumanni					
Rows/teeth	—	N.S.	N.S.	N.S.	N.S.
Length/rows	—	N.S.	N.S.	N.S.	N.S.
Width/teeth	—	—	N.S.	N.S.	N.S.
Length	N.S.	<0.001	N.S.	<0.01	<0.02
Width	<0.05	<0.001	<0.05	<0.01	<0.01
W:L ratio	N.S.	N.S.	N.S.	N.S.	N.S.
Rows	N.S.	N.S.	<0.001	N.S.	<0.01
Max. teeth	N.S.	<0.05	<0.001	<0.001	<0.01
galexorum					
Length		<0.02	<0.001	N.S.	<0.001
Width		<0.02	<0.001	N.S.	<0.001
W:L ratio		N.S.	<0.05	N.S.	N.S.
Rows		N.S.	N.S.	N.S.	<0.05
Max. teeth		<0.02	<0.001	N.S.	<0.01
marislae					
Rows/teeth			N.S.	N.S.	<0.01
Length/rows			N.S.	N.S.	N.S.
Length			<0.001	<0.02	<0.001
Width			<0.001	<0.01	<0.001
W:L ratio			<0.05	N.S.	N.S.
Rows			<0.001	N.S.	<0.001
Max. teeth			<0.001	N.S.	<0.001
mcfarlandi					
Rows/teeth				N.S.	N.S.
Length/rows				N.S.	N.S.
Width/teeth				N.S.	N.S.
Length				<0.001	<0.02
Width				<0.001	N.S.
W:L ratio				<0.001	N.S.
Rows				<0.001	N.S.
Max. teeth				<0.001	N.S.
norrisi					
Rows/teeth					N.S.
Length/rows					N.S.
Width/teeth					N.S.
Length					<0.001
Width					<0.001
W:L ratio					<0.01
Rows					<0.001
Max. teeth					<0.001

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The Family Columbellidae in the Western Atlantic

Part IIb. - The Pyreninae (Continued)

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(4 Plates; 1 Text figure)

IN THIS FINAL ARTICLE of the above-named series, monographing the buccinacean family Columbellidae in the western Atlantic, a total of 10 genera and 17 species assigned therein are treated. Genera covered are *Aesopus* Gould, 1860; *Amphissa* H. & A. Adams, 1853; *Columbellopsis* Bucquoy & Dautzenberg (*in* Bucquoy, Dautzenberg & Dollfus), 1882; *Conella* Swainson, 1840; *Cosmioconcha* Dall, 1913; *Decipifus* Olsson & McGinty, 1958; *Mazatlania* Dall, 1913; *Mitrella* Risso, 1826; *Strombina* Mörch, 1852; and *Suturoglypta* Radwin, 1968. These genera all belong in the subfamily Pyreninae, a group characterized by the narrower, lighter form of the lateral radular teeth. In addition, most pyrenine species are characterized by a slender, unshouldered shell form but, given the diversity of shell morphology seen in the family, it is not a completely consistent feature.

For standard abbreviations and basic ecological and zoogeographic information the reader is referred to Part I of this series of articles (The Veliger **19** (4): 403 - 417; 1977).

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I would like to acknowledge my appreciation to Dr. Harald Rehder, under whose direction this research was done; to Drs. Joseph Rosewater, Joseph P. E. Morrison, and Wendell P. Woodring, who contributed critical suggestions. Dr. Norman Tebble, formerly of the British Museum (Natural History) and Mr. Jack Scott and the staff of the Photographic Laboratory, National Museum of Natural History supplied photographs of specimens. Mr. Anthony D'Attilio, San Diego Natural History Museum re-illustrated the radulae. Thanks are also due to Drs. Kenneth J. Boss, Museum of Comparative Zoology, William K. Emerson, American Museum of Natural History, and R. Tucker Abbott, formerly of the Academy of Natural Sciences, Philadelphia, for permitting me to examine the mollusk collections of their respective institutions. In addition, I offer thanks to all individuals, too many to enumerate, who have helped me obtain additional specimens for study. The present research was carried out under a Smithsonian Predoctoral Internship.

Aesopus Gould, 1860

Aesopus Gould, 1860. Proc. Boston Soc. Nat. Hist. **7**: 383 (type species by M: *Aesopus japonicus* Gould, 1860) (Figure *1*)

Shell small (4 - 14mm), slender, cylindrical; spire high, subacute, suture shallow; body whorl small, aperture short, broad, apertural lip smooth, unthickened, columella straight, smooth, generally with a small, heavy anterior callus, siphonal canal very short; shell surface commonly glossy with very fine, partly obsolete spiral sculpture; protoconch of one or 2 bulbous unsculptured whorls. The radula of *Aesopus japonicus* was not available. The radulae of the 2 western Atlantic species, *A. stearnsi* and *A. metcalfei*, have subrectangular median teeth flanked on each side by a sigmoid, bicuspid lateral tooth (Figures *30* and *31*).

Remarks: The shell in this genus is so distinctive that confusion with most other columbellid genera is not a problem. Characters used are: 1) the proportionately great height of the spire; 2) the distinct anterior columellar callus, 3) the short, bulbous protoconch, and 4) the short-cusped lateral radular tooth.

Aesopus metcalfei (Reeve, 1860)

(Figure *3*)

> *Terebra metcalfei* Reeve, 1860. Conch. Icon. **12:** *Terebra*, sp. 139 (pages not numbered); "West Indies" (here restricted to Samaná Bay, Dominican Republic); representation of lectotype, Reeve, **1860:** fig. 139; holotype probably lost. According to a note in the Journ. Conchol. 1944, **22** (4): 95 (lines 34-35), the Metcalfe collection was probably sold and its whereabouts is unknown.

Shell moderate in size (9 - 14mm), and cylindrical; spire high (over $\frac{2}{3}$ total shell length), subacute, whorls barely convex, suture shallow; body whorl small, aperture moderately broad, outer lip not thickened, weakly lirate within, columella straight and non-denticulate, anterior canal very short and slightly bent; color glossy white, sculpture lacking or axial ribs on the spire whorls; protoconch of $1\frac{1}{2}$ bulbous whorls. Each radular row has a flat, subrectangular median tooth flanked on each side by a bicuspid lateral tooth (Figure *30*). The radular tooth of *Aesopus metcalfei* is essentially indistinguishable from that of *A. stearnsi* except for its larger size.

Remarks: No fossil record or clear ancestry is known for this species. Its closest relative appears to be the Panamic *Aesopus arestus* Dall, 1919.

Range: The collection records of this species give a range which is deceptive, as the northern limit is Samaná Bay, Dominican Republic and its southernmost record is from off Cape Bermeja, Argentina. The lack of collection records from the northern, Caribbean and the southern, Argentine collection sites suggests either 2 clusters (perhaps 2 distinct species or subspecies) or that additional collection in moderately deep water off northern and central South America will show a continuous distribution for this species.

Aesopus stearnsi (Tryon, 1883)

(Figure *2*)

> *Nitidella filosa* Stearns, 1873. Proc. Acad. Nat. Sci. Phila. **1873:** 345 - 356, not Angas, 1867 (Tampa Bay, Florida; **lectotype** here selected, USNM 54309)
>
> *Columbella (Seminella) stearnsi* Tryon, 1883. Manual of Conchol. **5:** 179; plt. 58, fig. 48 (new name for *Nitidella filosa* Stearns, 1873, not Angas 1867)

Shell small (4 - 5mm), cylindrical; spire high (more than $\frac{2}{3}$ total shell length), subacute, whorls slightly convex, suture shallow; body whorl small, aperture short and wide, outer lip not thickened, weakly lirate on its inner surface; columella straight, non-denticulate, anterior canal very short, slightly bent, weak anal groove present; sculpture of numerous fine spiral threads with finer axial threads between them, imparting a microscopically pitted appearance; color varying from white to light brown with darker brown spots; protoconch of one full translucent white, bulbous volution. Each radular row consists of a flat subrectangular median tooth, flanked on each side by a bicuspid lateral tooth. The cusps of the laterals are short and sharp (Figure *31*).

Remarks: *Nitidella filosa* Stearns, 1873 is a secondary homonym of *Aesopus filosus* Angas, 1867.

The known fossil record includes *Columbella peculiaris* Guppy, 1867, a very similar species from the Pliocene of Trinidad. A similar Recent species is *Aesopus sanctus* Dall, 1919, from the eastern Pacific.

Range: The range of *Aesopus stearnsi* encompasses a discontinuous distribution. Records from as far north as Bermuda and off Cape Hatteras, North Carolina, and as far south as the central Bahamas and off Tampa Bay, Florida can be documented. Within this range, however, are notable gaps in distribution. No records have been found from between the Carolina Capes and southeastern Florida, the distribution resuming in the Bahama Islands and on the western coast of Florida. The known distribution of *A. stearnsi* seems to support the contention that the southern half of Florida was an island in the Plio-Pleistocene. Several other columbellid species as well as species in other families show a similar distribution pattern (see Zoogeography Section in Part I).

Amphissa H. & A. Adams, 1853

> *Cominella (Amphissa)* H. & A. Adams, 1853. Gen. Rec. Moll.: 111
>
> *Amphissa* H. & A. Adams. Dall, 1871. Amer. Journ. Conch. 7 (2): 111 (type species by SD [Dall, 1871: 111], *Buccinum corrugatus* Reeve, 1847 (not Brocchi, 1814) (= *Amphissa columbiana* Dall, 1916) (see Figure *4*)

Shell moderate to large (10 - 25mm), and buccinoid; spire high and acute, whorls strongly convex, suture impressed; body whorl $\frac{1}{2}$ shell length, aperture broadly open, apertural lip unthickened, non-denticulate within, columella straight, smooth, siphonal canal short; sculpture generally of numerous strong axial ribs crossed by spiral elements of varying strength; color off-white to brown with a straw-colored periostracum. Each radular row has a flat, subrectangular median tooth flanked on each side by an elongate, sigmoid, tricuspid lateral tooth (see Figure *35*).

Remarks: *Amphissa*, *Parametaria*, *Strombina*, *Cosmioconcha*, and *Anachis s. s.*, all primarily eastern Pacific columbellid groups whose members have elongate, sigmoid lateral radular teeth, appear to be closely related. The range of *Amphissa* is now known to include the entire North Atlantic, with the present reassignment of *Columbella haliaeeti* Jeffreys, 1867 to it.

Amphissa haliaeeti (Jeffreys, 1867)

(Figure *5*)

Columbella haliaeeti Jeffreys, 1867. Brit. Conch. **4**: 356-360 (off Unst, Shetland Islands; holotype, US NM 191601)

Pyrene costulata (of ?Cantraine, 1835, and other authors) Sars, 1878. Moll. Reg. Arc. Nerv.: 252-253

Shell small to moderate in size (6.5 - 12.5 mm), buccinoid; spire moderately high (about ½ shell length), and subacute, whorls strongly convex, suture impressed; body whorl swollen and buccinoid, aperture wide, outer apertural lip flaring but unthickened, interior of apertural lip generally non-denticulate, columella straight and smooth, siphonal canal short to moderate in length and slightly bent; sculpture of numerous prominent axial ribs crossed by microscopic spiral threads; color white to pale yellow; protoconch of almost 4 full whorls overlaid by a thin calcareous layer bearing a peculiar sculpture of fine oblique lines.

Each radular row consists of a single, flat, subrectangular median tooth flanked on each side by a pair of lateral teeth. Each lateral tooth has 2 rather straight distal cusps and a peculiar proximal lump or lobe (Figure *36*), a feature held in common with *Amphissa columbiana*, the type species of the genus.

Remarks: This species has often been called *Columbella costulata* Cantraine, 1835 (Tertiary of Pélore). Cantraine did not figure his species and gave no clear indication of its identity. In addition, no trace of the type of Cantraine's species has been found. If the present species is identical to Cantraine's, *Amphissa costulata* should be the name. I have, however, found no evidence for such a determination and *A. haliaeeti* is the first unequivocally available name for the species in question.

Range: In the eastern Atlantic *Amphissa haliaeeti* ranges from the Lofoten Islands (Norway) in the north to off Portugal and west to Sicily in the Mediterranean. In the western Atlantic it ranges from off Nova Scotia to off Cape Lookout, North Carolina. *Amphissa haliaeeti*, inhabiting both sides of the Atlantic, has a broad distribution, but the temperature in its deepwater habitat probably does not change appreciably with geography. Other factors, however, may affect it at the southern limit of its range in the western Atlantic, as the size of the shell decreases with southward progress.

Explanation of Figures *1* to *17*

Figure *1*: *Aesopus japonicus* (Gould, 1860), USNM 343002, Osima, Osumi, Japan

Figure *2*: *Aesopus stearnsi* (Tryon, 1883), USNM 677137, 500 yds. north of Egmont Key, Fla.

Figure *3*: *Aesopus metcalfei* (Reeve, 1860), USNM 107824, St. Martin, West Indies

Figure *4*: *Amphissa columbiana* (Dall, 1916), USNM 126638, Vancouver Id., Canada

Figure *5*: *Amphissa haliaeeti* (Jeffreys, 1867), USNM 38739, off Martha's Vineyard, Mass.

Figure *6*: *Columbellopsis nycteis* (Duclos, 1846), USNM 663724, Water Id., Virgin Islands

Figure *7*: *Columbellopsis minor* (Scacchi, 1836), USNM 191687, no locality (Mediterranean)

Figure *8*: *Decipifus sixaolus* Olsson & McGinty, 1958, USNM 441-887, Jack's Bay, St. Mary, Jamaica

Figure *9*: *Conella ovulata* (Lamarck, 1822), USNM 416425, "Antilles"

Figure *10*: *Conella ovuloides* (C. B. Adams, 1850), USNM 416424, "Antilles"

Figure *11*: *Cosmioconcha modesta* (Powys, 1835), AMNH 90877, Gulf of Fonseca, El Salvador, 13°20'03"N; 87°49'26"W

Figure *12*: *Cosmioconcha calliglypta* (Dall & Simpson, 1901), US NM 608200, Off Mustang Id., Texas

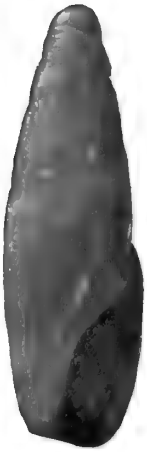
Figure *13*: *Cosmioconcha nitens* (C. B. Adams, 1850), USNM 429-305, Samaná Bay, Dominican Republic

Figure *14*: *Mitrella ocellata* (Gmelin, 1791), USNM 530185, St. Thomas, Virgin Islands

Figure *15*: *Mitrella scripta* (Linnaeus, 1758), USNM 191647, no locality (Mediterranean)

Figure *16*: *Mitrella dichroa* (Sowerby, 1844), USNM 599855, Off South Lake Worth Inlet, Palm Beach Co., Florida

Figure *17*: *Mitrella dichroa* (Sowerby, 1844), USNM 539121, Sacco São Francisco, Rio de Janeiro State, Brazil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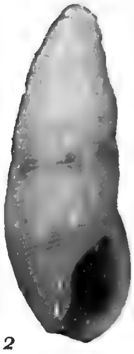
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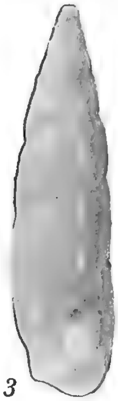
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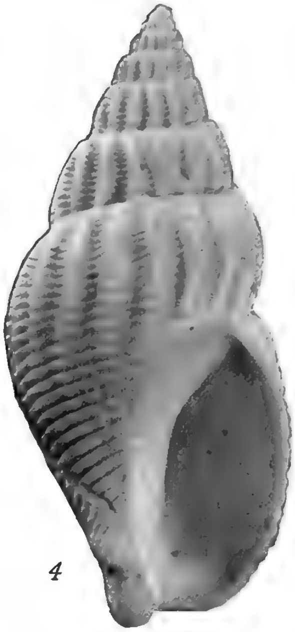
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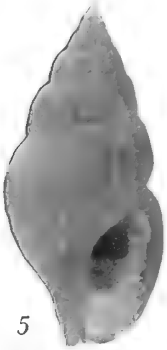
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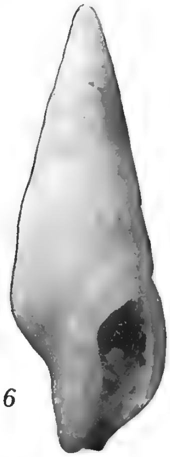
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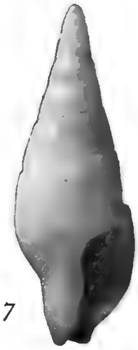
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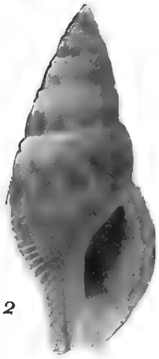
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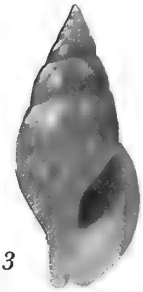
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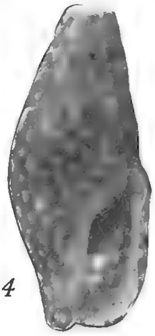
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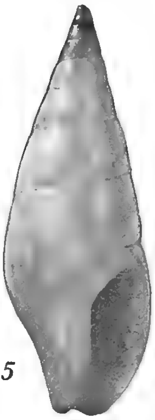
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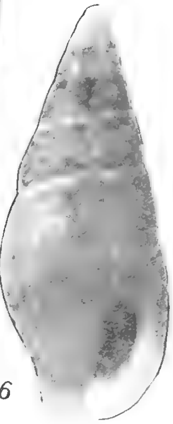
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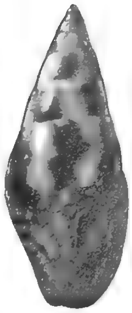
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Astyris H. & A. Adams, 1853

Astyris H. & A. Adams, 1853. Gen. Rec. Moll. 187 (type species by SD [Cossmann, 1901, 4: 238], *Buccinum rosaceum* Gould, 1839)

A complete treatment of the genus *Astyris* H. & A. Adams has been excluded from this paper because the subgeneric and specific interrelationships in this genus are not sufficiently understood to warrant such a treatment. Taxonomic criteria of value elsewhere in the family (*e. g.*, shell sculpture, shell proportion, and radular dentition), seem to be of negligible importance here. In several instances smoothly intergrading series of shell specimens have been seen with ornamentation varying from strong axial ribbing to a complete lack of sculpture, and shell form varying from slender and attenuate to truncate and obese. This extreme variability at the species level has made it difficult to segregate one species from another. A taxonomic treatment of *Astyris* cannot, therefore, be undertaken with the degree of confidence presently felt concerning the remainder of the western Atlantic genera.

The following is a compilation of all western Atlantic nominal species described under *Astyris*, and those that have subsequently been assigned there:

A. amphisella (Dall, 1881). Bull. Mus. Comp. Zool. 9 (2): 91
A. appressa Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 54
A. bonairense (Castellanos & Deambrosi, 1967). Neotropica 13 (41): 50
A. crumena Dall, 1924a. Proc. Biol. Soc. Wash. 37: 87
A. diaphana (Verrill, 1882). Trans. Conn. Acad. Sci. 5 (2): 513 - 515
A. dissimilis (Stimpson, 1851). Rev. Synon. Test. Moll. New England, pp. 47 - 48
A. duclosiana (d'Orbigny, 1842). Hist. Phys., Polit., Nat. Cuba, plt. 21, figs. 31 - 33
A. embusa Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 55
A. enida Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 57
A. euribia Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 56
A. georgiana Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 57
A. holbolli (Möller, 1842). Ind. Moll. Grön.: 15
A. lunata (Say, 1826). Journ. Acad. Nat. Sci. Phila. 5: 213
A. multilineata Dall, 1889. Bull. Mus. Comp. Zool. 18: 190
A. nivea (Ravenel, 1861). Proc. Acad. Nat. Sci. Phila. 11: 43
A. perlucida Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 53
A. profundi Dall, 1889. Bull. Mus. Comp. Zool. 18: 192
A. projecta Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 56
A. pura (Verrill, 1882). Trans. Conn. Acad. Sci. 5 (2): 515
A. pusilla (Sowerby, 1844). Proc. Zool. Soc. London 12: 53
A. raveneli Dall, 1889. Bull. Mus. Comp. Zool. 18: 190
A. rosacea (Gould, 1841). Rep. Invert. Mass. ... p. 197
A. rushii (Dall, 1889). Bull. Mus. Comp. Zool. 18: 188-189
A. sagenata Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 57
A. saintpairiana (Caillet, 1864). Journ. de Conchyl. 12: 279 - 282
A. spirantha (Ravenel, 1859). Proc. Elliott Soc.: 281-282
A. stemma Dall, 1927. Proc. U. S. Nat. Mus. 70 (2667): 53
A. stricta (Watson, 1882). Journ. Linn. Soc. London, Zool. 16 (93): 340 - 341
A. strix (Watson, 1882). Journ. Linn. Soc. London, Zool. 16 (93): 338 - 339
A. verrilli (Dall, 1881). Bull. Mus. Comp. Zool. 9 (2): 91-92
A. vidua Dall, 1924. Proc. Biol. Soc. Wash. 37: 87
A. wheatleyi (DeKay, 1843). Nat. Hist. N. Y. State p. 132

Columbellopsis Bucquoy & Dautzenberg, 1882

Columbellopsis Bucquoy & Dautzenberg *in* Bucquoy, Dautzenberg & Dollfus, 1882. Moll. Mar. Roussillon 1: 77 - 78; plt. 13, figs. 9, 10 (type species by OD, *Columbella minor* Scacchi, 1836) (see Figure 7)

Shell small (4 - 10mm), slender, fusiform; spire acute, more than ½ the total shell length, whorls flat-sided, suture very shallow, body whorl short, slightly inflated, aperture small, broad, outer lip thickened, denticulate on its inner surface, siphonal canal short to moderate in length, strongly constructed, slightly bent, columella denticulate; shell surface glossy, translucent, white in color, often with orange, brown or white markings. Each radular row consists of a flat rectangular median tooth flanked on each side by a sigmoid, bicuspid lateral tooth.

Remarks: *Atilia* H. & A. Adams, 1853 was first introduced without designation of a type species. Subsequent authors utilized the name for a *Mitrella*-like group of species, also without designating a type species. Cossmann (1901) was the first to designate a type for *Atilia.* He selected *Mitrella minor* Scacchi (the type species of *Columbellopsis*), a species not in the original list of H. & A. Adams and thus an invalid designation. The following year Pace (1902) designated *Columbella suffusa* Sowerby as the type species of *Atilia*, thereby completely removing *Mitrella minor* and its congeners from that genus. *Columbellopsis* appears to belong near *Mitrella* on the basis of shell morphology. It differs from the latter genus primarily in the slenderness of its shell and its more constricted and elongate siphonal canal. It shares with *Mitrella* the distinction of having the longest geologic record (first records are from the early Eocene).

Columbellopsis nycteis (Duclos, 1846)

(Figure *6*)

Columbella fusiformis d'Orbigny, 1842 *in* Sagra, Hist. Phys., Polit., Nat. Cuba: plt. 21, figs. 25-27, not Anton, 1839 (Martinique; holotype BM[NH])

Colombella nycteis Duclos, 1846 *in* Chenu, Illust. Conchyl. **4**: plt. 17, figs. 5 - 8 (type locality here designated as "one mile northwest of Fowey Light, Florida;" representation of **lectotype:** Duclos, **4**: plt. 17, figs. 5 - 8)

Colombella plutonida Duclos, 1846 *in* Chenu, Illust. Conchyl. **4**: plt. 16, figs. 1 - 2 (type locality not specified; representation of **lectotype**, Duclos, 1846, **4**: plt. 16, figs. 1 - 2)

Columbella belizana Duclos, 1848 *in* Chenu, Illust. Conchyl. **4**: plt. 22, figs. 9 - 10 (type locality not specified; representation of lectotype, Duclos, 1848, **4**: plt. 22, figs. 9 - 10)

Columbella fenestrata C. B. Adams, 1850b. Contrib. to Conch. **4**: 57 - 58 (Jamaica; holotype MCZ 186009)

Shell small (5 - 7mm), fusiform; spire acute, about $\frac{2}{3}$ total shell length, whorls flat-sided with very shallow suture; body whorl swollen, aperture moderately wide, outer lip thickened, weakly denticulate on its inner surface, columella bent, non-denticulate, siphonal canal short and bent; sculpture lacking, color translucent white with ephemeral white, yellow, red, or bluish flammules on part or all of the spire. Each radular row consists of a flat, rectangular median tooth flanked on each side by a sigmoid, bicuspid lateral tooth. Each of these bears, in addition to 2 sharp distal cusps, a more rounded proximal lobe (Figure *32*).

Remarks: *Columbellopsis nycteis* has a comparatively long fossil history. The earliest fossils of the species have been reported from the Pliocene of Florida (Olsson & Harbison, 1953: 237) as *Anachis (Alia)* cf. *fenestrata*. An earlier record of a *Mitrella (Columbellopsis)* aff. *M. fenestrata* (Woodring, 1964: 248) indicates a Miocene age, but, whereas the form reported is probably congeneric with the present species, it may not be conspecific with it.

Range: *Columbellopsis nycteis* exhibits a typical Caribbean distribution (see Part I of this series of articles) and ranges from Palm Beach County, Florida on the north to Curaçao, Dutch West Indies and Panamá on the south.

Conella Swainson, 1840

Conella Swainson, 1840. Treat. Malac.: 149, 151, 312 (type species by M, *Conella picata* Swainson, 1840 (= *Columbella ovulata* Lamarck, 1822) (Figure *9*)

Cionella Swainson, Gray, 1847. Proc. Zool. Soc. London **15**: 138 (error for *Conella*).

Shell moderate in size (12 - 16mm), biconic; spire low to moderate in height, acute, more or less convex, suture impressed; body whorl large ($\frac{3}{4}$ of total shell length), aperture long, narrow, apertural lip moderately thickened, weakly denticulate on its inner surface; swinging upward posteriorly where it joins the body whorl, columella straight, smooth, siphonal canal short, straight; shell surface smooth or with microscopic spiral striae; color orange to light or dark brown with irregular white blotches. Each radular row consists of a flat, subrectangular median tooth

Explanation of Figures *18*, *19*, *21* to *29*

Figure *18*: *Strombina lanceolata* (Sowerby, 1832), USNM, Galápagos Islands

Figure *19*: *Strombina pumilio* (Reeve, 1859), ANSP 240053, Off Punta de Piedras, Isla de Margarita, Venezuela

Figure *21*: *Suturoglypta albella* (C. B. Adams, 1850), USNM 64-396, Jamaica

Figure *22*: *Suturoglypta pretri* (Duclos, 1846), USNM 103412, St. Thomas, West Indies

Figure *23*: *Suturoglypta iontha* (Ravenel, 1861), USNM 53777, Pine Key, Florida

Figure *24*: *Mazatlania aciculata* (Lamarck, 1822), USNM 409845, Tobago, West Indies

Figure *25*: *Mazatlania fulgurata* (Philippi, 1846), USNM 59316, Acapulco, Mexico

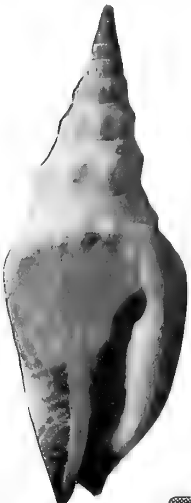
Figure *26*: ?*Mitrella rubra* Martens, 1881 (After Strebel, 1905)

Figure *27*: *Parvanachis decorata* (Strebel, 1905) (After Strebel, 1905)

Figure *28*: *Parvanachis paessleri* (Strebel, 1905) (After Strebel, 1905)

Figure *29*: *Parvanachis melvillei* (Strebel, 1905) (After Strebel, 1905)

[RADWIN] Figures *18*, *19*, *21* to *29*



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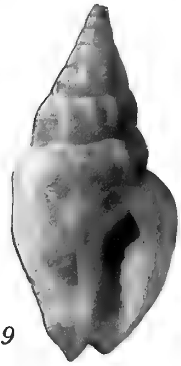

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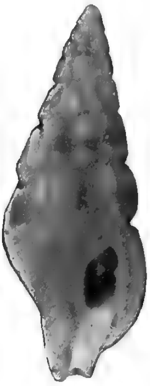

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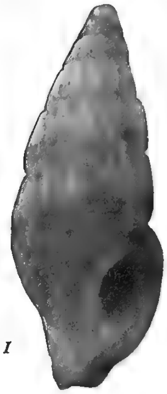

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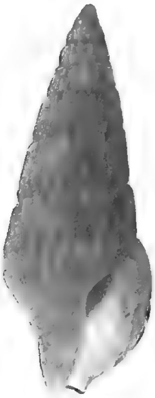

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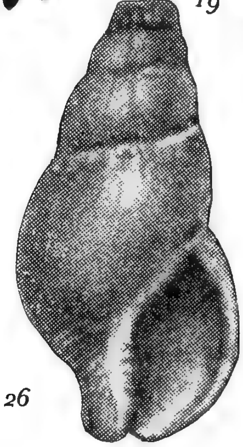

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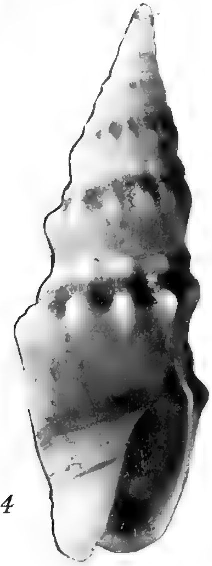

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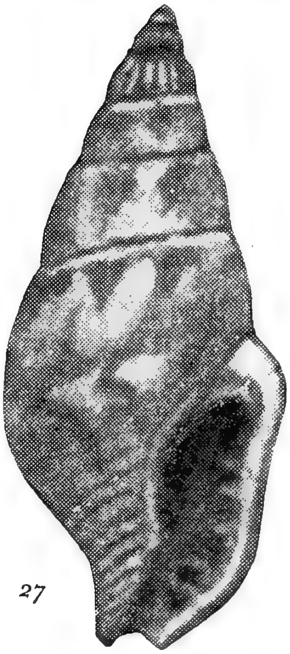

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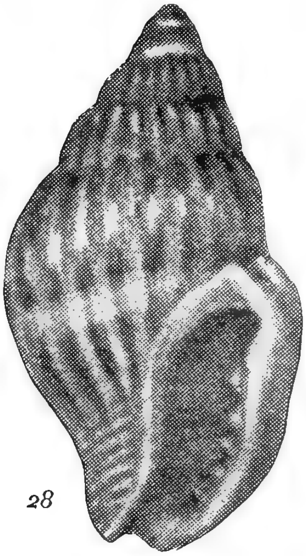

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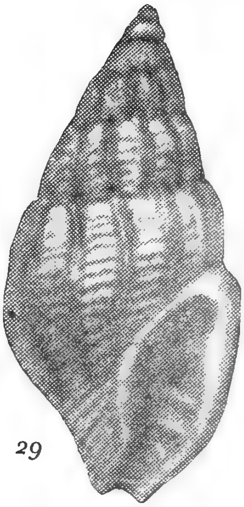

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flanked on each side by an elongate, sigmoid lateral tooth. Each of these teeth bears 2 sharp distal cusps (Figure *33*).

Remarks: The 2 Caribbean species of *Conella* have been assigned by some authors to *Pyrene* Röding, 1798, a genus limited to the Indo-Pacific region. *Pyrene* has a uniquely terraced spire configuration not found in *Conella* (Figure 20). Only Woodring (1928), in his discussion of *Eurypyrene*, has correctly indicated that *C. picata* Swainson, 1840 (= *C. ovulata* Lamarck, 1822) is the type species of *Conella* Swainson, 1840 by monotypy.

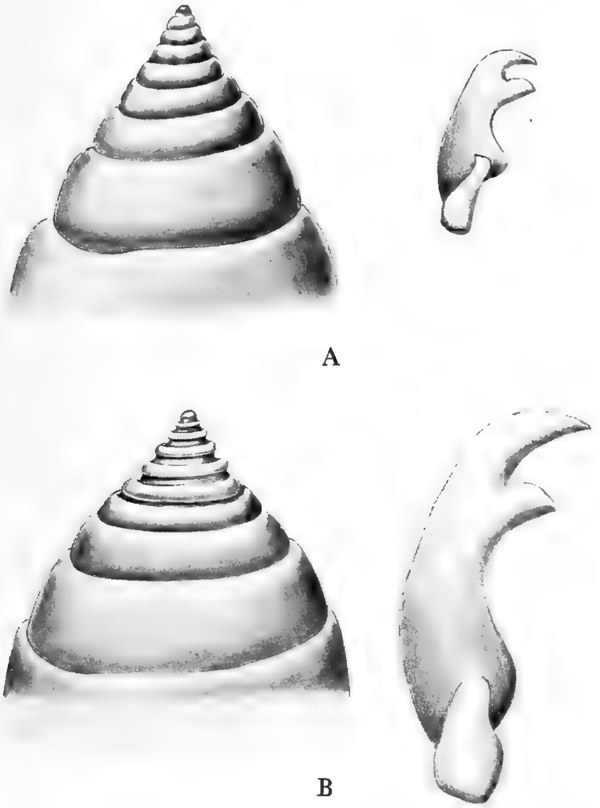


Figure 20

(A) *Conella ovulata* (Lamarck, 1822) vs. (B) *Pyrene punctata* comparison of spire form and lateral radular tooth

The radula of *Conella* suggests the placement of this genus near *Anachis*, *Strombina*, and *Parametaria*. On the basis of shell characters alone, however, this genus is most closely related to *Eurypyrene* Woodring, 1928, last encountered in the Pleistocene of Florida.

Conella ovulata (Lamarck, 1822)

(Figure *9*)

Columbella ovulata Lamarck, 1822. Hist. Nat. Anim. s. Vert. **7**: 295 (type locality here designated as "St. Thomas, Virgin Islands," holotype GM)

Conella picata Swainson, 1840. Treat. Malac.: 151, fig. 17a (new name for *Columbella ovulata* Lamarck)

Meta ovuloides Reeve, 1859 (part). Conch. Icon. **11** (*Meta*): plt. I, fig. 2a (not fig. 2b)

Shell moderately large (14 - 20mm), biconic; spire low, acute, with a slightly convex profile, whorls weakly convex, suture impressed; body whorl obesely cylindrical, tapering slightly anteriorly, aperture narrow, outer lip thickened, denticulate on its inner surface, curving upward toward its posterior point of contact with the body whorl, columella straight and smooth, siphonal canal short, straight; sculpture of weak spiral grooves and microscopic axial growth lines; color mahogany brown with irregular blotches of white and a white spire tip; protoconch of 2 full, opaque-white volutions. Each radular row has a flat subrectangular rachidian tooth flanked on each side by an elongate, sigmoid, distally bicuspid lateral tooth (Figure *33*).

Remarks: The features used to distinguish *Conella ovulata* from *C. ovuloides* may be found in the section on *C. ovuloides*. Additional distinctions may be discovered when the radular dentition of both species is known.

The earliest fossil record of the genus is *Meta perplexabilis* Maury, 1917, which appears to more nearly resemble *Conella ovuloides* than *C. ovulata*. No other direct progenitor of either species is known to me.

Range: *Conella ovulata* has a Caribbean distribution and ranges on the north to the Bahama Islands in the east and to British Honduras in the west. The southern end of its range is Barbados Island.

Conella ovuloides (C. B. Adams, 1850)

(Figure *10*)

Columbella ovuloides C. B. Adams, 1850a. Contrib. to Conch. **1** (4): 53 - 54 (Jamaica; lectotype MCZ 177372)

Columbella (Conoidea) ovuloides C. B. Adams, Tryon, 1883. Man. Conch. **5** (*Columbella*): 181; plt. 59, fig. 58

Shell moderately large (12 - 18mm), biconic; spire moderately high, acute, spire profile concave, whorls convex, suture impressed. Body whorl cylindrical, tapering anteriorly, aperture narrow, outer lip moderately thickened, denticulate on its inner surface, curving upward at its posterior point of contact with the body whorl, columella straight, smooth siphonal canal short, straight; sculpture of weak spiral grooves and microscopic axial growth lines; color orange-brown with irregular blotches of white and a white spire tip; protoconch of one full opaque-white volution. The radula of *Conella ovuloides* has not been seen.

Remarks: The close resemblance of *Conella ovuloides* to *C. ovulata*, here considered to be based on characters of generic value, has led to frequent synonymy of the 2 species. Pending the examination of the radulae of both species, the following distinctions may be made on the basis of shell morphology:

Conella ovuloides	*Conella ovulata*
average size smaller (12 to 18mm)	average size larger (14 to 20mm)
form more slender, attenuated	form more rounded, obese
shell moderately strong	shell very heavy and thick
spire moderately high, concave	spire moderately low to low, flatsided to slightly convex

As mentioned under *Conella ovulata, Meta perplexabilis* Maury, 1917 is either conspecific with the present form or is its direct fossil progenitor. The only other reference to the ancestry of this species is the report (Brown & Pilsbry, 1913) of *C. ovuloides* from the Pleistocene of Panamá.

Range: As with its congener, *Conella ovulata,* the distribution of *C. ovuloides* is of the Caribbean type, ranging north to the southern Bahama Islands in the east and to Yucatán in the west; and south to Curaçao. Its pattern of distribution differs, in the Greater Antilles, from that of *C. ovulata*. According to the data I have seen, the present species is present on Hispaniola and not on Puerto Rico, whereas its congener is apparently absent from Hispaniola and is present on Puerto Rico.

Cosmioconcha Dall, 1913

Amphissa (Cosmioconcha) Dall, 1913. Proc. U. S. Nat. Mus. 45 (2002): 589 (type species by O. D., *Buccinum modestum* Powys, 1835; see Figure *11*)

Shell buccinoid, small to moderately large (7 - 30mm); spire high, acute, whorls moderately convex; body whorl about ½ total shell length, aperture widely open, siphonal canal short, straight; sculpture variable. Several species have axial ribs, some only fine striae, and a few are almost entirely lacking in sculpture. Most species have a deep subsutural spiral groove. Color pattern of spiral bands of brown or orange flammules on a white, sometimes glossy background. Each radular row consists of a flat, rectangular median tooth flanked on each side by a single sigmoid, bicuspid lateral tooth. The laterals are somewhat longer and less strongly flexed than those of *Anachis* and *Mitrella* (Figure *37*).

Remarks: Previously thought to be represented only in the Panamic province of the eastern Pacific, this genus includes 2 western Atlantic species, *"Fusus" nitens* C. B. Adams, 1850b and *"Anachis" calliglypta* Dall & Simpson, 1901.

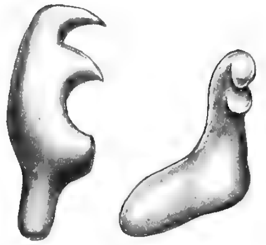
Dall originally described *Cosmioconcha* as a subgenus of *Amphissa* and suggested that on the Pacific coast of America the former supplants the latter in progress toward the tropics. Although there is certainly a close relationship between these 2 groups, they appear to have diverged sufficiently from each other to merit full generic separation.

Cosmioconcha seems to have followed the same pattern of evolutionary radiation as that of other Pacific genera. In genera with representatives in both the Caribbean and the Panamic regions, the Pacific species are generally more numerous, more diverse in form, and on the average larger.

Explanation of Figures *30* to *36*

Radular Dentition

Figure *30*: *Aesopus metcalfei* (Reeve, 1860)
Figure *31*: *Aesopus stearnsi* (Tryon, 1883)
Figure *32*: *Columbellopsis nycteis* (Duclos, 1846)
Figure *33*: *Conella ovulata* (Lamarck, 1822)
Figure *34*: *Decipifus sixaolus* Olsson & McGinty, 1958
Figure *35*: *Amphissa columbiana* Dall, 1916
Figure *36*: *Amphissa haliaeeti* (Jeffreys, 1867)



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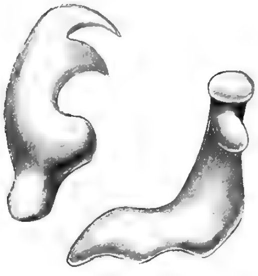

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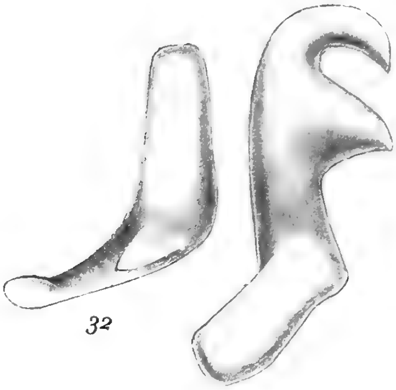

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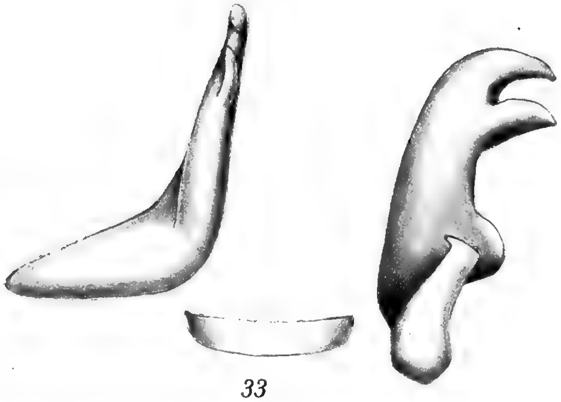

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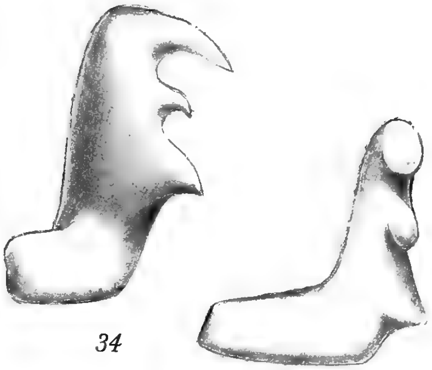

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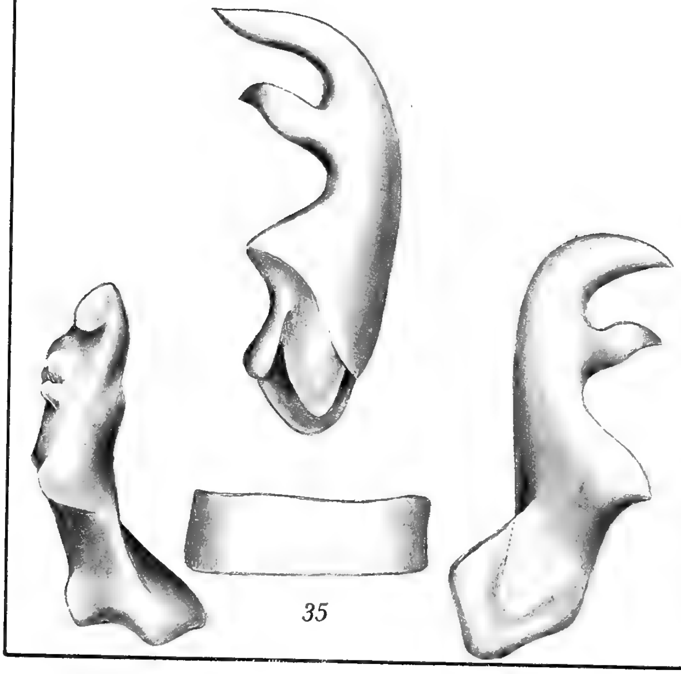

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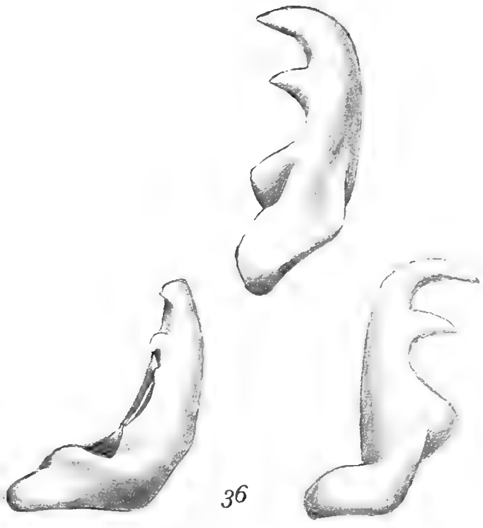

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Cosmioconcha calliglypta (Dall & Simpson, 1901)

(Figure *12*)

Anachis calliglypta Dall & Simpson, 1901. U. S. Fish Comm. Bull. **20** (1): 405; plt. 56, fig. 13 (Aguadilla, Puerto Rico; holotype, USNM 160201)

Shell moderately small (7 - 12 mm); spire high, acute, whorls moderately convex, suture impressed; body whorl sub-cylindrical, aperture moderately wide, apertural lip thickened, denticulate on its inner surface, columella straight, non-denticulate, siphonal canal moderately long, slight anal sinus present; sculpture erratic, predominantly axial, often absent on body whorl. Some specimens have all spire whorls axially ribbed, others lack axial sculpture on various parts of the spire. Color white with a pinkish or yellowish tinge and with spiral bands of brown flammules. The radula of this species has not been seen.

Remarks: This species, whose rarity in collections is probably related to the depth at which it lives (36+m), has been reported, with the exception of the type locality, only from the Gulf of Mexico. The holotype, collected at Aguadilla, Puerto Rico, is an empty, worn shell and, in addition, is a rather stunted individual.

Cosmioconcha calliglypta, with one exception, inhabits deep water in the Gulf of Mexico. No fossil examples of this species are known to me.

Cosmioconcha nitens (C. B. Adams, 1850)

(Figure *13*)

Fusus nitens C. B. Adams, 1850b. Contrib. to Conch. **4**: 60 - 61 (Jamaica; holotype, MCZ 186191, figured by Clench & Turner, 1950, Occas. Papers on Moll., MCZ **1** (15): 316 - 317; plt. 39, fig. 17)

Columbella (Astyris) perpicta Dall & Simpson, 1901. U. S. Fish. Comm. Bull. **20** (1): 316 - 317; plt. 57, fig. 12 (Mayaguez, Puerto Rico; holotype US NM159697)

Mitrella perpicata (Dall & Simpson), Woodring, 1928. Carnegie Inst. Wash. **385**: 275 (error for *M. perpicta*)

Shell moderately large (10 - 14 mm), fusiform; spire high (about ½ total shell-length), acute, whorls convex, suture impressed; body whorl inflated, fusoid, aperture broad, apertural lip thickened, faintly denticulate on its inner surface, columella straight, non-denticulate, siphonal canal short to moderate in length and slightly bent; sculpture lacking except for 1 or 2 faint subsutural spiral grooves, shell surface glossy, color white with 2 spiral rows of brown flammules on the body whorl and 1 row on each of the spire whorls. Each radular row consists of a flat, subrectangular median tooth, flanked on each side by a sigmoid, bicuspid lateral tooth. The laterals are slender and their cusps are short and only slightly bent (Figure *38*).

Remarks: The species in question agrees in color pattern, radular features, sculpture, and apertural form with the Panamic-Pacific genus *Cosmioconcha.* Another western Atlantic species, *Cosmioconcha calliglypta,* differs from *C. nitens* primarily in sculpture and in general habitat.

Range: Although it probably is much more widespread in the Caribbean, this species is known only from off Cuba and Puerto Rico in the east and from off British Honduras in the western Caribbean.

Decipifus Olsson & McGinty, 1958

Decipifus Olsson & McGinty, **1958**: 36 - 37; type species by OD, *Decipifus sixaolus* Olsson & McGinty, 1958

Shell tiny (3 - 5 mm), *Phos*-like; spire high, acute, whorls convex, suture impressed; body whorl cylindrical, moderately large (about ½ total shell length), aperture moderately wide, apertural lip slightly thickened, smooth on its inner surface, columella straight, smooth, siphonal canal very short and slightly bent; sculpture of low narrow axial riblets finely beaded by spiral cords; color chestnut brown, in some instances interspersed with patches of white. Radula minute; each row consists of a subrectangular median tooth flanked on each side by a strongly sigmoid lateral tooth, with 3 sharp distal cusps (Figure *8*).

Remarks: The type species is the only known species of *Decipifus.* Despite the *Phos*-like appearance of its shell, the radula of *D. sixaolus* is unquestionably columbellid.

The shell bears a superficial resemblance to *Zafrona,* but lacks the diagnostic bicuspid columella of species in that genus. The radular dentition of *Decipifus* is pyrenine, rather than columbelline as in *Zafrona.*

Decipifus sixaolus Olsson & McGinty, 1958

(Figure *8*)

Buccinum pulchellum C. B. Adams, 1851. Contrib. to Conch. **8**: 130 - 131, not Blainville, 1829 (Jamaica; holotype, MCZ 186110)

Decipifus sixaolus Olsson & McGinty, 1958. Bull. Amer. Paleo. 39 (177): 36 - 37; plt. 2, figs. 3, 3a (Bocas del Toro, Panamá; holotype, ANSP 211900)

Shell tiny (3 - 5mm) and *Phos*-like; spire moderately high, subacute; body whorl cylindrical, aperture moderately broad, apertural lip slightly thickened, non-denticulate, siphonal canal very short, slight anal groove present; sculpture of weak ribs crossed by more numerous strong spiral cords forming beads at their intersections; color mahogany or chestnut brown, occasionally with white blotches; protoconch of one large depressed whorl. Radula minute; each row consists of a single, flat, subrectangular median tooth flanked on each side by a short, sigmoid lateral tooth. Each of the latter bears 3 sharp cusps, the most proximal of which is strongly down-hooked (Figure 34).

Remarks: No fossil examples of this species are known to me.

Range: *Decipifus sixaolus* is known in the Caribbean from Jamaica and Yucatán, Mexico in the north to Curaçao and Panamá in the south. The seeming rarity of this species and its apparently erratic distribution pattern may be due to its small size and inconspicuous coloration.

Mazatlania Dall, 1900

Euryta H. & A. Adams, 1853. Gen. Rec. Moll. 1: 225, not Gistel, 1848 (no type species designated)

Mazatlania Dall, 1900. Nautilus 14 (4): 44 (new name for *Euryta* H. & A. Adams, 1853, not Gistel, 1848) (type species by OD *Buccinum aciculatum* Lamarck, 1822)

Shell moderately-sized (10 - 15mm) and *Terebra*-like; spire high ($\frac{3}{5}$ of total shell length), acute, whorls slightly convex, suture shallow; body whorl short, broad, aperture moderately wide, apertural lip flaring, thin, non-denticulate within, siphonal canal short, slightly bent, with a noticeable fasciole, columella smooth, slightly bent; sculpture consisting of a major spiral row of spinose nodules near the periphery of the whorl and a minor row immediately posterior to it; color buff with spiral bands of brown and purple suffusions. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid bicuspid lateral tooth. The bases of the laterals are unusually long; each bears a strong hook-like structure which appears to articulate with a depression in the side of the tooth behind it (Figure 39).

Remarks: A truly distinctive genus about whose identity there is little confusion, *Mazatlania* differs from other genera in its overall shell form, its unusual sculpture, its thin, non-denticulate apertural lip, the well developed siphonal fasciole, and the peculiarly developed base of the lateral radular teeth.

There are 2 distinct species of *Mazatlania* in the New World, *M. aciculata* (Lamarck) and *M. fulgurata* (Philippi), both amphi-American.

Mazatlania aciculata (Lamarck, 1822)

(Figure 24)

Buccinum aciculatum Lamarck, 1822. Anim. sans Vert. 7: 274 (type locality here designated as Margarita Island, Venezuela; holotype, GM)

Terebra consentini Philippi, 1826. Enum. Moll. Sicil.: 227; plt. XI, fig. 29 (?Sicily; holotype, ? GM)

Terebra nodosoplicata Dunker, 1853. Zeitschr. f. Malakoz. 10: 110 (type locality not specified, holotype, BM[NH])

Mazatlania hesperia Pilsbry & Lowe, 1932. Proc. Acad. Nat. Sci. Phila. 84: 74; plt. 1, figs. 8, 9 (Cape San Lucas, Baja California, Mexico; holotype, ANSP 156342).

Shell moderately large (14 - 25mm), turreted; spire high, acute, whorls shouldered, convex, suture moderately deep; body whorl short (about $\frac{1}{3}$ total shell length), wide, aperture broad, apertural lip not thickened, non-denticulate on its inner surface, columella short, smooth, straight, siphonal canal short, slightly bent, with a marked siphonal fasciole; sculpture consisting of 2 spiral rows of spinose nodes, the lower one usually stronger; color very variable, usual-

Explanation of Figures 37 to 42

Radular Dentition

Figure 37: *Cosmioconcha modesta* (Powys, 1835)
Figure 38: *Cosmioconcha nitens* (C. B. Adams, 1850)
Figure 39: *Mazatlania aciculata* (Lamarck, 1822)
Figure 40: *Mitrella scripta* (Linnaeus, 1758)
Figure 41: *Mazatlania fulgurata* (Philippi, 1846)
Figure 42: *Mitrella dichroa* (Sowerby, 1844)

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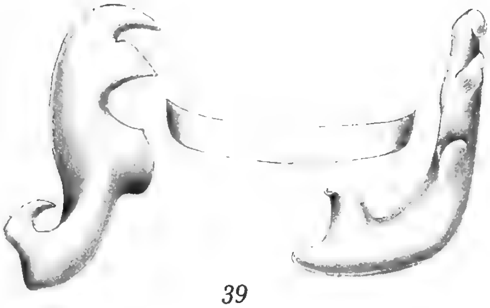

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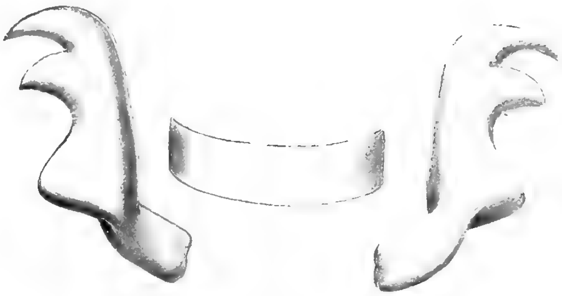

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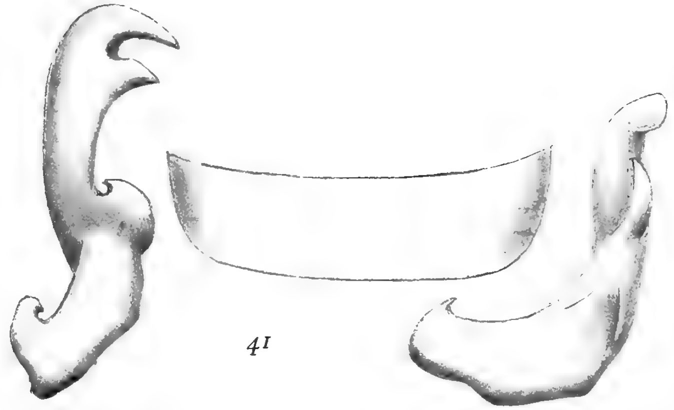

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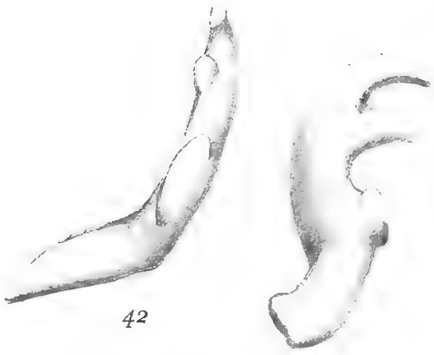

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ly white or yellowish with spiral bands of purple and brown; fine brown flammulations are often present. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid, bicuspid lateral tooth. The laterals are similar to those in *Costoanachis* but the base of each bears a peculiar hook-like process which is unique in *Mazatlania* (Figure 39).

Remarks: This species is very variable with regard to size, strength of sculpture, and color pattern. The presence of *Mazatlania aciculata* as well as *M. fulgurata* in both the Pacific and Atlantic indicates their presence in both prior to the closure of the seaways through Central America. There have been some minor changes in the shell in the 2 isolated populations of *M. aciculata*, but none which would, in my opinion, justify specific distinction.

Mazatlania hesperia Pilsbry & Lowe, 1932 is said to differ somewhat from *M. aciculata* in lacking strong spinose nodes of that species and in having noticeable fine spiral grooves over its entire surface. These distinctions do not appear to be of specific significance.

The earliest appearance of *Mazatlania aciculata* is in the Miocene of Limón, Costa Rica.

Range: Known in both the western Atlantic and the eastern Pacific, this species ranges in the former from southeastern Florida to Venezuela and Limón, Costa Rica, and in the latter from (?) Guadelupe Island and Magdalena Bay, Baja California, Mexico to Zorritos, Peru. Philippi's record from the Mediterranean (as *Terebra consentini*) is based on an apparently adventitious occurrence. The USNM collection also has lots labeled as from the Mediterranean.

Mazatlania fulgurata (Philippi, 1846)

(Figure 25)

Terebra fulgurata Philippi, 1846. Zeitschr. f. Malako. 3: 53 (type locality here designated as Mazatlán, Mexico; holotype, BM[NH])

Terebra arguta Gould, 1853. Proc. Boston Soc. Nat. Hist. 6: 374 (Gulf of California; holotype, MCZ 169044)

Aesopus goforthi Dall, 1912. Nautilus 25 (11): 127 (?Monterey, California; holotype, USNM 249624)

Shell small to moderate in size (8 - 15mm), terebriform; spire high, acute, whorls slightly convex, suture shallow, body whorl short (about ⅓ total shell length), moderately wide, aperture broad, apertural lip not thickened, nondenticulate on its inner surface, columella short, smooth, with a noticeable siphonal fasciole; sculpture consisting of weak axial riblets crossed by submicroscopic spiral grooves; axial elements occasionally entirely lacking; color yellow-white with a faint spiral band of purple-brown and rust-brown axial flammulations. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid bicuspid lateral tooth. As in *Mazatlania aciculata*, the laterals are similar to those of *Anachis*, except that each bears a hook-like process on its base. The hook, however, is neither as large nor as strong as that of *M. aciculata* (Figure 41).

Remarks: As in *Mazatlania aciculata*, the shell in this species is very variable with regard to size, strength of sculpture, and color pattern. Although more commonly collected in the eastern Pacific, populations of *M. fulgurata* occur in scattered localities throughout the Caribbean.

Range: Eastern Pacific – Cape San Lucas and Bahía Bacochibampo to Panamá; western Atlantic – Samaná Bay, Dominican Republic and Vera Cruz, Mexico to Colón, Panamá.

Mitrella Risso, 1826

Mitrella Risso, 1826 Hist. Nat. de l'Europe Mérid.: 247 - 248 (type species by SD [Cox, 1927: 28] *Mitrella flaminea* Risso, 1826 [= *Mitrella scripta* (Linnaeus, 1758)]) (Figure 15)

Mitsella "Risso" Mörch, 1859. Journ. de Conchyl. 7: 257 - 258, 260 (error for *Mitrella*)

Shell small to moderately large (4 - 20mm), fusiform; spire high, acute, whorls flat-sided, suture shallow; body whorl equal to or shorter than spire, aperture moderately broad, apertural lip denticulate, siphonal canal very short to moderately long, columella straight, denticulate; shell surface smooth, color variable with blotches of various shades of brown on a white background. Each radular row consists of a flat, rectangular rachidian tooth flanked on each side by a sigmoid, bicuspid lateral tooth (Figure 40).

Remarks: This genus has long been used as the "dumping ground" of the Columbellidae. All species with smooth or weakly sculptured shells not readily placed in other genera have been assigned to *Mitrella*. Species more properly assigned to *Anachis*, *Astyris*, and *Alia* are frequently placed here. An indication of this tendency may be seen in GRANT & GALE (1931), in which the authors considered *Alia*, *Astyris*, and *Alcira*, 3 quite distinctive genera, to be entirely synonymous with *Mitrella*.

Mitrella dichroa (Sowerby, 1844)

(Figures *16, 17*)

Columbella ocellata d'Orbigny, 1842. Hist. Phys., Polit., et Nat. de l'île de Cuba, Atlas: plt. XII, figs. 34 - 37 (not Gmelin, 1791) (type locality not specified; holotype not located)

Columbella dichroa Sowerby, 1844. Proc. Zool. Soc. London **1844:** 50 (St. Vincent, B. W.I.; representation of lectotype, Sowerby, 1847, Thes. Conch. 1 (10): plt. 40, figs. 168 - 169)

Columbella orphia Duclos, 1846. Illus. Conch. **4:** plt. 15, figs. 1, 2 (type locality not specified; representation of lectotype. Duclos, 1846, plt. 15, figs. 1, 2)

Buccinum parvulum Dunker, 1847. Zeitschr. Malak. **4:** 64 ("Ind. Occid."; holotype not located)

Columbella argus d'Orbigny, 1853. Hist. Phys., Polit., et Nat. de l'île de Cuba: 138 (Guadeloupe, F. W. I.; holotype ?BM[NH])

Columbella schrammi Petit de la Saussaye, 1853. Journ. de Conchyl. **4:** 364; plt.12, figs. 3, 4 (Pointe-à-Pitre, Guadéloupe, F. W. I.; holotype Mus. Rouen)

Nitidella elegans Dall, 1871. Amer. Journ. Conchol. **7** (2): 122 (Panamá – adventitious; holotype, USNM 182582)

Shell small (6 - 9mm); spire high (about $\frac{3}{5}$ total shell length), acute; whorls flat-sided, suture very shallow; body whorl sub-cylindrical, aperture moderately broad, interior of apertural lip denticulate, columella straight, weakly denticulate, siphonal canal short, slightly bent; sculpture entirely absent; color white with chestnut brown longitudinal bars. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid bicuspid lateral tooth with a proximal rounded projection (Figure *42*).

Remarks: Although said by Sowerby to be a part of the Cuming Collection, the type of this species was probably given or sold to a private party prior to the acquisition of the Cuming Collection by the British Museum (Natural History). According to Dr. Norman Tebble, former head of the Mollusca Section, it is not in the British Museum (N H), nor has it ever been catalogued in their collection. Its present whereabouts is unknown.

A table of size range for *Mitrella dichroa* shows a cline with regard to shell length. The specimens from the northern end of its range are small (6.0 - 6.4mm) and exhibit white and brown punctations overlying the typical zebra-striped color pattern. This form has been called *M. parvula* and *M. argus*. Specimens from the southern end of the species' range are appreciably larger (7.0 - 8.0mm) and generally have no overlaid pattern of punctations. This form has been called *M. dichroa*. These color patterns can be shown to intergrade gradually if specimens from localities throughout the geographical range are available.

No fossil examples of this species are known to me.

Range: *Mitrella dichroa* ranges from Palm Beach County, Florida, to the Lesser Antilles and from Vera Cruz, Mexico, to southern Brazil.

Mitrella ocellata (Gmelin, 1791)

(Figure *14*)

Voluta ocellata Gmelin, 1791. Syst. Nat. Ed. **13:** 3455 (type locality here designated as Nassau, New Providence Island, Bahama Islands; representation of lectotype, Martini & Chemnitz, Neues Syst. Conch.-Cab. **4:** plt. 150, fig. 1409)

Buccinum cribrarium Lamarck, 1822. Hist. Nat. Anim. s. Vert. **7:** 274 (type locality, Les mers de Java; holotype, GM)

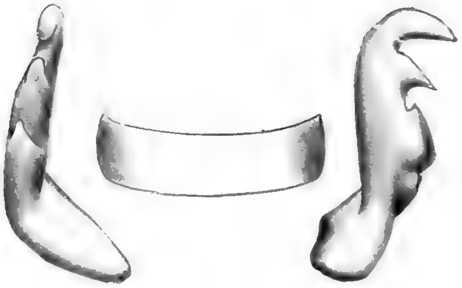
Columbella guttata Sowerby, 1832. Proc. Zool. Soc. London f. **1832:** 118 (type locality, Panamá, Pacific; holotype, BM[NH])

Shell moderate in size (11 - 13mm), fusiform; spire $\frac{3}{5}$ of total shell length, acute when complete (shell is usually decollate), whorls flat-sided, suture shallow; body whorl cylindrical, aperture moderately broad, apertural lip slightly thickened, denticulate on its inner surface, columella straight, smooth, siphonal canal very short, slight anal canal present; sculpture lacking, color usually consisting of white punctations on a black background. Other color variations include a completely yellow-white

Explanation of Figures *43* to *48*

Radular Dentition

Figure *43*: *Mitrella ocellata* (Gmelin, 1791)
Figure *44*: *Suturoglypta albella* (C. B. Adams, 1850)
Figure *45*: *Suturoglypta pretri* (Duclos, 1846)
Figure *46*: *Suturoglypta iontha* (Ravenel, 1861)
Figure *47*: *Strombina pumilio* (Reeve, 1859)
Figure *48*: *Strombina recurva* (Sowerby, 1832)



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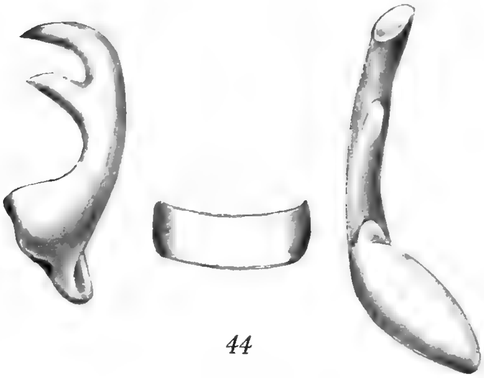

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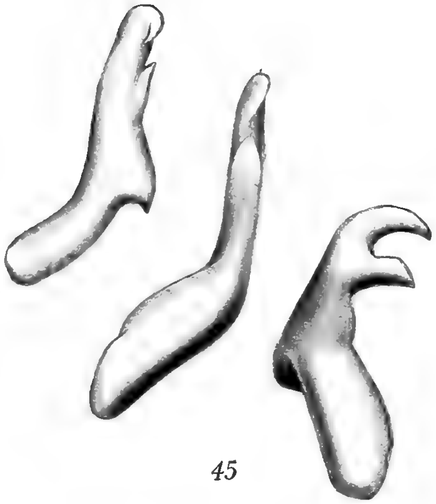

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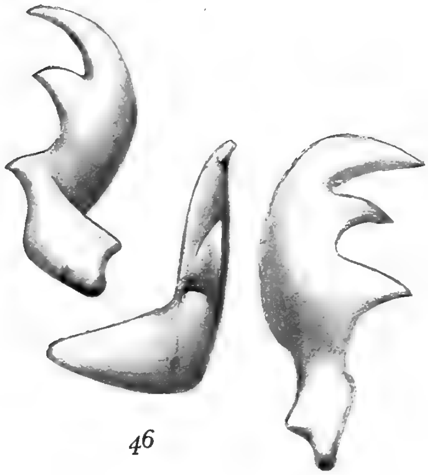

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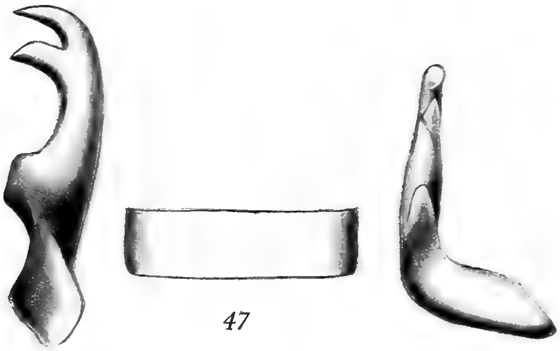

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48

shell and one in which the background is yellow or light brown with darker spots. Each radular row consists of a flat, subrectangular rachidian tooth flanked on each side by a sigmoid, bicuspid lateral tooth (Figure *43*).

Remarks: According to DANCE (1967), the figures referred to by Gmelin were based on specimens in the Spengler Collection and these must be considered the types of Gmelin's species. The specimen from which Gmelin's *Voluta ocellata* was described and upon which the figure, cited by Gmelin, in Martini & Chemnitz was based, is said to be in the Spengler Collection (Copenhagen Museum). Often assigned to *Nitidella*, REHDER (1962) has correctly assigned this species to *Mitrella.* In addition to shell characters, major radular differences exist between *Mitrella ocellata* and *Nitidella nitida*, the type species of *Nitidella*. Most striking is the disparity in the width and degree of flexure of the lateral radular teeth.

The shell of *Mitrella ocellata* is extremely variable with regard to color, color pattern, and overall proportions throughout its very wide geographic range. A slender form occurring in parts of the Panamic-Pacific region is known as *M. delicata* Sowerby, and the dark, stubby form from the coast of East Africa is known as *M. ocellata nomadica* (Melvill). There is also a very dark, stout form from the Galápagos Islands which is known as *Nitidella guttata baileyi* Bartsch & Rehder, 1939. It appears to be quite similar to certain populations of *M. ocellata* on the basis of shell characters but has a markedly different lateral radular tooth and appears to be a completely distinct species.

The only fossil examples of this species are known from the Pleistocene of Venezuela. WOODRING (1928) described a form from the Miocene of Jamaica as *Mitrella ocellata bowdenensis* and noted that it is so similar in shell characteristics to the living form that, perhaps, it should not be separated even subspecifically.

Range: This species, in one or another of its forms, is known from tropical areas almost entirely around the world. In the eastern Pacific it ranges from the central Gulf of California to Panamá and in the western Atlantic it ranges from Palm Beach County, Florida and the north-Bahama Islands to Trinidad and Panamá. In addition, I have seen scattered Museum records from the eastern and western coasts of Africa.

Strombina Mörch, 1852

Strombina Mörch, 1852. Cat. Conch. Yoldi: 85 (type species by SD (COSSMANN, 1901: 241) *Columbella lanceolata* Sowerby, 1832) (see Figure *18*)

Strombocolumbus Cossmann, 1901. Essais Paléoconch. Comp. 4: 241, objective synonym of *Strombina* Mörch, 1852

Shell large (20 - 40mm) and fusiform; spire moderately high, almost ½ total shell length), acute, whorls convex, shouldered, suture impressed; body whorl large, angulate, aperture long, narrow, apertural lip usually thickened with strong denticulate plates on its inner surface, columella bent, often with a strongly denticulate callus, siphonal canal short to moderate in length, bent; sculpture generally consisting of a row of strong axial knobs below the suture which become ephemeral anteriorly; color variable with whites, browns, and purples predominating. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a long, sigmoid lateral tooth similar in shape to those of *Anachis* (see Figure *48* for extrapolation to *Strombina lanceolata*).

Remarks: Considering the wealth of fossil species of this genus in the western Atlantic, the survival of only a single, rarely encountered species suggests that *Strombina* is approaching extinction in that region. Indeed, this genus, once widely distributed, seems to be flourishing today only in the Panamic Province of the eastern Pacific. In this it is not alone. A number of molluscan genera, represented sparsely or not at all in other regions, have undergone remarkable adaptive radiation in this region.

Strombina pumilio (Reeve, 1859)

(Figure *19*)

Columbella pumilio Reeve, 1859. Conch. Icon. **11** (*Columbella*): species 147; plt. 24, fig. 147 (type locality Cumaná, Venezuela; holotype ?BM[NH])

Strombina terquemi Jousseaume, 1876. Mém. Soc. Zool. France **1**: 265 - 266; plt. 5, figs. 1, 2 (type locality East Africa [erroneously]; holotype not located)

Strombina caboblanquensis Weisbord, 1962. Bull. Amer. Paleo. **42** (193): 323 (type locality, Venezuela – Pleistocene; holotype, Paleo. Res. Inst., Ithaca, N. Y.)

Shell moderately large (15 - 20mm), stromboid; spire high, acute, whorls moderately convex, suture impressed, body whorl large (⅗ of total shell length), ventricose, shouldered, aperture long and narrow, apertural lip strongly thickened, bearing a long denticulate plate on its inner surface, columella straight, non-denticulate, with a slight callus, whose raised edge extends along the anterior ⅔ of the aperture, siphonal canal short, bent; shell surface smooth; sculpture of axial riblets ending in round knobs at the shoulder of the body whorl and, in some instances, on the spire whorls, spire rarely with spiral threads; the periostracum is thin, brown, parchment-like. Shell color is chestnut-brown with irregular white blotches. Each radular row consists of a flat, subrectangular rachidian tooth flanked on each side by a sigmoid, bicuspid lateral tooth (Figure *47*).

Remarks: The earliest fossil example of this species is reported from the Pliocene of Venezuela (Weisbord, 1962).

Range: This species ranges from Jamaica to the northern coast of South America.

Suturoglypta Radwin, 1968

> *Anachis (Suturoglypta)* Radwin, 1968. Proc. Biol. Soc. Wash. **81**: 145 (type species by OD, *Colombella pretri* Duclos, 1846) (see Figure *22*)

Shell small (4 - 8mm), fusiform; spire high, whorls flat-sided, suture squarely incised; body whorl moderately small, aperture narrow, constricted anteriorly, apertural lip swollen, denticulate interiorly, columella slightly bent, non-denticulate, siphonal canal moderate to long; sculpture predominantly axial, ribs distinctly raised, almost square in cross-section; color wax yellow to white with pale brown axial flammules and, in one species, entirely translucent red-brown. Each radular row consists of a flat, subrectangular rachidian tooth flanked on each side by a sigmoid bicuspid lateral tooth (Figure *45*).

Remarks: Species in this group show great variability in the number and strength of the axial ribs. The 3 species included here may be distinguished by slight shell differences and consistent radular divergences. The most diagnostic features are the distinctly fusoid shell form, the strong, square-cut axial ribs, and the squarely incised suture.

Suturoglypta albella (C. B. Adams, 1850)

(Figure *21*)

> *Pleurotoma albella* C. B. Adams, 1850a. Contrib. to Conch. 1 (4): 63 (type locality, Jamaica; holotype, MCZ 186006)

Shell small (4 - 6mm); spire moderately high (about $\frac{3}{5}$ of total shell length) and acute, whorls slightly convex, more so toward the body whorl, suture deep, squarely chiseled; body whorl subcylindrical, aperture narrow, apertural lip slightly thickened, denticulate on its inner surface, columella bent, weakly denticulate, siphonal canal moderately long, somewhat bent, distinct anal sinus present; sculpture of square-cut prominent axial ribs with no spiral elements, color pure white, in some instances with rust-brown blotches or even entirely red-brown. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid lateral tooth. Each of the lateral teeth has 2 sharp distal cusps and 1 more rounded proximal lobe (Figure *44*).

Remarks: Assigned originally to the turrid genus *Pleurotoma* by C. B. Adams because of its size and marked anal sinus, this species is the smallest, least common species in *Suturoglypta*. Its distribution is apparently restricted to the Bahama Islands and the Greater Antilles. *Suturoglypta albella* differs from *S. iontha* and *S. pretri* by its smaller size, its more convex spire profile, its geographic distribution, its consistently shorter siphonal canal, and minor radular differences.

No fossil examples of this species are known to me.

Range: This species ranges from the central Bahamas Islands to Grand Cayman Island.

Suturoglypta iontha (Ravenel, 1861)

(Figure *23*)

> *Columbella iontha* Ravenel, 1861. Proc. Acad. Nat. Sci. Phila. 3: 41 - 42 (type locality off Charleston, South Carolina; holotype apparently destroyed)
> *Anachis acuta* Stearns, 1873. Proc. Acad. Nat. Sci. Phila. for **1873**: 344 - 347 (type locality, Tampa Bay, Florida; holotype, USNM 53779)

Shell moderately small (6 - 10mm); spire high ($\frac{3}{4}$ of total shell length), acute, whorls flat-sided; body whorl broad, fusoid, aperture moderately narrow, apertural lip thickened, flaring, denticulate interiorly, columella weakly denticulate, strongly bent, distinct anal sinus present; sculpture consists of strong, square-cut axial ribs, varying in number and spacing; color wax-yellow, in many cases with spiral strokes of chestnut-brown. Each radular row has a flat subrectangular median plate, flanked on each side by a sigmoid, bicuspid lateral tooth (Figure *46*).

Remarks: Although Dance (1967) claims that the Ravenel Collection is in the mollusk collection of the Charleston (South Carolina) Museum, according to Mrs. Amelia Scheltema, who visited the museum in 1965, the collection is not there (A. Scheltema, personal communication). Ravenel's entire collection was apparently moved from Charleston to Atlanta to avoid the Union Army's depredations, only to be burned with the remainder of that city. Apparently, the type of *Suturoglypta iontha* was destroyed at that time.

This species differs from *Suturoglypta pretri*, its closest relative, in having a broader and more foreshortened body whorl, a shorter, more bent, siphonal canal, differing details of axial ribbing, a distinctly more northern geographical distribution, and minor radular distinctions.

No fossil examples of this species are known to me.

Range: This species ranges from off Cape Hatteras, North Carolina to Key West, Florida and to South Padre Island, Texas.

Suturoglypta pretri (Duclos, 1846)

(Figure 22)

Colombella pretrii Duclos, 1846. (*in* Chenu) Illust. Conchyl. **4:** plt. 16, figs. 7, 8 (type locality here designated as Charlotte Amalie Harbor, St. Thomas; representation of lectotype, Duclos, 1846, **4:** plt. 16, figs. 7, 8).

Columbella mangelioides Reeve, 1859. Conch. Icon. **11** (*Columbella*): plt. 31, fig. 197 (type locality, West Indies; holotype, BM[NH])

Anachis samanensis Dall, 1889. Bull. Mus. Comp. Zool. **18:** 188 (type locality, Samaná Bay, Dominican Republic; holotype, USNM 54285)

Columbella pretrei Kobelt, 1897. Martin & Chemn. Conchyl.-Cab. **3-1d:** 252, 319; plt. 34, fig. 4; plt. 41, fig. 7 (error for *C. pretri*)

Shell moderately small (6 - 9mm), spire high (about $\frac{2}{3}$ total shell length), acute, whorls flat-sided, suture squarely incised and moderately deep; body whorl fusoid, aperture moderately narrow, apertural lip thickened, flaring, denticulate within, columella denticulate, bent, covered with a callus, siphonal canal moderately long, bent; anal sinus present. Sculpture of strong, square-cut axial ribs, color wax-yellow with brown spiral markings. Each radular row consists of a flat, subrectangular median tooth flanked on each side by a sigmoid lateral tooth. Each lateral has 2 sharp distal cusps and a rounded proximal lobe (Figure 45).

Remarks: *Suturoglypta pretri*, the type species of the genus, differs from *S. iontha* in having fewer and more broadly spaced axial ribs, a less inflated body whorl, less bent siphonal canal, a smaller apical angle, and a less thickened apertural lip. There are also minor radular differences. *Suturoglypta pretri* differs from *S. albella* in its consistently larger size, higher, more acute spire, flatter spire profile, and greater length and degree of curvature of its siphonal canal.

Populations of this species from the western end of Cuba and from Yucatan are very variable with regard to sculpture. Lots have been examined in which sculpture ranged from typical, strong, square-cut axial ribbing to weak, sinuous axial ribs to an almost complete absence of sculpture with complete intergradation between these forms.

The earliest fossils of this species have been reported from the Pleistocene of Panamá.

Range: This species ranges from southeastern Florida and eastern Mexico to Barbados and Curaçao.

OTHER REPORTED WESTERN ATLANTIC SPECIES

Several other columbellid species have been described from the Magellanic province of South America. Efforts to obtain specimens of these species have been almost entirely unsuccessful. The most extensive report on the mollusks of this area was made by Strebel (1905) in which 3 columbellid species were originally described and figured. These are the earlier treated *Parvanachis melvillei* (Figure 29), *P. paessleri* (Figure 28), and *P. decorata* (including the subspecies *P. decorata inornata* (Figure 27)). The first 2 species were mistakenly placed in the subgenus *Seminella* Pease. Another species, *Columbella rubra* Martens, 1881 (Figure 26), also inhabits the Magellanic province. Although no specimens were available for examination, the figure of this species accompanying the original description by Strebel suggests an affinity with the genus *Mitrella* Risso.

The adventitious occurrence of gastropod shells is no novelty in the history of malacology. During the period of history when the wooden sailing vessel was the sole form of transoceanic transportation, ship-bottom ballast in the form of beach sand and rocks was often necessary. Other material, such as beach-drifted shells, was often included and the entire load of ballast was then unloaded at another port of call where the vessel replaced the ballast with cargo.

Such a ballast origin may be suspected in the case of 2 supposedly western Atlantic species. The most obvious instance concerns *Anachis terpsichore* Sowerby, 1824. The type locality is western Atlantic and a number of worn shell specimens from several West Indian localities are in the collection of the Division of Mollusks, National Museum of Natural History. In none of these cases were the specimens collected alive. A large number of live-collected and freshly dead specimens from the east coast of India has been examined. This appears to be the true habitat of the species. A number of spurious Caribbean records of *A. terpsichore* has also been based on misidentification of *A. lyrata* Sowerby, 1833, another large species of *Anachis* that superficially resembles *A. terpsichore.* It differs from the latter species in having more regular spiral brown color bands and more convex whorls; those of *A. terpsichore* are flat at the periphery. *Anachis lyrata* occurs along the Pacific coast of Central and South America and on the Atlantic coast of Brazil. In addition, a few worn, empty shells have been collected in the Caribbean. These may also be examples of adventitious distribution.

Several empty shells of *Costoanachis varia*, a large species found throughout most of the Panamic province, have been collected at a single locality (Wounta Haulover, Nicaragua) on the Caribbean coast of Central America. An apparently close relative of *C. varia*, *C. asphaltoda* Maury, was common in Trinidad and elsewhere in the Caribbean during the Pliocene, but there is no clear indication that *C. varia* or *C. asphaltoda* occurs today in the Caribbean. The shells from the above locality are moderately fresh and may have been carried across the narrow part of Nicaragua by traders or other travelers, or they may be additional ballast-shell records. Until this species is found living in the Caribbean, its status as a bona fide western Atlantic species will remain doubtful.

The fate of the type specimens of the species described by Edmund Ravenel provides an ironic commentary on the Civil War period. SHERBORN (1940) located the above types at the Charleston Museum of Natural History. Authorities of the CNHM have been unable to locate this collection. As accurately as can be determined, during the Civil War the Ravenel collection, including the types, was moved from Charleston to protect it from Union troops then thought to be threatening the city. The collection was apparently moved to Atlanta, Georgia, shortly before Sherman's troops burned that city. This circumstance does not present a major difficulty in most cases. In one case, however, Ravenel's description is so unclear, ambiguous, and generally inadequate that there is doubt as to the species' identity. This is *Columbella similis* Ravenel, 1861. There are 2 apparently undescribed *Costoanachis* species or subspecies on the Atlantic and Gulf coasts of the United States. One is probably an unusual form of *C. avara* and the other may be the *C. similis* of Ravenel. It is unfortunate that with no extant type, an inadequate description, and no published figure, the assignment of this name to any biological entity is impossible.

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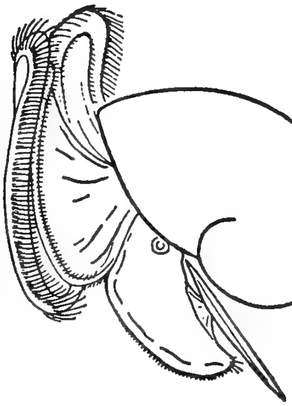
Editor's Note: This is the second time in 20 years of publishing The Veliger that an author died before proofs could be submitted to him. Responsibility for proof reading was shared in the present instance by Mr. Anthony D'Attilio, a former co-worker of Dr. Radwin, and an unnamed volunteer worker at the San Diego Museum of Natural History; Mrs. Jean M. Cate; Mrs. R. Stohler, and the editor. Any typographical errors remaining are the sole responsibility of the editor. Factual errors or errors of judgment and interpretation, if any, are the responsibility of the late Dr. George E. Radwin as is the credit for the work completed.



Two New Giant Epitoniids

(Mollusca : Gastropoda)

from West Africa

BY

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(1 Plate; 1 Text figure)

IN 1971, TWO SPECIES of Epitoniids of large size were found washed ashore after a storm near Rufisque (Senegal). One of them is identical with a gastropod trawled in 1964 off Pointe-Noire, Congo, in 300m and accessioned by MNHN in 1969. The second species has subsequently been found by various persons in West Africa. Surprisingly enough, the 2 species, both longer than 50mm, appear to be undescribed. They are to be added to the list of species described in recent years from the coast of Senegal (BOUCHET, 1975; ROSSO, 1976, 1977; BOUCHET & NICKLES, 1976) and show how little we know about even the larger species inhabiting the Senegalese shelf.

We shall first describe the species and then present a short synopsis of the family EPITONIIDAE in West Africa.

Amaea africana Bouchet & Tillier, spec. nov.

(Figures *1*, *2*, *6*, *7*, 8)

Type Material: Holotype (shell only) in MNHN (Kergroach coll., Lozet leg.).

Type Locality: Coastline near Rufisque, Senegal.

Material Examined: One adult shell, Bay of Gorée, Sénégal, MNHN (Marche-Marchad, coll.); one juvenile shell, Cavally, Ivory Coast, 50 - 55m, MNHN (Rancurel and Marchal, coll.); one adult shell from Senegal, without precise data, MNHN (Lozet leg.); 4 shells, off Grand Bassam, Ivory Coast, MNHN and IFAN (Le Loeuff, coll.); east of Sassandra, Ivory Coast, 56m, 1 shell; Grand Bereby, Ivory Coast, 56m, 1 live-taken specimen; south of Cavally River, Ivory Coast, 44m, 1 live-taken specimen: all MNHN (Le Loeuff leg.); 1 adult shell, Dakar area, coll. M. Pin.

Description: Holotype: shell slender, rather thin, fragile, composed of 13 whorls (the larval shell and about 1.5 postlarval whorls lacking); colour brownish orange with a narrow whitish subsutural band; columellar zone thickened, white; no umbilicus.

The sculpture is cancellate, composed of axial and spiral lines. On the "first" (see supra) postlarval whorl, there is a single, sharp, spiral cord forming a sort of keel visible down to the 5th whorl. On the second whorl 2 spiral lines appear under the keel; at the beginning of the 4th whorl a 3rd one appears under these 2, together with 2 other spiral lines above the keel. Along the 4th whorl, secondary spiral lines appear above and between the main lines. The number of lines increases in the following whorls: on the body-whorl a dozen main spiral lines can be counted, with 3 to 10 secondary ones between 2 adjacent main lines. The axial sculpture is formed by thin lamellae crossing over the spiral sculpture; these lamellae are straight and are bent only frontwards in the subsutural zone. On the body-whorl they show a tendency to merge together and we count 65 of them. The growth lines are hardly visible.

The basal disc is lined by a rather strong spiral cord; below this, the numerous spiral threads are thin and more regular than above.

Dimensions of the Shell: Height, 48mm, diameter, 18 mm.

Other Specimens: The juvenile shell also lacks the apex but probably only the protoconch has fallen off; this shell has 1.5 more upper whorls than the holotype. The keel is present up to the top; the mode of formation of the spiral sculpture is the same as in the holotype. All other specimens correspond well with the holotype with slight variation in colour and number and breadth of the spiral threads of the last whorls. At a diameter similar to that of the body-whorl of the holotype, the axial lamella-number varies from 50 to about 80.

The longest shell (M. Pin, coll.) is 55 mm high, with a diameter of 21 mm and 11.5 whorls (first whorls missing).

Radula: 53 × (46 - 50) · o · o · o · (46 - 50): Figure 8; operculum illustrated in Figure 7.

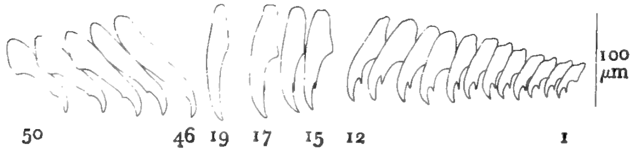


Figure 8

Amaea africana Bouchet & Tillier, spec. nov.

Half-row of the radula of a specimen from Grand Bereby, Ivory Coast, 56 m

Remarks: There is no doubt that this is the species figured by Caricati (1975: 235; plt. 4, figs. 1 - 2) as *Amaea* cf. *mitchelli* (Dall); Caricati mentioned West Africa only as the probable origin. Indeed, *A. africana* is not closely similar to any other West African species and is closer to *A. mitchelli* Dall, 1896 than to any other. We have compared *A. africana* with the plates of Clench & Turner (1950: plt. 106, figs. 5 - 7), Andrews (1971: 84), and with actual specimens of *A. mitchelli* from the coast of Texas, including the type (USNM 465611). The American species is more solid and has a coarser sculpture; it is white with a median brown band and with a similar band below the basal keel. *Amaea africana* also comes near *A. brunneopicta* (Dall, 1896) from the Panamic Province, but the latter is more slender and thinner.

We do not know any fossil from Europe to which it can be compared, but a few American fossils could be considered ancestors of the *africana-mitchelli-brunneopicta* group of species:

– *Epitonium eleutherium* Pilsbry & Olsson, 1941, from the Pliocene of Ecuador is very close to *Amaea brunneopicta*;

– *Ferminoscala pseudoleroyi* (Maury, 1925), from the Miocene of Jamaica, as illustrated by Woodring (1928: 402; plt. 32, figs. 3 - 4; ?= *Scalina gardnerae* Olsson, 1967: Miocene of Florida) differs by its slenderness and stronger spiral sculpture.

Amaea guineense Bouchet & Tillier, spec. nov.

(Figures 3, 4, 5)

Type Material: Holotype and one paratype (shells only) in MNHN (Kergroach coll., Lozet leg.).

Type Locality: Coastline near Rufisque, Senegal.

Material Examined: One shell, off Pointe-Noire, Congo, 300 m (Crosnier, Orstom leg.).

Description: Holotype: shell slender, solid, of a uniform creamy colour. There are 8 whorls, but the protoconch and several postlarval whorls have been broken off at a diameter of 5 mm. The whorls are twice as broad as high and the suture is deep. The columella is remarkably thickened for an *Amaea*. There is no umbilicus.

The sculpture is cancellate, composed of axial and spiral lines. The spiral sculpture is formed by 9 main threads, visible from the first postlarval whorl still present. From the 3rd preserved whorl, secondary threads appear between them: their number (1 to 3 between 2 adjacent main spiral threads) and importance are not constant. In the subsutural zone, there are 4 to 6 secondary spiral threads; they are oblique and cannot be followed from one side of any axial lamella to the other. The axial lamellae are developed to roughly the same degree as the main spiral threads and they deviate a little backwards when they cross over the latter. Near the upper

Explanation of Figures 1 to 7

Amaea africana Bouchet & Tillier, spec. nov.

Figure 1: Holotype, ventral view; length 48 mm; diameter 18 mm

Figure 2: Juvenile specimen, Cavally, Ivory Coast; ventral view; length 10 mm; diameter 4 mm

Figure 6: Holotype, view of the basal disc; diameter 18 mm

Figure 7: Operculum of a specimen from south of Cavally River, Ivory Coast, 44 m

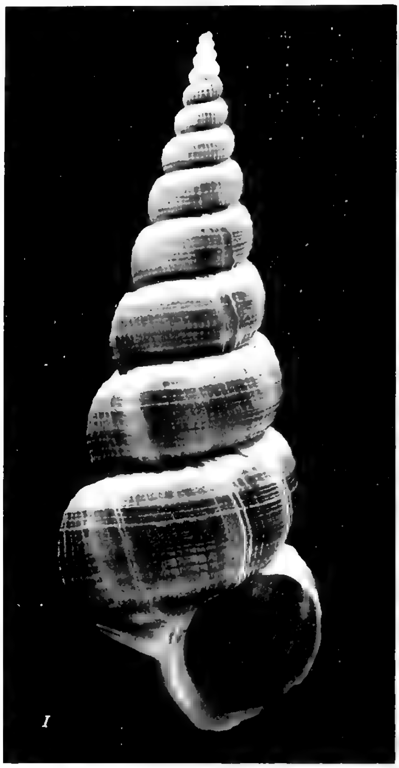
Amaea guineense Bouchet & Tillier, spec. nov.

Figure 3: Paratype, ventral view; length 39.5 mm; diameter 15.5 mm

Figure 4: Holotype, ventral view; length 64 mm; diameter 26 mm

Figure 5: Paratype, view of the basal disc; diameter 15.5 mm

(Photographs by A. Foubert)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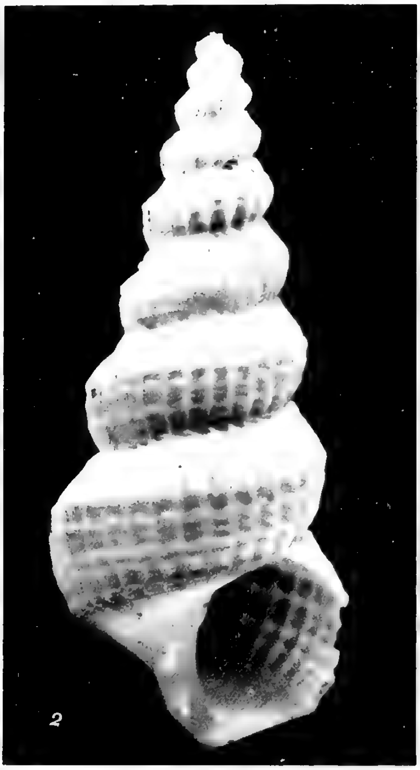
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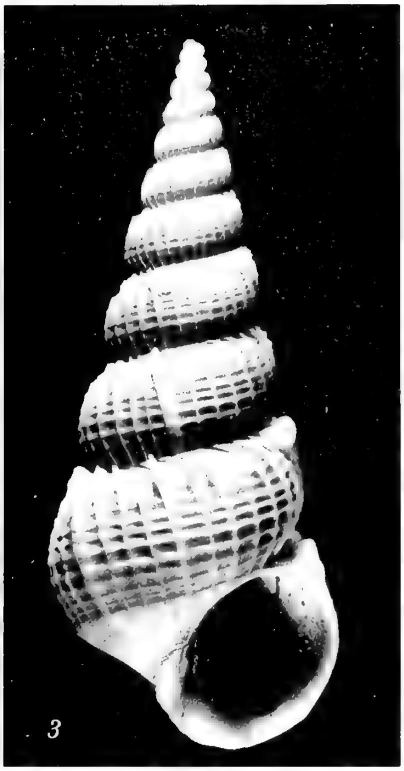
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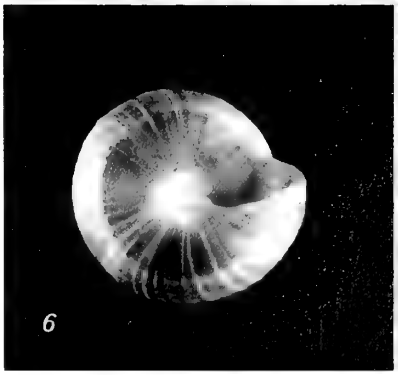
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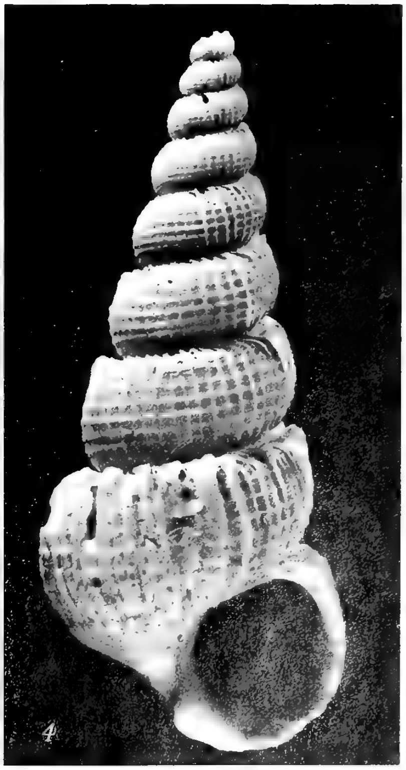
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suture they bend frontwards and show a winglike projection; the lamellae of 2 consecutive whorls do not join. As we approach the peristome the lamellae grow thicker and several of them may join to form varices: this is why the outer lip looks so thick. Because of these varices, the number of lamellae on the body-whorl is from 61 along the basal keel to 50 in the subsutural zone. From the 3rd whorl onwards, thin growth lines can be seen between the lamellae: there is a clear intersection with the secondary spiral threads, not with the main ones.

The basal disc is sculptured by many spiral threads, axial lamellae and growth lines.

Dimensions of the Shell: Height, 64 mm; diameter, 26 mm.

Other Specimens: The specimen from Congo is a 61 mm broken shell, on which a sea-anemone has grown. From the holotype, it differs mainly by showing a greater tendency to form varices so that only 30 axial lamellae can be counted on the body-whorl.

The paratype is a younger shell with the protoconch and at most 1 postlarval whorl broken. The 9 main spiral threads are present at the very top; secondary ones appear in the subsutural zone on the 4th whorl and between the main threads on the 5th whorl. The upper whorls are regularly convex in outline.

Remarks: We do not know any Atlantic species close to *Amaea guineense*; only the Panamic species *A. tehuanarum* DuShane & McLean, 1968 is similar but it has keeled upper whorls and as a result has a different pattern in sequence of appearance of spiral lines.

Apparently, there is no fossil in the American Cenozoic, but several in Europe which might be considered ancestors:

– *Amaea subreticula* (d'Orbigny, 1852), from the middle and upper Miocene, does not show any growth lines between axial lamellae (after the description of Glibert, 1952: 44); it has lower whorls and the main spiral threads are fewer.

– *Amaea pellati* (de Raincourt & Munier-Chalmas, 1863), from the Biarritz Oligocene (= *Acrilla amoena* var. *eosubcancellata* Sacco: see Boussac, 1911: 83) is closer to *A. subreticula* than to *A. guineense.*

– *Amaea phoenix* (de Boury, 1912) from the lower Miocene of Dax and Corsica has a rather similar sculpture, but is more slender and has a more oblique suture.

– *Amaea elegantissima* (Deshayes, 1861) from the Grignon Lutetian is also close to *A. phoenix* and *A. guineense,* but can be separated by a sculpture with fewer axial lamellae.

Amaea guineense then appears to be the living form of a lineage starting in the Paris Eocene, through the Miocene of southern France to present-day Gulf of Guinea. Unfortunately, we have too little information on the upper Cenozoic of northwestern Africa to be able to identify additional elements of this lineage.

The family Epitoniidae in West Africa

Over 20 Epitoniids have already been mentioned from tropical West Africa; however, many are known only from the original description and we have no idea on the distribution of most species. Also their biology is virtually unknown as far as feeding and larval development are concerned. To be added to the species already described, we have seen several undescribed ones, especially in the de Boury Collection and among recently collected material: when the family is better known, there will probably be more than 40 species from the shelf of tropical West Africa. It should also be remembered that the fauna of the slope is almost completely unknown.

LIST OF THE WEST AFRICAN SPECIES

Opalia crenata (Linnaeus, 1758): a Mediterranean species known from Mossamédès (Dautzenberg, 1913) and Sao Thomé (Tomlin & Shackleford, 1914)
Opalia gaini (deBoury in Lamy, 1923) from the Bissagos archipelago and Gaboon;
Opalia hellenica (Forbes, 1844)
Epitonium pulchellum (Bivona, 1832)
Epitonium grossicostatum (Nyst, 1873)
Epitonium candidissimum (Monterosato, 1877)
Amaea smithi (Watson, 1897 *non* Tryon, 1887)
– all mentioned from Sao Thomé by Tomlin & Shackleford (1914) together with
Epitonium commutatum (Monterosato, 1877), occurring from the Mediterranean to Angola (Lamy, 1907; 1908; Nobre, 1909; Hidalgo, 1910; Dautzenberg, 1913).

Two manuscript names, credited to de Boury, have been published by Tomlin & Shackleford (1914): *Epitonium atlanticum* and *E. tenuipunctatum.* These specimens are present in the de Boury collection but are apparently *nomina nuda.*

Smith (1871) has described 2 new species from Whydah (or Ouidah), Dahomey:
Scala miranda Smith, 1871, changed to *Scalaria smithii* by Tryon (1887) because he considered it to be preoccupied by *Crossea miranda* A. Adams;
Scala bairdi Smith, 1871.

In 1890, the same author mentioned 7 more species from Saint Helena, 5 of them being new:
Scalaria confusa Smith, 1890
Scalaria mellisii Smith, 1890
Scalaria sanctaehelenae Smith, 1890
Scalaria atomus Smith, 1890
Scalaria commoda Smith, 1890
Scalaria fragilis Hanley, 1842

Scalaria cf. multistriata Say, 1825,
the 2 last mentioned being already known from the West Indies. Other species:
Scalaria pachygyra Locard, 1896, dredged by the "*Travailleur*" in the Cape Verde Islands in 100 - 318m;
Scalaria cochlea Sowerby, 1844 from the coasts of Angola (Sowerby, 1847; Dunker, 1853);
Scalaria fusca Sowerby, 1844, from Sierra Leone (Sowerby, 1847);
Epitonium tenuicostatum von Martens, 1882, dredged by the "*Gazelle*" in Cape Verde Islands.

Finally, the following 3 species have been described from Gorée, Senegal, but never illustrated, by von Maltzan, (1885).
Scalaria boettgeri von Maltzan, 1885
Scalaria trochiformis von Maltzan, 1885
Scalaria senegalensis von Maltzan, 1885.

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Clonal Variation in the Parthenogenetic Snail *Campeloma decisa* (Viviparidae)

BY

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INTRODUCTION

Recent studies of clonal diversity in parthenogenetic animals, as revealed by electrophoretic analysis of allozymic variation, have contributed to an understanding of processes involved in the evolution of non-Mendelian genetic systems (review in Lokki, 1976; Parker & Selander, 1976; Parker *et al.*, 1977). We here report on clonal diversity and genic heterozygosity in several populations of the parthenogenetic aquatic snail *Campeloma decisa* (Say, 1822) in central New York.

MATERIALS AND METHODS

Samples of *Campeloma* were collected by hand or by baiting with meat (Allison, 1942) at 5 localities in New York: Song Lake, near Syracuse, Onondaga County; west side of Jamesville Reservoir at Craner Oil Depot, Jamesville, Onondaga County; north end of Honeoye Lake, Livingston County; Delaware River at Walton, Delaware County; and Dryden Lake, near spillway east of Dryden, Tompkins County. Individual snails were processed for electrophoresis according to the techniques of Selander & Hudson (1976). Allozymic variation at 13 enzyme systems encoded by 21 structural gene loci was assayed by horizontal starch-gel electrophoresis (techniques described by Selander *et al.*, 1971). The following enzyme loci were scored: 3 leucyl-alanine peptidases (*Pep-1, -2, -3*), 2 leucine aminopeptidases (*Lap-1, -2*), 2 esterases (*Est-1, -2*), 2 phosphoglucomutases (*Pgm-1, -2*), phosphoglucose isomerase (*Pgi*), mannose phosphate isomerase (*Mpi*), *β*-glucuronidase (*β-Glu*), 2 superoxide dismutases (*Sod -1, -2*), α-glycerophosphate dehydrogenase (*α-Gpd*), glucose-6-phosphate dehydrogenase (*G6pd*), 2 malate dehydrogenases (*Mdh-1, -2*), 2 isocitrate dehydrogenases (*Idh-1, -2*), and 6-phosphogluconate dehydrogenase (*6-Pgd*). Electromorphs (corresponding to allelic variants) at variable loci were numbered according to their relative mobility, the most common being designated *100* in all cases. Average individual heterozygosity (*H*) was determined by direct count of heterozgotes.

RESULTS AND DISCUSSION

Nine of the 21 loci assayed were polymorphic in the 5 samples of *Campeloma* examined (Table 1). Two clones

Table 1

Genetic diversity in clones of *Campeloma decisa*

Locus[1]	Genotype Clone I[2]	 Clone II[3]
Pep-2	100/100	100/95
Lap-1	100/100	100/90
Lap-2	null	100/100
Est-1	100/100	100/90
Pgm-1	110/100	100/100
Pgm-2	100/100	110/100
Sod-1	100/100	105/100
α-Gpd	100/100	100/90
Idh-1	100/90	110/100

[1] The following loci were monomorphic for the same allele in both clones: *Pep-1, Pep-3, Est-2, Pgi, Mpi, β-Glu, Sod-2, G6pd, Mdh-1, Mdh-2, Idh-2,* and *6-Pgd.*

[2] Clone I: Song Lake, N = 30 specimens; Walton, N = 11; Dryden Lake, N = 38.

[3] Clone II: Jamesville Reservoir, N = 30; Honeoye Lake, N = 1.

(designated I and II) can be distinguished, and these differ at each of the 9 variable loci. The nature of the difference is such that only at one locus (*Lap-2*) do the clones not share an allele. The clones are monomorphic and indistinguishable at the remaining 12 loci. Thus, the clones differ genotypically at 43% of the loci examined, but share alleles at 95% of the loci.

The clones differ in level of individual heterozygosity, with Clone I having 2 of 21 loci fixed in heterozygous condition ($H = 9.5\%$), and Clone II having 7 of 21 loci fixed as heterozygotes ($H = 33.3\%$). The occurrence of fixed heterozygosity in one or both clones at 9 loci strongly suggests that *Campeloma decisa* has an apomictic system of egg maturation in which recombination does not occur (UZZELL, 1970; NUR, 1971), since, in the absence of heterotic selection, recombination in parthenogenetic lineages should lead to homozygosity (ASHER, 1970). MATTOX's (1937) cytological work on the related parthenogenetic form *C. rufum* was interpreted by SUOMALAINEN (1950) as evidence that oögenesis is apomictic.

Without knowledge of the nature and extent of genetic diversity in the bisexual populations of *Campeloma* from which the parthenogens were derived, we can only speculate on the mode of origin of the clones. Because heterozygosity (and clonal diversity) is expected to increase in apomictic parthenogenetic lineages as a consequence of the accumulation of mutations (WHITE, 1973; LOKKI, 1976), it might be suggested that Clone II is older than Clone I. However, an alternative hypothesis is that the clones are equivalent in age but were derived from sexual individuals (belonging to the same or different populations) differing markedly in heterozygosity. A third possibility, which we regard as the least likely, is that the clones diverged genetically following the origin of a single parthenogenetic lineage from an individual of an ancestral sexual population.

Parthenogenetic forms of *Campeloma* apparently are confined to northeastern and north-central North America, while sexual species occur south of a line from Kentucky to Illinois (MATTOX, 1938; POLLISTER & POLLISTER, 1940; HUBRICHT, 1943; VAN DER SCHALIE, 1965; ANDERSON, 1966). This pattern of distribution suggests the possibility that the parthenogens evolved and colonized northern areas at the time of recession of the last Pleistocene glacier. A similar interpretation has been advanced by SUOMALAINEN (1962) to account for patterns of distribution of parthenogenetic insects in Europe.

Our findings for *Campeloma* are consistent with the results of previous work demonstrating that parthenogenetic "species" generally are clonally diverse (SUOMALAINEN & SAURA, 1973; LOKKI *et al.*, 1975; PARKER & SELANDER, 1976; PARKER *et al.*, 1977). Each of the 4 populations for which we have reasonably adequate samples apparently consists of individuals belonging to one clone. Because populations of *Campeloma* are widely spaced and isolated in central New York, migration probably is infrequent, and colonization normally may involve the transport of only one or a few individuals. Hence, the uniclonal composition of populations may merely reflect the founder effect. However, the possibility that interclonal competition is involved should also be considered. For a number of parthenogenetic "species" and strongly selfing species, studies already reported or currently in progress in our laboratory suggest that local areas are inhabited by a small number of clones or strains that are genetically very divergent and differ in habitat distribution. For example, populations of the self-fertilizing land snail *Rumina decollata* in southern France are composed of 2 strains differing at 50% of their loci and showing "preferences" for relatively xeric or humid microhabitats (SELANDER & HUDSON, 1976). Clones of the parthenogentic aquatic snail *Potamopyrgus jenkinsi* (WARWICK, 1952; WINTERBOURN, 1970) differ at about half their loci (SELANDER & JONES, in preparation). Similarly, many populations of the parthenogenetic earthworm *Octolasion tyrtaeum* in central New York consist of 2 clones differing at 40% of their loci (JOHN JAENIKE, in preparation). This pattern suggests that limiting similarity (MACARTHUR & LEVINS, 1967; MAY & MACARTHUR, 1972) is involved in determining the extent of interclonal and interstrain diversity in local populations of parthenogenetic and selfing organisms. Our findings for *Campeloma* are consistent with the genetic aspect of this hypothesis, but the number of populations sampled is too small to provide evidence regarding possible clonal differences in habitat utilization. The hypothesis that clones or selfing strains can coexist only if they are rather divergent in genetically-determined adaptive traits related to differential niche utilization (or if they are minimally distinct genetically and, hence, ecologically equivalent or nearly so) is, of course, simply an extension of current theories relating to interspecific competition and resource partitioning. It can be tested through intensive study of the genetic and ecological relationships of parthenogenetic organisms such as *Campeloma*.

SUMMARY

Populations of the parthenogenetic aquatic snail *Campeloma decisa* in central New York consist of one of two clones differing genotypically at 43% of their structural gene loci and sharing alleles at 95% of the loci. The occurrence of fixed heterozygosity at 9 loci in one or both clones suggests a non-recombinational system of egg ma-

turation. Individual heterozygosity was 9.5% in one clone and 33.3% in the other. It is suggested that both the founder effect and ecological limiting similarity potentially are important factors determining the clonal structure of parthenogenetic "species."

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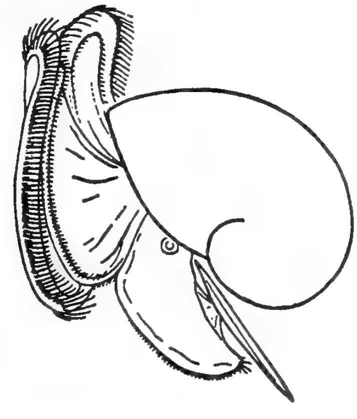

Effects of Cornstarch and Dextrose on Oysters [1]

BY

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INTRODUCTION

THE GROWTH AND FATTENING of the American oyster, *Crassostrea virginica* (Gmelin, 1791), has long been of interest to oyster biologists since the market value of oysters is directly related to the quantity and quality of "meat" obtained per bushel (= 35.2 L) of harvested oysters. Much of the early work done on the growth and fattening of oysters attempted to demonstrate the superior nutritional value of specific planktonic organisms and detritus (MOORE & POPE, 1910; MARTIN, 1923, 1927a, 1927b, 1928; GAVARD, 1927; NELSON, 1947). MITCHELL (1917) was the first to study the effects of carbohydrates of known composition on oysters. He reported that oysters held in standing seawater containing 0.25% glucose had higher glycogen levels than control oysters. YONGE (1928) showed that oysters were capable of removing dissolved carbohydrates from seawater. GILLESPIE, INGLE & HAVENS (1964) demonstrated that oysters receiving only dextrose at 30 mg/L lived an average of 68.2 days longer than starved oysters.

NELSON (1934) was the first to investigate effects of particulate carbohydrates on oysters. Although his report did not present quantitative data, he stated that only cornstarch was "successful." More recent investigators have studied the effects of particulate and dissolved carbohydrates on the glycogen content, tissue weight and shell size of oysters. HAVEN (1965) demonstrated that oysters receiving wheatflour or cornstarch at concentrations of 2 mg/L would, at certain seasons, have dry tissue weights significantly greater than controls receiving only flows of natural river waters. His results of supplemental feeding with dextrose were not definitive, and dextrose concentrations as high as 34 mg/L were required to produce a significant influence on dry tissue weight. These studies were corroborated by GILLESPIE, INGLE & HAVENS (1966). KUWATARI & NISHII (1967) showed that rice powder added to the diet of the pearl oyster resulted in a higher tissue weight. In a more recent study, CASTELL & TRIDER (1974) demonstrated the nutritional value of carbohydrates, lipids and other dietary substances of known composition in the diet of oysters.

Previous authors have suggested that stored glycogen is a major factor influencing the size and quality of oyster tissue and have shown that the level of stored glycogen on a dry weight basis varies seasonally with a minimum of about 3% in late summer and a maximum of about 24% in early spring and late fall (ENGLE, 1950; HOPKINS, MACKIN & MENZEL, 1953). As a consequence of this seasonal change in glycogen, effects of supplements added at various seasons might vary.

There were three purposes to this study. The first was to define the minimum quantity of particulate carbohydrate (in the form of partially hydrolyzed cornstarch) necessary to produce a measurable increase in glycogen content, tissue weight, shell height, underwater shell weight and total volume of oysters. The second was to determine if the effect of starch varied with season. The third was to eliminate some of the confusion concerning the uptake and utilization of dextrose. That is, does supplemental feeding with low levels of dextrose result in statistically significant increases in glycogen content, tissue weight, shell height, underwater shell weight and total volume. Also, are these increases, if they occur, statistically comparable to those produced by cornstarch. In order to answer these questions oysters were offered dextrose in two forms: 1) as a solution; and 2) mixed with clay. The rationale behind mixing dextrose with clay was that soluble sugars are known to be adsorbed on clay particles similar to those present in marine waters (BADER, 1962). It was theorized, therefore, that if oysters were offered clay particles coated with dextrose they would ingest the coated particle and the dextrose would be stripped from the particle and assimilated. The digestive diverticula of oysters are known to be quite acidic (GALTSOFF, 1964), a situation which would favor this process.

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MATERIALS AND METHODS

Four experiments were conducted during the summer and fall of 1966 and the spring of 1967 using different concentrations of cornstarch, dextrose and clay. The types of supplements added, size and treatment of experimental groups, sources of oysters, size, meat measurements and statistical treatment of data are presented in this section and in Table 1.

Oysters for all studies were obtained from Horsehead Bar in the James River, Virginia, an area free of known oyster diseases (Andrews, personal communication). Experimental oysters were selected for uniformity (40 to 45 mm in shell height), freed of attached fouling, randomly separated into groups of 20 and numbered with an enamel paint. Each group of 20 oysters became a "unit" which was subject to various experimental conditions.

One day prior to the start of an experiment, the following measurements were taken on individual oysters in all groups: 1) underwater shell weight to the nearest 0.01 g by the method of ANDREWS (1961); 2) shell height to the nearest 0.1 mm with vernier calipers; and 3) total volume to the nearest 0.1 cc by water displacement. In addition, one group of 20 oysters was sacrificed on the first day of each experiment to determine the following measurements: 1) wet tissue weights to the nearest 0.01 g; and 2) glycogen levels estimated to the nearest 0.01% of the wet tissue weight. Wet tissue weights were recorded after the tissues had drained for 1 minute on a fine mesh, metal grid. Glycogen was extracted by the method outlined by CALDERWOOD & ARMSTRONG (1941) with the exception that the precipitated glycogen, rather than being collected on filter paper, was centrifuged down and the supernatant discarded (Armstrong, unpublished). Glyco-

Table 1

Specific Details of Experiments I, II, III and IV Showing Dates, Water Temperatures, Salinities and Treatments.

Exp. No.	Date	Temp. Range and (mean) C	Salinity Range and (mean) %	Treatment
I	7/ 7/66-13/ 8/66	27.9-29.4 (25.6) Max. Summer Temp.	20.4-22.4 (21.6)	1. Cornst.—2 mg/L 2. Dext.—2 mg/L 3. Mont.—2 mg/L 4. Dext. & Mont.—2 mg/L each 5. Control—no supp. 6. Initial—sacrifice
II	27/ 7/66-11/10/66	27.2-17.2 (22.1) Decreasing Fall Temp.	21.3-24.2 (23.1)	1. Const.—2 mg/L 2. Const.—5 mg/L 3. Dext.—2 mg/L 4. Mont.—2 mg/L 5. Dext. & Mont.—2 mg/L each 6. Control—no supp. 7. Initial—sacrifice
III	21/10/66- 6/12/66	18.2- 5.6 (12.6) To Lowest Fall Temp.	22.0-23.3 (20.9)	1. Cornst.—2 mg/L 2. Cornst.—5 mg/L 3. Dext.—2 mg/L 4. Control—no supp. 5. Held in tray, York Rv. 6. Initial—sacrifice
IV	1/ 4/67-29/ 6/67	12.8-25.6 (18.2) Increasing Spring Temp.	20.7-17.9 (19.1)	1. Cornst.—0.25 mg/L 2. Cornst.—0.50 mg/L 3. Dext.—5 mg/L 4. Dext.—5 mg/L & Mont.—2 mg/L 5. Control—no supp. 6. Held in tray, York Rv. 7. Initial—sacrifice

gen levels were determined colorimetrically by the method of Kemp & Kits van Heijnigen (1954). Analysis of Variance testing (Sokal & Rohlf, 1969) showed that the initial mean underwater shell weights, shell heights and total volumes among the oyster groups in each experiment were statistically similar (*i. e.*, differences among the oyster groups were non-significant at the 5% significance level). Consequently it was assumed that, for each experiment, the sacrificed and experimental groups had statistically similar initial mean wet tissue weights and glycogen levels.

Oysters were held in Plexiglas troughs under running York River water. Troughs measured 36 cm long by 19 cm wide by 6 cm high and consisted of 5 compartments (4 oysters per compartment) and a baffle to insure thorough mixing of water and supplement. Oysters were oriented with bills facing the current and the right valve (flat side) up. Position of oysters in respect to the inflow was changed daily on a random basis. Troughs and oysters were cleaned of feces and pseudofeces every other day.

York River water was pumped to a large overhead trough in the laboratory, flowed into a conducting column of Plexiglas, through Tygon tubing to flow meters and then to the oyster-holding troughs through Tygon tubing. Water flow through the flow meters was checked twice a day and readjusted to the proper flow if necessary. In Experiments I, II and III, the water flow was 1 L/min.; in Experiment IV the water flow was 0.5 L/min. Water temperature and salinity were not regulated but were the same as that of the York River.

The dietary supplements were hydrolyzed cornstarch, dextrose in solution, and dextrose mixed with the clay mineral, montmorillonite. Montmorillonite alone was run as a "control" for the montmorillonite and dextrose mixtures in Experiments I and II but not in Experiment IV; the dextrose and montmorillonite mixture was not used in Experiment III. Individual supplements were prepared by mixing aliquots of either cornstarch, dextrose, montmorillonite or dextrose and montmorillonite mixed with 3 000 mL of tapwater in 4 000 mL Erlenmeyer flasks. The flasks were fitted with 2-holed rubber stoppers. One hole contained a short piece of glass tubing plugged with cotton which functioned as a vent. The second hole contained a glass tube which extended to near the bottom of the flask and served as a delivery tube. Before use, supplements in their flasks, rubber stoppers and glass tubing were autoclaved for 10 minutes at 10 pounds pressure (115° C). This treatment sterilized the supplements and suppressed bacterial growth in the holding flasks. It also converted part of the cornstarch into amylose and amylopectin through hydrolysis of the (#) 1-6 linkages.

Supplements were delivered to the experimental holding troughs through Tygon tubing attached to the glass delivery tube. Flows were regulated by peristaltic pumps and checked twice daily. Particulate supplements were kept in suspension by means of magnetic bars and stirrers. The contents of each flask lasted about 3 days and as the flasks became empty, they were replaced by full, presterilized, reserve flasks.

Addition of supplements to the oyster groups was stopped 24 hours prior to the end of each experiment, and oysters received only York River water during this period so that any undigested supplement might be eliminated from their digestive tracts. Individual oysters were then cleaned of particulate debris and measured for final underwater shell weight, shell height, total volume, wet tissue weight and glycogen level by the previously described methods.

For each experiment, statistical comparisons between initial and final measurements of each oyster group were conducted to determine if significant changes in the variables of interest occurred during the course of the experiment. Comparisons between initial and final mean underwater shell weights, shell heights and total volumes were facilitated by paired "t"tests (Sokal & Rohlf, 1969). Comparisons between mean wet tissue weights and glycogen contents of the sacrificed group to the final values of the control and test groups were carried out by single classification Analysis of Variance and the appropriate F-tests (Sokal & Rohlf, *op. cit.*). Statistical comparisons between the final mean measurements of the control group and those of the test groups were also conducted using single classification Analysis of Variance and the appropriate F-tests. All statistical tests were evaluated at the 5% significance level.

All oyster groups were held in the laboratory with the exception of Experiments III and IV where one group per experiment was maintained in a wire tray suspended in the York River to compare "natural changes" in variables to those of the laboratory control group.

RESULTS

EXPERIMENT I

This study was conducted during mid-summer when water temperatures were maximal and after most spawning had occurred.

Oyster groups receiving the cornstarch and dextrose supplements and the dextrose and montmorillonite mixture had final glycogen levels significantly higher than

Table 2

Experiment I: initial and final measurements on oysters (7 July 66-13 Aug. 66).

Group designation	Glycogen content	Wet tissue weight	Shell height mm		Underwater shell weight g		Total volume cc	
	%	g	Initial	Final	Initial	Final	Initial	Final
Initial	0.51	1.42	39.6	—	4.88	—	7.01	—
Control	0.47	1.50	42.5	45.5[1]	5.33	7.21[1]	7.51	9.13[1]
Cornst.—2 mg/L	1.06[1 2]	1.75[1]	40.1	45.0[1]	5.54	8.50[1]	7.08	9.75[1]
Dext.—2 mg/L	1.17[1 2]	1.31	38.9	44.0[1]	5.45	7.81[1]	7.05	9.19[1]
Mont.—2 mg/L	0.63	1.27	37.8	41.8[1]	5.18	7.35[1]	7.11	8.96[1]
Dext. & Mont.— 2 mg/L each	0.87[1 2]	1.40	41.5	46.1[1]	5.46	7.75[1]	7.37	9.55[1]

[1] Final mean value is significantly different from the initial mean value, $\alpha = 0.05$.

[2] Final mean value is significantly different from that of the control, $\alpha = 0.05$.

their initial mean levels (Table 2). The control group and the group receiving montmorillonite alone showed no significant change from initial levels. Only the group receiving cornstarch increased significantly in mean wet tissue weight. Final mean underwater shell weight, shell height and total volume of each oyster group were significantly greater than the initial mean values.

Comparison among final mean measurements showed that the oyster groups receiving cornstarch, dextrose and the dextrose and montmorillonite mixture had final glycogen levels significantly higher than that of the control group. Levels were respectively 2.2, 2.5, and 1.9 times greater than the control level of 0.47%. Final mean levels of the other variables of all test groups, however, were not significantly different from those of the control group.

EXPERIMENT II

This experiment was conducted during a period of falling water temperatures when oysters in nature normally begin to accumulate glycogen and spawning has ceased.

All oyster groups exhibited significant increases in all variables measured during this experiment (Table 3). Unfortunately, changes in glycogen levels could not be determined due to the failure of the freezer in which the initially sacrificed tissues were held.

Only the cornstarch and the dextrose in solution supplements produced final mean glycogen levels significantly higher than that of the control group. Final mean glycogen levels of the groups receiving cornstarch at 2 and 5 mg/L showed gains which were respectively 13.6 and 15.6

Table 3

Experiment II: initial and final measurements on oysters (27 August 1966-11 Sept. 66)

Group designation	Glycogen content	Wet tissue weight	Shell height mm		Underwater shell weight g		Total volume cc	
	%	g	Initial	Final	Initial	Final	Initial	Final
Initial	—	1.37	40.9	—	6.27	—	8.15	—
Control	0.68	1.88[1]	41.5	47.8[1]	6.08	8.40[1]	8.31	10.45[1]
Cornst.—2 mg/L	9.26[2]	2.92[1 2]	42.0	50.1[1]	6.15	9.99[1]	8.19	11.96[1]
Cornst.—5 mg/L	10.59[2]	3.24[1 2]	41.2	49.2[1]	6.28	9.70[1]	8.56	11.99[1]
Dext.—2 mg/L	1.62[2]	1.95[1]	41.7	48.9[1]	6.21	9.06[1]	8.08	11.01[1]
Mont.—2 mg/L	1.08	1.67[1]	41.8	46.1[1]	6.48	8.83[1]	8.14	10.33[1]
Dext. & Mont.— 2 mg/L each	1.23	2.00[1]	42.1	47.5[1]	6.46	9.23[1]	8.31	11.02[1]

[1] Final mean value is significantly different from the initial mean value, $\alpha = 0.05$.

[2] Final mean value is significantly different from that of the control, $\alpha = 0.05$.

times greater than the control level (0.68%). The group receiving dextrose in solution was only 2.4 times greater than the control level. The significantly higher glycogen levels in the cornstarch-fed groups were accompanied by significantly heavier mean wet tissue weights; this was not so for the dextrose-fed group. As in Experiment I, none of the supplements had a significant influence on shell height, underwater shell weight and total volume.

EXPERIMENT III

This study was conducted in late fall when all oyster spawning is over and oysters in nature have accumulated glycogen to maximal storage levels (based on the yearly cycle of glycogen accumulation).

Final mean measurements, with the exception of shell height, of all laboratory groups were significantly greater than initial measurements (Table 4). Only the group receiving cornstarch at 5 mg/L exhibited a significant increase in shell height. The York River group did not increase significantly in any of the variables measured.

At the end of the study, all supplements yielded final mean glycogen levels significantly higher than the control level of 2.8%. The groups receiving the cornstarch supplements had levels 3.2 (2 mg/L) and 4.1 (5 mg/L) times greater than that of the control group. The mean glycogen level of the dextrose-fed group was 1.6 times greater than the control level. However, only the cornstarch supplements resulted in final mean wet tissue weights significantly greater than that of the control group. The York River group had a final mean glycogen level and wet tissue weight which were significantly less than those of the control group, but did not differ significantly from the control group in the other variables measured. Again, supplements had no significant influence on shell height, underwater shell weight and total volume.

EXPERIMENT IV

This study was conducted in early spring during a period of rising water temperatures. Early spring is prior to spawning and is normally a period of glycogen accumulation after winter depletion in populations of oysters occurring in nature.

All oyster groups, including the York River group, increased significantly in all variables measured during this experiment (Table 5). The cornstarch supplements produced final mean glycogen levels significantly higher than that of the laboratory control group. These levels were approximately 1.5 times greater than the control level of 3.08%. Dextrose in both supplemental forms had no significant influence on glycogen levels. None of the supplements had a significant influence on mean wet tissue weights, shell heights, underwater shell weights and total volume. The oyster group held in the York River had final mean glycogen level significantly less than that of the control group, but did not significantly differ from the control group in the other variables measured.

DISCUSSION

It is assumed in this study, that significant differences between test and control oysters in final measurements were primarily due to the addition of supplements and not to adverse laboratory conditions. This assumption is sup-

Table 4

Experiment III: initial and final measurements on oysters (21 Oct. 66-6 Dec. 66).

Group designation	Glycogen content	Wet tissue weight	Shell height mm		Underwater shell weight g		Total volume cc	
	%	g	Initial	Final	Initial	Final	Initial	Final
Initial	1.84	1.86	43.0	—	6.73	—	9.00	—
York River	2.08[2]	1.80[2]	45.5	45.0	6.57	7.28	9.48	9.83
Control	2.84[1]	2.31[1]	44.1	46.4	6.92	8.43[1]	9.48	10.55[1]
Cornst.—2 mg/L	9.13[1 2]	3.10[1 2]	44.2	46.6	6.92	8.43[1]	9.55	10.79[1]
Cornst.—5 mg/L	11.48[1 2]	3.09[1 2]	44.9	47.3[1]	6.87	8.32[1]	9.84	10.90[1]
Dext.—2 mg/L	4.64[1 2]	2.49[1]	44.5	46.3	6.81	8.13[1]	9.29	10.43[1]

[1] Final mean value is significantly different from the initial mean value, $\alpha = 0.05$.

[2] Final mean value is significantly different from that of the control, $\alpha = 0.05$.

Table 5

Experiment IV: initial and final measurements on oysters (1 April 67-19 June 67).

Group designation	Glycogen content	Wet tissue weight	Shell height mm		Underwater shell weight g		Total volume cc	
	%	g	Initial	Final	Initial	Final	Initial	Final
Initial	1.67	1.91	46.1	—	6.88	—	9.84	—
York River	2.33[1 2]	2.94[1]	44.4	47.8[1]	6.82	10.30[1]	9.76	12.24[1]
Control	3.08[1]	2.46[1]	44.2	49.3[1]	6.98	9.47[1]	9.44	11.32[1]
Cornst.—0.25 mg/L	4.58[1 2]	2.33[1]	43.8	50.6[1]	6.98	9.59[1]	9.30	11.60[1]
Cornst.—0.50 mg/L	4.73[1 2]	2.83[1]	45.8	52.3[1]	6.68	9.47[1]	9.86	12.33[1]
Dext.—5 mg/L	3.48[1]	2.69[1]	45.2	50.9[1]	6.96	9.91[1]	9.52	12.09[1]
Dext.—5 mg/L & Mont.—2 mg/L	3.02[1]	2.49[1]	44.8	50.8[1]	7.08	10.10[1]	9.45	12.02[1]

[1] Final mean value is significantly different from the initial mean value, $\alpha = 0.05$.
[2] Final mean value is significantly different from that of the control, $\alpha = 0.05$.

ported by Experiments III and IV in which control oysters held in the laboratory showed increases equal to or exceeding those of oysters held in the York River.

Our studies showed that effects of carbohydrate supplements on glycogen levels varied with season. Seasonal changes in glycogen content are typical of oysters occurring naturally in Chesapeake Bay (Galtsoff, Chipman, Engle & Calderwood, 1947; Engle, 1950). These changes were reflected in glycogen levels among the control groups held in the laboratory; percentage change and absolute levels were lower in summer and early fall than they were in late fall and early spring. This agrees with known aspects with the oyster's spawning cycle. Fall and spring are periods of glycogen storage, while stored glycogen is utilized in the formation of sexual products during the summer months. Effects of cornstarch and dextrose in the fall and spring on glycogen levels paralleled this natural cycle. The oysters receiving cornstarch during these periods of glycogen storage had substantially higher glycogen levels than those normally found in oysters occurring in the natural environment. Consequently, utilization of carbohydrates as feeding supplements must be considered in relation to the natural glycogen cycle.

Comparison of the cornstarch and dextrose results clearly shows that cornstarch was the better supplemental food. Its effect was most noticeable in the fall. At this time concentrations of cornstarch ranging from 2 to 5 mg/L greatly influenced both glycogen levels and wet tissue weights, but dextrose influenced only glycogen levels and to a much lesser extent. Haven (1965) and Gillespie *et al.* (1966) concluded from their results that dextrose was limited in value as a carbohydrate supplement for oysters. It is noted that cornstarch at 2 and 5 mg/L in both fall experiments resulted in similar levels of percentage glycogen (approximately 9 to 11%). This suggests that cornstarch concentrations much over 2 mg/L could not be assimilated into stored glycogen.

The effect of mixture of dextrose and montmorillonite was, in absolute terms, minimal, the only positive influence on glycogen levels occurring in the summer experiment. Assuming that the dextrose was adsorbed on the clay, it is postulated that the oysters were not capable of stripping the adsorbed dextrose off the clay particles. Another possibility is that the uptake route of glucose is through bacteria and that bacteria can not strip the dextrose off the clay particles.

Cornstarch at the low concentrations of 0.25 and 0.50 mg/L in the spring experiments influenced glycogen levels, yields being only about one-half of those of the 2 and 5 mg/L concentrations in the fall experiments. This point is emphasized since it shows that during spring, cornstarch concentrations of only one-tenth of those used during the preceding fall yielded one-half of the glycogen yielded by the higher concentrations. It is also emphasized that during the spring study, water flows were only one-half of those used in the preceding study.

The lack of influence of cornstarch on shell height, underwater shell weight and total volume at any season agrees with the data of Haven (1965). Gillespie *et al.* (1966) concluded that cornstarch influenced various parameters of shell size as well as glycogen levels and tissue weight and volume. However, the lack of appropriate statistical comparisons in the presentation of their data makes their contention difficult to support. It is concluded that the influence of cornstarch as a supplement for oysters is limited to glycogen content and tissue size with the major influence being on glycogen levels. Thus, supplements which influence glycogen levels to a high degree can be expected to have a similar influence on tissue size. This relation supports the statement of Mitchell (1917) that investigations leading to increased meat yields must consider supplements which influence glycogen formation.

Haven (1965) pointed out that supplemental feeding with cornstarch offered promise as a cultural technique for increasing meat production. Recently the method has been used along with an algal supplement on a routine basis to condition oysters prior to their spawning in a hatchery (Dupuy & Rivkin, 1972).

It is quite probable that the seasonal changes in meat quality of oysters observed by Haven (1962) are associated with the natural fluctuation of a particulate carbohydrate in estuarine waters. Possible sources of this substance might be algal cells or detrital material originating from the breakdown of grasses such as *Spartina* or *Zostera*.

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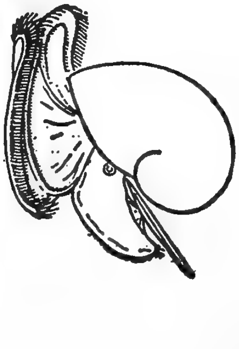

Further Field Notes on the Behavior of *Aplysia dactylomela*

BY

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On a recent collecting trip to the waters off La Parguera, Puerto Rico (21 V through 24 V 1977) 3 observations offer data supportive of previous reports of the behavior of *Aplysia dactylomela* Rang, 1828 (Tobach, Gold & Ziegler, 1965; Lederhendler, Bell & Tobach, 1975; Lederhendler, 1977; Lederhendler & Tobach, 1977) and *Aplysia californica* Cooper, 1863 (Kupfermann & Carew, 1974; Audesirk, 1976).

Because of weather conditions, it was only possible to collect on one afternoon (21 V) and 3 mornings (22 V, 23 V and 24 V). We searched 2 sites thoroughly on each occasion except as noted below: a reef lagoon called La Gata. The leeward side of La Gata is a shallow, sandy-bottomed area with coral rubble and rock bordering on a shallow water bed of *Thalassia. Ulva lactuca* and *Acanthophora spicifera* are found in abundance in the *Thalassia*, but in the rocky area close to the reef. Mangroves border the area in the north. The Enrique site is an extensive shallow water bed of *Thalassia,* with sandy bottoms, in which *A. spicifera*, *U. lactuca*, and *Laurencia obtusa* are found in profusion. The site is bordered by mangroves on the leeward side. The 3 species of algae are readily eaten by *Aplysia dactylomela* in the laboratory and they are found feeding on them in these waters (Lederhendler, 1977).

On the first afternoon, we tagged 8 animals in the La Gata lagoon in an area approximately 30 meters square. We also tagged 8 animals in an area approximately 40m by 20m in the Enrique area. Only 1 pair of these animals was found copulating. There was a significant difference between the weights of the 2 populations (Mann-Whitney "U" test, $p = 0.002$). The La Gata sea hares ranged in weight from 25g to 220g (median = 150g), while those found at Enrique ranged from 165g to 450g (median = 350g). The 2 copulating animals were found at La Gata; the sperm donor weighed 420g; the sperm receiver weighed 410g.

On the subsequent 3 mornings we found the following:

1. All 8 animals tagged at La Gata were recaptured. Only 2 were recaptured at Enrique. The recaptured pair were copulating; the sperm receiver was the same animal that was the sperm receiver the first afternoon; the sperm donor was a different animal and weighed 450g.

2. An additional 20 animals were captured. On the first morning, 2 of 10 animals were copulating; on the second morning, the ratio was 2/7; on the third day, 6 of 8 were found copulating (see Table 1).

Table 1

Reproductive Behavior of *Aplysia dactylomela*
La Parguera, Puerto Rico (1977)

	Enrique Reef		La Gata Reef	
	Copulating	Not Copulating	Copulating	Not Copulating
PM: 5/21	2	6	0	8
AM: 5/22	0	0	2	10
5/23	2	1	0	4
5/24	6	2	—	—[1]

[1] Not visited because of weather

$X^2 = 3.08$. d.f. = 1, $0.10 > p > 0.05$

3. At the Enrique area on the third morning, the 8 animals collected were all in a sandy area approximately 10 meters square which was not as rich as surrounding areas in *Ulva lactuca* and *Acanthophora spicifera.* No *Laurencia* was seen. This area had been searched during the previous afternoon and morning visits. We did not find any copulating animals in that area or in the nearby areas where the algae were thick on those occasions, or on the third morning.

The recapture of animals in the same area over a 3-day period is not unusual for *Aplysia dactylomela* as we had previously been able to recapture large numbers of animals over a 12-day period in Bimini (LEDERHENDLER, BELL & TOBACH, 1975). The difference in numbers of animals found copulating during the morning and afternoon conforms with previous findings (see LEDERHENDLER *et al.*, 1975; LEDERHENDLER & TOBACH, 1977). The gathering of copulating animals in a small area is reminiscent of the observations made by KUPFERMANN & CAREW (1974) and AUDESIRK (1976) of *Aplysia californica.*

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Flight Responses of Two Intertidal Gastropods

(Prosobranchia : Trochidae)

to Sympatric Predatory Gastropods from Barbados

BY

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INTRODUCTION

THE ROCKY INTERTIDAL ZONE of Barbados is exceedingly rich in species of gastropods. LEWIS (1960) records over 20 different species of prosobranchs inhabiting the narrow littoral zone. At the present time there is an inverse relationship between the number of species and the published reports concerning any aspects of their natural history and behavior. While in residence at the Bellairs Institute of McGill University on Barbados during January, 1977, we studied the escape responses of 2 species of top shells (Prosobranchia, Trochidae), *Tegula excavata* (Lamarck, 1822), the Green-based *Tegula*, and *Cittarium pica* (Linnaeus, 1758), the West Indian Top Shell. These herbivorous gastropods are ideal for studying escape behavior in that they are available in sufficient numbers and that they share their rocky habitat with at least 4 species of carnivorous gastropods (Prosobranchia, Thaididae): *Purpura patula* (Linnaeus, 1758), the wide-mouthed Purpura; *Thais haemastoma floridana* (Conrad, 1837), the Florida Rock Shell; *Thais rustica* (Lamarck, 1822), the Rustic Rock Shell; and *Thais deltoidea* (Lamarck, 1822), the Deltoid Rock Shell. Although temperate water species of top shells show well defined flight responses to asteroids (FEDER, 1963; YARNALL, 1964), the tropical top shells have been reported to show flight behavior to the presence of thaidid gastropods (CLARK, 1958). In a region of the Caribbean that is depauperate in predatory asteroids (LEWIS, *op. cit.*), the only carnivores that could be implicated as gastropod predators are the thaidids. Although the temperate species of *Thais* (now *Nucella*, ABBOTT, 1974) have been identified as predators of acorn barnacles (CONNELL, 1961, 1970), the number of acorn barnacles that were noted in the rocky intertidal zone of Barbados is extremely sparse and would preclude them from being a major food resource by the gastropods.

Through a study of the behavior of the 2 species of trochid gastropods presented with possible predators, we wish to demonstrate the flight responses and shed light on possible trophic relationships among this assemblage of intertidal gastropods.

DESCRIPTION OF SPECIES

Observations on all species of gastropods were made both in the field and in the laboratory during January, 1977. Field data were obtained and collections for laboratory experiments were made at 2 small indentations on the northeast exposed rocky coast of Barbados, River Bay (13°19′N; 59°36′W) and Little Bay (13°18′N; 59°35′W). In the laboratory the carnivorous species were kept separate from the herbivorous forms using 2 separate concrete holding tanks, both of which were supplied with running sea water, the temperature of which varied from 25.5 to 28° C during the period of the experiments. No attempt was made to provide any of the snails with food while in the laboratory, although the carnivorous forms were found to prey on each other.

The Herbivorous Gastropods

Tegula excavata is a common intertidal gastropod that ranges throughout the rocky shoreline of the Caribbean (ABBOTT, 1974). On Barbados the species is found in moderately large numbers under rocks and small boulders at the mean low water level, just in or below the "pink zone" of LEWIS (1960). There is little published information concerning the biology of this species. Approximately 150 specimens were collected at River Bay and ranged in shell axis length from 0.5 to 1.2 cm. From the size range for this species by WARMKE & ABBOTT (1962), both juvenile and adult specimens were used in our experiments.

Cittarium pica, an economically important species, ranges throughout the rocky intertidal zone of the Caribbean, but it appears only as fossils in Florida and Bermuda, although it apparently died out in these 2 areas in comparatively recent times (Clench & Abbott, 1943). Lewis (1960) reports that the juvenile stages occur in the "pink zone" above mean low water at Barbados. The adults are found from slightly above the water level to several decimeters below, usually within 60 cm of the surface (Randall, 1964). Many of the natives of Barbados supplement their diet with these large "whelks," often attaining diameters of over 10 cm. Almost all the adult animals that we were able to find were located in grooves and pits on the underside of large rocks and boulders below the mean water level at River Bay; whereas the juvenile animals were collected on the surface of exposed ledges at low tide in the "pink zone" above the mean low water mark at Little Bay. Approximately 100 specimens of *C. pica* were collected and ranged in shell axis length from 1.0 to 4.8 cm, mean length 1.9 ± 2.94 S. D.

The Carnivorous Gastropods

Purpura patula ranges in the Caribbean from Palm Beach, Florida south to Trinidad (Clench, 1947). Lewis states that the Barbados population is most abundant from mean sea level to a few decimeters above mean high water, regions Lewis has named the "black zone" and the "green zone." We have found many specimens of *P. patula* on the surface of exposed rocks as well as hidden in pits and depressions. Man appears to be the only real predator of this high intertidal gastropod, as many of the natives along the east coast collect them for food. According to Lewis (1960) the diet of *P. patula* consists primarily of the chiton *Acanthopleura granulata* (Gmelin, 1791) and the barnacle, *Tetraclita squamosa* Darwin, 1854.

Thais haemastoma floridana again has a rather broad distribution from North Carolina, south through the West Indies and along the Central American Coast to Trinidad (Clench, 1947). On Barbados, *Th. haemastoma floridana* is an open coast inhabitant found in the "pink zone" of Lewis from below mean low water to mean sea level. Many of the specimens that we collected had shell lengths in excess of 4.0 cm. Lewis (1960) again reports that "*T. floridana* is carnivorous and feeds upon barnacles, chitons and other molluscs."

Also found in the same "pink zone," but ranging below mean sea level, *Thais rustica* can be readily confused with the preceding species, although adults rarely exceed 3.0 cm in length (Abbott, 1974). At River Bay we observed many juvenile specimens between 0.4 and 1.2 cm below the mean low water mark in the surf zone of Lewis, beneath the algal canopy or among the clusters of the vermetid, *Spiroglyphus irregularis* (d'Orbigny, 1842). This species ranges from South Florida through the Caribbean south to the coast of Brazil (Clench, 1947). Lewis makes no mention of this species in his monograph, and little is known of its diet.

Thais deltoidea is found still further down in the rocky intertidal zone, generally below the low water level, although it does range upward to the lower portion of the "pink zone." Abbott (1974) reports that this species ranges from Jupiter Inlet, Florida, and Bermuda throughout the Caribbean southward to Brazil, and that it is "an abundant species where intertidal rocks are exposed to the ocean surf." At River Bay and Little Bay, most of the specimens of *Th. deltoidea* were quite large, shell length 3.0 to 4.5 cm, and heavily encrusted with coralline algae. Little is known of its feeding preferences.

EXPERIMENTAL METHODS

The following experiments were designed to test whether the 2 species of top shells would demonstrate escape responses to specific carnivorous gastropods, and to determine whether such behavior was induced by contact or distance chemoreception. Six to 10 specimens of either *Tegula excavata* or *Cittarium pica* were placed in glass finger bowls (top diameter 11.5 cm), each of which contained approximately 150 mL of sea water. The *T. excavata* ranged in shell length from 0.5 to 1.2 cm, whereas the *C. pica* were all juvenile animals with shell length varying from 1.0 to 2.6 cm (Randall, 1964). The experiments were designed to collect both descriptive and quantitative data by counting the number of top shells to leave the water in an arbitrarily determined time of 10 minutes after adding either the predator or an aliquot of sea water that contained the predator's "scent." In order to standardize the procedures the following steps were taken:
1) After being placed in the bowls, the snails were allowed to come to rest, usually 20 minutes before adding the carnivorous snails, 2) the experiments were performed between 0800 and 1100 Barbados time under the subdued lighting conditions of the laboratory, 3) an herbivorous gastropod, *Nerita versicolor* (Gmelin, 1791) was added to each of the control bowls in order to mimic the predator's presence by moving about the bowl acting as a potential disruptive agent, 4) to test for distance chemoreception, approximately 25 mL of sea water taken from a container that held one carnivorous snail per 100 mL of sea water was slowly added to a finger bowl that contained top shells.

The control for this experiment was adding an equal volume of sea water from the intake sea water valve to a bowl with snails. When it appeared necessary, the data were tested for significance using the X^2 test for 2 independent samples (SIEGEL, 1956).

After some initial observations, it became apparent that there may be a differential size response of *Cittarium pica* to predatory gastropods. To test this hypothesis, the following experiment was performed: 6 small, juvenile *C. pica* (1.0 to 2.6cm) and 6 large specimens (3.5 to 4.8cm) were placed into each of four 2L bowls that were half filled with sea water. After all locomotory activity had ceased in the bowls, usually 15 minutes, a specimen of *Thais deltoidea* (4.0 to 4.2cm) was placed into each of 2 bowls, and a specimen of *Nerita versicolor* (3.0 to 3.5cm) was added to each of the remaining 2 bowls as controls. The experiment was designed to measure the number of snails, and the size of these snails, to evacuate the bowls in 10 minutes.

RESULTS

1. Laboratory Experiments

Flight responses were elicited in ***Tegula excavata*** and ***Cittarium pica*** juveniles by 3 of 4 sympatric gastropod species that were tested in the laboratory (Table 1). A strong response was elicited when contact was made between the top shells and the carnivores. This was most apparent with *T. excavata*, for actual contact was not necessary to elicit a strong response in *C. pica*. The significance of contact to elicit a strong response in *T. excavata* can be seen in Table 1. The top shells that remain in the bowls, even after adding the carnivores, is almost half the total number. These top shells were not brought into direct contact with the carnivores, a case especially true for *Th. deltoidea* which is far less active than *Th. haemastoma floridana*. Generally the flight behaviors of both species were identical. The initial response was a slight elevation of the shell to expose the head, followed by a rapid flailing of the cephalic and epipodial tentacles. The top shells then exhibited increased locomotory activity, which usually resulted in the evacuation of the bowl of water. The behavior of *Te. excavata* differed from that of *C. pica* juveniles in that contact with such carnivorous species as *Th. haemastoma floridana* and *Th. deltoidea* often elicited a rapid, jerky torsion or twisting of the shell through an arc of 180°. This was most apparent when contact was made between the propodium of the carnivore and the soft parts or shell of the top shell. No such shell torsion or twisting was demonstrated by *C. pica* juveniles. On 3 separate occasions during the experiments, a specimen of

Table 1

	Size of Test Snail in cm	# of topshells in exptl. bowls at T_O	# to leave exptl. bowls in 10 min.	# topshells in control bowls at T_O	# to leave control bowls in 10 min.	Chi-Square Value
Tegula excavata	0.5-1.2					
Thais haemastoma floridana	3.0-4.2	75	62	75	0	—
Thais deltoidea	2.5-4.0	90	41	90	1	—
Thais rustica	2.0-3.0	40	21	40	1	—
Purpura patula	2.5-3.2	40	1	40	2	—
T. h. floridana water		32	5	32	0	3.471[1]
T. deltoidea water		32	11	32	2	6.178[1]
T. rustica water		32	8	32	1	4.655[1]
Cittarium pica (juveniles)	1.0-2.6					
Thais haemastoma floridana	3.0-4.2	40	36	40	0	—
Thais deltoidea	2.5-4.2	40	38	40	0	—
Thais rustica	2.0-3.0	24	16	24	0	—
Purpura patula	2.8-3.3	24	0	24	0	—
T. h. floridana water		40	35	40	0	—
T. deltoidea water		32	31	32	0	—
T. rustica water		24	3	24	1	—

[1] The difference between the experimental and control counts is significant ($p = 0.05$) when chi-square is greater than 3.840.

Te. excavata was captured, inverted and eaten by a specimen of *Th. haematoma floridana.* This occurred when the path to escape was blocked by other top shells in the bowl.

As well as exhibiting a strong response to contact, *Cittarium pica* juveniles react strongly to water that contained the "scent" of both *Thais haemastoma floridana* and *Th. deltoidea* (Table 1). When *Thais* water was added to a bowl of quiescent top shells, the snails became agitated and began to move about the bowls to the extent that most evacuated the bowls *en masse* within the first 3 minutes. On the other hand, *Tegula excavata* react less strongly to such water samples. Although there was tentacular flagellation, movement in the bowls tended to be slower and less direct. Even though a statistically significant number did vacate the bowls (Table 1), they did not do so simultaneously, and after 10 minutes those that did remain in the bowls had once more become quiescent.

There appeared to be a relationship between the age or size of *Cittarium pica* and its ability to respond to a predator (Table 2). Only the smaller, juvenile animals, with shell lengths between 1.0 and 2.6 cm, would respond to the presence of *Thais deltoidea.* The response was spectacular for in most cases the small top shells would evacuate the bowl not only within 3 minutes after adding the predator, but in unison. Although no motion was observed in the larger top shells with shell lengths between 3.5 and 4.8 cm, the cephalic tentacles did show slight flailing. When bowls that contained similar numbers and sizes of *C. pica* were moved out of doors in bright light or direct sunlight, all the top shells became highly agitated before the addition of the predator, although they would not evacuate the bowls.

Table 2

Differential size response of *Cittarium pica* to *Thais deltoidea*

	Experimental Group	Control Group
Number of Large Topshells (3.5-4.8 cm) to vacate bowls in ten minutes or less (n = 12 per group)	0	0
Number of Small Topshells (1.0-2.6 cm) to vacate bowls in ten minutes or less (n = 12 per group)	11	0

2. Field Observations

During our residence on Barbados, field trips were made on a daily basis with one purpose being to observe possible feeding behavior of the carnivorous gastropods. Barbados is characterized by mixed semidiurnal tides. All observations were made during the lowest low tide sequence at either Little Bay or River Bay.

Purpura patula was observed feeding on 13 separate occasions on the striped nerite, *Nerita tessellata* (Gmelin, 1791). In all cases the carnivores were small specimens, averaging about 2.4 cm in length. The nerites had been flipped over and the purple shell was covering the ventral surface with its large foot. On 3 separate occasions we noted larger specimens of *P. patula* (average size, 4.0 cm)' feeding on the chiton, *Acanthochiton granulata.* The chitons had also been flipped over and the purple shell had initially drilled (eaten) a hole through the center of the large foot to get at the viscera.

Thais haemastoma floridana and *Th. rustica* were not observed feeding in the field, although the former was a most opportunistic carnivore, even cannibal, in the laboratory holding tank. We did note a large number of *Tegula excavata* shells that were either empty or inhabited by small hermit crabs at River Bay. Generally we would find large specimens of both *Th. haemastoma floridana* and *Th. rustica,* in excess of 2.5 cm in association with *Te. excavata.* So they may be guilty of preying on them, guilty at least by association.

We did observe a *Thais deltoidea* (shell length 4.5 cm) in the process of consuming a carved star shell, *Astraea caelata* (Gmelin, 1791) with a shell length of 3.0 cm. We were unable to collect large numbers of star shells to test for flight behavior, but in 2 cases we did observe, under the laboratory conditions previously described, the shell twisting phenomenon when this species of star shell was presented to *Th. deltoidea.*

Although we did not make an actual count, we observed numerous large empty *Cittarium pica* shells scattered in the intertidal zone of River Bay. Many of these shells were broken at the apical end, exposing the dorsal visceral chamber. The only large carnivore besides man that was in evidence on the beach were the Sally Lightfoot crabs, *Grapsus grapsus.* Although they easily avoided capture and thus made direct measurements impossible, many of the males appeared to have carapace widths in excess of 15 cm.

DISCUSSION

Tegula excavata and juvenile *Cittarium pica* exhibit flight behavior that is typical of trochid gastropods (see ANSELL, 1969 for a review). The differences between these 2 species appear to be in the sensory cues used to elicit the response, the complexity of the response, and most importantly, the age or size of the responding snail. The responses of *Tegula excavata* to carnivorous gastropods are mediated primarily through contact and in this regard differ from the responses of *C. pica* juveniles where predator detection appears to involve distance chemoreception. Clearly, there is an advantage conferred to a snail able to detect predators from a distance since contact with some carnivorous gastropods may be fatal; for example, contact with cone species where a toxin is injected by means of radular teeth in the eversible proboscis (KOHN, 1959). In the course of our experiments, we have observed that *T. excavata,* a snail that responds primarily to contact, was captured and eaten by *Thais haemastoma floridana* on 3 separate occasions, whereas under similar experimental conditions no *C. pica* were ever captured.

Shell twisting in *Tegula excavata* may be an additional adaptation to contact induced flight behavior as it would serve to extricate the top shell from the grasp of the prehensible foot of a carnivorous gastropod. Shell twisting was initially reported in Australian trochid gastropods, induced by thaidid snails (CLARK, 1958). Apparently it is also quite commonly induced by molluscivorous echinoderms and gastropods in such genera as *Tegula* (FEDER, 1963), *Gibbula* and, in addition to the more vigorous shell rolling movements, *Calliostoma* (FEDER, 1967). The ability to twist the shell around the long axis of the visceral mass does cross familial boundaries in that we have observed it in the turbinids, *Astraea caelata* and *Turbo castanea* (Gmelin, 1791), although in this latter species, the response was elicited by handling and not by a specific predator.

The apparent dichotomy in response between adult and juvenile *Cittarium pica* is noteworthy. Differential size responsiveness has been reported only once. MONTGOMERY (1967) reports that larger specimens of *Haliotis rufescens* Swainson, 1822 and *H. assimilis* Dall, 1878, are unresponsive to predatory asteroids, while smaller specimens exhibit shell twisting, mantle covering, and mucus expulsion. However, the possible significance of this phenomenon is not discussed.

Failure of the large specimens to respond can have several explanations, not mutually exclusive: 1) the larger snails may move into a zone unoccupied by predators, flight to which would confer an advantage; 2) the snails may attain a size relative to their predators at which they would be less susceptible to predatory tactics; 3) especially where contact is important, larger specimens may not receive stimulation sufficient to elicit a flight response; or 4) in a case where shell twisting is part of the flight repertoire, the shell may reach a bulk at which it would be energetically unfavorable to shell twist. In the case of *Cittarium pica*, the adults appear to migrate downward, entering a zone where different predators are encountered. RANDALL (1964) notes that one of the large top shells was found in the arms of a small octopus, and that octopods readily feed on live top shells. In addition, Randall has discovered top shells or their opercula in fish stomachs. Whatever the significance, we feel that it is important that future investigations address themselves to the possibility of size being a relatively important factor in the behavior of mollusks.

The 2 species of Barbadian trochids exhibit a strong response to those 3 species of *Thais* that share their habitat in the mid to lower intertidal zones. Although RANDALL (1964) observed a 3.5 cm specimen of *Purpura patula* feeding on a 3.7 cm specimen of *Cittarium pica,* neither species demonstrated a response to the presence or contact of *P. patula,* which from field observations appears to prey on other species of mollusks. *Purpura patula* is a high intertidal carnivore that may only on rare occasions be found in the lower zone inhabited by the 2 species of top shells. This situation may be similar to that of *Acmaea scabra* (Gould, 1846) which does not show an escape response to *Pisaster ochraceus,* with which it overlaps only at the lower extreme of its range in the intertidal zone, yet ranks high on a percentage basis of food for the asteroid (FEDER, 1963). We feel that the relatively strong response of both *Tegula excavata* and juvenile *Cittarium pica* to *Thais haemastoma floridana, Th. deltoidea* and *Th. rustica* has ramifications in the predator-prey interactions of these species. Whether or not top shells comprise the major portion of the thaidids' diet and the extent to which the flight responses of potential prey are involved, remain unanswered until more ecological data are available.

SUMMARY

Two species of mid to lower intertidal top shells, *Tegula excavata* and *Cittarium pica,* exhibit flight behavior to the presence of 3 sympatric thaidid gastropods. The former species tends to respond strongly to contact with predatory

forms; whereas the latter primarily responds to distance chemoreception. Neither of the snail species responds to a high intertidal predatory gastropod, *Purpura patula.*

Also, there are 2 major differences in the behavior of the 2 top shell species in that only *Tegula excavata* shows the shell twisting response to contact and it is only the small or juvenile *Cittarium pica* that have a flight reaction to the predators, the adults being relatively unresponsive.

ACKNOWLEDGMENTS

We wish to thank Dr. Finn Sander, Director of the Bellairs Research Institute of McGill University for facilities and warm hospitality afforded us while in Barbados. Also Dr. Joseph Rosewater, Division of Malacology, the U. S. National Museum for identifying several of the species of gastropods reported in this study. And finally Debbie Barnard, Joe McGinley and Jeff Churchill for their much appreciated assistance in the field and laboratory.

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Notes on the Spawning and Egg Capsules of Two Prosobranch Gastropods: *Nassarius tiarula* (Kiener, 1841) and *Solenosteira macrospira* (Berry, 1957)

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(2 Text figures)

BOTH *Nassarius tiarula* (Kiener, 1841) and *Solenosteira macrospira* (Berry, 1957) occur intertidally on mudflats throughout the Gulf of California. According to KEEN (1971), *S. macrospira* is endemic to the Gulf, but *N. tiarula* ranges as far south as Panamá. Collections and observations for this study were made at Cholla Bay, 11 km north of Puerto Peñasco in the northern Gulf of California.

Spawning can be observed from April through the last part of June for *Nassarius tiarula*. Females deposit pale yellow egg capsules in clusters of 15 to 30 on empty shells lying just beneath the surface of the mud. The capsules are vase-shaped and have 4 sides. The front and back are flat with slightly convex sides (Figure 1a). Each has an opening at the top fitted with a mucous plug. The bottom of the capsule tapers to a long, narrow stalk, which is attached to an adhesive disk. The entire capsule measures 13 mm high and about 3 mm wide. Each capsule contains about 50 eggs which float in an albuminous fluid.

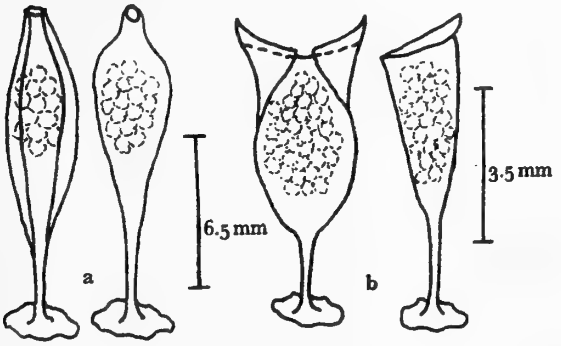

Figure 1

Egg capsules: a - *Nassarius tiarula*; b - *Solenosteira macrospira*

During dissection of gravid females, egg capsules were released from the genital opening. First a small transparent bubble appeared which proved to be the basal region of the capsule. As the bubble was squeezed out, the opening was distended to about 3 times its normal diameter. Shortly after, the eggs were released and appeared initially as a single string surrounded by albuminous fluid. Prior to release of the capsule, the eggs clumped into a central mass. The top of the capsule with the mucous plug intact was the last to leave the nidamental opening. This newly formed capsule was soft and transparent. It was then transported along a ciliated groove to the foot.

Histological sections reveal the 5 layers that compose the capsule wall (Figure 2a). An innermost mucous layer (mu) is surrounded by a coat of circular fibers (ci). Peripheral to this is a loose network of fibers interspersed by lacunae (mpl), which are filled with a mucoid substance. The 4th layer is another stratum of circular fibers. The final layer is a tenuous mucous coat surrounding the entire capsule.

Solenosteira macrospira begins spawning in March and continues through the first week of June. This is an interesting species because the female deposits the capsules on the shell of a living male buried beneath the mud. On many occasions the shell of the male was completely covered by the capsules. GEMMELL (1973) first reported this behavior in populations of *S. macrospira* near San Felipe, Baja California.

The capsules are transparent and the reddish-brown eggs can be observed inside floating in the albuminous fluid. The flask-shaped capsules stand about 7 mm high and are attached to the shell by a long, slender stalk similar to that of *Nassarius tiarula* (Figure 1b). In each

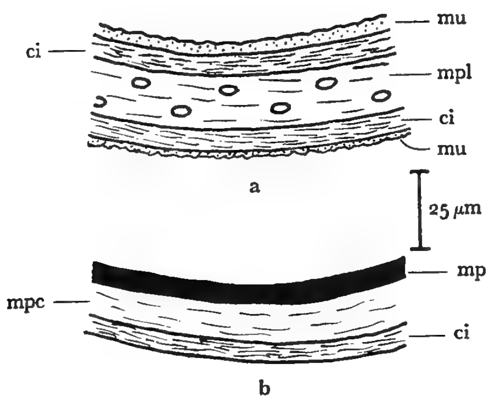

Figure 2

Egg Capsule Histology

a - *Nassarius tiarula* b - *Solenosteira macrospira*
ci – circular protein fibers mp – muco-protein
mpl – muco-protein fibers interspersed by lacunae
mpc – muco-protein fibers mu – mucus

capsule there are up to 500 eggs averaging 200 μm in diameter.

The wall of the egg capsule consists of 3 layers (Figure 2b). The inner region is a muco-protein layer (mp), not a mucous one as in *Nassarius tiarula*. The middle layer is a thick, fibrous muco-protein coat (mpc). This is covered by an outer layer consisting of circular fibers (ci). Similar conditions were observed by Fretter (1941) for egg capsules of *Nucella lapillus* (Linnaeus, 1758). Ankel (1937) suggested that the egg capsules of *N. lapillus* are composed of 2 substances, the protein and conchiolin intermixed with mucus or a mucoid substance. This has been substantiated in histochemical studies by Bayne (1968), in which acid mucopolysaccharides and conchiolin were found to be the major components of the capsule wall.

The long slender stalks allow the egg capsules to extend above the mud where the developing embryos are exposed to ample water circulation. Since competition for hard substrates is severe, females of *Solenosteira macrospira* have overcome this problem by depositing egg capsules on the shells of their mates.

ACKNOWLEDGMENT

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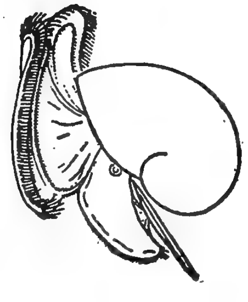

Additional Molluscan Records from Bahía de Los Angeles, Baja California Norte

BY

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Los Angeles County Museum of Natural History

(1 Map)

Bahía de Los Angeles is located on the east side of the Baja California Peninsula about 440 km south of the United States Border (29°00'N; 113°30'W). The area covers approximately 63 square kilometers and is protected on the east side by about 15 small islands, with Isla Smith as the largest.

The literature records a number of expeditions which collected in this part of the Gulf of California. The earliest of these was the *Albatross* in 1911. Although several of the expeditions did collect in the bahía, most attention was given to dredging around Isla Angel de la Guarda, more than 30 km offshore. The reports of the molluscan fauna of the bahía were scarcely significant, the largest number of species reported being 28 by Steinbeck & Ricketts (1941).

Two more recent papers have been published in the Transactions of the San Diego Society of Natural History, reporting on the mollusks collected at Bahía de Los Angeles. McLean (1961) reported on the mollusks collected from shore and beach drift. This paper included records from his collection and 4 other sources. Coan (1968) reported benthic species from the inner part of the bahía. Collecting for that report was done with an orange peel grab and followed a grid over the southern part of the bahía where the bottom is primarily silty mud.

Accompanied by Carl and Laura Shy of Westminster, California, we have made 3 collecting trips of about 10 days each to this area in recent years. Base camp was at Punta la Gringa, a small point of land about 14 km by road north of the village. Using small boats and hand-operated dredging equipment, we made approximately 240 drags in depths of 20 - 30 m. The maximum depth recorded in the bahía is 40 m (Barnard & Grady, 1968). The bottom was primarily broken rock and shell but included samplings of other substrates as indicated on the map.

Each trip was associated with periods of extreme low tides, so we did extensive intertidal collecting. Some of this was done along the rocky reefs between Punta la Gringa and the sand spit north of the village. Much time was spent along the rocky shore several kilometers north of camp and along the west side of Isla Smith. A number of species of marine algae and sponges cover the rocky intertidal areas and extend out to about 10 m.

Many of the specimens obtained at the bahía have been significantly larger than the average sizes indicated in Keen (1971), and have been registered with the Lost Operculum Club, a project of the Conchological Club of Southern California. Roden & Groves (1959) report, "An area of low temperatures around Isla Angel de la Guarda is found throughout the year." This is the second largest island in the Gulf of California and parallels the coast about 32 km from the bahía. The channel between reaches a depth of more than 600 fathoms (1096 m). Strong tidal currents force cold water from these depths into the bahía. The maximum temperature in the bahía was reported to be 29.8° C in August, 1962, and the minimum temperature was reported to be 15° C in February, 1962 (Barnard & Grady, 1968). The unusually cold water together with the abundance of algae, sponges, coral, and other food sources may contribute to an explanation of why so many "giants of the species" are found here.

A total of 510 different identified mollusks was included in the papers by McLean and Coan. Only 67 species were reported by both authors. This paper adds 160 identified species to their total, which increases the recorded molluscan fauna for Bahía de los Angeles by 36% for a total of 603 species.

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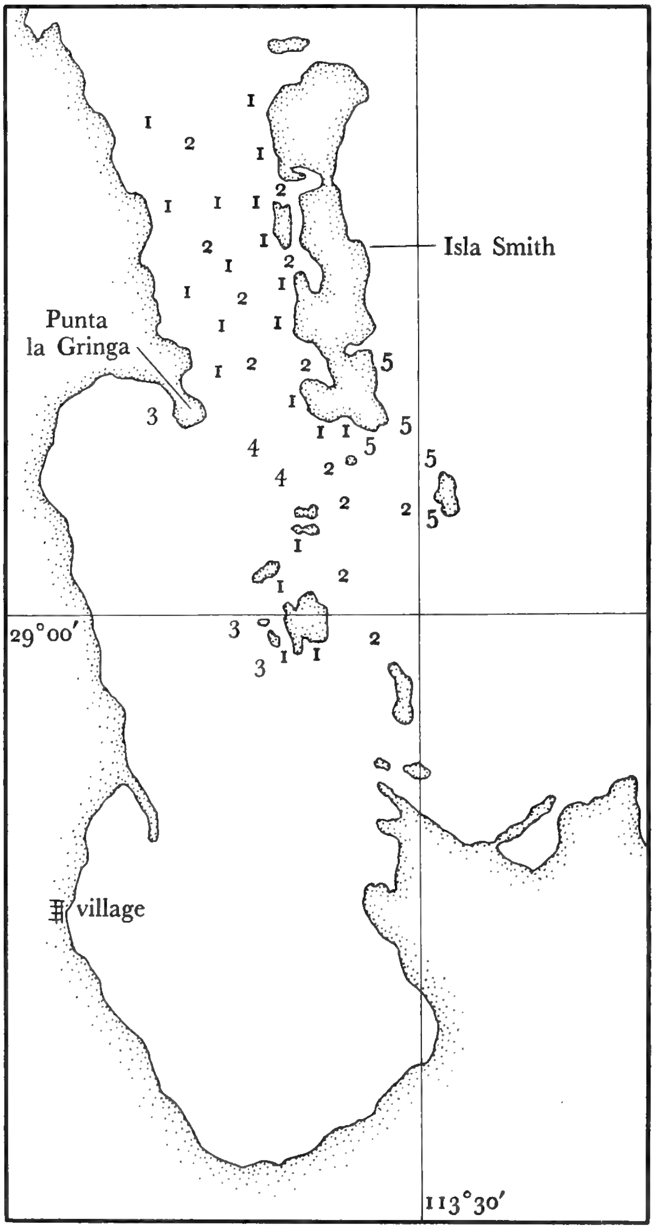
The following list includes those mollusks collected by the Shys and the Poormans and which were not reported in either of the other 2 papers. Identifying numbers from KEEN (1971) precede the names of each species listed. Dredging or intertidal records are indicated by D or S after each species name. Significant range extensions are also included. Several undescribed opisthobranchs and chitons were taken and are now in manuscript.



Bahía de Los Angeles,, Baja California Norte, Mexico

1. broken rock and shell 3. silty mud
2. fine sand and shell 4. fine living coral
5. valves of *Pecten vogdesi*

Our appreciation is extended to Gale Sphon, Los Angeles County Museum of Natural History, for his help in identifying opisthobranch species, and to George Hanselman, San Diego, for help with the chitons.

PELECYPODA

ARCIDAE

77 *Anadara (Anadara) adamsi* Olsson, 1961 D (Panama)
92 *Anadara (Rasia) formosa* (Sowerby, 1833) D (Cedros Isld.)

GLYCYMERIDIDAE

117 *Glycymeris (Tucetona) strigilata* (Sowerby, 1833) D

MYTILIDAE

119 *Brachidontes adamsianus* (Dunker, 1857) S
122 *Brachidontes semilaevis* (Menke, 1849) S

PECTINIDAE

183 *Chlamys lowei* (Hertlein, 1935) D
187 *Cyclopecten exquisitus* Grau, 1959 D
194 *Delectopecten zacae* (Hertlein, 1935) D

PLICATULIDAE

207 *Plicatula inezana* Durham, 1950 S (Southern Gulf of California)
208 *Plicatula penicillata* Carpenter, 1857 D (Southern Gulf of California)

SPONDYLIDAE

213 *Spondylus ursipes* Berry, 1959 D

LUCINIDAE

271 *Lucina (Here) excavata* Carpenter, 1857 D
277 *Lucina (Pleurolucina) leucocymoides* (Lowe, 1935) D
278 *Lucina (Pleurolucina) undatoides* Hertlein & Strong, 1945 D

UNGULINIDAE

293 *Diplodonta suprema* Olsson, 1961 S (Panama)
296 *Phlyctiderma (Phlyctiderma) discrepans* (Carpenter, 1857) D

SPORTELLIDAE

343 *Basterotia (Basterotella) hertleini* Durham, 1950 S

CHAMIDAE

348 *Chama frondosa* Broderip, 1835 D
352 *Chama venosa* Reeve, 1847 D
357 *Pseudochama janus* (Reeve, 1847) D

CARDIIDAE

373 *Lophocardium annettae* (Dall, 1889) D

VENERIDAE

381 *Ventricolaria isocardia* (Verrill, 1870) D
401 *Pitar (Pitar) helenae* Olsson, 1961 D
414 *Pitar (Lamelliconcha) frizzelli* Hertlein & Strong, 1948 D (Southern Gulf of California)
424 *Megapitaria aurantiaca* (Sowerby, 1831) D
456 *Chione (Chionopsis) purpurissata* Dall, 1902 D

MACTRIDAE

490 *Mactra (Mactrotoma) nasuta* Gould, 1851 D
497 *Anatina cyprinus* (Wood, 1828) D

TELLINIDAE

517 *Tellina (Angulus) meropsis* Dall, 1900 D
546 *Tellina (Phyllodina) pristiphora* Dall, 1900 D
551 *Tellina (Tellinella) cumingii* Hanley, 1844 D

PSAMMOBIIDAE

603 *Gari (Gobraeus) helenae* Olsson, 1961 D

SOLECURTIDAE

614 *Solecurtus guaymasensis* Lowe, 1935 D (Guaymas, Sonora)

SEMELIDAE

626 *Semele californica* (Reeve, 1853 *ex* A. Adams, MS) S (Cabo San Lucas)
634 *Semele junonia* (Verrill, 1870) D
636 *Semele lenticularis* (Sowerby, 1833) DS (Barra de Navidad, Jalisco)
647 *Semele simplicissima* Pilsbry & Lowe, 1932 D

MYIDAE

673 *Sphenia fragilis* (H. & A. Adams, 1854) D

CORBULIDAE

687 *Corbula (Juliacorbula) ira* Dall, 1908 D (Panama)
692 *Corbula (Varicorbula) speciosa* Reeve, 1843 D

PANDORIDAE

733 *Pandora (Pandora) uncifera* Pilsbry & Lowe, 1932 D
738 *Pandora (Pandorella) cornuta* C. B. Adams, 1852 D (Panama)
739 *Pandora (Pandorella) granulata* Dall, 1915 D

LYONSIIDAE

747 *Entodesma (Phlycticoncha) lucasanum* (Bartsch & Rehder, 1939) D

THRACIIDAE

764 *Cyathodonta dubiosa* Dall, 1915 D

VERTICORDIIDAE

789 *Verticordia (Verticordia) ornata* (Orbigny, 1846) D

GASTROPODA

FISSURELLIDAE

13 *Rimula mexicana* Berry, 1969 D
22 *Diodora pusilla* Berry, 1959 S
23 *Diodora saturnalis* (Carpenter, 1864) D
43 *Leurolepas roseola* McLean, 1970 D

TROCHIDAE

86 *Calliostoma mcleani* Shasky & Campbell, 1964 D
97 *Tegula (Agathistoma) corteziana* McLean, 1970 S

SKENEIDAE

124 *Parviturbo stearnsii* (Dall, 1918) D

LIOTIIDAE

130 *Arene (Arene) lurida* (Dall, 1913) D
134 *Arene (Marevalvata) balboai* (Strong & Hertlein, 1939) D
135 *Arene (Otollonia) fricki* (Crosse, 1865) D
138 *Macrarene lepidotera* McLean, 1970 D (Socorro Island)

TURBINIDAE

149 *Turbo (Marmarostoma) squamiger* Reeve, 1843 D

LITTORINIDAE

179 *Littorina aberrans* Philippi, 1846 S

VITRINELLIDAE

393 *Teinostoma (Teinostoma) politum* A. Adams, 1851 S (Ecuador)

ARCHITECTONICIDAE

429 *Heliacus caelatus* (Hinds, 1844) D

TURRITELLIDAE

441 *Turritella mariana* Dall, 1908 D (Guaymas, Sonora)
442 *Turritella nodulosa* King & Broderip, 1832 D (Guaymas, Sonora)
445 *Turritella rubescens* Reeve, 1849 D
447 *Vermicularia frisbeyae* McLean, 1970 DS (Bahía de Tenacatita, Jalisco)

CERITHIIDAE

558 *Diastoma chrysalloidea* Bartsch, 1911 S

EPITONIIDAE

633 *Epitonium (Cirsotrema) togatum* Hertlein & Strong, 1951 D
634 *Epitonium (Cirsotrema) vulpinum* (Hinds, 1844) D
636 *Epitonium (Hirtoscala) reflexum* (Carpenter, 1856) S
678 *Opalia (Dentiscala) crenatoides* (Carpenter, 1864) D
686 *Opalia (Nodiscala) spongiosa* Carpenter, 1864 D

EULIMIDAE

707 *Eulima townsendi* (Bartsch, 1917) D
752 *Niso (Niso) splendidula* (Sowerby, 1834) D

VANIKORIDAE

797 *Vanikoro aperta* (Carpenter, 1864) D

CALYPTRAEIDAE

817 *Crepidula striolata* Menke, 1851 D
822 *Crucibulum (Crucibulum) lignarium* (Broderip, 1834) D
828 *Crucibulum (Dispotaea) concameratum* Reeve, 1859 D

NATICIDAE

866 *Natica (Natica) scethra* Dall, 1908 D (Panama)
893 *Sinum sanctijohannis* (Pilsbry & Lowe, 1932) D (Nicaragua)

COLUBRARIIDAE

972 *Colubraria (Colubraria) siphonata* (Reeve, 1844) D

MURICIDAE

988 *Murexiella humilis* (Broderip, 1833) D
1019 *Aspella (Trialatella) cunninghamae* (Berry, 1964) D
1020 *Attiliosa carmen* (Lowe, 1935) D
1021 *Attiliosa incompta* (Berry, 1960) D
1058 *Pterotyphis (Tripterotyphis) lowei* (Pilsbry, 1931) D

CORALLIOPHILIDAE

1063 *Coralliophila (Pseudomurex) costata* (Blainville, 1832) S

THAIDIDAE

1093 *Morula (Morunella) lugubris* (C. B. Adams, 1852) D

BUCCINIDAE

1099 *Caducifer (Monostiolum) biliratus* (Reeve, 1846) D
1124 *Engina fusiformis* Stearns, 1894 D

COLUMBELLIDAE

1252 *Nassarina (Steironepion) tincta* (Carpenter, 1864) D
1261 *Parametaria dupontii* (Kiener, 1849-50) S
1265 *Strombina (Strombina) angularis* (Sowerby, 1832) D
1273 *Strombina (Strombina) gibberula* (Sowerby, 1832) D

NASSARIIDAE

1293 *Nassarius cerritensis* (Arnold, 1903) D
1304 *Nassarius insculptus* (Carpenter, 1864) D

OLIVIDAE

1363 *Oliva (Oliva) polpasta* Duclos, 1833 DS
1379 *Olivella (Olivella) gracilis* (Broderip & Sowerby, 1829) D
1382 *Olivella (Olivella) sphoni* Burch & Campbell, 1963 D

CONIDAE

1510 *Conus (Lithoconus) archon* Broderip, 1833 D

TEREBRIDAE

1531 *Terebra crenifera* Deshayes, 1859 D
1535 *Terebra elata* Hinds, 1844 D
1538 *Terebra glauca* Hinds, 1844 D
1554 *Terebra ornata* Gray, 1834 D

TURRIDAE

1579 *Calliclava alcmene* (Dall, 1919) D
1599 *Kylix paziana* (Dall, 1919) D
1615 *Drillia (Drillia) acapulcana* (Lowe, 1935) D
1637 *Splendrillia bratcherae* McLean & Poorman, 1971 D
1641 *Bellaspira acclivicosta* McLean & Poorman, 1970 D
1643 *Bellaspira melea* Dall, 1919 D
1648 *Polystira oxytropis* (Sowerby, 1834) D
1656 *Knefastia dalli* Bartsch, 1944 S
1663 *Pyrgospira obeliscus* (Reeve, 1843) D
1676 *Crassispira (Crassispira) maura* (Sowerby, 1834) D
1688 *Crassispira (Crassispirella) rustica* (Sowerby, 1834) D
1691 *Crassispira (Dallspira) bifurca* (E. A. Smith, 1888) S
1699 *Crassispira (Striospira) kluthi* E. K. Jordan, 1936 D
1701 *Crassispira (Striospira) tepocana* Dall, 1919 D
1702 *Crassispira (Striospira) xanti* Hertlein & Strong, 1951 D
1723 *Carinodrillia dichroa* Pilsbry & Lowe, 1932 D
1727 *Strictispira ericana* (Hertlein & Strong, 1951) D
1777 *Nannodiella fraternalis* (Dall, 1919) D
1791 *Kurtziella (Granoturris) antipyrgus* (Pilsbry & Lowe, 1932) D
1810 *Kurtzia arteaga* (Dall & Bartsch, 1910) D
1813 *Kurtzia granulatissima* (Mörch, 1860) D
1839 *Daphnella mazatlanica* Pilsbry & Lowe, 1932 S

ACTEONIDAE

2229 *Acteon panamensis* Dall, 1908 D (Guaymas, Sonora)

ATYIDAE

2245 *Haminoea virescens* (Sowerby, 1833) S

AGLAJIDAE

2254 *Chelidonura inermis* (Cooper, 1863) S

APLYSIIDAE

2296 *Aplysia (Neaplysia) californica* Cooper, 1863 S
—— *Phyllaplysia padina* Williams & Gosliner, 1973 S

PLEUROBRANCHIDAE

2306 *Pleurobranchus areolatus* (Mörch, 1863) S
—— *Berthellina citrina* (Rüppell & Leuckart, 1828) S

DORIDIDAE

2327 *Conualevia mizuna* Marcus & Marcus, 1967 S

CHROMODORIDIDAE

2328 *Chromodoris banksi* Farmer, 1963 S

POLYCERATIDAE

2350 *Polycera alabe* Collier & Farmer, 1964 S
2352 *Polycera hedgpethi* Marcus, 1964 S
2353 *Laila cockerelli* MacFarland, 1905 DS

GYMNODORIDIDAE

2354 *Nembrotha eliora* Marcus & Marcus, 1967 DS

DENDRODORIDIDAE

2359 *Dendrodoris krebsii* (Mörch, 1863) S
—— *Dendrodoris fulva* (MacFarland, 1905) S
2360 *Doriopsilla albopunctata* (Cooper, 1863) S
2362 *Doriopsilla rowena* Marcus & Marcus, 1967 S

TETHYIDAE

2370 *Melibe leonina* (Gould, 1852) S

ARMINIDAE

2373 *Armina californica* (Cooper, 1862) DS
2374 *Histiomena convolvula* (Lance, 1962) D

FLABELLINIDAE

2382 *Coryphella iodinea* (Cooper, 1863) D

AEOLIDIIDAE

2388 *Spurilla chromosoma* Cockerell & Eliot, 1905 S

ONCHIDIIDAE

2395 *Onchidella binneyi* Stearns, 1893 S

MELAMPIDAE

2399 *Melampus (Melampus) mousleyi* Berry, 1964 S

POLYPLACOPHORA

ISCHNOCHITONIDAE

16a *Radsiella eucosmius* (Dall, 1919) D
23x *Stenoplax circumsenta* Berry, 1956 D
32 *Lepidozona crockeri* (Willett *in* Hertlein & Strong, 1951) D
35 *Lepidozona formosa* Ferreira, 1974 D
37 *Lepidozona serrata* (Carpenter, 1864) D

MOPALIIDAE

48 *Dendrochiton lirulatus* Berry, 1963 D
50 *Placiphorella velata* Dall, 1879 S

SCAPHOPODA

DENTALIIDAE

7 *Dentalium (Graptacme) sectum* Deshayes, 1826 D
11 *Dentalium (Tesseracme) tesseragonum* Sowerby, 1832 D

SIPHONODENTALIIDAE

17 *Siphonodentalium quadrifissatum* (Pilsbry & Sharp, 1898) D

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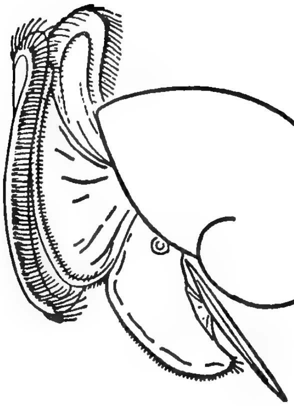

Tambja and *Roboastra*

(Mollusca : Opisthobranchia)

from the Gulf of California and the Galápagos Islands

BY

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(20 Text figures)

EVELINE AND ERNST MARCUS and James R. Lance published a description of *Nembrotha eliora* Marcus & Marcus, 1967, and *Nembrotha hubbsi* Lance, 1968, respectively. The papers describe the same animal species as shown by photographs, illustrations, and descriptions. Further work now shows that Marcus & Marcus' *N. eliora* was described from 2 lots of material. Their "material one" is similar to Lance's species and therefore *N. hubbsi* is considered a junior synonym of *N. eliora*. The Marcuses have 2 species in their description. Their "material two" is of a new species of *Tambja*. Lance's *N. hubbsi* also involves 2 different species. His description of *N. hubbsi* is correct, except the radula figure is that of a *Roboastra*.

The members of the genus *Nembrotha* as used by Marcus & Marcus have denticles or serrations on the leading edge of the teeth. In *Tambja*, the leading edge of the rachidian is smooth.

NUDIBRANCHIA

Doridoidea

PHANEROBRANCHIA

NONSUCTORIA

GYMNODORIDIDAE

Tambja Burn, 1962

Type species: *Nembrotha (?) verconis* BASEDOW & HEDLEY, 1905; 29: 146, 158, 159; plt. 2, figs. 1 - 3

"Rachidian is rectangular with notched or smooth upper margin, lateral tooth has a bifid or simple cusp with 3 - 7 marginal plates. The buccal collar is strong; a labial armature is absent. The small prostate gland is confined to a glandular section of the vas deferens." (BURN, 1967: 214).

Tambja eliora (Marcus & Marcus, 1967)

(Figures 1 - 3, 18)

Nembrotha eliora MARCUS & MARCUS, 1967: 194 - 196; figs. 57, 58; – FARMER, 1968: 26, 27 (fig.); – 1970a: 16; – 1970b: 73, 75, 78 (figs. 6, 8), 79, 84; – 1970c: 5, 12, figs.; –KEEN, 1971: 827, 828; plt. XX, fig.3; – ABBOTT, 1974: 358; – SKOGLUND, 1974: 5

Nembrotha hubbsi LANCE, 1968: 6 - 8; plt. 1, fig. 6

Syntypic material (*eliora*): the holotype number is USNM 678410 and radular slide no. 915.6. One specimen and its radula are represented. The type of *N. hubbsi* is an intact specimen, CASIZ type series no. 315. The radula illustrated is of a *Roboastra* from another specimen no longer intact.

Type Locality: Puerto Lobos, Sonora, Mexico.

Distribution: Angel de la Guarda Island, Guaymas, Escondido Bay, Carmen Island, Monserrate Island, San

Figure 1

Tambja eliora (Marcus & Marcus, 1967)

Diego Island, Punta Entrada, Espiritu Santo Island, La Paz, Cerralvo Island, and Magdalena Bay, Mexico.

Description: The radula, based on a minimum of specimens, is typically that of a *Tambja* with the formula $15 \times 5\text{-}4 \cdot 1 \cdot 1 \cdot 1 \cdot 4\text{-}5$ (Figure 2). No labial armature is evident. The animal can attain a length of 50 mm and is limaciform. The foot color is gray; the edge of the foot is blue. Three marked turquoise blue stripes on the dorsum are bordered by black. The rhinophores have 22 leaves. The gills are unipinnate and nearly black in color; the axis of the gills is marked with turquoise, black, and yellow ochre. The morphology of the head is characteristic in this animal where the cephalic shield dips into a "V" or "U" shape (Figure 1). The cephalic tentacles are broad and flat.

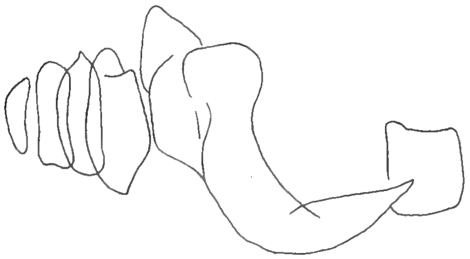

Figure 2

Radula of *Tambja eliora* (Marcus & Marcus, 1967)

A dorsal orientation of the reproductive system shows many of the parts in surface view. Carefully teasing the organs apart (Figure 3), the atrium is found to be enlarged. The hermaphrodite duct leads into the large vaginal gland by way of an ampulla. A thin sac-like structure is connected to the nidamental duct as is the adjacent round spermatotheca.

Behavior: *Tambja eliora* swims by undulating the body from side to side (Farmer, 1970b). This is an escape response to the advances of the predatory slug, *Roboastra tigris* Farmer (spec. nov., herein) (Figure 18). Other possible reasons for swimming are not known.

Discussion: The "material one" of Marcus & Marcus, 1967, is compatible with the above description. Their "material two" is also part of the original material, but it represents another species, which is described below as *Tambja abdere*.

Lance's work with *Nembrotha hubbsi* was nearly concurrent with that of Marcus & Marcus, although each was unaware of the other's involvement.

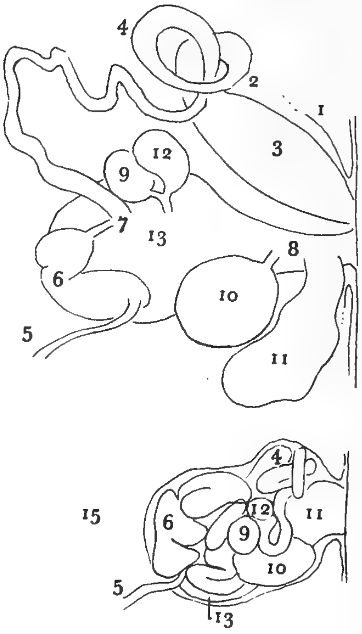

Figure 3

Gonads of *Tambja eliora* (Marcus & Marcus, 1967)

1 – capsule membrane
2 – penis
3 – atrium
4 – prostate
5 – hermaphrodite duct
6 – ampulla
7 – oviduct
8 – nidamental duct
9 – spermatocyst
10 – spermatotheca
11 – Sac
12 – Ampulla
13 – vaginal gland
15 – gonad in dorsal orientation

Specimen distribution of *Tambja eliora* and the number of specimens include:

CASIZ 003565 San Pedro Island, 32 km N of Guaymas, Mexico, in 24 – 27 m of water. Leg. Bill Van Zandt, (2 specimens).

USNM 709790 San Pedro Island, 32 km N of Guaymas, Mexico, in 24 – 27 m of water. Leg. Bill Van Zandt, (1 specimen).

LACMNH 71-14 3 – 15 m, east side of Punta Entrada at Sail Rock (N entrance to Magdalena Bay), Baja California, Mexico (24° 32.4′ N, 112° 04′ W). Leg. James H. McLean, 30 – 31 January, 1971. (1 specimen).

LACMNH 16904 La Paz area, Baja California, Mexico. Leg. Edwin Janss. May, 1972 (3 specimens).

LACMNH A.9942 Near Escondido Bay, Carmen Island, Baja California, Mexico. Leg. Carl Gage and Chuck Fisher, March 28, 1974. (1 specimen).

LACMNH A.9555 Isla Monserrate, Baja California, Mexico. Leg. Edwin Janss, April, 1974. (2 specimens).

LACMNH A.9555 13.5 m, S end of Isla San Diego, Baja California, Mexico. Leg. Edwin Janss, April, 1974. (6 specimens and 1 *Tambja abdere* Farmer).

SDMNH 63051 Isla Monserrate, Baja California, Mexico, April 13, 1969. Leg. Bill Van Zandt. (1 specimen).

DMNH 92182 San Pedro Island, 32 km N of Guaymas, Mexico in 24 – 27 m of water, April, 1969. Leg. Bill Van Zandt. (1 specimen).

BMNH 197936 San Pedro Island, 32 km N of Guaymas, Mexico in 24 – 27 m of water, April 13, 1969. Leg. Bill Van Zandt. WMF # 650. (1 specimen).

WMF 651 San Pedro Island, 32 km N of Guaymas, Mexico. 24 – 27 m of water. Leg. Bill Van Zandt, April 13, 1969. (12 specimens).

Tambja abdere Farmer, spec. nov.

(Figures 4 - 6)

Nembrotha eliora Marcus & Marcus, 1967: 195 (original "material two" only)
Nembrotha sp. Farmer, 1970a: 16

Holotype: CASIZ No. 687. An egg mass is also included.

Paratypes: USNM 709791; LACM 1717; SDSNH 63052; DMNH 92183; and BM[NH] 997838.

Type Locality: La Paz, Baja California, Mexico. Edwin Janss, Jr., coll. May 1972.

Distribution: Punta Lobos, Guaymas, Danzante Island, San Diego Island, San Francisco Island, and La Paz, Mexico.

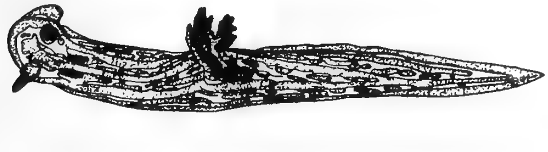

Figure 4

Tambja abdere Farmer, spec. nov.

Description: The 80mm long type specimen is limaciform (Figure 4). The sole of the foot is brown and the foot margin is ochre. The general color is yellow ochre with 4 distinct areas of turquoise, 2 on each side and 2 dorsal. These areas extend the length of the body, and within them are irregular patches of yellow ochre. Between the turquoise and yellow ochre is black. The head shield is horizontal across the front. Two flat cephalic flaps under the head shield of yellow ochre have turquoise between them. The blue-black rhinophores are retractile into highly set shields. The eye spots are prominent and blue-black. The gills (one unipinnate and 2 bipinnate) are dark and are set on a yellow ochre axis anterior to the anus. The radular formula, based on a minimum of preparations (Figure 5) is $17 \times 4 \cdot 1 \cdot 1 \cdot 1 \cdot 4$. The labial armature is weak.

Dorsal observation of the reproductive system shows surface areas and placement of the organs before they are teased apart. The penis is a narrow structure proximally. Distally the spring-like prostate narrows to a very thin tube at its apex (Figure 6) and descends through the center of the coils, merging into an ampulla. The hermaphrodite duct leads into the vaginal gland by way of an enlarged, convoluted ampulla. A small round spermatocyst is connected to the nidamental duct at the site of

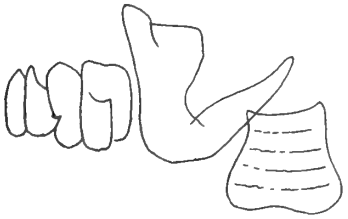

Figure 5

Radula of *Tambja abdere* Farmer, spec. nov.

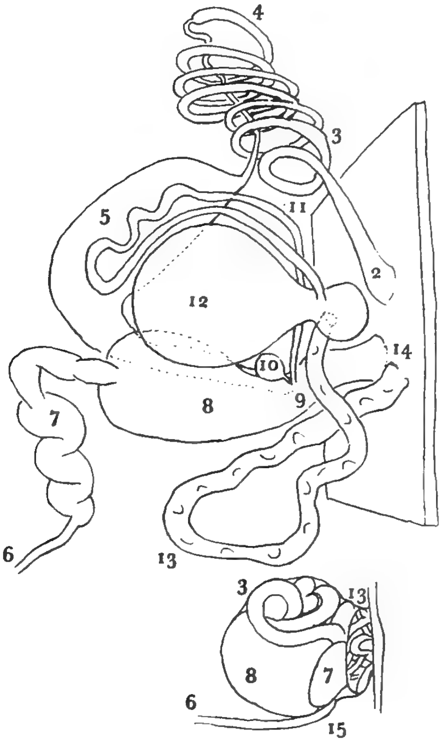

Figure 6

Gonads of *Tambja abdere* Farmer, spec. nov.

1 – capsule membrane
2 – penis
3 – vas deferens
4 – prostate
5 – ampulla
6 – hermaphrodite duct
7 – ampulla
8 – vaginal gland
9 – nidamental duct
10 – spermatocyst
11 – insemination duct
12 – spermatotheca
13 – vagina
14 – aperture of outer oviduct
15 – dorsal orientation of gonad

the insemination duct. The long insemination duct connects at a small bulbous portion of the bi-bulbar spermatotheca. Also connected to this small bulbar area of the spermatotheca at the opposite side is the lengthy vagina.

Behavior: *Tambja **abdere*** secretes great amounts of a substance from numerous goblet cells found in the skin. The reaction, triggered by the advances of ***Roboastra,*** is depicted in Figure 19.

Discussion: This species represents the "number two" material of MARCUS & MARCUS, 1967. The authors did not illustrate the species, and it was presented only in the text. However, the text revealed the difference between the 2 materials. This difference was seen in Dr. Pickens' photographs as well as in the text. *Tambja **eliora*** has blue-black rhinophoral sheaths and dark foot margins; *T. **abdere*** has yellow or yellow ochre sheaths and "bright yellow" foot margins.

Specimen distribution of *Tambja **abdere*** and the number of specimens included are:

CASIZ 687 La Paz area, Baja California, Mexico. Leg. Edwin Janss. Microscope slide of radula No. 497 specimen egg mass included. (1 specimen).
USNM 709791 La Paz area, Baja California, Mexico, May, 1972. Leg. Edwin Janss. (1 specimen).
LACM 1717 La Paz area, Baja California, Mexico, May, 1972. Leg. Edwin Janss. (1 specimen).
LACM A.9555 Subtidal, Isla de San Francisco, Baja California, Mexico. Leg. Edwin Janss, February, 1974. (Specimen label incorrectly labeled *Roboastra*. 3 specimens).
SDSNH 63052 La Paz area, Baja California, Mexico, May, 1972. Leg. Edwin Janss. (1 specimen).
DMNH 92183 La Paz area, Baja California, Mexico, May, 1972. Leg. Edwin Janss. (1 specimen).
BMNH 197438 San Pedro Island, 32 km N of Guaymas, Mexico in 24 – 27 m of water, April 13, 1969. Leg. Bill Van Zandt. (1 specimen).
WMF 461 La Paz, Baja California, Mexico, 19 April, 1964. Leg. Richard Adcock. (1 specimen).

Etymology: The specific name ***abdere***, which is Latin and Greek, meaning "away from" and "skin," is selected to call attention to the ability of the animal to produce copious amounts of defensive secretions.

*Tambja **fusca*** Farmer, spec nov.

(Figures 7 - 9)

Holotype: CASIZ No. 688. It consists of a dissected animal and a radula slide.

Paratypes: USNM 709792; LACM 1719; SDSNH 63052; DMNH 92184; and BM[NH] 197435.

Type Locality: Isla Monserrate, Baja California, Mexico; Edwin Janss, Jr. coll. April 1964.

Distribution: Concepçion Bay, La Paz, and Cabo San Lucas, Baja California, Mexico.

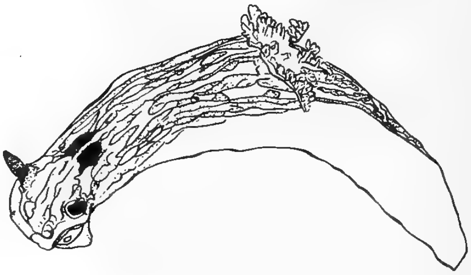

Figure 7

*Tambja **fusca*** Farmer, spec nov.

Description: The 40 - 50 mm long animal is limaciform (Figure 7). The sole margin is ochre and is bordered by a black line. The general color is a dark yellow ochre with areas of turquoise of an irregular pattern. Between the ochre and turquoise is a thin line of black. The retractile rhinophores are ruddy with dark tips. They have 19 leaves. One unipinnate and 2 bipinnate gills are set about half way on the back of the animal. The gills are dark tipped with slightly lighter areas attached to the ochre axis of the gill supports. The anal papilla is located just posterior of and next to the gills. The eye spots are dark in color, easily recognizable, and set posterior of and medial to the rhinophores.

The radular formula, based on a minimum of preparations, is $15 \times 4 - 3 \cdot 1 \cdot 1 \cdot 1 \cdot 3 - 4$ (Figure 8). A thin labial armature is present.

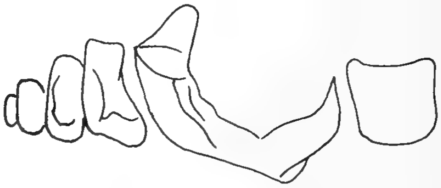

Figure 8

Radula of *Tambja **fusca*** Farmer, spec. nov.

Viewing the reproductive system dorsally before the capsule membrane is removed, many tubules and a wide surface of the vaginal gland are observed. Careful teasing of the system reveals the spermatotheca to be bi-bulbar (Figure 9) with a relatively short insemination duct. The spermatocyst is attached to the insemination duct, but not directly to the vaginal gland. The spring-like coils of the vas deferens and prostate surround the thin ascending

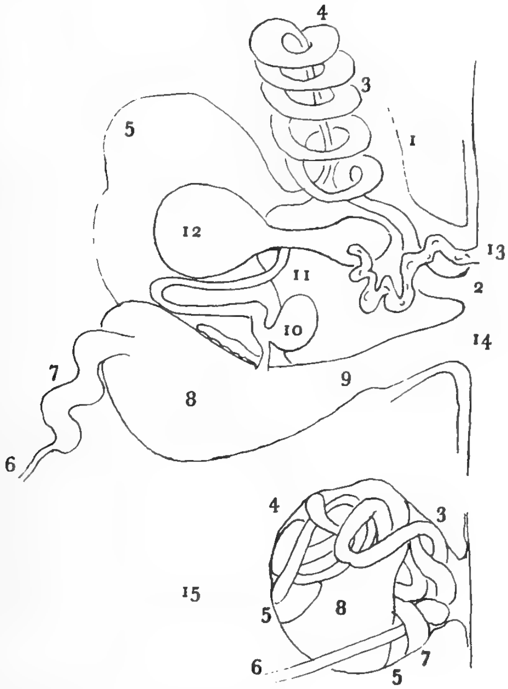

Figure 9

Gonads of *Tambja fusca* Farmer, spec. nov.

1 – capsule membrane 2 – penis 3 – vas deferens
4 – prostate 5 – ampulla 6 – hermaphrodite duct
7 – ampulla 8 – vaginal gland 9 – nidamental duct
10 – spermatocyst 11 – insemination duct 12 – spermatotheca
13 – vagina 14 – aperture of outer oviduct
15 – gonad in dorsal orientation

tube from an ampulla. The hermaphrodite duct leads into the vaginal gland through a thicker ampulla.

Discussion: The lateral teeth variations are from 3 - 4 in *Tambja fusca*, and only 4 laterals in *T. abdere*. The first tooth appears to be more robust in *T. fusca* than in *T. abdere*.

Specimen distribution of *Tambja fusca* and the number of specimens identified include:

CASIZ 688 Isla Monserrate, Baja California, Mexico. Leg. Edwin Janss, April, 1974. Radula on microscope slide No. 498. (1 specimen).
USNM 709792 Isla Monserrate, Baja California, Mexico, April, 1974. Leg. Edwin Janss. (1 specimen).
LACM 1719 Isla Monserrate, Baja California, Mexico. April, 1974. Leg. Edwin Janss. (1 specimen).
LACM A-9555 Gulf of California. Leg. Edwin Janss, 1972. (Not a *Roboastra* as per LACM label, 1 specimen).
SDSNH 63053 Isla Monserrate, Baja California, Mexico. April, 1974. Leg. Edwin Janss. (1 specimen).
DMNH 92184 Isla Monserrate, Baja California, Mexico. April, 1974. Leg. Edwin Jansa. (1 specimen).
BMNH 197435 La Paz area, Baja California, Mexico. April, 1972. Leg. Edwin Janss. (1 specimen).
WMF 649 San Pedro Island, 32 km N of Guaymas, Mexico. April 13, 1969. Leg. Bill Van Zandt. (4 specimens).

Etymology: The specific name *fusca*, the feminine form of the Latin adjective *fuscus* (meaning dark, blackish) is selected to emphasize the relatively dark coloration of *Tambja fusca* as compared to the lighter color of *T. abdere*.

Tambja mullineri Farmer, spec. nov.

(Figures 10 - 12)

Holotype: CASIZ No. 689, a dissected specimen and a microscope radula slide.

Paratypes: LACM 1718; SDSNH 63052; DMNH 92185; BM[NH] 197437.

Type Locality: Academy Bay, Santa Cruz Island, Galápagos Islands, Ecuador. David Mulliner and Gale G. Sphon, coll. 18 March, 1971.

Distribution: James Island; Jerris Island; Academy Bay, Santa Cruz Island; NW Onslow Island, and Floreana, Galápagos Islands.

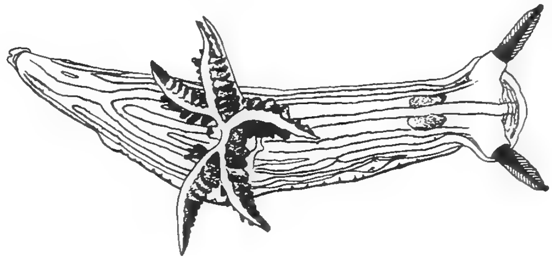

Figure 10

Tambja mullineri Farmer, spec. nov.

Description: The 15 mm long animal is limaciform (Figure 10). The foot of the living animal is like the general background color of ochre-turquoise grading into a lighter shade. Broad turquoise stripes are bordered by a thin line of navy blue. The colors are noted from a photograph by David K. Mulliner.

The one unpinnate and 2 bipinnate gills are navy blue with a light ochre-turquoise trunk supporting the gill filaments. A wide turquoise stripe extends from the gill, anteriorly between the rhinophores, to the cephalic rim. How the stripe ends anteriorly is not known since it has not been observed in relaxed living material or photographed from the front. Two dark areas are behind the rhinophores adjacent to the medial stripe.

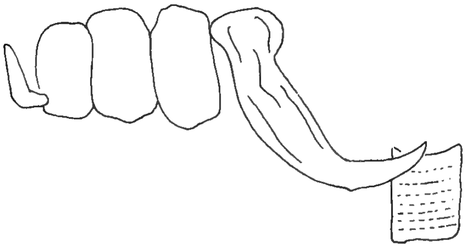

Figure 11

Radula of *Tambja mullineri* Farmer, spec. nov.

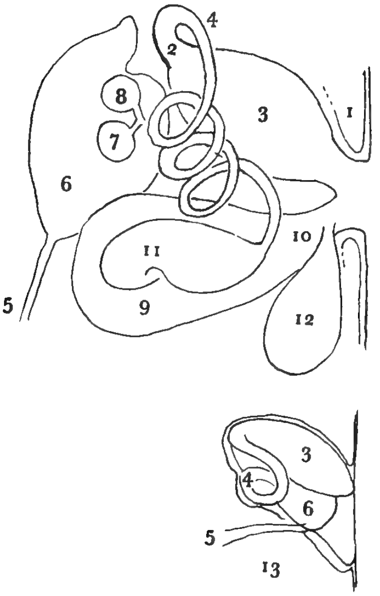

Figure 12

Gonads of *Tambja mullineri* Farmer, spec. nov.

1 – capsule membrane 2 – penis 3 – atrium 4 – prostate
5 – hermaphrodite duct 6 – ampulla 7 – spermatocyst
8 – spermatotheca 9 – vaginal gland 10 – nidamental duct
11 – ampulla 12 – vagina 13 – gonad in dorsal orientation

The rhinophores are navy-blue with ochre-turquoise leaves. The rhinophoral sheaths are thick and stout in appearance. The blunt navy-blue tipped rhinophores have 12 or 13 leaves; they are retractile. The eye spots are moderately dark.

The reproductive system, viewed dorsally with the capsule membrane intact, shows a large atrium extending to the far side. At this point, the prostate arises with a loop descending into the inner part of the mass. The hermaphrodite duct enters the mass posteriorly about $\frac{1}{3}$ the distance from the inside of the snail. Teasing apart of the reproductive system (Figure 12) reveals a large atrium and coiled prostate of uniform diameter connected to an ampulla. This ampulla rests on and is connected to the vaginal gland. The hermaphrodite duct connects to a large ampulla. A small round spermatotheca of equal size and shape and the spermatocyst join to this ampulla by a common duct. This ampulla's connection to the rest of the system has yet to be uncovered.

The radular formula (Figure 11) from a few preparations is $15 \times 4 \cdot 1 \cdot 1 \cdot 1 \cdot 4$. The labial armature is moderately stout.

Discussion: *Tambja mullineri* is similar to *T. eliora* in appearance. The frontal veil suggests a uniform sweep across the animal, unlike that of *T. eliora* which dips down the front of the head. The blue stripes are wider in *T. mullineri* than in *T. eliora*. The first lateral tooth in *T. mullineri* has a hook, but it is absent in *T. eliora*.

The distribution of specimens of *Tambja mullineri* and the number of specimens identified include:

CASIZ 689 Academy Bay, Santa Cruz Island, Galápagos Islands, Ecuador, on a reef in 22 – 30 m of water. Leg. Los Angeles County Museum of Natural History # 18171, August 26, 1974. Radula on microscope slide, No. 499 (1 specimen).

LACM 1718 James Bay, James Island, Galápagos Island, Galápagos Islands, March, 1971. Leg. Los Angeles County Museum of Natural History. (1 specimen).

LACM 1718 Jerris Island, Galápagos Islands, March, 1971. Leg. Los Angeles County Museum, David K. Mulliner and Gale Sphon. (1 specimen).

LACM 16905 On nullipores, North West of Isla Onslow, Floreana Island, Galápagos Islands, Ecuador, in 20 m. Leg. Gerard M. Wellington, January 13, 1975. Dissected gonad. (2 specimens 13 mm long each).

SDSNH 63056 Jerris Island, Galápagos Islands, March, 1971, in 10.5 m of water. (1 specimen).

BMNH 197437 Academy Bay, Santa Cruz Island, Galápagos Islands, Ecuador, in 22 – 30 m of water on reef, March 18, 1971. Leg. Los Angeles County Museum of Natural History. (1 specimen).

Etymology: *Tambja mullineri* is named for David K. Mulliner, a member of the Ameripagos Expedition, whose photographs have been useful in this study.

Roboastra Bergh, 1877

Type species: *Roboastra gracilis* Bergh, 1877: 458; plt. 56; fig. 12

"Oral tentacles are strongly developed as dorsolaterally grooved cylindrical projections equal in length to the rhinophores. Rachidian teeth are reduced to three prongs of well defined denticles. The lateral tooth is deeply bifid. Marginal plates are reduced and linear, 1 - 3 in number. The buccal collar is very weak. A labial armature is absent. A small prostate gland is confined to a coiled glandular section of the vas deferens." (Burn, 1967: 215).

Roboastra tigris Farmer, spec. nov.

(Figures 13 - 19)

Roboastra sp. Farmer, 1970a: 16

Holotype: CASIZ No. 690; it is entire. A microscope slide of the radula from another animal is with the specimen.

Paratypes: CASIZ No. 691; LACM 1720; SDSNH 63054; DMNH 92186; and BM[NH] 197439.

Type Locality: San Pedro Island, 32 km N of Guaymas, Sonora, Mexico, in 24 - 27 m.

Distribution: Los Angeles Bay, Guaymas, Monserrate Island, San Diego Island, and La Paz, Mexico.

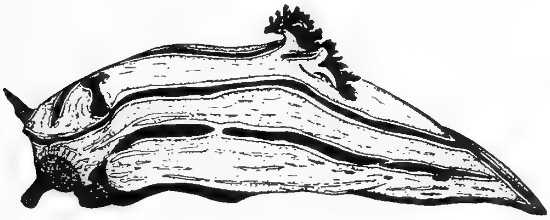

Figure 13

Roboastra tigris Farmer, spec. nov.

Description: The 200 to 300 mm long animal is limaciform (Figure 13). The sole is blue-black; the foot margin is blue. The basic color is yellow ochre with 5 black stripes bordered by bluish green. The sides may have an interrupted stripe. The retractile rhinophores are blue-black, surrounded by a rhinophore sheath, also blue-black. The cephalic tentacles are placed anterior laterally and folded with the rib of the fold downward. The eye spots are generally bluish in color and well defined. The anterior cephalic shield is marked by a slight ridge.

The radular formula, based on a few microscope slide preparations, is $35 \times 4 - 3 \cdot 1 \cdot 1 \cdot 1 \cdot 3 - 4$. The radula is typically that of a *Roboastra*. The rachidian tooth has lateral prongs. The lateral teeth vary in number from 3 or 4 and are without prongs (Figure 14). Lance (1968) figures *Roboastra* radula for *Nembrotha hubbsi* or *Tambja (Nembrotha) eliora.* One should also keep in mind that there is another *Roboastra* species living in the Gulf of California.

Figure 14

Radula of *Roboastra tigris* Farmer, spec. nov.

The oral area is cobalt blue and everts to surround its prey. Two cephalic tentacles are internal, proximal to the mouth. The radula is distal to the mouth in the buccal cavity (Figure 17).

The body is primarily a hydrocoel, which plays an important role in the swift eversion of the buccal envelope used to capture prey (Figures 18, 19).

The digestive system is a centrally located tube in the coelomic cavity. There is a digestive gland at the junction of the esophagus and stomach. The intestine has its insertion antero-dorsally to the stomach.

The cephalic ganglia produce 4 neurons of large diameter involving the external cephalic tentacles and the rhinophores.

The genital pores are located on the right side and are cobalt blue. Viewing the encapsulated reproductive system from the dorsal side, the hermaphrodite duct and ampulla overlying the vaginal gland can be seen. The round spermatotheca, vas deferens and prostate are also seen at the surface. The teased reproductive system (Figure 15) shows a uniform diameter vas deferens and slightly larger diameter prostate connected to a thin tube, the oviduct. The ampulla from the hermaphrodite duct is also connected to the oviduct. The elongate spermatocyst and round spermatotheca are situated over the large vaginal gland. An ampulla is attached to a Y-shaped tube leading

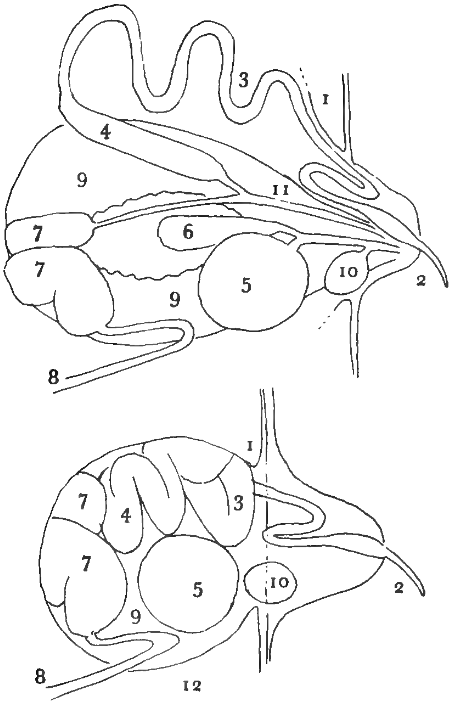

Figure 15

Gonads of *Roboastra tigris* Farmer, spec. nov.

1 – capsule membrane 2 – penis 3 – vas deferens
4 – prostate 5 – spermatotheca 6 – spermatocyst
7 – ampulla 8 – hermaphrodite duct 9 – vaginal gland
10 – ampulla 11 – oviduct 12 – gonad in dorsal orientation

from the spermatocyst and spermatotheca. The penis is armed with hooks (Figure 16). The 5 unipinnate gills are blue-black; the anus is centrally located.

An underwater photograph by Boris Innocenti clearly indicates that *Roboastra tigris* attains a length of 300 mm.

Figure 16

Penial hooks of *Roboastra tigris* Farmer, spec. nov.

The large size of this predatory slug might be linked to its feeding mechanism. A slug of such large size has mostly fluid within the coelomic cavity. This reservoir of fluid can be used to operate the rapid eversion of the buccal envelope to capture the rapidly swimming *Tambja eliora.*

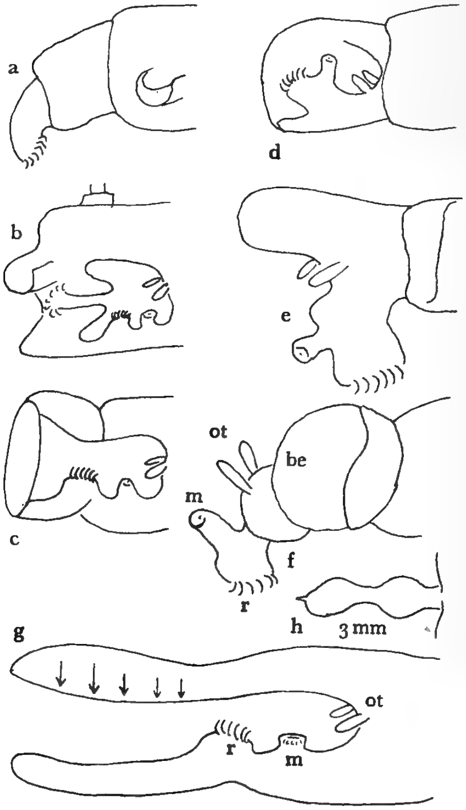

Figure 17

Roboastra tigris Farmer, spec. nov.

Illustrations of moribund specimen (a, e, f)

h – oral tentacle, swellings indicate mode of peristalsis along the length of the oral tentacle m – mouth ot – oral tentacle
be – buccal envelope r – radula

In the type species description no mention is made of the feeding apparatus seen in *Roboastra tigris.* The oral tentacles are strongly developed as dorso-laterally grooved cylindrical projections. *Roboastra tigris* has these projections; however, they cannot be called oral tentacles; they might rightly be called cephalic projections since the oral tentacles are inside the buccal area behind and above the mouth. The oral tentacles are not merely static organs but undergo peristalsis as illustrated in Figure 17h.

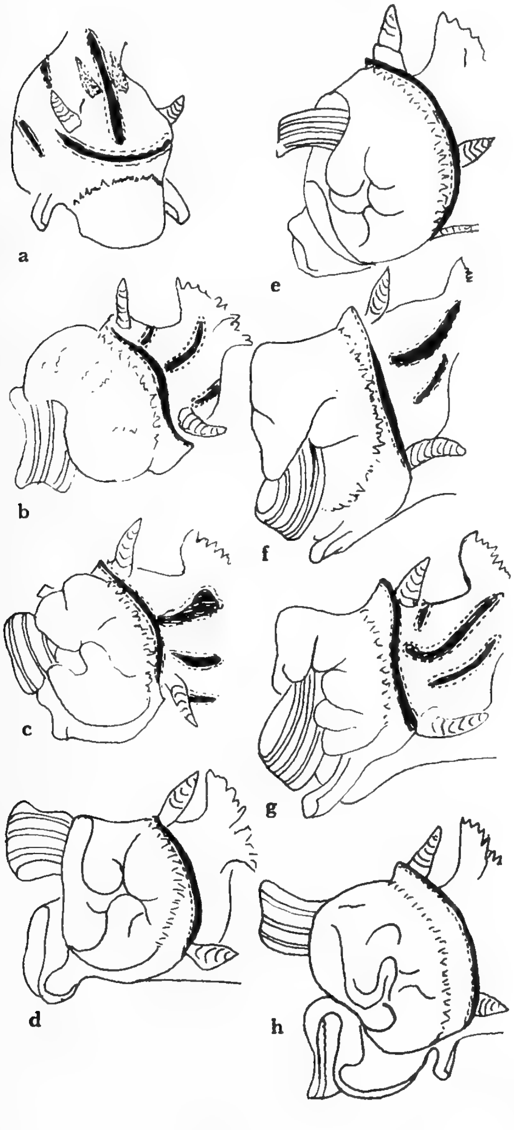

Figure 18

Sketches from selected motion picture frames of *Roboastra tigris* capturing *Tambja eliora*

Behavior: *Roboastra tigris* is photographically recorded as attempting to feed on a large specimen of *Tambja abdere* (Figure 19). Motion pictures of one feeding on *T. eliora* are partially illustrated here. It is the first known nudibranch as a predator of another nudibranch. It is known to live in a rocky environment and to attain a size of 300 mm. *Chelidonura inermis* (Cooper, 1862), a cephalaspidian, also preys upon sea slugs.

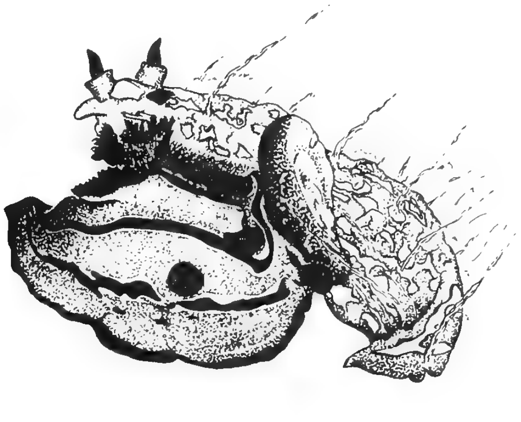

Figure 19

Roboastra tigris attempting to capture *Tambja abdere*

A color photograph illustrating the unusual feeding behavior of *Roboastra tigris* is reproduced in Sea Frontiers as *Nembrotha* sp.

The distribution of specimens of *Roboastra tigris* and the number of specimens identified are as follows:

CASIZ 690 San Pedro Island, 32 km N of Guaymas, Mexico in 24 – 27 m of water. April 13, 1969. Leg. Bill Van Zandt. WMF 650. (1 specimen).
CASIZ 691 La Paz, Baja California, Mexico, 1964. Leg. Dick Adcock. WMF 392. A specimen and microscope slide of radula No. 500.
USNM 708793 La Paz, Baja California, Mexico. May, 1972. Leg. Edwin Janss. (1 specimen).
LACM 1720 San Pedro Island, 32 km N of Guaymas, Mexico in 24 – 27 m of water, April 13, 1969. Leg. Bill Van Zandt. WMF 650. (1 specimen).
LACM 16906 La Paz, Baja California, Mexico. Leg. Edwin Janss. April, 1972. (1 specimen).
LACM A.9555 S End of Isla San Diego, Baja California, Mexico, in 13.5 m. Leg. Edwin Janss, April, 1974.
LACM A.9555 Isla Monserrate, Baja California, Mexico. Leg. Edwin Janss, April, 1974. (1 specimen).
SDSNH 63054 San Pedro Island, 32 km N of Guaymas, Mexico, in 24 – 27 m of water, April 13, 1969. Leg. Bill Van Zandt. WMF 650. (1 specimen).
DMNH 92186 La Paz area, Baja California, Mexico. May, 1972. Leg. Edwin Janss. (1 specimen).
BMNH 197439 San Pedro Island, 32 km N of Guaymas, Mexico in 24 – 27 m of water, April 13, 1969. Leg. Bill Van Zandt. WMF 650. (1 specimen).
WMF 392 La Paz, Baja California, Mexico. 1964. Leg. Richard Adcock. (1 specimen).
WMF 650 San Pedro Island, 32 km N of Guaymas, Mexico. 24 – 27 m of water. April 13, 1969. Leg. Bill Van Zandt. (1 specimen).

Etymology: *Roboastra tigris* is so named for its stripes and carnivorous appetite similar to the tiger.

Roboastra sp.

(Figure 20)

Edwin Janss snapped a photograph of *Roboastra* sp. near La Paz in June 1972 (Figure 20). It shows an animal similar to *Roboastra tigris,* but differing in detail of color and patterns, suggesting that another species of *Roboastra* may be present in the Gulf of California. Unfortunately, the specimen was devoured by one of its *Roboastra* companions in transit from the field to the laboratory. A strong resemblance in dorsally grooved oral tentacles (or cephalic tentacles) is noted between the "new" species and *Roboastra.* However, it differs by having orange-tipped rhinophores, white gills, and many more stripes on the body.

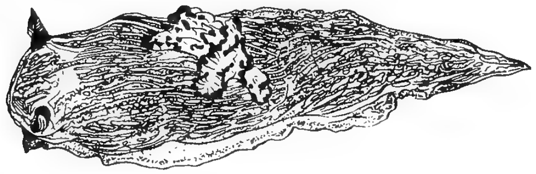

Figure 20

Roboastra sp.

Color Notes: The limaciform animal is about 60 mm long. The edge of the foot is blue-black; the body is marked with numerous stripes of yellow ochre and bluish-black. Some of the stripes are lighter in shade. The eye spots are white. The cephalic basal folds are blue-black. The base of the rhinophores is blue-black with a similar core; the leaves are bright orange. The rhinophores are tipped in blue-black; the gills are blue-black distally and white proximally. There are 5 unipinnate gills. The mouth area could not be seen in the photographs.

Abbreviations used are:

BM[NH] – British Museum [Natural History]
CASIZ – California Academy of Sciences, Invertebrate Zoology
DMNH – Delaware Museum of Natural History
LACM – Los Angeles County Museum of Natural History
SDSNH – San Diego Society of Natural History
USNM – United States National Museum
WMF – Wesley M. Farmer collection.

Key to the Eastern Pacific Species of *Roboastra* and *Tambja*

1 Mouth anterior and centrally located in the head 2
– Mouth located antero-ventrally near the foot 3
2 Rhinophores blue-black, black stripes on body few, bordered by light blue .... *Roboastra tigris*
– Rhinophores red, stripes on body numerous .... *Roboastra* sp.
3 Frontal veil horizontal 4
– Frontal veil dips into "V" or "U" shape .... *Tambja eliora*
4 Turquoise blue areas with "islands" of yellow ochre 5
– Turquoise blue stripes with "islands" of yellow ochre; both stripe colors of equal width .... *Tambja mullineri*
5 Yellow ochre dark, turquoise blue areas with "islands" of yellow ochre appearing "irregular" with variable interface between ochre and turquoise .... *Tambja abdere*
– Yellow ochre light, turquoise blue areas with "islands" of yellow ochre appearing "organized" with uniform appearing interface between ochre and turquoise .... *Tambja fusca*

ACKNOWLEDGMENTS

The author appreciates the help and support of James Lance for his contributions of literature; and Bill Van Zandt and Boris Innocenti for initial collections of 3 species of sea slugs and photographs. David K. Mulliner and Edwin Janss are responsible for the fine photographs of sea slugs, specimens, and data. Robert Burn and Eveline Marcus offered many excellent comments on procedure. Type material was sent for examination by Walter J. Byas and Clyde F. E. Roper of the Smithsonian Institution; the late Allyn G. Smith of the California Academy of Sciences; and the Santa Barbara Museum of Natural History. The manuscript was read by several friends who wish to remain anonymous; they offered editorial suggestions for the manuscript. The combined efforts of these people helped to bring this work to completion.

The author described the species; his wife, Michaelene Farmer, worked with the historical aspects of the manuscript.

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METHODS & TECHNIQUES

Air Drying Giemsa Technique for Gastropod Chromosomes

BY

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(1 Plate)

INTRODUCTION

PERHAPS NOT MORE than 0.5% of the known species of molluscs are known karyologically. Again, most of the chromosomal studies in this group have been undertaken rather recently (PATTERSON, 1971). Unfortunately, the available information on the morphology of somatic metaphase chromosomes and behaviour of germinal chromosomes during meiosis lacks details in many of the investigated species and thus needs reinvestigation. Recently several new techniques for preparations of meiotic and mitotic chromosomes of Mollusca have been described (BURCH, 1968; PATTERSON, *op. cit.*; STERN, 1975a), but most of these consume much time and labour. The present authors wish to describe here a technique for gastropod chromosomes which is quite simple and takes much less time.

MATERIALS AND METHODS

Ovo-testes of a land snail, *Euplecta subdecussata* (Pfeiffer), a pulmonate, constitute the material for the present study. The specimens received an injection of 0.1 mL of 0.025% colchicine solution directly through the apex of the shell. Two hours after the injection the shell was removed, the ovo-testes were taken out and placed in distilled water at room temperature for 45 minutes. Incubation for less than 45 minutes yielded poor spreading of chromosomes. These ovo-testes were minced and flushed in a 0.9% sodium citrate solution to obtain a thin emulsion which was centrifuged for 5 - 10 minutes. The tissue precipitate was fixed in freshly prepared aceto-methanol mixture (1 : 3). The latter was thoroughly flushed and after 10 minutes the fixative was replaced with fresh fixative. After 45 minutes of final fixation the suspended material was spread on chilled slides (stored in 50% alcohol), which were exposed to flame and then air dried.

On being dried for 24 hours or more the slides were stained with Giemsa stain (stock solution diluted 1 : 10) for 1 hour, the excess of stain being removed by washing in tap water. The dried slides were then ready for microscopic examination.

DISCUSSION

The aceto-orcein squash technique used by STERN (1975a, 1975b) for the study of chromosomes from gonads and embryonic tissue of molluscs was undoubtedly an improvement over the techniques for the chromosome cytology of Mollusca previously employed by HUSTED & BURCH (1946) since the latter required an elaborate fixing and sectioning procedure. And yet this technique failed to resolve the precise morphology, chiasma frequency, etc. of chromosomes.

Sometime earlier, BURCH (1968) has described a tissue culture technique for karyotype analysis of pulmonate land snails. However, as noted by PATTERSON (1971), tissue culture is not only time-consuming but is very expensive and requires sterile conditions.

The present authors, using the air-drying technique, obtained excellent preparations of meiotic chromosomes. The chromosomes were very well spread and thus rendered the study of their morphology, chiasma frequency, etc., extremely easy. The diploid number of *Euplecta subdecussata*, as revealed by the gonial metaphases, was found to be 54 (Figure *1*). The chromosomes were rod-

Explanation of Figures *1* to *3*

Chromosomes of *Euplecta decussata* (Pfeiffer)
Figure *1*: Gonial metaphase **Figure *2*: Pachytene stage**
Figure *3*: Diakinesis stage

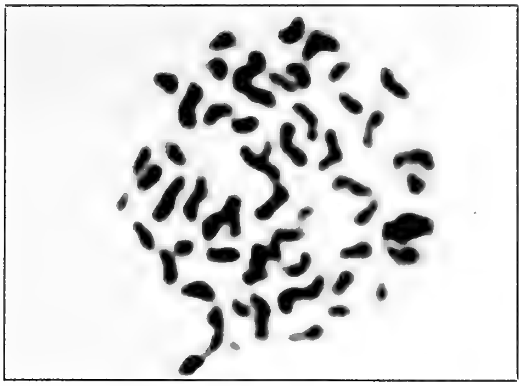

Figure *1*

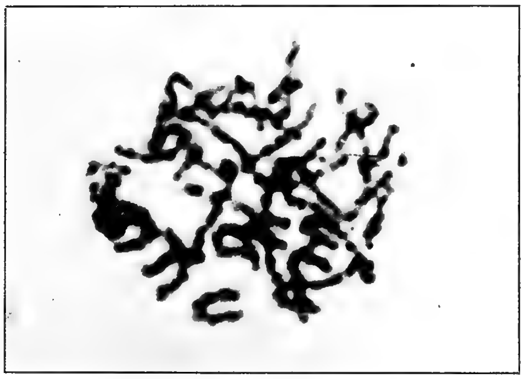

Figure *2*

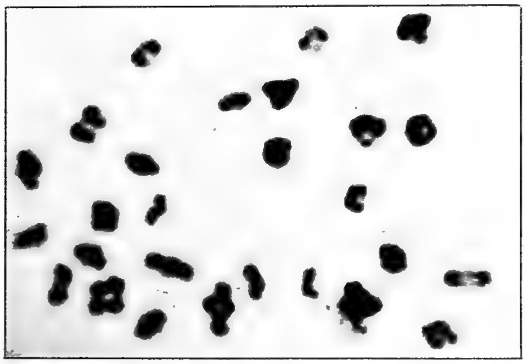

Figure *3*

Chromosomes of *Euplecta decussata* (Pfeiffer)

Figure *1*: Gonial metaphase Figure *2*: Pachytene stage
Figure *3*: Diakinesis stage

shaped and none of them could be considered a "marker chromosome" in the complement. The early stages of meiosis represent a growth phase (Figure 2) and the haploid number of 27 bivalents could be confirmed from diakinesis and subsequent stages (Figure 3). Most of the bivalents at diakinesis stage contained a single interstitial chiasma each and had undergone extreme condensation and terminalization at metaphase I. A heteromorphic or heteropycnotic sex-element could not be marked in any of the stages.

ACKNOWLEDGMENTS

The authors wish to thank the Director, Zoological Survey of India, Calcutta, for his kind help in the identification of the specimens.

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1975a. A technique for the preparation of gastropod chromosomes. The Veliger 17 (3): 296 - 298; 2 text figs. (1 January 1975)
1975b. The chromosomes of *Viviparus subpurpureus* (Say). Malacol. Rev. 8: 107 - 108; 5 text figs.

INFORMATION DESK

What's the Difference?

The Role of the Editorial Referee

BY

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We who set out to publish our work are rarely aware of the number of people who will have handled the script before it appears in print. We negotiate with the editor, but there are many back-stage workers, such as typesetters, proof-readers, layout designers, and printers. Also there are the referees who form the most faceless category of all, and to whom the editor soon relays the paper. (I use the term "referee" in the sense of "consultant," not in the sports sense of "umpire"; an alternative term, "reviewer," I prefer to reserve for one who writes a critique after publication, not before.) My purpose here is to give young authors some tips on how the process of publication can be expedited, because understanding the tasks of the editor and the referees may enable the writer to forestall much of their criticism, thus saving both time and the fraying of nerves.

The referee is usually someone who has special knowledge of the field of the paper and who thus can advise the editor on its merits as well as its faults, catch inaccuracies of text or outright errors, point out inadequate coverage of literature, and in general provide an impartial judgment of value as a contribution to science. The editor, of course, has the responsibility of seeing that the paper then is put into optimum condition before it goes to press. With what finesse he can muster, he relays the referee's criticisms (if any) to the author and works with the author in getting the paper into acceptable form. Somewhere along the line a decision must come from among four alternatives: to accept the paper in its submitted form, to take on the task of correcting minor errors, to send it back to the author for further work, or to reject it entirely. No one feels easy about making such decisions alone, so that here the referee can be of service in reinforcing the editorial judgment. Often more than one referee examines the paper. This is a way modern journals have for maintaining publication standards. Because of the frank appraisals the referees must make, they normally are happy to remain nameless and unacknowledged, and the breaching of their protective anonymity can lead to no little embarrassment.

Many editors, having had experience with typescripts of less-than-polished quality, supply their referees with a list of suggestions for evaluating papers, designed to help watch for common faults. One such list starts with the title (is it clear, concise, informative?); then it asks about the general organization (is it logical, with well-chosen subheads?); the text itself (is the sentence structure free of ambiguities, vagueness, indefinite references, superfluous words and phrases?); the illustrative matter (are tables consistent and essential?); literature cited (is the reference list adequate but not over-long, and is it properly cued in the text?); figures (are they essential, of a quality to reproduce well, and are the captions clear?); footnotes (are they properly indicated in the text, and are they appropriately placed?); lastly, the abstract, if there is one (is it a concise summary?).

How does the referee work? Well, hope greets each new script — maybe this will be the near-perfect one. It's a good omen if the word "Acknowledgments" is correctly spelled. Next comes a glance to see whether words and phrases like those in Table 1 are sprinkled too liberally through the first pages (if so, that's a bad omen). Most of these terms are correct if rightly used, but unwary writers overwork them to the point of obscuring meaning. The referee becomes hypercritical when too many of them interfere with the author's line of thought, and reading becomes a struggle through the verbal shrubbery.

Table 1

Words and phrases that frequently occur in poor writing

as to
but which
different than
etc.
found to be
in case of
instance
interesting
located
often
so that
standpoint
the fact that
very
was found

Next, the referee begins to watch for some of the common terms that authors frequently use incorrectly, such as those listed in Table 2. Misuse of any of these signals a lack of sensitivity to meanings. Some phrases even betray a failure to think clearly. For example, can anything be *quite unique*? Or an idea be *utterly basic* or have *first priority*? Are there any other than *true facts*? Yet, authors have committed these and similar infelicities in manuscripts!

Table 2

Words and phrases frequently misused

appears is not an exact synonym of *seem* and should be reserved for the meaning, "becomes visible"
around is not a synonym of *about*
curious is only in part a synonym of *strange* or *unusual*
due to is not an adequate substitute for *because of*
presently refers to the future, not to *now*
quite means *entirely* or *completely*; it is not a comparative term
which and *that* are not interchangeable ("which is non-defining and should be used only after a comma" [see Fowler (1926)])
while and *since* are time terms, inappropriate as synonyms of *whereas* and *although*

Matters of syntax should not have to concern the referee, but they do. The dangling participle, the unclear antecedent, the indefinite "it," and erratic shifts in tense or number all may slide in and make for hard reading. Such redundancies as, "measuring x mm in length" are a distraction. Logical defects may trip up the writer whose mind is more on content than on form. Kesling (1958) quotes several examples of fuzzy writing: "The ends of the spines are 2 mm. long." "The average length is about 25 mm. but it varies greatly." "Certain crabs spend all their lives in empty gastropod shells."

These, then, are some of the pitfalls that the referee hopes the author will have avoided, so that there would be no need to alert the editor about awkward usages.

Malacologists (and for that matter biologists in general) have some peculiarities of style that need examination. Here is a gem culled from a manual on invertebrates that manages five faults in three short sentences [emphasis and commentary are mine]: "A large slender *species* [1] *found* [2] in mud at low water. *It* [3] sometimes grows to nearly two feet in length. Only the *curious* [4] head is shown, which *bears* [5] four short curved hooks. ..."

Commentary: 1) A *species* is a concept, drawn up from the study of specimens. Only the specimens, then, really can have the morphological characteristics of size, shape, color, texture, etc.; the species itself has only relatedness to other forms and distribution in time and space. 2) Here the animal described *occurs* in mud; finding it has nothing to do with its ecological niche. 3) "*It*" is an indefinite reference word, presumably applying to "species," but if so, the *species* cannot grow in any such fashion; the animal does the growing. 4) Whether the animal was *curious* (*i. e.*, inquisitive) or not we really cannot judge; the illustration of it shows a bulbous head studded near the end with four recurved hooks. 5) *Bear* is a word that Fowler (1926) classes as formal or pretentious; its synonym *carry* is preferable. Formal words tend to be polysyllabic and much longer than their plainer synonyms; here, though, the formal word is actually the shorter. Another formal word that appeals to many malacologists is *possess*. A clam, as I used to point out to my students, may *have* siphons, but — I asked — does it really "possess," *i. e.*, "own" them?

A confusion between verb forms and adjectives creeps into many a species description with the use of such terms "imbricated," "angulated," and the like. The *-ed* ending implies a process. Thus "elongated" may be justifiable, for growth is a process that can increase length. Mainly, however, the use of these terms implies the adjectival or descriptive aspect — elongate, angulate, imbricate, etc.

The word "intertidal" often appears as a noun, which grates on the sensitive ear; one should say either "intertidal zone" or "intertidally" to be etymologically correct.

Another word often misused in descriptions is *prominent*, which may indeed mean *evident* or *conspicuous*. However, it really denotes something that juts out or is elevated. An umbilicus may be *well-marked*, but it can hardly be *prominent*.

Paleontologists and stratigraphers are prone to err in use of the word *interval* when they imply it to be the actual rock stratum — a "sandstone interval." An *interval* is a hiatus or gap, not a physical entity.

Telegraphic style is almost universally adopted in writing of species descriptions. Achieving consistency in its use is not always easy, however. I have discussed this in a recent note (KEEN, 1977).

How, then, should the aspiring author go about preparation of a paper? The first need is a good outline, to arrange the ideas in a logical sequence, to clarify the scope, and to put the study in its proper setting. Before starting the actual composition one should take time to read or re-read any of several available style manuals (a few are listed in Table 3) or some of the useful short papers cited under "References." That is, one should give oneself a refresher course on good writing, after which it is only human to feel a creeping paralysis, what with all the do's and don'ts that must be remembered, like the victim in this bit of verse (author unknown):

> A centipede was happy quite
> Until a frog in fun
> Said, "Pray, which leg goes after which?"
> This raised her mind to such a pitch
> She lay distracted in the ditch,
> Considering how to run!

According to a Chinese proverb, the longest journey begins with a single step. Therefore, the wise course at this point is to exert some will-power, to sit down, and to start writing. Let the words flow — visualizing it as a conversation with the prospective reader — until the first draft has been knocked into a semblance of shape. Scan it and make whatever corrections seem immediately needed, based on the previous reading. For the next step, two courses are open, and it doesn't matter which comes first: either find someone who will give the work a critical reading and point out weaknesses; or put it aside for a while before the critic sees it. MCCARTNEY (1954) tells us that the Roman teacher Quintilian advised his students to let a manuscript rest until it would seem, upon re-reading, the work of another. Our modern pace rarely permits such refrigeration, but a pause of a few days or weeks can give enough perspective to enable a more critical review of one's own work, which then should be read for order, for clarity of presentation, for correctness of wording and spelling, and for consistency between parts. Reading it aloud may help, especially if one has a friend do the reading and can listen, as the French zoologist Buffon did — for passages where the reader halts or fails to catch the meaning at once. Buffon revised or rewrote these. Soliciting criticism before publication is wise insurance against adverse reviews that could come later. Having taken these precautions the author makes the paper really ready to go to the editor.

Table 3

Style Manuals

Geowriting, a Guide to Writing, Editing, and Printing in Earth Science. American Geological Inst., Falls Church, VA. 2nd ed., 1974. 80 pp.

Manual of Style for Authors, Editors, and Copywriters. Univ. Chicago Press. 12th ed., 1969. 546 pp.

Style Manual for Biological Journals. American Inst. Biological Sciences, Washington, D. C. 3rd ed. 1972. 97 pp.

Lest anyone reading this feels that I am more prone to give advice than to act upon it, I would point out that this entire paper has been framed with almost no reverting to use of the passive voice or to those words "perhaps" and "apparently" that have hitherto been a part of my writing kit. The passive voice is a useful device, at times, especially for avoiding the forthright "I" or the wordy "the writer," and "perhaps" may be a way of softening didactic statements. However, while doing for myself the advance reading that I had recommended, I noticed such frequent injunctions against these mannerisms — for example, STRUCK (1954) says that "every passive should be considered sick until proved healthy" — that I resolved to write one paper without using them. I found it possible to change my habits, but not easy. In fact, I had to omit one sentence: in introducing the gem that manages five faults in three sentences I wanted to recount the tale of the politician who *is said* to have established an all-time record of three errors in only two words: "Them's them." But I could see no way to do it, because I could not positively document the story.

I also had the intention, when I sat down to write, to stress the modern lack of drill in school training (what child nowadays learns to parse or diagram a sentence?). Those who are not taught to distinguish between counterfeit and genuine verbal coins, who find half-a-dozen repetitions of "you know" quite acceptable in a spoken sentence, can hardly be expected to be skillful at writing. But then, in my reading, I found that Lane (1935) was quoting an editor who as long ago as 1915 deplored the then poor quality of English training in the schools! It may be that anyone, with determination, can learn to write; but writing, like any other craft, requires practice. That practice must be coupled with a constant awareness: we learn only when we begin to notice our own mistakes.

ACKNOWLEDGMENTS

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Suggestions to authors of papers submitted for publication by the United States Geological Survey. U. S. Govt. Printing Office, Washington, D. C., 4th ed., 126 pp. (later revised but now out of print; available in libraries)
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1954. Does writing make an exact man? Science 119 (3095): 525 - 528 (23 April 1954)
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NOTES & NEWS

Soviet Contributions to Malacology in 1976

BY

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We once again provide a listing of malacological publications which appeared in the Soviet Union and were abstracted in the Referativnyy Zhurnal during the year 1976. This annual resumé has appeared previously (see The Veliger 19 (4): 440 for last year's report and reference to earlier ones). The editors of the Referativnyy Zhurnal have altered the arrangement of the categories in their format, and we have followed their procedures herein.

Published malacological research in the Soviet Union shows no marked departure in quantity or quality during 1976. Several important papers appeared concerning the phylogeny, and thus, the evolutionary biology and systematics of the Mollusca during the last year. Most noteworthy is probably Shileiko's study of the excretory apparatus of the stylommatophoran Pulmonata. Since the higher categories in the taxonomy of this group are defined largely in reference to the configuration of visceral organs, especially the ureter, any evidence which questions the stability or phyletic importance of these structures demands attention. Shileiko points out that the sigmurethrous condition found among the higher pulmonates may have been independently derived more than once from the more primitive, simple orthurethrous stocks.

Minichev and Starobogatov propose a rather questionable system for the phylogeny of the Mollusca, deriving the phylum from *Dinophilus*-like annelids; such a scheme seems somewhat dated when very strong evidence indicates direct molluscan-turbellarian affinities. Starobogatov also wrote a review of the phyletic relationship among the Lymnaeidae while Zuev and his colleagues discussed the systematics of a number of cephalopod genera. Sirenko also provided some phyletic re-arrangements within the Polyplacophora.

Several new taxa were introduced and many of these in turn are doubtful, being established not only on typological criteria but rather weak biological evidence. Sirenko introduced a new subfamily, several new genera and a number of new species of chitons. Among terrestrial pulmonates, Sklyar described a new *Deroceras* from the Crimea and Shileiko established a couple of new subgenera and several new species of lauriine pupillids as well as two further new subgenera of orculids. Krivosheina added 5 new species of *Euglesa* (Sphaeriidae) from montane lakes in the Altai while Timms studied and 'revised' the finger-nail clams of an Estonian lake-reservoir system, introducing 3 more new *Euglesa*. Nominally the remarkable malacofauna of Lake Baikal has been increased by the introduction of about 4 new subgenera and 13 new species of freshwater gastropods, both pulmonate and prosobranch (see the paper by Bekman and Starobogatov).

However, several other studies tended more fully to appreciate species as biological entities with their concomitant genetic, populational, and behavioral characteristics: Alimov on *Sphaerium*, Chukhchin on hydrobiids, Mikulich and Biryulina on *Crenomytilus*, Khokhutkin on polytypy in terrestrial gastropods, and Bogatov on variability in *Lymnaea stagnalis*.

The molluscan faunas of zoologically poorly known geographical regions were studied in some detail: Arutyunova on terrestrial mollusks in the Crimea, Izzatullaev on Central Asian and Tadzhikistani land snails, Gul'bin on shallow water marine gastropods of the Kurile Islands, and Uvalieva and Mukhitdinov on Kazakhstan. Several investigations dealt with physiological problems attendant upon the adaptation to waters of varying salinities, especially in the White and Barents Seas.

Researches which reviewed or discussed other regional faunal assemblages include Govberg on the White Sea and Ignat'ev *et al.* on the Okhotsk Sea and the Sea of Japan. Roginskaya investigated the Opisthobranchia of Sosnovets Island in the White Sea, while Zuev *et al.* studied the populations of various cephalopods in the Atlantic Ocean.

Certain researches centered on the autoecology of marine and freshwater forms: Shustov on *Bythinia leachi*, Klebovich on *Hydrobia ulvae*, Spiridonov on *Dreissena*, Berger on *Littorina*, Potafeev on *Lymnaea truncatula* and Zhuravleva and Prazdnikov on *Mytilus edulis*.

Biochemical analyses stressed adaptations to new environments: Petkevich *et al.* on *Mya arenaria* in the Black Sea, while several papers were concerned with physiological parameters, most notably those concerning the reproductive biology of squids (Shevtsov) and scallops (Mal'tsev).

Several studies reported the occurrences of mollusks introduced into the territory of the USSR; namely *Mya arenaria* in the Black Sea (Petkevich *et al.*), *Melanoides tuberculatus pamirensis* in the Pamirs (Akhrorov and Churshina) and *Physodon integrum* in Tadzhikistan (Izzatullaev).

We have provided below a listing of abbreviations and acronyms which we have utilized in this compilation.

AN – Akademiya nauk (Academy of Science)
Biol. Morya – Biologiya Morya (Marine Biology)
Biol. Morya Resp. Mezhved. sb. – (Interrepublic Marine Biology Collection)
BSV – Biol. Shel'fa Tezisy dokl. Vses. Konf. Vladivostok (Scientific theses on ocean shelf biology from the All Union Conference in Vladivostok)
ES – English summary.
GZ – Gidrobiol. Zhurnal (Hydrobiological Journal)
IANT – Izvestiya Akad. Nauk Tadzh. SSR. Otd. biol. (Bulletin of the Academy of Sciences of Tadzhikistan, Department of Biological Sciences)
IFML – Issled. fauny morei, Leningrad, Nauka (Studies of marine fauna, Leningrad Science Press)
ITNIIRKO – Izv. Tikho-okeansk. nauch.-issled instituta rybn. khoziaistva i okeanogr. (Bulletin of the Pacific Scientific Research Institute of Fisheries and Oceanography)
LMA – Lietuvos TSR mosklu Akademija DARBAI (Trudy Akademiya Nauk Litovskoi SSSR). Vilna. (Works of the Academy of Sciences of the Lithuanian Republic of the USSR)
NDVS – Nauch. Dokl. Vyssh. Shkol. Biol. Nauk. (Scientific Reports of the Higher Educational School for Biological Sciences)
TLOE – Trudy Leningradskogo Obshchestva Estestvoispytatelei (Works of the Society of Leningrad Naturalists)
TRO – Trudy Instituta Okeanologii. Akademiya Nauk SSSR. (Works of the Institute of Oceanology, Academy of Science, USSR)
TVNIIMRXO – Trudy Vsesoiuznogo Nauchno-Issledovatel'skogo Instituta morskogo rybnogo Khozyaistva i okeanografii. (Articles of the All-Union Research Institute of Marine Fisheries and Oceanography)
Vestn. Zool. – Vestnik Zoologii (Zoological News)
VLGU – Vestnik Leningr. Gosudarstvennogo Universiteta (News from Leningrad State University)
ZOB – Zhur. Obshch. Biol. (Journal of General Biology)
ZZ – Zoologicheskii Zhurnal. (Zoological Journal)

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GENERAL

Golikov, A. N.
1976. Regularities in the growth and variability of some mollusks. Gidrobiol. issled. samoochishcheniya vodoemov (Hydrobiological investigations of self-cleaning reservoirs), Leningrad, pp. 97 - 118

[Variability is reflected in phenotypical modifications correlated with environmental influences, of which temperature is of prime importance]

Govberg, L. I.
1975. The formation of the mollusk fauna of the White Sea. BSV, pp. 28 - 29

[Four faunistic complexes are distinguished, beginning in pre-boreal times and corresponding to 4 stages of development. The malacofauna derives from the Barents Sea]

Ignat'ev, A. V., E. V. Krasnov & V. E. Sheigus
1975. The determination [of the effects] of temperature on growth of mollusks in the Sea of Japan and the Sea of Okhotsk by the isotopic oxygen method. BSV, pp. 62 - 63

[Analyses of isotopic oxygen in the calcite of the shells of 7 species of bivalves were made]

Izzatullaev, Z.
1975. Little known land mollusks (Mollusca, Gastropoda) of the fauna of Central Asia. IANT, No. 2, pp. 39 - 45

[A description of the shell and partial genital anatomy, as well as the ecology, taxonomy, and geographic distribution are represented for 4 species of terrestrial mollusks]

Kozlitina, L. M.
1976. Cellular stability in certain mollusks to changes in salinity. Biol. Morya, No. 1, pp. 36 - 40 (ES)

[The stability of ciliated epithelium and isolated muscle of marine mollusks was studied. The damaging effect of low salinity depends on its low tonicity. Addition of saccharose to the saline solution considerably increases the duration of tissue sensitivity]

Krivosheina, L. V.
1976. On the molluscan fauna of the mountain lakes of South Altai. KazSSR Fylym Akad. Khabarlary Izv. AN KazSSR (Bulletin of the Khabarlary Academy of Science of Kazakhstan) (Biol.) No. 3, pp. 26 - 32

[5 new species of *Euglesa* (Sphaeriidae) are proposed. Remarks on the distribution of mollusks and the reduced diversity along the gradient, plains-foothills-montane lakes, are provided]

Minichev, Yu. S. & Ya. I. Starobogatov
1976. On the phylogeny of mollusks. TLOE 84 (1): 37 - 42

[The hypothesis is proposed that the mollusks were derived from a *Dinophilus*-like ancestor. A new system of mollusks is proposed: 2 basic branches appeared at different stages of evolution, 1) mollusks with an internal cavity (coelom?) — the subtype Cochleophora; and, 2) mollusks without such an internal cavity – the subtype Peltophora. The latter diverged into 2 lineages: the Bivalvia and the Loricata, from which the Aplacophora developed. The Cephalopoda and Monoplacophora arose independently within the limits of the Cochleophora, and the latter, in turn, led to the Gastropoda]

Starobogatov, Ya. I.
1975. 5th All-Union Conference on the study of mollusks. Symposium: 'New methods of studying mollusks.' ZZ 54 (9): 1423

[56 reports were given on the biology of mollusks]

Vorob'ev, V. I.
1975. Dynamics of trace elements in the mollusks of the Volga Delta. Nekotoriye probl. ekol. zhivotnikh Nizhn. Povolzh'ya i sev. Kavkaza (Some problems of the ecology of the fauna of the lower Volga and northern Caucasus), Volgograd, pp. 3 - 13

[Aluminum, cobalt, manganese, nickel, molybdenum, zinc, lead, vanadium, titanium and silver were detected both in gastropods and bivalves. These elements were also noted in the sediments and waters of reservoirs]

Zhgenti, E. M.
1976. The Lutetiidae of the Middle Miocene, their evolution and stratigraphic significance. Metsniereba Tbilisi, 156 pp.

[The systematics, phylogeny, ecology, extinction and geochronological distribution of the family are reviewed]

APLACOPHORA and POLYPLACOPHORA

Sirenko, B. I.
1975. On the systematics of the chiton genus *Lepidozona* Pilsbry. Biol. Morya, No. 3, pp. 13 - 28 (ES)

[Seven species of *Lepidozona* inhabit the seas of the USSR: data are provided on their distribution (including Asiatic and American waters), ecology and biology. *Gurjanovillia* is synonymous with *Lepidozona*, and the species *G. derjugini* with *L. kobjakovae*. New taxa are *L. thielei*, *L. multigranosa*, *L. ima* and *L. kobjakovae kamtchatkana*]

———
1975. A new chiton subfamily — Juvenichitoninae (Ischnochitonidae) from the northwest Pacific. ZZ 54 (10): 1442 - 1451 (ES)

[A new subfamily with 3 new genera (*Juvenichiton*, *Micichiton* and *Nanichiton*) and 5 new species is erected primarily on the basis of the radula's having only 11 to 13 teeth per transverse row rather than, as the author states, the usual 17. Sirenko terms this putative reduction in the number of teeth: hypomorphosis]

———
1976. The systematics of the chiton genus *Spongioradsia* Pilsbry, 1893 (Ischnochitonina, Ischnochitonidae). Vestn. Zool. No. 2, pp. 50 - 55 (ES)

[The status of the genus is verified and a diagnosis given. *Spongioradsia* includes 3 species distributed in the Pacific, including a new one from the shores of the Kuril Islands]

GASTROPODA, GENERAL

Akhrorov, F. & N. M. Churshina

1976. The tropical mollusk *Melanoides tuberculatus pamirensis* Lindh. in the Pamirs. ZZ 55 (5): 767 - 768 (ES)

[In 1973 and 1974, large numbers of this snail, described from excavated material, were found living in Dzhaushangoz Springs in the Pamirs]

Beer, S. A., A. V. Lifshits, L. K. Maslova & V. D. Zavoikin

1976. Localized distribution and ecology of *Bythinia inflata* in the northern Tomsk Region. Report 1: The influence of abiotic factors on the distribution of *Bithynia*. Med. parazitol. i parazitar bolezni (Medical parasitology and parasitic diseases) 45 (1): 74 - 81 (ES)

[Abiotic, hydrological factors affect the occurrence of *B. inflata* which was found locally at 54 of 439 stations throughout the flood plain of the Ob River]

Gavrilov, S. I. & I. I. Desyatik

1975. The gastropods of Naroch' Lake. Vestn. Belorus. un-ta (Reports of the White Russian University), ser. 2, No. 3, pp. 47 - 50

[28 species are listed, most of which are littoral; greatest population densities are found in lightly silted substrates with rich vegetation]

Gul'bin, V. V.

1975. The distribution and biogeographical composition of the gastropod fauna of the higher portions of the Middle Kurile Shelf (Urup and Simushir). Biol. Morya, No. 4, pp. 46 - 50 (ES)

[The complex of hydrological conditions, especially water temperature, influences most the vertical and horizontal distribution of the 81 species of snails]

Uvalieva, K. K.

1976. The land mollusks of Kazakhstan and the problem of their further study. Chteniya Pamyati akad. E. N. Pavloskogo Dokl. prochit. na 8-om (1973) i 9-om (1974) ezhegodn. chteniyakh. Nauka (Lectures of the Memorial Academy of E. N. Pavlov. Reports delivered at the 8th (1973) and 9th (1974) Annual Lectures (Science). Alma-Ata, pp. 25 - 35

[Discussed are the roles of land mollusks in agriculture, in geology, and in the dispersal of helminths]

PROSOBRANCHIA

Bekman, M. Yu. & Ya. I. Starobogatov

1975. Deep water Baikal mollusks and their related forms. Tr. Limnol. in-ta. sib. Otd. Acad. Nauk. SSSR (Works of the Limnological Inst. of the Siberian branch of the AN SSSR) 18 (38): 92 - 111

[6 new deep water species (from up to 200 m) and 7 new shallow water species are described from Baikal. The latter, while showing clear relationship with the deep water forms, nevertheless point to the formation of an abyssal Baikal fauna. Intraspecific subdivisions of the genera *Benedictia* and *Choanomphalus* are discussed. Within the limits of the latter, 4 new subgenera are established. A revision of the systematics of the Baikal species of the subgenus *Gyraulus* of the genus *Anisus* shows that the only species of this genus in the "sors" zone (shallow peripheral lagoons) is *A. (G.) ignotellus* with 2 subspecies. It is also observed that among the Baikal deep water species there are certain ones not present in shallow water forms]

Berger, V. Ya.

1976. On the adaptation to decreasing salinity of several littoral White Sea mollusks. IFML, AN SSSR 17 (25): 59 - 111

[The molecular, cytological, and organismic reactions to changing salinity by *Littorina littorea, L. obtusata, L. saxatilis* and *Hydrobia ulvae* were studied, especially in differing ecological settings]

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1976. A comparison of the reactions of Barents Sea and White Sea *Littorina* to variations in environmental salinity and a discussion of the criteria of physiological races. IFML, AN SSSR 17 (25): 112 - 123

[In regard to respiratory and hematological activity, *L. obtusata* and *L. littorea* transferred from one sea to another adapted phenotypically to the different salinity regimes]

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1976. Seasonal changes in the sensitivity of White Sea *Littorina obtusata* (L.) to salinity in its habitat. IFML, AN SSSR 17 (25): 155 - 159

Berger, V. Ya. & N. N. Chernysheva

1975. A comparative study of the reaction of White Sea and Barents Sea *Littorina* to altered salinities. Ekologiya 5: 49 - 53

[Samples from populations of *L. littorea* and *L. obtusata* eventually acclimatize to salinity regimes of respective seas]

Chukhchin, V. D.

1976. The systematic placement and ecology of Hydrobiidae of the Black Sea. Biol. morya Resp. mezhved. sb. vyp. 36, pp. 65 - 75

[Black Sea hydrobiids are closely related to *H. ventrosa* of the Atlantic. Several ecological varieties appear and are correlated with such factors as depth distribution, growth, sexual dimorphism and parasitical gigantism. There are species with pelagic larvae (*H. acuta*) and those with direct development (*H. ventrosa* and *H. pusilla*). Although *H. acuta* has the greatest geographical distribution, *H. ventrosa* exhibits a wider salinity tolerance]

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1976. The life cycle and growth rate of *Hydrobia acuta* (Drap.) and *H. ventrosa* (Mont.) in the Black Sea. Biol. morya Resp. mezhved. sb., vyp. 37, pp. 85 - 90

[Both species have a one-year life cycle. From numerous diminutive eggs, benthic larvae develop directly in *H. ventrosa* while they become pelagic in *H. acuta*]

Khlebovich, V. V. & A. P. Kondratenkov

1976. The influence of hydrolized albumen on the adaptability of *Hydrobia ulvae* to reduced salinities. IFML, AN SSSR 17 (25): 132 - 135

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1976. Influence of catabolic products of some marine organisms on the saline adaptability of *Hydrobia ulvae*. IFML, AN SSSR 17 (25): 136 - 141

[The generation of metabolic products of low molecular weight facilitates adaptability to different salinity regimes]

Khlebovich, V. V. & O. Yu. Mikhailova
1975. The influence of periodic changes in salinity on the activity of *Hydrobia ulvae*. ZZ 54 (10): 1452 - 1456 (ES)

[Experimental evidence illustrates the acclimatization of this euryhaline snail to different and variable salinity regimes (6 - 24‰)]

Kondratenkov, A. P.
1976. Analysis of inter-populational differences of *Hydrobia ulvae* using gradual acclimatization. IFML, AN SSSR 17 (25): 124 - 131

[Between populations, clear differences in salinity tolerances are shown]

Korzhuev, P. A. & I. O. Alyakrinskaya
1976. Biochemical characteristics of the hemolymph of some hemocyanin-bearing gastropods. Dokl. AN SSSR (Reports, AN USSR) 228 (1): 239 - 241

[The quantitative contents of hemocyanin in the hemolymph of *Littorina littorea* and *Viviparus contectus* were examined]

Polishchuk, V. V. & I. B. Lyurin
1976. The occurrence of *Potamopyrgus jenkinsi* (Smith, 1889) in the Pripyatskii Forest. Dokl. AN SSSR (Reports, AN USSR) (B) No. 4, pp. 367 - 369 (ES)

[*P. jenkinsi*, usually an inhabitant of zones near the ocean, was collected in the Pripyatsky River]

Radoman, Pavle
1975. Species formation in the genus *Belgrandiella* and related genera in the Balkans. Glasnik Prir. Muzeya Beogradu (Public Natural History Museum of Belgrade) (B) 30: 29 - 69 (Serbian, ES)

[A new monotypic genus (*Sarajana*) and 13 new species of the 3 other genera in the subfamily Horatiinae, family Orientaliidae, are introduced. The name *Frauenfeldia* Clessin (*non* Eger) is replaced by *Graziana* (*novum*). Some remarks on the distribution of the forms are provided]

Shustov, A. I.
1975. Characteristics of the biology of *Bithynia leachi* (Shep.) in the reservoirs of Central Kazakhstan. Inst. Zool. AN KazSSR, Alma-Ata, pp. 131 - 141

[Snails are active from the end of April to early October. Data on their abundance and some of their environmental tolerances are provided]

OPISTHOBRANCHIA

Kharazova, A. D. & V. V. Rostova
1976. A study in the changes of synthesis of albumens and RNA in the tissues of the White Sea *Coryphella rufibranchialis* in reduced environmental salinity. IFML, AN SSSR 17 (25): 142 - 154

[Synthesis is reduced in hyposaline conditions and sharply restored with the return to normal salinities]

Roginskaya, I. S.
1976. Opisthobranchia of Sosnovets Island (White Sea). ZZ 55 (1): 23 - 28 (ES)

[Three littoral opisthobranchs, along with data of their ecology and reproductive biology, are recorded from Sosnovets: the sacoglossan *Acteonia cocksi* and the nudibranchs, *Onchidoris fusca* and *Ancula cristata*]

PULMONATA, LAND

Arutyunova, L. D.
1975. Notes on some land mollusks along the southern shore of Crimea. Biol. zh. Armenia (Biological Journal of Armenia) 28 (10): 104 - 109 (Armenian Summary)

[8 species of stylommatophorans are noted; descriptions of genital morphology and anatomical variability are provided]

Bratchik, R. Ya.
1976. A method for the rapid fixation of land snails. ZZ 55 (7): 1078 - 1079 (ES)

Harris, S. V.
1976. The vertical stratification of the distribution of land mollusks on the Iraqi slope of the Persian Mountains and in the Skaly Hills of Alberta, Canada. Vysokogorn. Geoekologiya (High Mountain Ecology), Moscow, pp. 101 - 102

Izzatullaev, Z.
1975. Some notes on the biology of slugs (Mollusca; Pulmonata) which are harmful to agriculture in Tadzhikistan. IANT, No. 4, pp. 22 - 24

[*Deroceras caucasicum* and *Parmacella levanderi* are especially deleterious to agriculture in the autumn and spring, respectively]

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1975. Characteristics of the distribution of land mollusks in the Gissarskii Mountain Ridge and contiguous regions of Tadzhikistan. Zool. sb. ch. 1 (Zool. Coll. Pt. 1), Dushanbe "Donish", pp. 212 - 224

[The malacofauna falls into 5 groups: 15 widely spread species, 7 species from the mountain areas of Europe and Eastern Asia, 27 Central Asian endemics, 6 tropical species or endemics with tropical relationships, and 3 introduced species]

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1975. A study of the molluscan fauna in the environs of Khorog City. Zool. sb. ch. 2 (Zool. Coll. Prt. 2), Dushanbe "Donish", pp. 5 - 7

[On the plains of the Gunt, Shakhdara, and Pyandzh Rivers, 9 species of land mollusks occur. *Nesovitrea petronella* is reported for the first time and 3 species of freshwater pulmonates are also recorded]

Khokhutkin, I. M.
1975. Polymorphisms and [population] structure of land snail taxa in the molluscan fauna of the USSR. Trudy in-ta ekol. rast. zhivotnikh. Uralsk nauch. tsentr AN SSSR (Transactions of the Institute of floral and faunal Ecology, Ural Sci. Center, Acad. Sci. USSR) 96, pp. 116 - 138

[Polytypic land mollusks have large numbers of subspecies]

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1976. On the physiological differentiation of populations of the molluscan genus *Bradybaena*. NDVS, No. 7, pp. 54 - 57

[No differences were detected in carbon dioxide respiration between *Bradybaena fruticum* and various morphs of *B. lantzi*]

Khokhutin, I. M. & A. I. Lazareva
1975. Polymorphism and imitative coloring in populations of land mollusks. ZOB 36 (6): 863 - 869 (ES)

[Polymorphism occurs more frequently than usually appreciated. A complex of phenotypic variants in 3 helicid species in the Caucasus is discussed]

Lyurin, I. B.
1975. Seasonal changes in several morphological and physiological features in mollusks from the Loess of the Ukraine. Prirod. obstanovka i fauny proshlogo (Natural Conditions and Fauna of the Past) 9, Nauk dumka, Kiev, pp. 57 - 67

[An investigation of the tempo of evolution in land and freshwater mollusks of the Loess shows that changes in temperature to extremely high or low values led to a reduction in the range of phenotypic variations]

Mukhitdinov, A. B.
1975. Zoogeographical characteristics of the land molluscan fauna of northern Tadzhikistan. IANT, No. 4, pp. 18 - 21 (Tadzhik Summary)

[42 species, some endemic, are listed from this mountainous region of Central Asia. Notes on local distribution in the Gissaro-Darvasskii Region of the Afghano-Turkestani frontier are presented]

Namatov, T. N.
1976. Respiration of some land mollusks at various temperatures. Perekrestn. adaptatsii k prirod. faktoram sredy (Correlation of adaptations to natural environmental factors), Frunze, Ilim, pp. 59 - 65

[Metabolic rate depends on body weight. Respiratory rates are lower at 20° C than at 10° C]

Ostroumova, N. K.
1976. The fine structures of neural fibres terminating in the pericardium of the cardiac muscles of *Achatina*. Fiziol. i biokhimiya mediator. protsessov. (Physiology and Biochemical Mediating Processes), Moskva, pp. 99 - 100

Pakhorukova, L. V.
1976. A quantitative assay of feeding in *Deroceras agrestis* and *D. reticulatum*. ZZ 55 (1): 29 - 33 (ES)

[Feeding and assimilation were studied in these 2 species of slugs. Bioenergetically, *D. agrestis* was more efficient. As total weight of the animals increases, the amount of food consumed decreases]

Runkova, G. G., V. N. Maksimov, L. A. Koval'chuk & I. M. Khokhutkin
1975. Extra-mitochondrial and mitochondrial oxidative pathways in sinistral and dextral morphs of the snail, *Bradybaena lantzi*, at various temperatures. Trudy Inst. Ekol. rast. i zhivotnikh, Uralsk, nauch. tsentr AN SSSR (Transactions of the Inst. of floral and faunal Ecology, Ural Sci. Center, Acad. Sci. USSR) 97: 113 - 116

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1975. Thyroxin sensitivity of endogenous oxidase in homogenates of 2 morphs of *Bradybaena lantzi*. Trudy Inst. Ekol. rast. i zhivotnikh, Uralsk, nauch. tsentr AN SSSR (Transactions of the Institute of floral and faunal Ecology, Ural Sci. Center, Acad. Sci. USSR) 97: 117 - 120

[Although some distinctions were shown, no consistent differences occur between sinistral and dextral snails]

Shileiko, A. A.
1975. The mollusks of the subfamily Lauriinae in the USSR (Pulmonata, Pupillidae). ZZ 54 (12): 1767 - 1782 (ES)

[The Caucasian Lauriinae show considerable conchological and anatomical variation, especially in the structure of the male sexual apparatus. In the Caucasus the Lauriinae include the genus *Euxinolauria* with 4 subgenera: *Matschachelia* (new subgenus), *Caucasipupa*, *Euxinolauria*, and *Neolauria* (new subgenus), and the single species *Lauria cylindracea* in the genus Lauria. The subfamily Argninae has the single Carpathian species *Orna bielzi*. 3 new species of the genus *Euxinolauria* are also described]

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1976. Characteristics of the organization and systematics of the family Orculidae (Gastropoda). NDVS, No. 4, pp. 47 - 58

[In conchological characteristics and in genital anatomy, the family is one of the more unique groups of Paleoarctic Orthurethra. The complex of shell characters indicates the primitiveness of the group while the structure of the penial appendix testifies to an advanced degree of specialization. The family is composed of 2 subfamilies, the Orculinae and the Pagodulininae, the former with 3 genera, the latter with 1. Two new subgenera are introduced: *Mesorculella* (of *Orculella*) and *Crystallifera* (of *Pagodulina*)]

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1976. Evolutionary pathways and the phylogenetic significance of the excretory apparatus of the Pulmonata. ZZ 55(2): 215 - 225 (ES)

[Really limited to the Stylommatophora, this study points out that from the primitive orthurethrous condition, wherein the ureter consists of open ciliated grooves, several advance stages in the evolution of the excretory apparatus can be recognized: Mesurethra (shortened kidney); Sigmurethra (ureters closed); Heterurethra (lung shorter and wider). The Orthurethra represent a phylogenetically primitive unit whereas the other presently recognized taxonomic grouping may consist of heterogeneous components independently evolved]

Sklyar, I. Ya.
1975. A new slug of the genus *Deroceras* (Gastropoda, Limacidae) from the Crimea. Vestn. zoologii, No. 6, pp. 79 - 82 (ES)

[Distinguished chiefly by its penial structure, *D. ramosum* is described as new from the forest zone on the Crimean peninsula]

PULMONATA, AQUATIC

Bogatov, V. V.
1975. Variability of *Lymnaea stagnalis* L. in small reservoirs. Vopr. ekol. zhivotnykh (Problems in animal ecology) 2, Kalinin, pp. 3 - 10

[Populations of snails in 6 small reservoirs in the Kalinin Region were studied. The shape of the shell is influenced by the OLA (Oscillating Level of Amplitude) of the reservoir. As the OLA increases, the shell increases in length; this effect is especially marked from May 1 to September, the period of the major blooms of macrophytes upon which the snails feed]

Izzatullaev, Z.
1975. On the discovery of the freshwater mollusk *Physodon integrum* (Haldeman) (Mollusca, Basommatophora, Physidae) in Tadzhikistan. Zool. sb. ch. 2 (Zool. Coll. Prt. 2), Dushanbe "Donish", pp. 8 - 12

[This is the first recorded occurrence of the species in Central Asia in the Plain of Vakhshskya; the shell and the genital anatomy are illustrated]

Kamardin, N. N.
1976. The structure and cellular organization of the osphradium of *Lymnaea stagnalis* L. Arkhiv anatomii gistologii, i embriologii 71 (8): 87 - 90 (ES)

[The osphradium consists of epithelial canals composed of 3 types of cells (secretory, filamentous, and epithelial) connected to basal ganglia which provide fine sensory innervations]

Kruglov, N. D.
1975. On an analysis of contemporary methods of molluscan systematics and the limit of their applications in the case of the lymnaeids. Vopr. Biol. i sistematiki zhivotnikh Smolensk. i sopredel'n obl. (Problems of biology and faunal systematics of Smolensk and the surrounding region), Smolensk, pp. 12 - 28

Kruglov, N. D., S. D. Drozdova & T. N. Makarova
1975. An ecological and morphological study of *Lymnaea corvus* (Gmelin, 1778) and *L. corviformis* (Bourgignat in Servain, 1881). Vopr. biol. i sistematiki zhivotnikh Smolensk. i sopredel'n obl. (Problems of biology and faunal systematics of Smolensk and the surrounding region), Smolensk, pp. 29 - 35

Leibson, N. L. & L. T. Frolova
1975. Localization of cell division in the intestinal epithelium of marine animals. 1. *Crenomytilus grayanus*. Biol. Morya, No. 5: 15 - 22 (ES)

[Autoradiographic methods using thymidine-H^3 noted no special localization of mitoses along the gut of the mussel, a condition unlike that found in higher vertebrates]

Maiorova, V. G. & I. V. Chernova
1976. Selective sensitivity to traces of acetylcholine in separate neurons in the large parietal and visceral ganglia of pond snails. Fiziol. i Biokhimiya mediator. protsessov. (Physiology and Biochemical Mediating Processes), Moskva, pp. 85 - 86

Potafeev, N. E.
1975. Some data on the ecology of *Lymnaea truncatula* in the Kursk region. Ekol. i eksperim. parazitol. (Ecology and experimental parasitology), Leningrad Univ., 1: 154 - 160 (ES)

[*L. truncatula* is an intermediate host of *Fasciola hepatica*. Its seasonal and diurnal activity was studied; 2 main biotopes, based on hydrological conditions, were recognized and infected snails were limited to one of the biotopes]

Potapina, N. V.
1976. A study of the amebocytes in the blood of *Lymnaea stagnalis* by autoradiography. Materialy III. Nauch. Konf. molodykh uchenykh-morfologov Moskvy (Materials of the 3rd scientific conference of young student morphologists), First Moscow Med. Inst., Mosk. Univ., pp. 34 - 37

Starobogatov, Ya. I.
1976. The systematics and phylogeny of the Lymnaeidae (Gastropoda, Pulmonata, Basommatophora). Probl. zoologii, Leningrad, Nauka, pp. 79 - 81

BIVALVIA

Alimov, A. F.
1976. Notes on the variability of some mollusks of the family Sphaeriidae. Gidrobiol. issled. samoochishcheniya vodoemov (Hydrobiological investigations of self-cleaning reservoirs), Leningrad, pp. 119 - 128

[Variability in the shells of *Sphaerium corneum, S. scaldianum, S. solidum* and *Sphaeristrum rivicola* was examined. As might be expected, stenotopic species exhibited little variation while eurytopic species, such as *S. corneum*, exhibited the greatest variability]

Belogrudov, E. A. & V. N. Mal'tsev
1975. The spawning of scallops in Pos'et Bay. ITNIIRKO 96: 273 - 278 (ES)

[Spawning takes place earlier in shallow water coves than in the open parts of the bay. Spawning continues for about 10 days in each different portion of the bay and lasts about 1.5 months in the bay as a whole]

Berger, V. Z.
1976. The effect of several physiologically active materials on the adaptive reaction of ciliated epithelial cells on the ctenidia of mussels in changing saline conditions. Tsitologiya 18 (8): 981 - 984 (ES)

Egereva, I. V.
1976. Novelties in the fauna of the Kuibyshev Reservoir. Ryb. khozyaistvo (Fisheries), No. 3, p. 29

[From 1966 to 1970 1 615 000 specimens of *Monodacna colorata* from Taganrogsky Bay were introduced, and in September 1975, only 12 specimens, measuring 4 to 22 mm, were recovered]

Gorbarenko, S. A. & A. V. Ignat'ev

1975. Changes in isotopic oxygen concentration in shells [in relation] to temperatures during growth of deep-water bivalves in the Japan Sea. BSV, pp. 32 - 33

Gurina, V. I.

1976. An autoradiographic study of the synthesis of albumen and RNA in the intestinal epithelium of White Sea mussels in relation to differing degrees of salinity. VLGU, No. 3, pp. 59 - 63 (ES)

Ivantsiv, V. V.

1975. Features of the distribution of the Unionidae in Kremenchusky Reservoir. Vestn. zoologii. No. 6, pp. 82 - 84

Kafanov, A. I.

1975. General conformity of variability in marine bivalves. BSV, pp. 74 - 75

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1975. On the interpretation of the logarithmic spiral in connection with the analysis of the variability and growth of bivalve mollusks. ZZ 54 (10): 1457 - 1467 (ES)

[Equations are provided which describe the dynamics of growth components in bivalves]

Kharchenko, T. A.

1975. The Dniepr sea-roach as a factor in the control of dreissenids in the canals. Biol. samoochishchenie i formir. kachestva vody (Biological methods for producing cleaner water). Nauka, pp. 73 - 74

[Since the sea-roach feeds on *Dreissena polymorpha* and *D. bugensis*, introduction of this fish into the Kakhovsky reservoir and elsewhere would help in the control of the bivalve]

Kodolova, O. P. & B. M. Logvinenko

1976. Electrophoresis of muscle albumens of freshwater unionids. NDVS, No. 4, pp. 142 - 144

[Differences were detected in the 2 different contractile elements of the adductor muscle]

Korchagin, V. P. & E. V. Krasnov

1975. A comparative study of the amino acid contents of albumen of the shells and byssus of several species of mussels in Peter the Great Bay (Sea of Japan). BSV, pp. 87 - 88

[*Mytilus edulis*, *Modiolus modiolus*, and *Crenomytilus grayanus* were studied; the amino acid contents of the periostracum, the byssus and the ligament are species specific]

Kulakovskii, E. E.

1976. The influence of reduced salinity on the neuro-secretory system of *Mytilus edulis* (L.). IFML, AN SSSR 17 (25): 160 - 166

[In the cerebral ganglia, 3 morphologically and topographically distinct types of neurosecretory cells occur. Although neurosecretion is altered under reduced salinity, our data are insufficient to quantify the response]

Kuz'movich, L. G., I. V. Shust & I. M. Kostnik

1976. Histological characteristics of the gonads of *Anodonta piscinalis* Nilss. NDVS, No. 6, pp. 63 - 68

[Histochemical analysis of lipids, neutral fats, and polysaccharides of unparasitized sex cells]

Mal'tsev, V. N.

1975. Some regularity in the settling of *Pecten* larvae in collectors in Pos'et Bay. ITNIIRKO 96: 179 - 282 (ES)

[The extent, date, and density of spat by depths are given for Peter the Great Bay; data on the dependence of the date of settling on the temperature of the water are provided]

Mikulich, L. V. & M. G. Biryulina

1975. On the problem of the species-concept for *Crenomytilus grayanus* (Dunker). Trudy Tikhookean. in-ta (Transactions of the Pacific Ocean Institute) 9: 114 - 118

[The length/width index varies between 1.4 and 2.7 in populations from various localities and different ecological stations. These differences in the form of the shell reflect the range of intraspecific variation, and all individuals with different indices form a single species]

Naumov, A. D.

1976. Variability of *Portlandia arctica* (Gray) in the complex of [environmental] characteristics of the White Sea. Probl. zoologii, Leningrad, Nauka, pp. 67 - 69

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1976. The adaptation of *Portlandia arctica* var. *portlandica* (Taxodonta) of the White Sea to waters of lower salinity. ZZ 55 (3): 449 - 453 (ES)

[Differences were noted in the physiological activity of individuals from shallow and deep water; it is suggested that in the White Sea there are 2 races, with the deep water one being euryhaline]

Petkevich, T. A., R. P. Kandyuk & I. A. Stepanyuk

1975. On the biochemistry of the mollusk *Mya arenaria* (L.), newly discovered in the Black Sea. GZ, 11 (5): 101 - 106

Rakov, V. A.

1975. Changes in the shell shape of *Swiftopecten swifti* during growth. ITNIIRKO 96: 302 - 304 (ES)

Sanina, L. V.

1975. Preliminary estimates of the nutrient requirements for filter-feeding mollusks in the northern Caspian. TVNIIMRXO 107: 43 - 47 (ES)

Skirkyavichene, Z. Yu.

1975. Amino acid content of the soft parts of dreissenids in Kurshyu-Mares Bay. 2. Free amino acids at various times of the year. LMA (B), No. 3 (71): 127 - 133 (ES)

[Chromatographs from dreissenid tissue taken in 1967 and 1968 showed a content of 21 free amino acids; seasonal variations were noted]

Spiridonov, Yu. I.

1975. The growth structure of a population and persistence of life of *Dreissena* in the Volgograd reservoir. Tr. kompleks. ekspeditsii Saratov. un-ta po izuch. Volgogr. i Saratov vodokhranilishch. (Transactions of the Combined Expedition of Saratov University to Study Volgograd and Saratov Water Reservoirs) 5, pp. 84 - 86

Tadić, Ante
1975. Some *Unio* and *Anodonta* species in various habitats. Glasnik. Prir. Muzyea Beogradu (Public Natural History Museum of Belgrade) (B), 30: 103 - 118 (Serbian, German S.)

[Studies of 10 species of *Anodonta* and 2 species of *Unio* show that shell morphology is correlated with environmental conditions]

Timm, Viivi
1976. On the Pisidiidae of the lakes of the Chudsky-Pskov Region (Lake Peipsi-Pihkva). Izv. AN EstSSR, Biologiya (Bulletin of the Academy of Science of Estonia, Biology) 25 (1): 37 - 52 (ES)

[30 species of 6 genera were collected from 1964 to 1974: *Sphaerium*, 1; *Amesoda*, 1; *Musculium*, 1; *Pisidium*, 2; *Euglesa*, 22; *Neopisidium*, 3. 26 species were collected for the first time in reservoirs, 2 of which are new to Estonia, and 3 species are new to science (*E. peipsi*, *E. pihkva*, and *N. stelfoxi*). Although the majority of species occurs in all the reservoirs, none appears in large numbers. Data are provided on the depth distribution and bottom preferences of *Pisidium*]

Zhuravleva, N. G. & E. V. Prazdnikov
1975. The ecology, reproduction, and development of the mussel *Mytilus edulis* in the Barents Sea. BSV, pp. 52 - 53

CEPHALOPODA

Bityukova, Yu. E. & G. V. Zuev
1976. The asymmetrical eyes of the Histioteuthidae in connection with their ecology. Biol. morya. Resp. mezhved. sb., vyp. 38, pp. 63 - 67

[It is concluded that the larger eye functions on the surface, the smaller in the depths]

Nesis, K. N.
1975. Evolution of adaptive forms in Recent cephalopods. TRO 101: 124 - 142 (ES)

[The morphological adaptations to diverse habitats (*i. e.* benthopelagic, nectobenthic, nektonic, benthic and planktonic) are considered]

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1976. Stimulation of bioluminescence in cephalopods. Okeanologiya 16 (1): 150 - 154 (ES)

[A weak solution of hydrogen peroxide intensifies the luciferin-luciferase reaction and was used on ship-board to stimulate the photophores in several species of epipelagic squids]

Shchepkin, V. Ya., G. E. Shul'man & T. G. Sigaeva
1976. Features of the lipid content in Mediterranean squids in various ecologies. GZ 12 (3): 76 - 79

Shevtsov, G. A.
1975. Spawning in the Pacific Ocean squid, *Todarodes pacificus* Steenstrup, in the southern part of the Sea of Okhotsk. ITNII RKO 96: 121 - 127 (ES)

[A population appears in the Okhotsk in autumn; length-weight measurements are given for males and females]

Zuev, G. V.
1975. Some notes on the intraspecific grouping of *Ommastrephes pteropus* (Cephalopoda, Mollusca) in the tropical Atlantic. Biol. issled. v. tropich. zonye okeana (Biological studies of the tropical zone of the ocean), Kiev, Nauk dumka, pp. 68 - 76

[In this zone, the epipelagic *Ommastrephes pteropus* forms 3 biologically specific populations: Canarian, mid-passage and equatorial]

Zuev, G. V., K. N. Nesis & Ch. M. Nigmatullin
1975. The systematics and evolution of the squid genera *Ommastrephes and Symplectoteuthis* (Cephalopoda, Ommastrephidae). ZZ 54 (10): 1468 - 1479 (ES)

[The authors claim that photophores are the most significant taxobases in deducing the phylogenetic relationships of several ommastrephid squids. As is general in teuthology, most of the genera are monotypic. Some paleontological speculation based on the modern distribution of the species as well as a phylogenetic dendrogram are provided]

———
1976. The distribution of the genera *Ommastrephes* d'Orbigny 1835, *Stenoteuthis* Verrill 1880, and *Todarodes* Steenstrup, 1880 (Cephalopoda, Oegopsidae) in the Atlantic Ocean. Biol. Mosk. ob-va ispyt. prirody (Bull. Moscow Naturalists Soc.) 81 (4): 53 - 63 (ES)

[From field observations and the literature, it is concluded that *S. pteropus* consists of no fewer than 9 partially sympatric populations mainly equatorial, that *O. bartrami* is subtropical, and that *T. sagittatus* occurs in subtropical and boreal waters of the northwestern Atlantic. Another species of *Todarodes*, *T. angolensis*, is of a more southerly distribution in sub-Antarctic waters]

Zuev, G. V. & Ch. M. Nigmatullin
1975. The spatial structure of the distribution of the ocean squid *Ommastrephes pteropus* Steenstrup in the Eastern Atlantic. Biol. issled. v tropich. zonye okeana (Biological studies of the tropical zone of the ocean), Kiev, Nauk dumka, pp. 56 - 67

[The Atlantic distribution of the species includes the entire tropical zone with northern limits in Africa at 20° to 22° N in winter and in summer to 30° or 32° N. The southern limit is 20° - 23° S throughout the year. Productivity depends on variations of the vertical circulation of the water, and the population density of the squid increases in the winter]

A Note on Changes in Marine Intertidal Fungus Taxonomy

BY

DAVID R. LINDBERG
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With ever increasing literature and specialization in the natural sciences it is becoming increasingly difficult for workers to keep abreast of developments within their respective fields. It is even more difficult to be aware of the developments and changes within areas or with organisms only tangentially associated with one's specialty. So while a worker may publish a modern up-to-date monograph or revision of his or her specialty, he or she may unknowingly include incorrect information on other organisms in the same text. I recently came across one of these problems in my work and since it involves an organism familiar to many malacologists, cirripedologists, and intertidal ecologists, I am calling attention to the taxonomic status of this species.

The marine fungus *Didymella conchae* Bonar, 1936, infects mollusks, barnacles, and other calcium carbonate secreting organisms, and is a major biological modifier of color patterns and morphologies of these organisms. This fungus is easily identified by the spongy appearance of the substratum and the black fruiting bodies visible at low magnification at the surface of the infected area. However, the name *D. conchae* is a junior synonym of *Pharcidia balani* (Winter) Bauch, 1936 (J. J. Kohlmeyer, *in litt.* July, 1977) and the usage of *D. conchae* is incorrect. Dr. Kohlmeyer further advises that this species could also be treated as a lichen as it sometimes forms associations with blue-green algae. The lichen name *Arthopyrenia sublitoralis* (Leighton) Arnold, 1891 is available, but junior to *P. balani*. However, the genus *Arthopyrenia* is in need of revision and an earlier available lichen name may be found, again changing the name of the shell-infecting organism. Until that time, Dr. Kohlmeyer considers *P. balani* the valid name for this fungus. For further information on marine fungi see Kohlmeyer & Kohlmeyer (1964 - 1969).

Literature Cited

Kohlmeyer, J. & E. Kohlmeyer
1964-1969. Icones Fungorum Maris. J. Cramer, Weinheim & Lehre, Germany. 7 vols.

A Rectification of a Statement Regarding the Lamarckian Collection in the Book "Murex Shells of the World" by George E. Radwin and Anthony D'Attilio

BY

ANTHONY D'ATTILIO

Shortly after the untimely death of Dr. George E. Radwin, senior author of "Murex Shells of the World" (Stanford University Press, Stanford, California, U. S. A., 1976, 284 pp.) an unfortunate situation has come to light. On page 58, the following sentence appears:

"Cernohorsky's assertion of having located this and other Lamarckian types is open to question, for Dr. Binder, of the Muséum d'Histoire Naturelle, Geneva, has stated (*in litteris*) to both of us separately that it is essentially impossible to determine the identity of Lamarck's types."

The basis of this statement is unknown, and the statement is completely erroneous. The junior author never corresponded with Dr. Binder on this or any other matter. Furthermore, in inventorying Dr. Radwin's professional papers following his death, no correspondence relating to the above matter was found. Because the junior author failed to notice this strange statement during proof-reading of the book, it was unfortunately printed.

As Dr. Radwin is deceased, the unusual circumstances responsible for the above matter may never be known. However, it is hoped that this notice will help clarify the regrettable situation for all, especially the most affected parties, Walter O. Cernohorsky and Dr. E. Binder.

Deshayes Types in the National Museum, Paris

BY

TWILA BRATCHER

In a personal communication from Dr. Philippe Bouchet, he states that the Deshayes types, formerly in the École des Mînes, Paris, have been accessioned by the Muséum Nationale d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et de Malacologie, 55 Rue de Buffon, 75005 Paris, France.

A very Generous Contribution from the Conchological Club of Southern California

A FEW DAYS AFTER our January issue had gone to press, a very generous donation to the Veliger Endowment Fund was received from the officers and members of the Conchological Club of Southern California. We express not only the thanks of the C. M. S., Inc., but of malacologists in general since all benefit from this gift, at least indirectly. As we have had occasion to point out on previous occasions, the income from the Endowment Fund helps the Society to keep the level of the dues as well as the subscription rate for the journal from rising as rapidly as the pressures of inflation would otherwise make necessary.

W. S. M.

THE WESTERN SOCIETY OF MALACOLOGISTS gave their 1977 Honor Award to Dr. Rudolf Stohler in appreciation for his many years as Editor of The Veliger, and for his continued support of the field of Malacology.

Helen DuShane, *President,* 1977
Western Society of Malacologists

Important

If the address sheet of this issue is **PINK**, it is to indicate that your dues remittance had not arrived at the time the mailing was prepared (*i. e.* by March 1, 1978). We wish to take this opportunity to remind our Members that a reinstatement fee of one dollar becomes due if membership renewals have not been received by C. M. S., Inc. by April 15, 1978. However, in view of the unreliability of the postal service, members should not be alarmed by this notice as their remittances may be received between the first of March and the date of mailing this issue on April 1. From overseas addresses we must allow a minimum of 6 weeks for surface mail. On the other hand, it is possible that the envelope and dues notice enclosed between pages 299 and 300 of the January issue have escaped your attention. If so, now is the time to use them to avoid interruption in the delivery of this periodical.

Sale of C. M. S. Publications:

Effective January 1, 1978, all back volumes still in print, both paper covered and cloth bound, will be available only from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644, at the prices indicated in our Notes and News section, plus postage and, where applicable, California State Sales Tax. The same will apply to the Supplements that are still in print, except for supplements to vol. 7 (Glossary) and 15 (Ovulidae), which are sold by The Shell Cabinet, P. O. Box 29, Falls Church, VI(rginia) 22046; and supplement to volume 18 (Chitons) which is available from Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Single Copies of "The Veliger":

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 will be presented in a forthcoming issue in the Notes and News section.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

California Malacozoological Society, Inc.
announces

Backnumbers of
THE VELIGER
and other publications

Volumes 1 through 8 and 10 through 12 are out of print.

Volume 9: $22.- – Volume 13: $24.- – Volume 14: $28.-
Volume 15: $28.- Volume 16: $32.-
Volumes 17, 18 and 19: $34.- each.

We have a limited number of volumes 9, 11, 13, 14 to 19 available bound in full library buckram, black with gold title. These volumes sell as follows: 9 - $27.-; 11 and 13 - $29.- each; 14 and 15 - $33.- each; 16 - $38.-; 17, 18 and 19 - $41.75 each.

Supplements

Supplement to Volume 3: $6.-
[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;
Part 2: The Anaspidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]
[The two parts are available separately at $3.- each]
Supplement to Volume 6: out of print.
Supplement to Volume 7: available again; see announcement below.
Supplement to Volume 11: $6.-.
[The Biology of *Acmaea* by Prof. D. P. Abbott *et al.*, ed.]
Supplement to Volume 14: $6.-.
[The Northwest American Tellinidae by Dr. E. V. Coan]
Supplement to Volume 15: Our stock is exhausted, but copies are still available from The Shell Cabinet, P. O. Box 29, Falls Church, Virginia 22046.
[A systematic Revision of the Recent Cypraeid Family Ovulidae by Crawford Neill Cate]
Supplement to Volume 16: $8.-.
[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]
Supplement to Volume 17: Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U. S. Naval Post-Graduate School, Monterey, CA(lifornia) 93940.
[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]
Supplement to Volume 18: $10.-.
[The Biology of Chitons by Robin Burnett *et al.*].
(Our supply of this supplement is exhausted; however, copies may be available by making application to the Secretary, Hopkins Marine Station, Pacific Grove, California 93950.)

Prices subject to change without notice.

Subscription rate to Volume 21 is $30.- plus postage.

We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US$12.- to US$24.-, depending on the cost to us.
Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

The Veliger is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

A Glossary of A Thousand-and-One Terms Used in Conchology
by Winifred H. Arnold

originally published as a supplement to volume 7 of the Veliger has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US$ 3.50 postpaid if remittance is sent with the order.

We are pleased to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. 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:

Volume 1:	$1.50	Volume 6:	$4.50
Volume 2:	$3.00	Volume 7:	$6.00
Volume 3:	$3.00	Volume 8:	$6.00
Volume 4:	$4.50	Volume 10:	$9.00
Volume 5:	$4.50	Volume 11:	$9.00

Volume 12: $9.00
Supplement to Volume 6: $1.50; to Volume 18: $3.00

California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, P. O. Box 243, Santa Maria, CA 93454.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644. Orders should be sent directly to Mr. West.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of $1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Supplements

Many of our members desire to receive all supplements published by the Society. Since heretofore we have sent supplements only on separate order, some members have missed the chance of obtaining their copies through oversight or because of absence from home. It has been suggested to us that we should accept "standing orders" from individuals to include all supplements published in the future. After careful consideration we have agreed to the proposal. We will accept written requests from individuals to place their names on our list to receive all future supplements upon publication; we will enclose our invoice at the same time. The members' only obligation will be to pay promptly upon receipt of the invoice.

Requests to be placed on this special mailing list should be sent to Dr. George V. Shkurkin, *Manager*, 1332 Spruce Street, California 94709

However, until further notice, we are suspending the publication of supplements until it will be reasonably certain that we will not be forced to spend many hours in tracing of lost insured or registered parcels and entering claims for indemnification. The special mailing list of members and subscribers who have entered an "including all supplements" will be preserved because of our innate optimism that sometime within our lifetime the postal services throughout the world will return to the former excellent and reliable performance.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims of missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues. This refusal is necessary as we have received an increasing number of "claims" as much as 6 months before the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address – $1.-

change of address and re-mailing of a returned issue – $2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of $12.50 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 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); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of $1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of $5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is $25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

REGARDING POSTAL SERVICE

Complaints regarding late arrival of our journal are increasing in number, steadily, continually. However, we very conscientiously dispatch our journal on the printed publication dates. What happens after deposition at the Post Office is, of course, beyond our control. From some of our members we have been able to construct a sort of probable delivery schedule. In general, within California, 8 days is usual; outside of California, the time lapse increases with the distance; the East Coast can consider a lapse of "only" two weeks as rapid service; 4 to 5 weeks are not uncommon. Foreign countries may count on a minimum of one month, six weeks being the more usual time requirement and over two months not rare!

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address).

New Postage Rates

The U. S. Postal Service has increased second class mail rates, effective on July 6, 1977. We will, however, not increase our charges for mailing The Veliger, but must insist that we are reimbursed in all cases for returned copies and for the expenses involved in remailing such copies to a new address. It is very important for our members to realize: a) the postal service will not forward any mail other than first class for more than 90 days, even though forwarding postage may be guaranteed by the addressee; and b) it is totally impossible for us to make changes in addresses in less than 6 weeks.

We must make an address change even if only one digit in the ZIP code is changed, and the cost to us is the same as for a completely new address.

Under no circumstances are we able to supply free replacement copies of issues that fail to reach their proper destination. However, we will ship by insured mail replacement copies at half the announced single copy rate of the particular issue plus postage. We have developed a triple check system so that, if we say that a copy has been mailed, we are absolutely certain that we delivered that copy to the post office in Berkeley and on the date we indicate. From our experience with the loss of insured mail, we are tempted to suggest that subscribers figure on a 10% reserve fund for the purchase of replacement copies. The only alternative remaining would be for us to increase subscription rates and membership dues by at least 10%. This, however, does not seem quite fair to us as some of our subscribers in almost 20 years have never failed to receive their copies.

On July 6 the rates for book parcels and the library rate have been increased. This necessitates that we must increase the postage charges on back volumes, supplements and individual back numbers. The charges stated must be increased by 20¢ for one item and by 8¢ for each additional item.

It has been announced by the Postal Service that no increase in postage rates would be asked during the current year; it was not stressed sufficiently that this applies only to the so-called first class mail. Second class mail rates are "phased," that is, they are scheduled to be increased each year until the rates are sufficiently high to pay the actual cost of handling that type of mail. While it is true that the rates have been very low, it should be borne in mind that the original intent of the special low rates was to aid in the dissemination of knowledge. This philosophy has, seemingly, been abandoned.

The regulations pertaining to second class mailing require "pre-sorting" of the mail which involves a large amount of time, especially if the total number of pieces is too small to warrant the employment of computerization. This requirement seems justified as long as the rates for second class matter remain substantially below those for first class matter. However, our members should be aware of the fact that postal regulations rule that second class matter cannot be forwarded three months after an address change, even though the addressee guarantees forwarding postage (in contrast, first class mail, at least for the time being, is forwarded for one year and that without charge!). Thus, issues mailed to the "old" address will be returned to the publisher if return postage is guaranteed at a rate that is considerably higher; we have been charged as much as $1.45 for such returned copies. There is also a charge of 25¢ for a postal notification of the new address. It must be obvious that we cannot keep absorbing such extra expenses and keep membership dues and subscription rate at the current low rate. We must ask for the wholehearted cooperation of all concerned to help us to hold the line against increases. Also, if a copy is returned we will, as in the past, advise the member of this fact and indicate the total costs incurred for which we must seek reimbursement. If this reimbursement is not made, we cannot continue to send future issues to the delinquent member. Membership will have to be considered as terminated and can be re-instated only upon payment of all arrears. We regret that this apparently hard rule is necessary, but we wish to continue publishing the Veliger – which will not be possible if these rules are not observed.

Although the Postal Service continues to deteriorate consistently, the postal rates are increased by 30 to 100%. We are, therefore, forced to increase the handling charges as well as the postage charges on the subscription. The following rates will be in effect on all new subscriptions and subscription renewals as of December 28, 1975:
$1.- on subscriptions and memberships in the U. S. A.;
$2.50 on memberships and subscriptions to PUAS countries (Mexico, Central and South America and Spain);
$3.50 to all other foreign countries, including Canada.
We wish to stress that we are NOT INCREASING either membership dues or subscription rates, in spite of increased printing costs. But at the same time, we wish to call the attention to our Endowment Fund, the income from which enables us, in part, to keep these charges at the established levels. Contributions (tax deductible in the U. S. A.) are always welcome.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed $200.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, $200.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office, in other words, it is destroyed.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $4.25 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

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. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

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 specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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