THE VELIGER

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CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

Volume 23

July 1, 1980 to April 1, 1981

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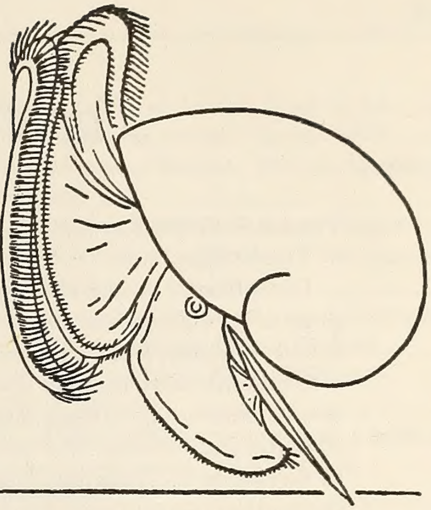

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Foreword to Volume 25

THE COMPLETION of volume 25 may be an appropriate time to review the development of The Veliger.

The physical facts are simple: from 40 pages in the first volume, the size has gradually increased to an average of over 400 pages; from a local distribution to a world-wide one; from mimeographed to printed; from text only to richly illustrated.

While this development was originally the dream of the now retiring editor, the result could not have been achieved without the generous and unselfish cooperation of many individuals. The endowment fund, the income of which is used to assist in defraying the expenses, has grown through generous gifts from many friends of the journal; several very large donations have been received; three of $1 000.00 each and one, in the aggregate over a number of years of over $25 000.00. Two shell clubs, the Conchological Club of Southern California and the San Diego Shell Club, have, for a number of years, made annual donations.

It is the purpose of this foreword to convey the editor's thanks to all for all the help received. While it is impossible to name each and every person whose help in one way or another has been received, two should be mentioned: Mrs. Jean M. Cate has made both financial contributions as well as much volunteer work as manager and proof reader for almost 20 years; Mrs. Emily Reid, who for all 25 years has contributed her matchless artistic skills.

In addition to these special individuals, the members of the Executive Board of the California Malacozoological Society have played an important role through lending their unflagging moral support and giving their wise counsel. Among them Dr. Cadet H. Hand, as President and Dr. Ralph I. Smith as Secretary deserve special thanks; the latter, in addition to the secretarial duties, has on many occasions taken on additional duties, relieving the editor when he was indisposed or on vacation. A special thank you to both.

A very large number of scientific specialists throughout the world have freely contributed their expertise in reviewing manuscripts submitted for publication in The Veliger.

It is not false pride when we believe that the journal has not only served the scientific community, but that it has served with special dignity and superb craftsmanship in the illustrations accompanying the articles. For the halftone plates the craftsmen of the Printing Department of the University of California deserve praise; for the photocomposition in the present volume the exceptional adaptability, intelligence and patience of Mr. Allin Taplin deserve special notice.

The point of special satisfaction to the editor is the fact that the development has been achieved without subsidies from any governmental agency.

With our sincere thanks to all those, named and unnamed, who have in one way or another helped and with our hope that this same kind of help will be extended to our successor, Dr. David W. Phillips, we say

Vale!

Rudolf Stohler.

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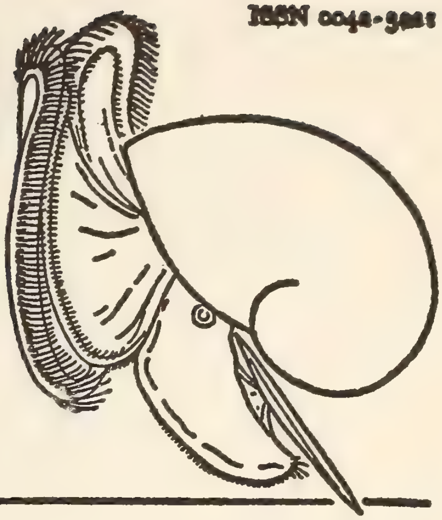

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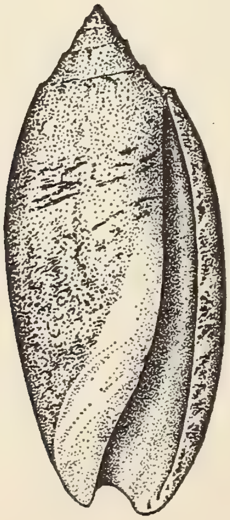

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
Superfamily, **Family**, **Subfamily**, ***Genus***, ***(Subgenus)***
New Taxa

Western Atlantic Species of *Nodilittorina*

(Gastropoda : Prosobranchia):

Comparative Morphology and its Functional, Ecological, Phylogenetic and Taxonomic Implications

BY

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(8 Plates; 11 Text figures)

INTRODUCTION

THE PRESENT STUDY started with the taxonomic review of some of the species dealt with herein. Soon it became apparent that not only a full-scale taxonomic revision of all the species would be the only satisfactory answer to several taxonomic and nomenclatorial problems, but that the taxonomic significance of the organs commonly utilised for classification, *i. e.,* shell, operculum, penis, radula and spawn, had to be re-assessed. This goal prompted a review of the functional morphology and the adaptational value to the animal of a given feature. Though much is left to do to answer such questions satisfactorily, there are indications that similar ecological pressures are prone to generate homoeomorphic properties in closely related species (*i. e.,* related on the genus and family level), and to recognise this, taxonomy must take account of as many organs and their properties as possible.

It may be worthwhile to recall the historical development of the taxonomic classification of our species. In the earlier part of the 19th century, all species were placed in the genus *Littorina.* Already in these early days, all nodulose shells were grouped together, although this was not always expressed in the generic classification (*e.g.,* PHILIPPI, 1846-48; REEVE, 1857-58). Later the genus *Littorina s. lat.* was split in various ways; without enumerating these taxonomic arguments, it may be said that the classification pattern common to all of them was to put the spirally sculptured species in *Littorina,* and all nodulose-species in *Tectarius,* except *Echininus cumingi* because of its multispiral operculum (*e.g.,* TROSCHEL, 1856-63; TRYON, 1887; THIELE, 1929; WENZ, 1939; CLENCH & ABBOTT, 1942). Only ABBOTT (1954a) recognised the close relationships between nodulose *Nodilittorina* and some of the spirally sculptured *"Littorina"* species and he separated *Tectarius* and *Nodilittorina.* But up to now all generic and subgeneric definitions of littorinid genera and subgenera coincide with the occurrence, resp. absence of nodulose or granulose sculpture (ABBOTT, 1954, 1974; ROSEWATER, 1970-73, 1981), in spite of the fact that the anatomical data described by these authors suggest many close relationships across the limits based upon shell sculpture.

The species concepts of West Atlantic Nodilittorinae reflect the development from a shell classification to a biologically oriented species classification and may be illustrated by the spirally sculptured *Nodilittorina* species. In the 19th century, all new species were proposed upon shell (and operculum) characters alone. As the differences were relatively slight and variability inevitably perceptible, BEQUAERT (1943) united all nominal species in *"Littorina ziczac,"* explaining some of the shell variations by sexual dimorphism of a single species; this interpretation proved to be entirely speculative. It was not until 1969 when BORKOWSKI & BORKOWSKI (1969) split *"Littorina ziczac"* into three species, utilising radula and spawn characters for the first time in this group. By the same criteria, Bandel (1974) recognized a fourth species, then cautiously named *"Littorina* sp.". In this paper, Bequaert's *"Littorina ziczac"* is shown to be composed of seven species, three of which can be distinguished only by radula characters, while the remaining four are also recognized by their shells, and in some instances also by spawn and operculum characteristics. Also, it proved that nearly all species were inadequately named, which was due to unresolved taxonomic problems as well as to misidentifications of type material and to nomenclatorial complications.

ACKNOWLEDGMENTS

We wish to express our thanks to all persons who supported our studies by providing information, giving recently collected specimens or enabling the examination of type specimens: C. V. A. Adams (Royal Albert Memorial Museum, Exeter, England); E. Binder (MHNG), Th. Borkowski (Chapel Hill, North Carolina), K. J. Boss (MCZ), C. E. Edwards (Miami), E. Gittenberger (RMNHL), M. Glibert (IRSNB), J. Knudsen (ZMK), E. du Bois-Reymond Marcus (São Paulo), P. B. Mordan (BMNH), G. J. Vermeij (Baltimore), A. Zilch (SMF); Mrs. Ch. Hemmer (Bonn) made the SEM photographs. Financial support of the Deutsche Forschungsgemeinschaft for one of the authors (K. B.) is gratefully acknowledged. We thank especially Prof. Dr. H. K. Erben (Paleontological Institute, University of Bonn, W. Germany) for his support.

ABBREVIATIONS

B/K	Collections of the authors (now largely in USNM, except few retained specimens of each sample.)
BMNH	British Museum (Natural History), London, England
IRSNB	Institut royal des Sciences Naturelles de Belgique, Bruxelles
MCZ	Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts
MHNG	Muséum d'Histoire Naturelle de Genève, Switzerland
RMNHL	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
SMF	Forschungsinstitut Senckenberg, Frankfurt a. M., Germany
USNM	United States National Museum of Natural History, Washington, USA.
ZMK	Universitetets Zoologiske Museum, København, Denmark

Explanations: An asterisk in synonymy lists denotes the introduction of a new name of the species group applicable to the species dealt with. Localities in the "Material examined" paragraphs are proven by radula examination unless otherwise stated.

In the plate explanations, "FN" denotes the photograph number of a SEM photograph taken and filed in the Institute for Paleontology of the University of Bonn.

Comparative Morphology and its Functional Interpretation

Anatomy of Soft Parts

General Remarks: The anatomy of *Littorina littorea* was described in great detail by Fretter & Graham (1962). These authors based their description on the accounts published by Linke (1933) and Johansson (1939) on the anatomy of *Littorina littorea, L. obtusata* and *L. saxatilis.* Marcus & Marcus (1963) dissected *"Littorina ziczac" (= Nodilittorina lineolata)* from Brazil and compared their anatomical data with those of Johansson, Fretter and Graham, and other authors. With exception of the morphology of the penis, Marcus & Marcus have noted no fundamental differences in the anatomy of *Littorina littorea* and *Nodilittorina lineolata.*

Penis: The species of the genus *Nodilittorina* described in this paper possess, where known, a slender verge with an open, but deeply folded spermiduct and with one large gland at its outer side. A basal enlargement is always present.

The penis gland was described in detail by Marcus & Marcus (1963, fig. 16). They found that it contained glandular cells lining a central cavity with a distal opening. The gland is similar in morphology to the numerous glands described in the genera *Littorina s. str., Tectarius* and *Echininus.* The genera *Littoraria, Cenchritis, Fossarilittorina* and *Melarhaphe* do not have this organ.

The penis morphology of West Atlantic species is not sufficiently known to allow subgeneric groupings in the genus *Nodilittorina.* Available data are depicted in Figures 1A-1D. Information published so far on Atlantic and Indo-Pacific species suggests a six-fold subdivision of the genus *Nodilittorina.* No consistent correlation between penis morphology and other properties of the species emerges from this, but very close relationships between nodulose and non-nodulose species can be assumed:

Group 1 (Figures 1A-1C): Penis with basal enlargement, adhesive flagellum ("Haftlappen" Marcus & Marcus (1963)) and one gland (rarely none or two) standing upright on

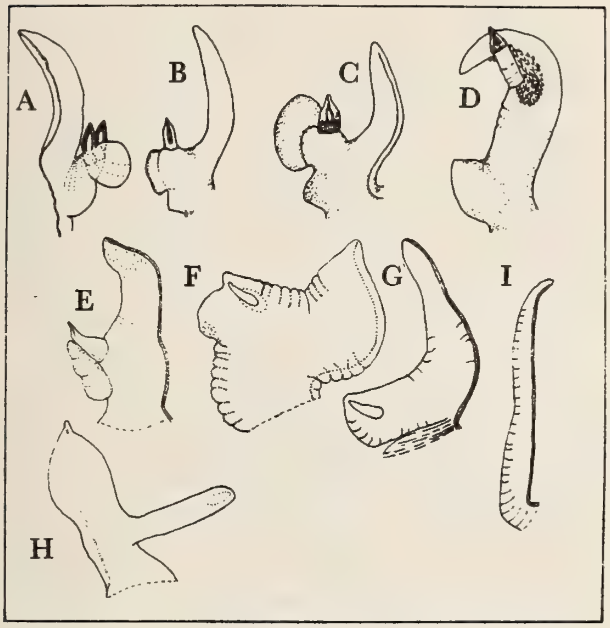


Figure 1

Penis Morphology

A) *Nodilittorina (Nodilittorina) lineolata* (Orbigny) after Marcus & Marcus, 1963 (*"Littorina ziczac,"* São Paulo)

B) *Nodilittorina (Nodilittorina)* sp. after Abbott, 1954a (*"Littorina ziczac"* from the Bahamas; may be *N. ziczac* (Gmelin) *s. str.*, *N. angustior* (Mörch) or *N.* **mordax** spec. nov.)

C) *Nodilittorina (Nodilittorina) tuberculata* (Menke) after Abbott, 1954a

D) *Nodilittorina (Tectininus) antoni* (Philippi) after Abbott, 1954a (*"Echininus nodulosus"*)

E) *Nodilittorina (Nodilittorina) pyramidalis* (Quoy & Gaimard) after Rosewater, 1970

F) *Nodilittorina (Nodilittorina) praetermissa* (May) after Ponder & Rosewater, 1979 (penis probably strongly contracted)

G) *Nodilittorina (Nodilittorina) sundaica* (Regteren-Altena) after Ponder & Rosewater, 1979

H) *Nodilittorina (Nodilittorina) acutispira* (E. A. Smith) after Ponder & Rosewater, 1979

I) *Nodilittorina (Liralittorina) striata* (King & Broderip) after Rosewater, 1981

the distal end of the basal enlargement. Caribbean species only: *Nodilittorina tuberculata*, *N. lineolata* and *N. spec. dub.* (*"Littorina ziczac"* of Abbott, 1954a).

Group 2 (Figure 1E): Penis with basal enlargement, and one gland recumbent on it; an adhesive flagellum is not always described: Indo-Pacific and Eastern Atlantic nodulose species placed by Rosewater (1970, 1981) in the subgenera *N. (Nodilittorina)* and *N. (Granulilittorina)*: *N. pyramidalis*, *N. millegrana*, *N. granosa*, *N. helenae.*

Group 3 (Figures 1F-1G): Penis with basal enlargement and one gland incorporated in its distal part. Apparently no adhesive flagellum: Indo-Pacific and Eastern Atlantic non-nodulose species placed by Rosewater (1970, 1981) and Ponder & Rosewater (1979) in *Littorina (Austrolittorina)*: *N. sundaica*, *N. unifasciata*, *N. knysnaensis*, *N. praetermissa*, *N. cincta*, *N. punctata*, *N. africana.*

Group 4 (Figure 1H): Penial gland on a long, upright projection inserting near outer, proximal end of penis, *i. e.*, at the same place as the basal enlargement of groups 1, 2, 3, 5; apparently no adhesive flagellum: the Australian *N. acutispira* only (Ponder & Rosewater (1979)).

Group 5 (Figure 1D): Penis with basal enlargement; single gland remote from it on the distal part of the verge, surrounded by "numerous, small, fleshy, opaque-white papillae" (Abbott, 1954a: *N. (Tectininus) antoni*, then named *Echininus nodulosus).*

Group 6 (Figure 1I): Penis slender, without any appendages: the West African *N. (Liralittorina) striata* only (Rosewater, 1981).

The first three groups are most closely related to each other. If the differences of the Caribbean species (group 1) prove to be significant and consistent throughout the species not yet investigated, they would be related more closely to each other than to Indo-Pacific species (groups 2, 3, 4), regardless of the presence or absence of nodulose sculpture, differences in operculum morphology and the considerable modifications of the radula in *Nodilittorina tuberculata* and *N. mordax.* In the Indo-Pacific, however, shell sculpture seems to be correlated with a penis feature, but even so the Indo-Pacific species of groups 2 and 3 would have more penis characters in common than they have with the Caribbean forms. The subgeneric name *Echinolittorina* Habe, 1956 is available for the latter, and should further anatomical evidence prove that such species as *N. tuberculata*, *N. lineolata* etc. are more closely related to each other than to their apparent Pacific analogues, *e. g.*, *N. pyramidalis*, resp. *N. paytensis*, they would have to be classified accordingly.

The fourth group is probably related to the third; the peculiarities can be seen as modifications of the characters of the third group.

The fifth, monospecific group is sufficiently different from the rest to warrant the retention of a particular subgenus, *Nodilittorina (Tectininus)* Clench & Abbott, 1942.

The sixth group, also monospecific, has been raised to subgeneric rank recently (Rosewater, 1981). The penis characters fully justify this, while radula and shell properties are well within the range observed in groups 1-4.

The differences between the four first-mentioned groups appear to be minor, and in view of the number of species not yet investigated, and the impossibility in the Caribbean species of correlating these penis properties consistently with other morphological features, these groups are united in the subgenus *Nodilittorina (Nodilittorina)* Martens, 1897. Synonyms of this are *Echinolittorina* Habe, 1956a, *Granulilittorina* Habe & Kosuge, 1966 and *Austrolittorina* Rosewater, 1970.

Little is known about the functional morphology of the penis appendages. It has been suggested that the gland and the flagellum secure the adhesion of the distal part of the penis in the mantle cavity of the female during copulation (Linke 1933, 1934: "Klebdrüsen" = "sticking glands" in *Littorina littorea;* Marcus & Marcus 1963: "Haftlappen" = "adhesive velum" in *Nodilittorina lineolata*).

Radula: Troschel (1856-63: 129) noted as a constant character of representatives of the Littorinae (in Troschel's terminology uniting the families Lacunidae and Littorinidae of Thiele's (1929-35) terminology) a low and wide lateral tooth with a characteristically extended gutter-like, outer posterior corner connected to an embayment of the outer posterior edge. Troschel expressed the opinion that generic differences in the Littorinae of his terminology showed up in the shape of the central tooth. So, for example, the members of the genus *Lacuna* are characterized as typical representatives of the Littorinae by the morphology of their lateral teeth, and as belonging in the genus *Lacuna* by the hexagonal outline of the central teeth.

Within the genus *Littorina* Troschel differentiated 3 subgenera: *Littorina, "Tectus" (= Tectarius)* and *"Nina" (= Echininus).* In order to do so he used as characters the morphology (number of whorls) of the operculum and the length-width relationship of the central tooth of the radula. In his scheme Troschel came to the assumption that *Nodilittorina pyramidalis* belonged to the subgenus *Tectus* of the genus *Littorina* along with others, as for example, *Cenchritis muricatus.*

Thiele (1929: 124-127) includes *Nodilittorina* as subgenus in the genus *Tectarius* (subgenus *Tectus* of Troschel). *Tectarius* is characterised by Thiele in regard to its radula morphology in such general terms that it cannot be differentiated with these features from members of the genus *Littorina* (subgenus *Littorina* of Troschel) in contrast to Troschel's earlier proposal. Thiele held the members of both genera *Tectarius* and *Littorina* apart only by differences in the number of whorls present on the operculum and by presence or absence of nodular sculpture of the shell.

Ponder (1976) and Arnaud & Bandel (1978) have found in their studies of radulae of Antarctic Littorinidae that there are many features to be found transitional between Lacunidae and Littorinidae. Troschel's (1856-63) assumption that the group Littorinae, encompassing both Lacunidae and Littorinidae of Thiele's classification, holds closely related species which can best be differentiated and classified by their radula morphology, was confirmed by their studies. Thus, no clear dividing line may be drawn between Thiele's families Littorinidae on one side and Lacunidae on the other side. Arnaud & Bandel (1978) noted a transition from the radula morphology of members of the genus *Laevilitorina* to that typical for the genus *Lacuna.* The members of the species of *Laevilitorina* studied show a radula morphology similar to typical representatives of the genus *Littorina* in the broad sense, including such shapes as are present in the radula of *Nodilittorina pyramidalis.*

Outside of the Antarctic region, as, for example, in the Caribbean area, Littorinidae are restricted to the intertidal and supratidal zones. In contrast to this circumstance in the Antarctic region, *Laevilitorina* lives continuously below water. There is a transition of morphological features from the radula present in *Laevilitorina* to radulae typical for representatives of the genus *Lacuna* of the northern hemisphere to be found in the southern region. Arnaud & Bandel (1978) suggested that this mode of life is, therefore, not to be considered as secondary adaptation but reflects the mode of life of the ancestors of the intertidal littorinids. However, as the taxonomic and phylogenetic relationships of the numerous taxa of the New Zealand and Antarctic region are not sufficiently known, and as the presence of *Littoraria*-like species as early as the Cenomanian points to an early adaptation to the intertidal habitat, it is not shown which taxa exhibit more primitive properties. It is even conceivable that in Antarctic waters species adapted secondarily to subtidal habitats, forced by the formation of inland and pack ice.

The radulae of 18 species of Littorinidae from the Atlantic, the Caribbean Sea and the Mediterranean Sea were described by Bandel (1974). He differentiated, by the radula function and the radula morphology derived from that function, two different groups of littorinid species. The first of these groups was exemplified by the radula of *Littorina littorea* (Figure 2B), the function of which has been described and analysed in detail by Ankel (1936, 1937). Reviews of these studies along with new observations were presented by Fretter & Graham (1962), Richter (1962) and Rosewater (1980), who divided this group in four, using details of radula morphology: "rhomboidal, hooded, moderate and pick." Into the first group of Bandel, a number of members of the genus *Nodilittorina* can be included, as for example the type species of the genus *Nodilittorina, N. pyramidalis* and also *N. ziczac, N. lineolata, N. interrupta, N. dilatata, N. vermeiji, N. glaucocincta, N. angustior* and *N. riisei.* This radula can be considered to be closely linked in its general morphology to the assumed original littorinid radula still found in some Antarctic representa-

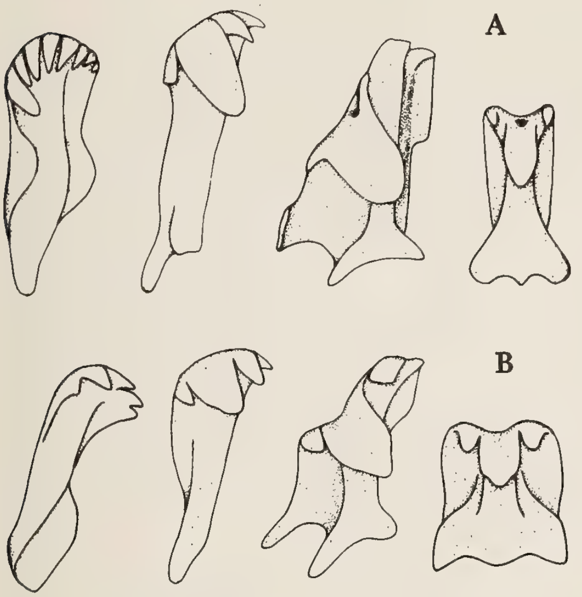


Figure 2

Radulae

A) *Nodilittorina (N.) pyramidalis* (Quoy & Gaimard), Indo-Pacific; B) *Littorina (L.) littorea* (Linnaeus), European Atlantic coast

tives of this family that live below the intertidal zone. It is found among most littorinids modified only in small, but characteristic details. This type of dentition is used to rake in detritus, bite off plant material, to scrape algal crusts and shovel loose material into the mouth. It can be considered as an all-purpose instrument.

The second group of radulae described by Bandel (1974) includes only a few species of the genus *Nodilittorina,* as for example *Nodilittorina tuberculata, N. mordax* and *N. antoni.* Here the lateral teeth have lost their shovel-like, concave shape and have become solid, massive cusps, larger and longer than all other teeth in each transverse row of the radula ribbon. The central tooth is reduced in size to such a degree that it has lost its function. This radula is used mainly for scraping and scratching over rock surfaces. Food material will be scratched from surfaces mainly with the lateral teeth and only the transport of loosened food material to the radula-midline is aided by the shorter marginal teeth.

Both groups of radulae found within the genus *Nodilittorina* are connected to each other by intermediate forms most probably not forming one line of descent but, at least, two (Figure 5).

The type species of the genus *Nodilittorina, N. pyramidalis* (Figure 2A) has a radula that in all essential features is like that of *N. ziczac.* The central tooth is about 2 times higher than wide. Its anterior front is evenly concave and the anterior corners are rounded forming the base of the 2 flanking cusps that accompany the solid, much larger, central, main cusp. A broad central swelling of the basal platform of the central tooth is continuous into the main cusp. The anterior corners of the central tooth are extended into narrow, wing-like structures that form the anterior portion of the straight margins of the tooth. In the posterior half of the basal platform the central swelling widens to form the rounded posterior corners. The lateral wings are in contact with this swelling in the posterior third of the margins. The posterior edge of the central tooth is formed by the rounded corners and, between them, an evenly concave embayment with a rounded or pointed central tongue projecting from it.

The central tooth and the lateral teeth of each row are hinged to each other in such a way that the inner raised margins of the lateral teeth rest in the concavities formed by the marginal wings and the central swelling of the central tooth. On the other hand the solid, rounded posterior corners of the central tooth project over and rest on the lower, wing-like inner margin of the lateral teeth. When the teeth are erected at the moment the radula ribbon is drawn over the front of the odontophore, the movement of the central and the lateral teeth, because of their being hinged with each other, occurs in phase with each other.

The lateral teeth also make up the largest teeth in each transverse row of teeth in the radula. It shows a wide cutting edge on its anterior front, dominated by two solid, central cusps. The inner of these cusps forms an angle larger than 90° with the basal platform of the tooth, while the outer cusp forms an angle of about 90° with it and in the folded radula stands up vertically. Both central cusps continue with their bases into a solid central swelling of the basal platform that becomes narrowest in the posterior center of the basal platform. The swelling widens again at its approach to the posterior edge. Here it forms a solid, short, thumb-like projection or denticle on the inner side that also forms the inner posterior corner. On the other side the posterior end of the central swelling ends without projection before the onset of a deep indentation of the posterior edge. This indentation forms the outer portion of the posterior edge between the central swelling and the projecting outer corner. The latter is the end of the outer margin that continues into the cutting edge. Near its outer, posterior end this margin is folded up, and, therefore, the basal platform between central swelling and outer margin is of gutter-like shape and deeply concave.

The two main cusps of the cutting edge of the lateral tooth are accompanied on both sides by one smaller denticle. The inner of these denticles is continuous into a shouldered wing with a raised inner rim. It is this wing that rests on the wing-like margin of the central tooth. The shoulder is found only in the anterior portion of the inner margin. Its raised rim ends at about half of the length of the margin, and a low, wing-like structure is present from rim end to the thumb-like, inner, posterior corner. Onto this posterior portion of the inner wing of the lateral tooth the solid, swollen bases of the central tooth are resting in the relaxed radula.

The outer raised margin of the lateral tooth will project over the outer margin of the inner marginal tooth in the relaxed radula. The inner marginal tooth rests within the gutter-like, outer, concave portion of the lateral tooth. It is attached to the radula ribbon in such a way that its cutting edge with its four cusps can be rested on the lateral tooth against the slope formed by its two outer cusps and their continuation into the central swelling. The inner marginal tooth shows a cutting edge with pointed, upturned cusps, the second outer of which is the largest. The cutting edge and the upper portion of the basal platform form a spoon-like concavity. The posterior portion of the platform is shaped like the solid, bilaterally flattened shaft of this spoon. The inner and the outer margins are straight and there may be a basal knob present at the pointed posterior edge.

The outer marginal tooth, in the relaxed radula, rests upon the upper, flat side of the inner marginal tooth. Its upturned cutting edge then is fitted into the spoon-like cavity of the inner marginal tooth. The outer marginal tooth is claw-like in shape and may be quite variable between species with otherwise very similar teeth. The number of cusps on the cutting edge is characteristic for species, and in this group around the type species of the genus *Nodilittorina* it counts between 6 and 9. The innermost of the cusps is the largest and commonly of triangular outline. The others are pointed and narrow. The central shaft is solid, straight and thickened by a ridge. There are wing-like lamellae present both on the inner and on the outer margin. The lamellae are not continuous into the claw-like apical region of the tooth, but end in indentations before reaching it. The inner lamella is narrow and little prominent, while the outer forms a wide, projecting wing on the lower half of the shaft. The posterior corner is pointed. With the inner marginal lamella the base of the outer marginal tooth is hinged to the inner marginal tooth. This lamella fits into the depression present on the base of the inner marginal tooth. The marginal teeth are not only erected, but also spread sideways when the radula ribbon is pulled over the edge of the odontophore.

The radula typical of *Nodilittorina*, as described above, shows many similarities to the typical radula of *Littorina* as present in *L. littorea* (Figure 2). But there are also sufficient differences in morphology as well as in other organs to be seen to separate both genera. The central tooth of *L. littorea* is hinged with the lateral tooth just as described above for *Nodilittorina*. But in contrast to the latter the central tooth of *L. littorea* is much wider and of more rectangular shape. The lateral tooth is very similar to that of *N. pyramidalis* with only the exception that the margin of the inner wing shows less upturned anterior shoulders. The inner marginal tooth also is very similar in *L. littorea* and the discussed group of *Nodilittorina*. It also rests in the gutter-like groove present on the outer platform of the lateral tooth. The outer marginal tooth of *L. littorea*, in contrast, is quite different from that of *Nodilittorina*. In *L. littorea* the base of the outer marginal tooth is twisted off from the main shaft and forms a separate wide base for attachment on the membrane. Aside from this base forming an angle with the shaft the latter is rounded and shows no marginal lamellae. Its claw-like apex only has five cusps.

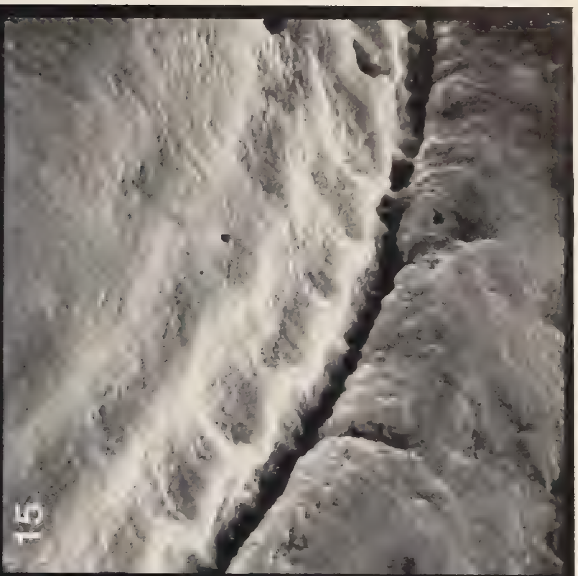
So major differences between *Nodilittorina pyramidalis*, *N. ziczac*, *N. lineolata* and *N. interrupta* on the one hand and *Littorina littorea* on the other may be found in the shape of

Explanation of Figures *12* to *17*

The early ontogenetic shell

Figure *12: Nodilittorina (N.) millegrana* (Philippi, 1848) Port Sudan, Red Sea.
(a) Overview; × 100 FN 1714/22
(b) Overview; × 170 FN 1714/17
(c) Sculpture of larval shell; × 500 FN 1714/23
Figure *13: Nodilittorina (N.) tuberculata* (Menke, 1828) FN 1165/6A

Nodilittorina (N.) ziczac (Gmelin, 1791)
Figure *14:* Embryonic shell; × 290 FN 1168/33A
Figure *15:* Sculpture of larval shell; Colombia, Santa Marta; × 650 FN 2150/13
Nodilittorina (N.) interrupta (C. B. Adams *in* Philippi, 1847)
Figure *16:* Overview. Colombia, Santa Marta. × 175 FN 2180/2
Figure *17:* Embryonic shell. × 450 FN 903/29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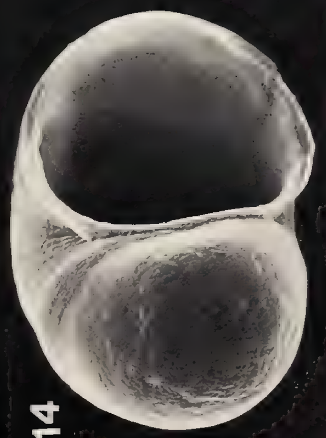
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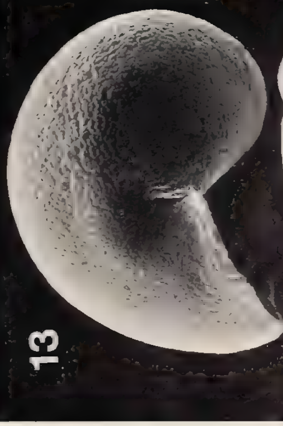
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the central tooth which is wider and more solid in *L. littorea,* and in the shape of the outer marginal tooth. The latter shows a twisted off, wide, flattened base, a rounded main shaft without marginal lamellae and fewer cusps present on the cutting edge. Such characteristics as present in *L. littorea* can also be noted, for example, in *L. saxatilis, L. obtusata, Littoraria angulifera, Fossarilittorina meleagris* and also in *Cenchritis muricatus* (see BANDEL, 1974).

Within members of the genus *Nodilittorina* the radula morphology as present in *N. pyramidalis, N. ziczac, N. lineolata* and *N. interrupta* is very close to that commonly present within the Littorinidae in general. But in other members of the genus *Nodilittorina* the teeth of the radula become continuously more modified until a radula morphology is reached that resembles that of *Nodilittorina antoni.*

In *Nodilittorina antoni* the central tooth has developed into a rudimentary, very narrow rod that is not solid enough to serve a function in the use of the radula. It lies almost completely hidden between the two lateral teeth. Here, on the inner margin of the solid, hammer-shaped lateral teeth a groove is present into which the narrow, flexible, central tooth can be fitted with its posterior two thirds. Therefore, only the uppermost portion of the central tooth is visible with its small, rudimentary, main cusp. Members of this species from San Salvador and Haiti, usually, show a better developed central tooth than members of this species from the Bahama Islands, where central teeth, in general, are more rudimentary.

The lateral teeth have become the dominating features in the radula of *Nodilittorina antoni.* They are large and solid and with the width of their anterior portions they also represent the width of the whole radula ribbon. The central tooth is, as we have seen above, held in a groove on their inner margins. The inner and outer marginal teeth, in the relaxed radula, are rested in the pockets formed by the lower, posterior portion of the outer margin. The inner marginal rim is present only as a narrow rudimentary projection on the inner side of the main cusp. The outer posterior corner, in its typical littorinid morphology, has disappeared and there is only a narrow lower terrace that follows the outer margin. On this terrace the marginal teeth may be rested. The cutting edge is formed mainly by a very solid, main cusp that stands vertically on the anterior portion of the tooth. There is an additional smaller outer cusp that projects sideways and forms the point of the greatest width of the radula in each transverse row of teeth. The posterior edge of the lateral tooth is rounded and formed by the end of the solid, swollen basal platform. There is no trace of a basal denticle. Aside from the longitudinal groove a crescentic depression is present on the flat, vertical inner margin of the tooth. This groove serves no apparent function. The posterior end of each lateral tooth fits into a groove present below the cutting edge of the posteriorly following row of teeth.

The marginal teeth are very slender with straight shaft and vertically upturned cusps. The inner marginal tooth is more solid than the outer marginal tooth and shows only one solid cusp. The posterior end is pointed and flattened. The outer marginal tooth shows 2-3 cusps and a slender, rounded shaft. Individuals from San Salvador and Haiti, here again, show less reduction and, usually, 3 cusps on the outer marginal tooth. Those representatives of this species collected at Nassau show 2 to 3 cusps.

In action the teeth of the *Nodilittorina antoni* radula will spread only very little and the scraping action is carried out by the dominating lateral teeth, while the central tooth is without function and the marginal teeth can only aid in catching material scraped off by the action of the laterals. Strong wear of the main cusps of the lateral teeth is the result of this activity, while the inner marginals show less wear and the outer marginal teeth no wear.

The development of the morphology of teeth as present in *Nodilittorina antoni* can be traced step by step in intermediate species starting with the type of radula present in *N. pyramidalis.* But the radula teeth morphology of different species does not show one direct trend to develop this modified radula type. In different species, different teeth acquire new features while others may show conservative trends.

In the differentiation and reduction of the central tooth we can trace a line, as follows. The already (in comparison with most other littorinids) slender teeth of *Nodilittorina pyramidalis, N. ziczac, N. lineolata* and *N. interrupta* show all typical features, as, for example, solid main cusp of the cutting edge accompanied on its sides by smaller cusp, wing-like upper margins, and a swelling extended into the posterior basal platform. In *N. vermeiji* the general shape of the central tooth has remained like that of the former species but the marginal wings have become narrower. In the case of *N. dilatata* and *N. angustior,* in addition, the tooth becomes more elongated and is now higher than twice its width. In *N. riisei* the marginal cusps of the cutting edge have migrated partially to the front of the central cusp and have split into smaller cusps. The lateral wings are extremely narrow here and the basal edge between posterior curves and central tongue is no longer concave. In *N. glaucocincta* a frontal rim has developed which carries the marginal cusps in such a way that they form a raised rim. The lateral wings are lost and the central tooth has become about 3 times higher than wide. In addition, there is no more hinging between central and lateral teeth of each row. In *N. mordax* these tendencies have increased. A pointed long rim with raised margins forms the anterior front. In contrast to *N. tuberculata, N. mordax* still shows rounded basal corners, while in *N. tuberculata* these corners are angular. In *N. mordax* and *N. tuberculata* the lower margins of the central tooth can be fitted into furrows present on the inner marginal flanks of the lateral teeth. In *N. antoni,* finally, the central tooth is almost hidden in these furrows of the neighbouring lateral teeth.

We can also trace the development of the chisel-like laterals, as present in *N. antoni,* step by step. The lateral teeth of *N. ziczac, N. lineolata, N. interrupta* and *N. pyramidalis* reflect the shape which is generally found among littorinids. Typical features are seen in the wide inner rim and the marginal lamella, the central swelling which continues into the main cusps of the cutting edge, and the basal thickening of the inner posterior edge forming the thumb-like inner corner. Typical is also the extended outer corner with upturned outer margin and deep indentation between this corner and the end of the central swelling.

In *Nodilittorina dilatata, N. vermeiji, N. angustior* and *N. riisei* the two main cusps of the lateral tooth become strengthened and more prominent. The length-width relationship changes in favour of the length of the tooth. The thumb-like projection of the inner posterior corner is less pronounced than in the former group of species. In. *N. glaucocincta* the lateral tooth has acquired a greater length than width and the central cusps have increased in strength even more. The major difference from the group with *N. dilatata* lies in *N. glaucocincta* in the formation of the inner flank of the tooth. Here, the marginal rim and wing is present only in the anterior portion of the inner margin. The posterior portion of this marginal flank shows a deep furrow without lamella. A thumb-like, inner base of the central swelling is present no longer.

In *Nodilittorina mordax* marginal cusps have disappeared on the cutting edge of the lateral tooth. *Nodilittorina tuberculata* no longer shows a raised rim of the outer margin, which could hold the inner marginal tooth at its place of rest, as is present in all other species mentioned before. It is only a short step away from this still wide lamella of the outer margin of *N. tuberculata* to the narrow, terrace-like outer margin of *N. antoni.* In the latter, the cutting edge of the lateral tooth has become more hammer-like in shape.

In regard to the inner marginal tooth very little difference can be seen in most of the *Nodilittorina* species discussed here. A reduction of the number of cusps is noted from the usual four to three in *N. glaucocincta,* two to three in *N. mordax* and 1 cusp only in *N. antoni.*

The outer marginal tooth again shows a different line of morphological development. The largest number of cusps is observed in *Nodilittorina ziczac* (8-9) and *N. vermeiji* (9). The former species has wide marginal lamellae while in *N. vermeiji* these lamellae are narrow. *Nodilittorina interrupta* and *N. dilatata* show 7-8 cusps; *N. lineolata, N. angustior* and *N. riisei* have 6-7 cusps. Here, *N. lineolata* and *N. angustior* show wide marginal lamellae while *N. riisei* has narrow lamellae. *Nodilittorina glaucocincta* and *N. mordax* have 5-6 cusps, *N. tuberculata* and *N. antoni* 2-3 cusps. All these species show no marginal lamellae.

The difference of development of these teeth demonstrates that the discussed species are not related to each other in a straight line of descent. The representatives of the genus *Nodilittorina* from the Caribbean Sea can be considered as branches of one phylogenetic line with the tendency to develop a radula with a scraping function rather than a raking and biting function as is present in littorinids in general. This circumstance enables us to differentiate, by radula features, species which otherwise show very little differences. Since we can still trace the different steps of the development towards the radula of *N. antoni* in our living fauna within the general area of the Caribbean Sea, it is quite probable that this development reflects a rather new phylogenetic achievement, restricted to the Caribbean area. This would explain the absence of similar radula features in the Indo-Pacific area. The radula type present in *Nodilittorina pyramidalis* and the group around *N. ziczac,* which must be considered as the pool from which our species development of the scraping radula has arisen, is commonly found among tropical and subtropical littorinid species from the Atlantic (see Bandel, 1974) and the Indo-Pacific (see Rosewater, 1970).

This closely linking chain of development of the morphology of radula teeth demonstrates the close relation between the Caribbean species of the genus *Nodilittorina,* even though the extremes, seen isolated, seem to be quite apart. It is, therefore, considered to be of no value to construct a subgeneric differentiation of these species on radula characters alone, even though it would be a simple task to do so with the help of the radula characters demonstrated above. Radula characters have developed in different lines to similar shapes; lines that are differentiated from each other by shell characters and morphology of the egg capsules (Figure 5).

Spawn (Figure 5): Within the family Littorinidae there exists quite some diversity of the morphology and consistency of the egg masses. There are species with gelatinous egg masses, with young hatching as miniature adults from a brood pouch, with young hatching as veliger larvae from a brood pouch and with concrete, unattached, floating egg capsules released into the water of the sea. MILEIKOVSKY (1975) has reviewed data on 39 species of littorinids from various regions of the world regarding the types of larval development. All members of the genus *Nodilittorina* listed by this author show a completely pelagic development of their larvae.

Egg capsules of members of the genus *Nodilittorina* were described by LEBOUR (1945), TOKIOKA & HABE (1953), HABE (1956b), KOJIMA (1957), WHIPPLE (1965), STRUHSAKER (1966), BORKOWSKI & BORKOWSKI (1969), ROSEWATER (1970), BORKOWSKI (1971), BANDEL (1974), ROBERTSON (1974). BANDEL (1974) has also presented a generalised scheme to show littorinid spawn as known from the literature. Here it becomes evident, that spawn is to be considered as of restricted taxonomic value within the littorinids in general. The closely related species *Littorina littorea, L. obtusata* and *L. saxatilis,* for example, hatch from very different egg masses. In *L. littorea* free floating egg capsules are produced from which veligers will hatch with a long free larval life. In *L. obtusata* gelatinous egg masses are glued to algal substrates. From these crawling young will hatch after a completed metamorphosis within the egg masses. In *L. saxatilis (s.l.)* crawling young will hatch after completed metamorphosis within the brood pouch of the female.

Members of the genus *Nodilittorina,* as far as is known at present, only produce spawn consisting of free floating egg capsules holding usually one egg only. Differences can be observed again within the floating egg capsules produced by many littorinids. These may be grouped in two ways, the first of which is by content: Many or few eggs per capsule, as, for example, in *Littorina littorea,* and 1 egg per capsule, as, for example, in the known representatives of *Nodilittorina.* Within such species having one egg capsule only, the shape of the capsules differentiates several groups (see BANDEL, 1974). The egg capsules of species of the genus *Nodilittorina* are characterized by a basal, watch-glass-shaped or flat wall and an upper cupola projecting over the base with a more or less wide rim. The cupola is sculptured by ridges and may show quite different ornamentation and shape, which could prove to be of taxonomic value within the genus *Nodilittorina.*

Nodilittorina interrupta, N. lineolata, N. ziczac and *N. dilatata* capsules show a broad, vertical, unsculptured, basal portion in their upper cupola and a species-specific number of ridges on the top of the cupola. In *N. tuberculata* and *N. angustior* the cupola extends into the basal rim, and a large number of step-like ridges is present. In *N. riisei* and *N. antoni* the vertical basal portion of the cupola shows additional, inclined, transversal stripes.

Egg capsules from Pacific representatives of the genus *Nodilittorina* resemble those from the Caribbean Sea. The capsules of *N. picta* (WHIPPLE, 1965, STRUHSAKER & COSTLOW, 1969) from Hawaii (= *N. hawaiiensis* Rosewater & Kadolsky) are similar to those found in *N. ziczac. Nodilittorina millegrana* (HABE, 1956 (as *picta*); TOKIOKA & HABE, 1953; ROBERTSON, 1974) shows a striated basal portion and, therefore, resembles the egg capsules of *N. antoni; N. pyramidalis* egg capsules (TOKIOKA, 1950; ROBERTSON, 1974) resemble again those of *N. ziczac.*

Each spawn of *Nodilittorina* consists of a large number of egg capsules. STRUHSAKER & COSTLOW (1969) have counted between 10 and 1000 eggs per spawn on *N. picta (= N. hawaiiensis).* The egg masses may show some minor variation in the ornamentation of individual capsules which is not so large as to dominate their species characteristics. Spawn of *N. ziczac* from Florida (BORKOWSKI & BORKOWSKI, 1969) is quite like that of members of this species from Colombia (BANDEL, 1974).

SHELL

General Remarks: The *Nodilittorina* species dealt with here can (all but three) be distinguished by their shell characters. The differences are sometimes subtle, but are always corroborated by more obvious differences of other organs. Only *Nodilittorina riisei, N. glaucocincta* and *N. mordax* have virtually identical shells, but very distinct radulae. As in this case the shell was phylogenetically more conservative than the radula, it seems that shell characters are not always that variable and hence of minor taxonomic significance as is sometimes expressed in literature. Obviously, lumping of seven non-nodulose species and two nodulose species into one each, as for example, BEQUAERT (1943) and CLENCH & ABBOTT (1942) did, respectively, gave the illusion of highly variable shell characters of these assumed "species." Certainly, as all species established in the 19th century were defined by shell characters alone, it was science at its best to question the importance placed on shell characters, unless anatomical data confirmed the "conchological" concept. The data now available show that many of the ancient species have been correctly proposed. It is noteworthy that a similar process of recognition occurred in European littorinids, when HELLER (1975a) realised that at least four species had been lumped under the name of *Littorina saxatilis* (Olivi), again resulting in the deceptive picture of a "species" with extreme shell variability.

Shell Sculpture: Individual species may frequently be distinguished by their sculpture. The number of primary, secondary and tertiary spirals, the profile of spiral ridges and furrows, the occurrence, shape and strength of nodulose beads and the way they merge or stay apart or divide themselves are useful criteria. In the genus *Nodilittorina*, however, the existence of nodulose sculpture cannot be consistently linked to other properties of the species, *e.g.*, radula, penis, operculum or spawn characters. In fact, all anatomical and even conchological characters apart from the sculpture, the nodulose species prove to be very closely related to the non-nodulose species classified by Rosewater, 1970 as *Littorina (Austrolittorina)*, while no particular relationships to other Littorinid genera with nodulose sculpture can be recognized. Furthermore, in some species *(Nodilittorina australis* (Gray), *N. millegrana* (Philippi), *N. hawaiiensis* Rosewater & Kadolsky, *N. cinerea* (Pease), *N. quadricincta* (Mühlfeld), *N. striata* (King & Broderip)) the infraspecific variability of sculpture ranges from spirally striated to granose or nodulose. A review of the entire family Littorinidae shows that nodulose sculpture has originated several times independently, as taxa showing this property have either close relationships to non-nodulose species or no particular relationships at all, not even to other nodulose taxa. These groups of nodulose species are (for genus definitions, see Table 1):

1. *Tectarius:* an Indo-Pacific group without close allies (Rosewater, 1972-73, as *Tectarius (Tectarius))*.
2. *Echininus:* another Indo-Pacific group without close allies (Rosewater, 1972, as *Echininus (Echininus))*.
3. *Cenchritis:* comprises one Caribbean species only; possibly related to *Littoraria* (Abbott, 1954, as *Tectarius (Cenchritis);* P. H. Fischer, 1971).
4. *Nodilittorina:* worldwide, tropical and subtropical; close anatomical relations to non-nodulose species do not justify a subgeneric separation of nodulose species; even the nodulose species in this genus may be of polyphyletic origin, as they form five groups which did not necessarily originate from a common nodulose ancestor: (a) *N. pyramidalis-miliaris (-dilatata?)* group, (b) *N. tuberculata*, (c) *N. millegrana* group, (d) *N. (Tectininus) antoni*, (e) *N. (Liralittorina) striata.*
5. *Littorina aleutica* Dall, 1872: A nodulose species probably related to *Littorina sitchana* (Philippi), *L. atkana* Dall and *L. obtusata* (Linnaeus) (see P. H. Fischer, 1967a).
6. *Littorina brevicula* (Philippi, 1844): A species with spiral ornamentation sometimes growing rugose or nodulose; not closely related to *L. aleutica*, although to be placed in the same genus.
7. *Melarhaphe nodulifera* (Kadolsky, 1973): a European Oligocene form originated from the sympatric *M. obtusangula* (Sandberger, 1859) which is entirely smooth, as are all other species of *Melarhaphe.*

These examples demonstrate the impossibility of utilising the nodulose sculpture by itself in littorinid taxonomy; however, combined with other shell and anatomical features it may be helpful to recognise related groups of species, hence genera and subgenera (compare Table 1).

Colour Pattern: Highly variable colour patterns in some Gastropods (*e.g.*, the land snail *Cepaea*) led to the conclusion that colour patterns can be assigned no or little taxonomic value. Also, this study has been conducted disregarding colour patterns of *Nodilittorina.* However, once the species were defined utilising other shell characters as well as operculum, radula and spawn characters, they turned out to have also fairly characteristic colour patterns. There is considerable variation; in our group, the most variable features are the inconstancy of ziczac lines which easily turn into straight or only slightly bent lines, and the extent of the dark brown pigmented zone in the middle of the whorls: sometimes being only a darker shade, sometimes seen in full intensity on the outer surface, it may also vary considerably in width.

Interestingly, only spirally sculptured and weakly granulose species of *Nodilittorina* seem to develop colour markings, as strong nodules certainly will obscure any markings. This, and the fact that the range of colour patterns in each species is relatively small, suggest that each particular colour pattern, or more generally speaking, the appearance of the shell surface (thus including obvious sculptures) is biologically meaningful in a given habitat. Its value in

Explanation of Figures *18* to *22*

Nodilittorina (N.) ziczac (Gmelin, 1791)

Figure *18:* Martinique. BMNH 1854. 10.4.13.; lectotype of *Litorina d'Orbignyana* Philippi, 1847; probably original of Orbigny, 1842 (plt. 15, figs. 5, 8). Shell: 24.2×14.0mm. Radula: × 280 FN 1465/11

Figure *19:* Locality unknown. BMNH 1968.222. Lectotype of *Littorina debilis* Philippi, 1846. Shell: 9.2×6.4mm. Radula:
a) × 280 FN 1600/30
b) × 280 FN 1600/28

Nodilittorina (N.) lineolata (Orbigny, 1840)

Figure *20:* Rio de Janeiro, part. BMNH 1854.12.4. 363. Lectotype. Shell: 8.2×5.1mm, Radula: × 480 FN 1465/63

Figure *21:* Rio de Janeiro, Hapuca in Niteroi. SMF 110777. Shell: 9.6×6.7mm, Radula: × 370 FN 1600/1A

Figure *22:* São Vicente near Santos. Marcus & Marcus leg. USNM 749802. Shell: 7.9×4.1mm

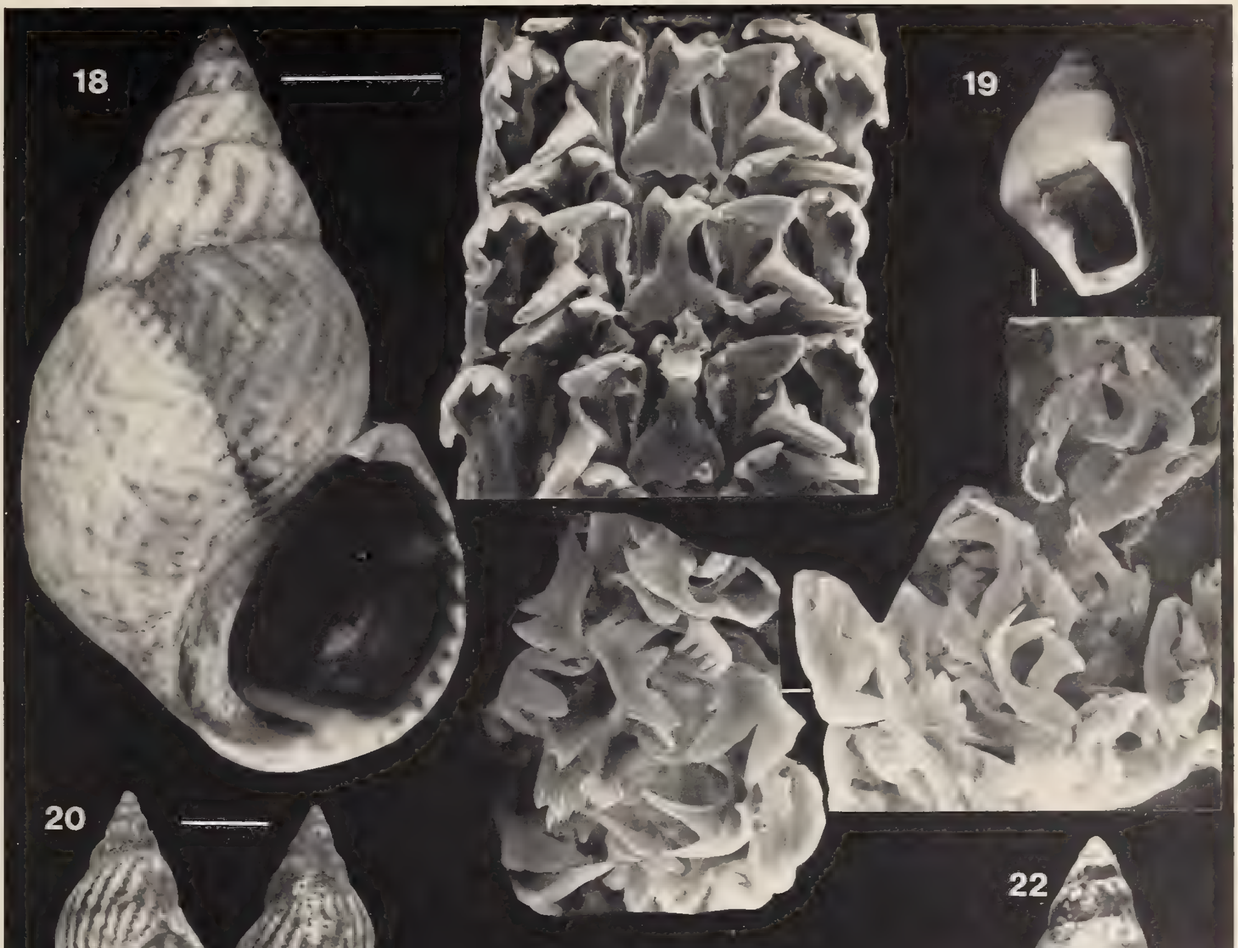
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Table 1

Synopsis of the characters of the genera of the family Littorinidae *s. str.*

Genus (with type species)	Shell			Penis	Operculum	Spawn, Ontogeny	Radula	Shell structure and mineralogy	Distribution, Remarks
	Size, Shape	Colour Pattern	Sculpture						
Littorina Ferussac, 1822 (*Turbo littoreus* Linnaeus, 1758)	Large to medium; ovate to conical	Uniform or broad spiral bands, or chessboard pattern; interior brown, no white zones; columella white	Elevated spiral striae, may become very faint or nodulose	Open spermoduct; numerous glands	Horny, paucispiral types A and B	Pelagic egg capsule with numerous eggs, veliger hatching; or egg masses or ovoviviparous without veliger stage	Central tooth broad, with 3 cusps in one level; cusps of lateral and marginal teeth show minor size differentiation	Main layer calcitic: irregular prism sectors with variable orientation of prisms; inner layer of aragonitic cross lamellae may be present	Northern Hemisphere, moderate and cold zones. Subgeneric division possible
Littoraria Gray in Griffith & Pidgeon, 1834 (*Littorina pulchra* Sowerby, 1832)	Large, rarely medium or small; ovate-conical, periphery often angulate	Brown dots and oblique axial or zigzag bands, often on yellow background; interior and columella only slightly pigmented	Elevated or flattened spiral striae	Spermoduct mostly open, rarely closed; no glands, often an accessory flagellum	Horny, paucispiral type A	Pelagic egg capsule with one egg, flat shape, veliger hatching or ovoviviparous	Broad central tooth with 3-5 cusps and usually a "cockscomb" at its distal end ("hooded" type of Rosewater, 1981); very little size differentiation in cusps of lateral and marginal teeth	Crosslamellae; aragonite	Worldwide, tropic and subtropic seas. Subgeneric division including *Littorinopsis* Mörch necessary, pending anatomical data on the type species, *pulchra* Sowerby (= *zebra* Donovan, 1825)
Cenchritis Martens, 1900 (*Turbo muricatus* Linnaeus, 1758)	Large; ovately top-shaped; pseudumbilicate.	Surface white with rudimentary brown dots; interior dark brown; columella white	Rows of rounded nodules; 3 primary, equal rows	Spermoduct open; no glands nor appendages	Horny, paucispiral type B	As in *Littoraria*	Similar to *Littorina*	Crosslamellae; aragonite	Caribbean. Probably related to *Littoraria*
Tectarius Valenciennes 1832 (*Tectarius coronatus* Valenciennes, 1832)	Large, conically top-shaped; thickening at columella, interior with raised spiral ridges	Sparse brown dots or bands; columella and interior light-coloured	Rows of spiny to rounded tubercules; 1 primary row	Spermoduct open; numerous glands on lateral edge; papillose surface on opposite edge	Horny, mesospiral	Unknown	Narrow central tooth; lateral and marginal with low number of cusps	Crosslamellae; aragonite	Indopacific, tropical seas
Echininus Clench & Abbott, 1942 (*Trochus cumingi* Philippi, 1844)	Large, top-shaped, umbilicated; interior with raised spiral ridges	As in *Tectarius*	As in *Tectarius*	Spermoduct open, with internal fold; numerous glands near base; swelling at base	Calcareous;	Unknown	As in *Tectarius*	Crosslamellae; aragonite	Indopacific, tropical seas
Nodilittorina Martens, 1897 (*Littorina pyramidalis* Quoy & Gaimard, 1833)	Medium sized, ovate-conical, periphery often angulate	Uniform, or chessboard pattern, or axial zigzag lines; often dark median zone on whorls; columella and interior dark brown, one light band on umbilical side, occ. several more	Incised spiral lines or rows of granules or nodules; primary rows unequal	Spermoduct open; usually with basal enlargement and one penial gland, occ. a flagellum, rarely no appendages	Horny, paucispiral types A and B, or mesospiral	Pelagic egg capsule with one egg, one side flat, the other convex with spiral ridges; veliger hatching	Central tooth narrow, occ. reduced, its 2 lateral cusps overtop the central cusps; cusps of lateral and inner marginal teeth of markedly different size	Crosslamellae; aragonite	Circumtropical; subtropical and tropical seas. Three subgenera: *Nodilittorina s. str.*, *Tectininus* and *Liralittorina*
Rissolittorina Ponder, 1966 (*Zelaxitas alta* Powell, 1940)	Very small, obtusely conical	Uniform brown, white band on umbilical side	Smooth	Spermoduct unknown; 1 long and slender 'filament'	Horny, paucispiral type A	Unknown	Central tooth broad, 5 cusps; cusps of all teeth show very little size differentiation	Unknown	New Zealand, moderate zone
Melarhaphe Mühlfeld in Menke, 1828 (*Turbo neritoides* Linnaeus, 1758)	Small, ovate-conical, periphery angulate; columella and parietal margins continuous	Uniform brown, white band on umbilical side	Smooth, rarely rounded nodules	Spermoduct partly closed; no appendages	Horny, paucispiral type A	Pelagic egg capsule flat, with one egg, veliger hatching	Central tooth broad, with basal denticles	Crosslamellae; aragonite	Europe, subtropical to moderate seas
Fossarilittorina Rosewater, 1981 (*Phasianella meleagris* Potiez & Michaud, 1838)	Small, ovate-conical, periphery angulate; pseudumbilicus	White dots, flammules and stripes on dark brown background; interior dark brown, white band on umbilical side	Spiral sculpture	Spermoduct closed; no appendages	Horny, paucispiral type A	Pelagic egg capsule with one egg, one side flat, the other convex with spiral ridges; veliger hatching	Central tooth moderately broad, with 3 cusps, the lateral ones not overtopping the central cusps; cusps of lateral and marginal teeth similar to primitive *Nodilittorina* teeth	Crosslamellae; aragonite	Atlantic; prob. American Pacific coast and Galapagos; tropical

natural selection, however, is at present not fully understood. Heller (1975b) demonstrated that red shells of *Littorina nigrolineata* Gray and *L. rudis* (Maton) are significantly more frequent on red-brown cliff rocks than on others, thus acting as camouflage against visual selection by predators. Also in the West Atlantic species, protection against visual selection predators could be more important than protection against desiccation by enhanced shell reflectivity, as there seems to be no correlation between light-coloured shells and their supratidal habitat.

Even on the genus level, some elements of the colour pattern are constant in *Nodilittorina:* The major portion of the shell's interior is pigmented dark brown except a narrow band on the umbilical side. In the family Littorinidae, the genera *Melarhaphe* and *Fossarilittorina* have this same colour pattern, but *Melarhaphe* is very different in every other respect, while *Fossarilittorina* appears to be more closely related to *Nodilittorina* in relation to its spawn and, to some degree, its radula characters. Yet there is no support in the fossil record to confirm the hypothesis that *Melarhaphe, Fossarilittorina* and *Nodilittorina* share a common ancestor with the same colour pattern, although this cannot be excluded with certainty.

Another colour character indicating relationships of *Nodilittorina* species is probably the fact that external colour markings in spirally sculptured species are present only in species living on American and African coasts; they are missing in the Australian and Pacific species, except in *N. acutispira* (E. A. Smith), which differs in penis characters from the other Pacific and Australian species.

In summary, if the range of colour patterns is considered, they may be of diagnostic value for both species and supraspecific groups, but they cannot be utilised isolated from other characters.

Embryonic and Larval Shells (Figures *12-17*): The embryonic shell of the Caribbean representatives of *Nodilittorina* does not differ in general from such embryonic shells found among other littorinids with young hatching as veliger larvae (Bandel, 1975a, b; Richter & Thorson, 1975). All embryonic shells studied up to now show weakly tuberculated to more coarsely tuberculated shells, which may or may not show growth lines. The embryonic shell of the Hawaiian *N. picta (= hawaiiensis)* is no exception (Struhsaker, 1968) and also demonstrates a finely granular sculpture.

The larval shell, secreted by the free swimming pelagic larva during its life as a member of the plankton, in contrast to the embryonic shell, shows more characteristics in its sculpture that may prove to be of high taxonomic value, if more species are studied. Up to now only the larval shell of *Nodilittorina hawaiiensis* (by Struhsaker, 1968, as *picta*), *N. striata* and *N. miliaris* (by Rosewater, 1981: plt. 6, figs. E, F), *N. millegrana, N. striata, N. ziczac* and *N. interrupta* (own studies) are known from members of *Nodilittorina.* The larval shell of *Littorina littorea* was recently studied by Bandel (1975b) and that of *"Littorina" neritoides (= Melarhaphe neritoides)* by Richter & Thorson (1975). The larval shell of *Littoraria angulifera* was also studied by us to serve for comparison with *Nodilittorina.*

Common to all Littorinidae species mentioned with a free living veliger phase is the change in the course of growth lines after hatching. While in the embryonic shell the apertural lips were straight and show no undulations, the larval shell develops, right from first shell secretion onwards, a hooked outer lip of the aperture. Growth lines now are situated following the outline of the aperture with a strong saddle between a shallow umbilical lobe and deep apical lobe at the apertural lip. While the embryonic whorl of the shell is planispirally arranged, the 1 or 1.5 larval whorls now show a clear conispiral coiling.

Growth lines in the embryonic shell usually are weak and difficult to trace. With the onset of the growth of the larval shell growth lines become more prominent. The larval shell shows a deep and wide umbilicus. Aside from the more pronounced growth lines and their sinuous course also a more characteristic sculpture is to be seen on the larval shell in comparison to the embryonic shell. This sculpture, in the case of *Littorina littorea,* consists of tubercles of about 1 μm width that arrange themselves into 7-8 spiral rows (Bandel, 1975b). In *Melarhaphe neritoides* tubercles at first form rows, later fuse partly to form 1-2 μm wide discontinuous spiral ridges on a smooth surface (Richter & Thorson, 1975, and own observations). The larval shell here shows tubercles on the apical portion of each whorl and discontinuous ridges on the umbilical side of the larval whorl.

The larval shell of *Littoraria angulifera* encompasses 3.6 whorls and is strongly sculptured by 6-7 spiral ridges separated from each other by even, rounded grooves between them. The spiral ridges themselves are undulating in their course or straight.

The larval shell among the studied members of the genus *Nodilittorina* could be found best preserved in the species *N. millegrana* from the Red Sea (Figure *12*). It consists of 3 whorls with a strong apical sinus in the outer lip. Growth lines, therefore, show a deep apical lobe and a wide, high saddle umbilically. Following the embryonic shell, that is sculptured like those of the Caribbean representatives of the genus (Bandel, 1975a), along with the abrupt change in the course of the growth lines from straight to lobed, a rapid change in sculpture is observed. On the first half whorl produced by the free swimming larva 8-9 spiral rows consisting of strong tubercles are present. In the following larval shell the tubercles are fused to form zic-zac shaped ridges, 7-10 on each whorl. There are quite strong individual differences to be noted in the number and the shape of these ridges. They may have a regular zic-zac course, or they may break up into rows of tubercles with short inclined ridges included, also giving a zic-zac appearance in the whole spirally arranged ornamental structure.

Nodilittorina ziczac and *N. interrupta* from Santa Marta (Figures *14-17*) show a larval ornamentation very much like that seen in *N. millegrana.* But the preservation of the studied material from the Caribbean Sea was not as good as that from the Red Sea. The number of the whorls of the larval shell of individuals ready to metamorphose is 2.5-3 in the case of *N. ziczac.* The ornamentation consists of ziczac ridges as in the case of *N. millegrana,* and also 7-10 such spiral ridges are present on each whorl. In the larval shell of *N. interrupta* the zic-zac pattern is not as strongly developed as in *N. ziczac,* but still well traceable.

The larval shell of *N. striata* from Gran Canaria (Canary Islands) also shows a sculpture very much like that of the three other representatives of the genus *Nodilittorina,* thus demonstrating its close affinities to this group.

Struhsaker (1968, fig. 8) described and presented a drawing of the larval shell of *Nodilittorina picta (= hawaiiensis* Rosewater & Kadolsky) from Hawaii. The author had found that the larval life lasts 3-4 weeks from spawning to settling; 3.5 whorls are present before the larvae settle and before the animal finishes its metamorphosis from veliger to the crawling young. The larval shell of *N. picta,* according to Struhsaker, shows a more or less coarse spirally arranged zic-zac ribbing, similar to that of the members of the genus *Nodilittorina* described above.

Shell Structure: The shell structure of all members of the genus *Nodilittorina* here studied is aragonitic in composition. The needle-like biocrystals are arranged in the crossed lamella structure as is described in detail by Bandel (1979). It is also like that of Antarctic littorinids as described by Arnaud & Bandel (1978).

The structure of the shell of Caribbean littorinids is like that of most marine mesogastropods. Usually two layers of the crossed lamellae structure are arranged in such a way that the plane of the lamellae of the first order of the outer layer forms almost a right angle with the plane of the lamellae of the first order of the inner layer. No differences in shell structure enabling the differentiation of species were found in the genus *Nodilittorina.*

Operculum

Characters: The common characters of all *Nodilittorina* opercula are: Operculum spirally coiled, composed of brown organic matter, edges thin and flexible, growth edge position opposite the parietal wall, spiral part opposite the columellar margin.

According to the type of coiling, three opercula types are recognised amongst West Atlantic species (Figure 3):

Type A: Operculum paucispiral, elongate, last whorl very large, its width is more than half of the operculum length; *Nodilittorina ziczac, N. interrupta, N. lineolata, N. riisei, N. mordax;* operculum not seen: *N. glaucocincta.*

Type B: Operculum paucispiral, more circular, width of last whorl equal or less than half of operculum length: *Nodilittorina angustior, N. dilatata, N. tuberculata, N. vermeiji.*

Type C: Operculum mesospiral, nearly circular, width of last whorl about one fifth of operculum length: *Nodilittorina (Tectininus) antoni.*

Functional Morphology: It has been suggested (Stanley, 1979) that in Gastropod phylogeny the acquisition of the operculum afforded an improved protection against predators. In the intertidal and supratidal habitats, however, the protection against desiccation may become a more important task for the operculum (Vermeij, 1973). One important measure to accomplish this is the acquisition of the thin and flexible edge of the operculum: when the operculum is strongly withdrawn into the shell interior, this edge bends outwards and provides an improved closure. The flexible portion is largest at the adapical side of the operculum and least at the abapical side, so the operculum can be withdrawn further on its adapical side.

Muscle impressions on the interior side of the operculum suggest that about half of its surface is only loosely attached to the flesh and that the retractor muscle inserts on the side adjacent to the columella and the parietal wall. The insertion area is oval with a central constriction, whose tip points to the nucleus of the operculum (Figure 3B). During growth, this impression migrates in a rotating sense, marking its previous positions by internal growth lines, which are perpendicular to the external growth lines. Apparently additional operculum material is accreted on the edge of the retractor muscle scar adjacent to the palatal wall of the shell. Thickening of the operculum can be achieved best if the rotation of the muscle scar and the subsequent material accretion occur as often as possible. With the

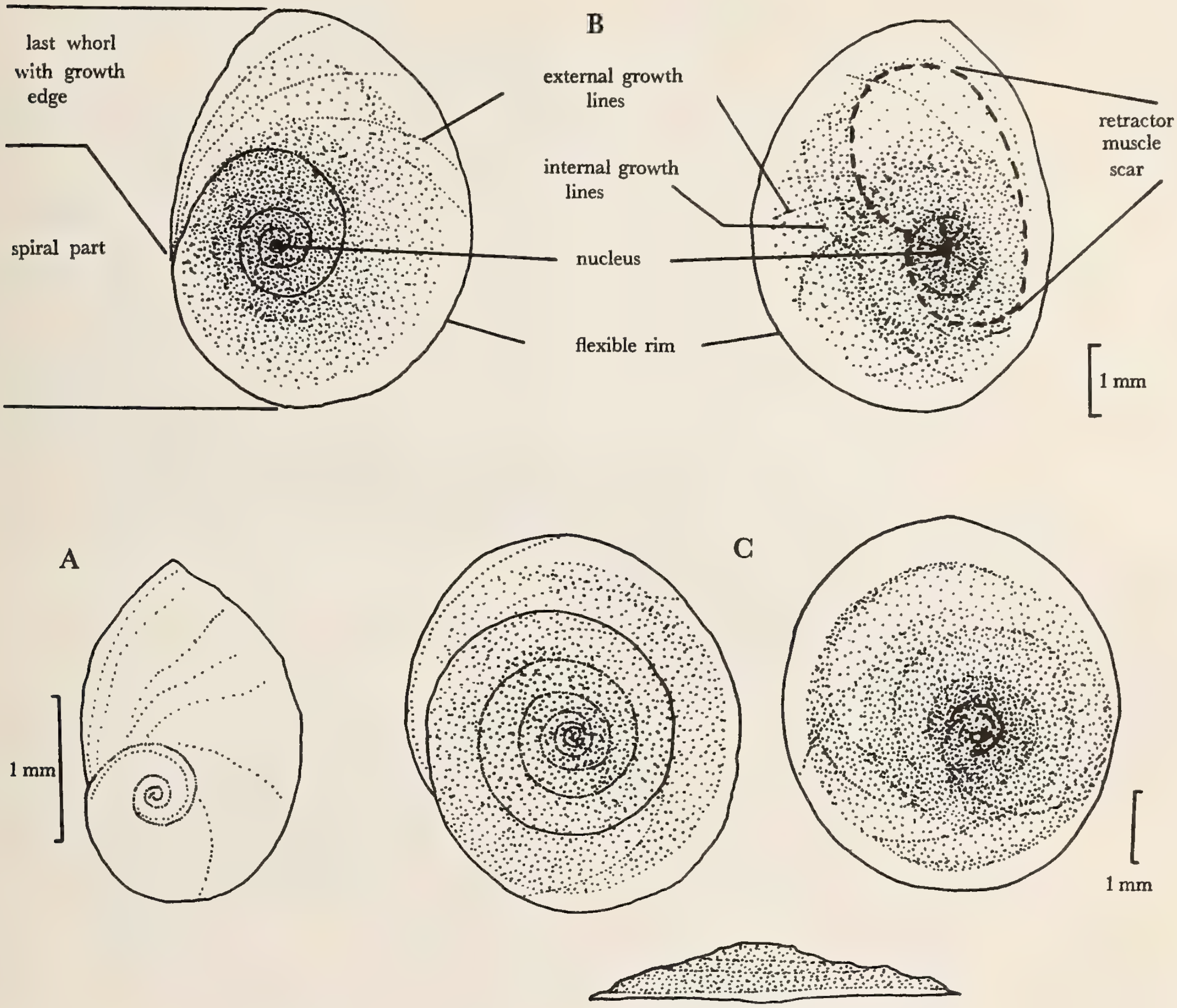


Figure 3

Opercula of *Nodilittorina* species

A) *N. lineolata* (Orbigny): paucispiral, widely coiled (type A). Pernambuco (BMNH)

B) *N. tuberculata* (Menke): paucispiral, narrowly coiled (type B). Santa Marta, Colombia (B/K)

C) *N. (Tectininus) antoni* (Philippi): mesospiral (type C). Nassau, Bahamas (B/K); left: outer surface; right: inner surface; below: side view with inner side pointing upwards

aperture size tending to become smaller in high supratidal species as compared to low supratidal ones, this can only be accomplished by narrowing the operculum whorls to leave space for more gyrations. In fact, the most densely coiled *Nodilittorina* species, *N. antoni*, has the thickest operculum. Its flexible edge has become very narrow, but as it is markedly concave on the exterior and convex on the interior surface, it will still provide a good closure.

The tendency of high supratidal species to build a smaller and more circular aperture coincides with the increase of the number of operculum whorls, which cause the operculum to acquire a more circular shape. So in the family Littorinidae the dense operculum coiling is a double purpose adaptation: to fit into a circular aperture and to enable the animal to thicken the operculum. In other Gastropod taxa living submerged, *e.g.*, many Trochacea (marine) and Valvatacea (freshwater), the multi-spiral operculum appears to be just an adaptation to fit into a circular aperture.

As a third measure to prevent desiccation, the operculum may become calcified, as it is in the Indo-Pacific genus *Echininus.*

Taxonomic significance: Amongst marine Littorinidae *s. lat.,* apart from the above-mentioned West Atlantic species, the paucispiral type A was found in: *Littoraria angulifera* (Lamarck), *L. flava* (King & Broderip), *L. pintado* (Wood), *L. glabrata* (Philippi), *L. nebulosa* (Lamarck), *L. undulata* (Gray), *L. tesselata* (Philippi), *L. scabra* (Linnaeus), *L. cingulifera* (Dunker); *Fossarilittorina meleagris* (Potiez & Michaud); *Nodilittorina miliaris* (Quoy & Gaimard), *N. millegrana* (Philippi), *N. peruviana* (Lamarck), *N. punctata* (Gmelin), *N. striata* (King & Broderip); *Littorina littorea* (Linnaeus), *L. obtusata* (Linnaeus); *Melarhaphe neritoides* (Linnaeus); *Laevilittorina johnstoni* (Cotton); *Macquariella kingensis* (May); *Rissolittorina alta* (Powell); *Laevilacunaria bennetti* (Preston).

The paucispiral operculum type B was observed in *Nodilittorina granosa* (Dunker), *N. pyramïdalis* (Quoy & Gaimard), *N. subnodosa* (Philippi); *Littorina saxatilis* (Olivi) group; *Risellopsis varia* (Hutton); *Cenchritis muricatus* (Linnaeus) (transitional to mesospiral); *Algamorda newcombiana* (Hemphill); *Rufolacuna bruniensis* (Beddome); *Macquariella hamiltoni* (E. A. Smith).

The mesospiral operculum (type C) is known from the genus *Tectarius* and the multispiral operculum from the genera *Echininus* and *Peasiella.*

In some instances, species with different opercula have been placed in the same genus (see *Nodilittorina, Littorina* and *Macquariella*), due to a combined evaluation of shell, radula, penis, spawn and operculum characters. From the considerations on the functional morphology and ecological adaptations of the operculum it is conceivable that from a stock of originally type A operculated littorinids the types B, C and the multispiral operculum evolved repeatedly, according to the pressure the supratidal environment exerted. So again, in taxonomy the operculum characters may be very misleading when considered isolated from other properties of the species, but in combination with as many other features as possible they will prove useful in recognising species groups and hence, subgenera and genera.

The subfamilies Echinininae Rosewater, 1972 and Tectariinae Rosewater, 1972, founded solely on operculum characters, are thus considered unnecessary: As opercula cannot have more weight in taxonomy than any other organs, these subfamilies either have to be withdrawn or, for the sake of a consistent classification, numerous subfamilies, each comprising only one or a very few genera, would have to be created (probably one subfamily for each genus as defined in Table 1). So it is preferred to postpone a subfamiliar division of the family Littorinidae until further anatomical data are known. The Risellidae and Lacunidae and the numerous taxa restricted to the Southern Pacific area (not mentioned in Table 1) would have to be considered in such a reclassification.

In the genus *Nodilittorina,* the mesospiral *N. antoni* constitutes the sufficiently well defined subgenus *Tectininus.* The paucispiral operculum type A occurs in most spirally striated and in the granulose species, for which the subgenera *Austrolittorina* Rosewater, 1970 and *Granulilittorina* Habe & Kosuge, 1966 have been proposed. However the penis of the spirally striated ones seems to differ between Indo-Pacific plus African species on the one hand and Western Atlantic species on the other; and there is the spirally sculptured *N. angustior* with operculum type B. These facts suggest that a subgenus *Austrolittorina* including all spirally striated Nodilittorinae would not represent natural groupings. The paucispiral operculum type B is found in *N. angustior* and in all more strongly nodulose species *(Nodilittorina s. str.).* It seems to be premature to attempt further subgeneric subdivisions based on shell and operculum characters before more anatomical data on *Nodilittorina* species are available.

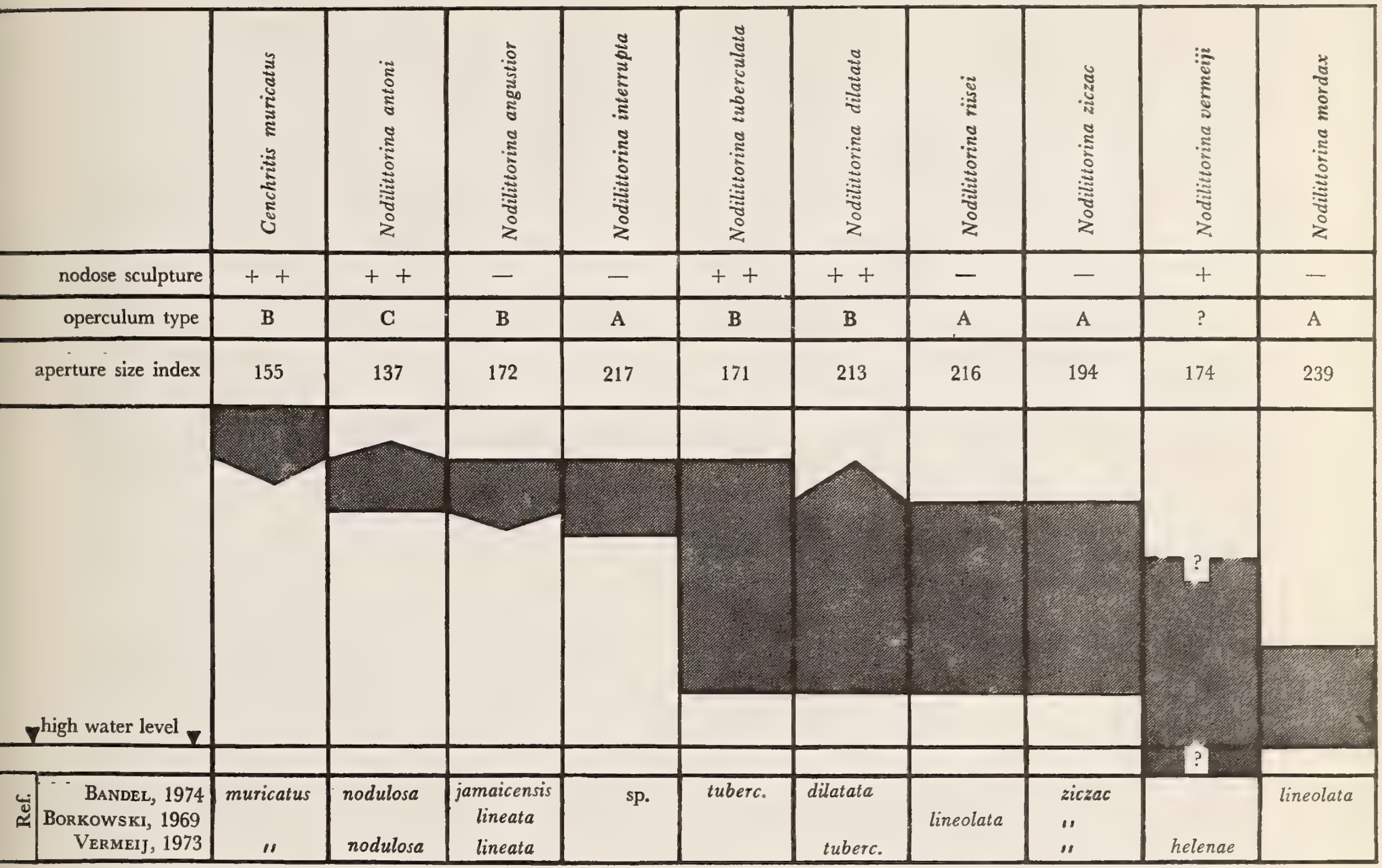
Ecology and Morphological Adaptation

(Figure 4)

All species treated here live on the shoreline above medium high water level on hard substrata, mainly rocks. They remain quiescent during dry periods and become active when wetted with seawater spray by wave action. Then they feed upon films and crusts of algae, lichens, and probably also fungi and microscopic animals. All species produce pelagic egg capsules; thus, even those living most distant from the water level have to descend for spawning; correspondingly, the juveniles originating from the planktonic veliger larva have to crawl upwards from the sea level to the usual living area of the animal.

Figure 4 depicts the relative levels of habitat. No absolute heights can be given as these vary according to the coast topography and the hydrographic conditions; *e.g.,* tide and wave action. Also this zonation will be found valid only on sea cliffs with a certain amount of slope, as on flat rock benches both high and low supratidal species may live together (Bandel, 1974a: Curaçao). For reference purposes, *Cenchritis muricatus* (Linnaeus) is also shown in Figure 4 as this is the littorinid species living most remote from the sea level.

Several papers deal with the morphological adaptations of littorinids to suit the supratidal habitat. Vermeij (1973) described from several localities all over the world gradients of littorinid shell morphology related to the distance of the living areas from the sea level; *i.e.,* related to the degree of desiccation and heat resistance of the animals. As a general trend, he recognised the increase of shell ornamentation and shell size and the decrease of the rela-



	Cenchritis muricatus	*Nodilittorina antoni*	*Nodilittorina angustior*	*Nodilittorina interrupta*	*Nodilittorina tuberculata*	*Nodilittorina dilatata*	*Nodilittorina riisei*	*Nodilittorina ziczac*	*Nodilittorina vermeiji*	*Nodilittorina mordax*
nodose sculpture	+ +	+ +	—	—	+ +	+ +	—	—	+	—
operculum type	B	C	B	A	B	B	A	A	?	A
aperture size index	155	137	172	217	171	213	216	194	174	239
Ref. Bandel, 1974	*muricatus*	*nodulosa*	*jamaicensis*	sp.	*tuberc.*	*dilatata*		*ziczac*		*lineolata*
Ref. Borkowski, 1969			*lineata*				*lineolata*	"		
Ref. Vermeij, 1973	"	*nodulosa*	*lineata*			*tuberc.*		"	*helenae*	

Figure 4

Supratidal zonation of West Atlantic species of *Nodilittorina* and their morphological adaptations to drought and heat

it cannot be compared accurately to habitats of the other species. Operculum type: A) paucispiral, last whorl wider than spiral part; B) paucispiral, last whorl narrower than spiral part; C) mesospiral. The aperture size index is the Ratio aperture surface : shell surface. Shell surface approximated as cone surface with base diameter = shell width, cone height = shell height; aperture surface approximated as ellipsis with long axis = mouth height, short axis = mouth width

The relative heights of the species habitats are indicated by reference to the mean high water level and to the zones of *N. ziczac*, *N. angustior* and *Cenchritis muricatus* (Linnaeus). The latter species is unrelated to *Nodilittorina* and included only for reference, as it is the littorinid living highest above sea level. Not shown are: *N. glaucocincta* (may live in the same zone as *N. ziczac*, if *"Littorina lineolata"* of Vermeij, 1973 from Jamaica is this species), and *N. lineolata*. Note that *N. vermeiji* is the sole species in its habitat, thus

(achieved by size increase) will minimise desiccation, and temperature intake will be minimised by avoiding the contact of the foot sole with the substratum, by avoiding creation of metabolic heat during dry periods and by mini-

tive mouth height with increasing distance of the habitat from the sea level. He interpreted this as an adaptation to desiccation and overheating, as a small aperture capable of being closed by an operculum and a low specific surface mising the shell surface exposed to radiation; cooling of the animal body is maximised by a strong sculpture which increases the surface exposed to wind convection without increasing the surface liable to evaporation and to reception of radiation.

Similarly, **Struhsaker** (1968) showed that the nodulose morph of *Nodilittorina hawaiiensis* Rosewater & Kadolsky (= *Litorina picta* Philippi, 1846, non *Litorina obtusata picta* Menke, 1845) living on steep cliff slopes is larger than the smoother morph and is better adapted to dryness, high temperatures and hypersalinity, while the smooth morph living on shallow benches is much more capable of withstanding strong surges and submersion. In this species wave action is obviously another relevant selective factor not dealt with by Vermeij.

In the Red Sea, one of the authors (K.B.) observed the habitats of the nodulose, top-shaped *Nodilittorina subnodosa* (Philippi) with operculum type B and of *N. millegrana* (Philippi), which has a relatively larger aperture, an operculum type A and only beads of faint nodules (rather: granules). Confirming the trends observed by Vermeij and Struhsaker, *N. subnodosa* lives in the supratidal zone above the usual splash zone and is therefore rarely active; *N. millegrana*, however, lives in the lower part of the supratidal zone, which is frequently wetted by wave splash, down to the upper part of the permanently wet zone, enabling the animals to be more frequently active.

Heller (1975b) indicated the importance of the camouflage effect of the shell colour in *Littorina nigrolineata* Gray and *L. rudis* (Maton), suggesting that protection against visual selection by predators is another essential selection mechanism.

Certainly there are many selection mechanisms; the littorinids have to cope, for example, with desiccation, high and low temperatures, hypersalinity and fresh water, wave action, gain of food, finding of sexual partners, maintenance of a sufficient fertility rate, protection against predators, resistance against parasites and epidemics. Also, each selection factor possibly can be tackled in several ways. As a result, the morphological features of a species are bound to reflect a complex pattern of adaptation. It will take years of research to elucidate some of these adaptations, as Struhsaker's studies on *Nodilittorina hawaiiensis* have shown. Every simplistic approach to explain morphological features by adaptation to a certain factor of the environment may be valid within narrow ranges, but cannot be generalised, as the following exceptions to Vermeij's and Struhsaker's findings demonstrate:

- In Europe, the littorinid species living highest above sea level, *Melarhaphe neritoides* (Linnaeus), is nearly the smallest European species, certainly the least sculptured one and has still an unusually large aperture.
- In the Indo-Pacific, nodilittorines are described as living intertidally and supratidally (**Rosewater**, 1970). Amongst the intertidal species, there are several nodulose and granulose ones (*Nodilittorina quadricincta quadricincta* (Mühlfeld, 1824) (syn. *N. leucosticta* (Philippi, 1847)), *N. quadricincta biangulata* (Martens), *N. nodosa* (Gray), *N. australis* (Gray), while non-nodulose species frequently live supratidally (*N. unifasciata* (Gray), *N. punctata* (Gmelin), *N. praetermissa* (May), *N. africana* (Philippi)).
- The colour pattern of West Atlantic nodilittorines appears not to be optimal for temperature insolation, as it is mostly fairly dark. However, the intertidal Australian *N. australis* and the not particularly high living Caribbean *N. ziczac* have very light-coloured shells. The unexpectedly low variability of colour patterns suggests that they are preferentially selected, only leaving a limited variety of them to survive. Probably the protection against predators is an environmental factor exerting stronger selective pressure than the reflectivity of the shell.

Figure 4 shows also some of the properties probably related to desiccation resistance. The trends noted by **Vermeij** (1973) are clearly visible: The aperture becomes relatively smaller, and nodulose sculpture is more frequently found in species living high above water level. Also, the operculum tends to become more narrowly coiled. However, the many exceptions from this trend can be seen

Explanation of Figures *23* to *29*

Nodilittorina (N.) interrupta (C. B. Adams *in* Philippi, 1847)

Figure *23:* "Antilles." MHNG 1096/87/2. Paratype of *Phasianella lineata* Lamarck, 1822. Shell: 14.3×8.4mm, Radula: × 360 FN 1599/14

Figure *24:* Jamaica, MCZ 186123. Topotype of *Litorina ziczac interrupta* C. B. Adams in Philippi, 1847 (figured by **Clench & Turner**, plt. 38, fig. 18). Shell: 7.8×6.0mm, Radula: × 400 FN 1599/18

Figure *25:* Lesser Antilles, St. Thomas, ZMK: Lectotype of *Littorina (Melaraphe) floccosa* Mörch, 1876. Shell: 11.7×7.5mm, Radula: × 420 FN 1394/2

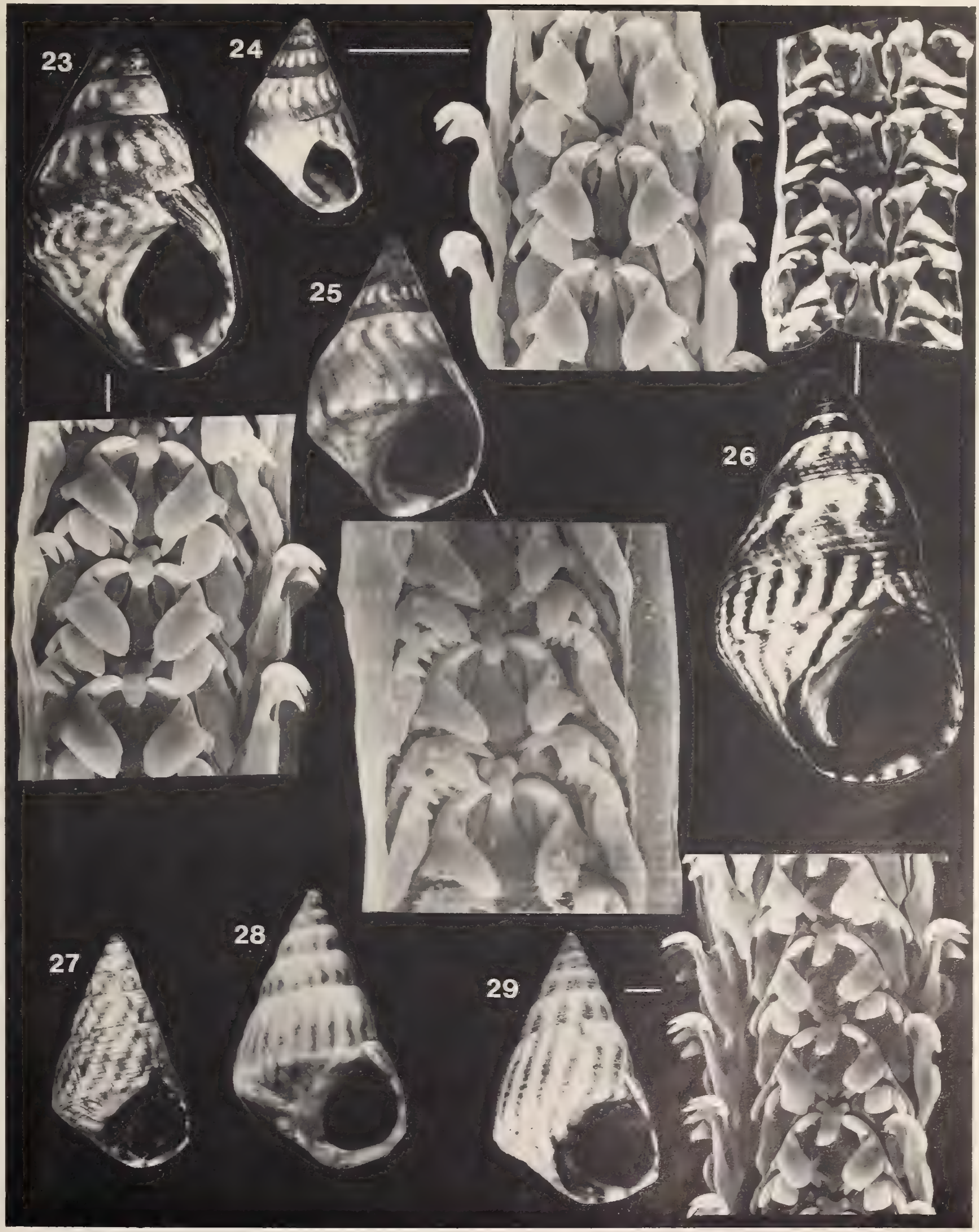
Figure *26:* Lesser Antilles, St. Vincent. BMNH. Height, 16.0mm. Radula: × 330 University Erlangen-Nürnberg FN 1491

Nodilittorina (N.) angustior (Mörch, 1876)

Figure *27:* Cuba, Havana. ZMK. Lectotype of *Littorina (Melaraphe) angustior* Mörch, 1876. Shell: 10.4×5.2mm

Figure *28:* Cuba. BMNH 1854.10.4.128. Lectotype of *Littorina carinata* Orbigny, 1842. 11.6×7.0mm

Figure *29:* Curaçao, Cornelisbaai. USNM 749809. Shell: 11.6× 6.8 mm, Radula: × 280 FN 1903/26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as well: *Nodilittorina interrupta* seems to have no adaptation at all to its elevated habitat, and *N. dilatata* seems to live too close to the water level, according to the criteria outlined above.

TAXONOMY

The Genus *Nodilittorina* Martens, 1897 in the Western Atlantic

Diagnosis.

Shell ovate to conical, solid; larval shell 2.5 to 3 obtusely conical whorls with spiral ziczac lines; postlarval shell sculptured with spirals or spirally arranged rows of nodules, tubercles or granules; whorls more or less angulate at periphery (may be superseded by nodules); interior of shell pigmented brown with a colourless or yellow band on the umbilical side, more unpigmented bands may be present; outer surface unicoloured, or with a broad dark median zone or axial brown stripes or both; no umbilicus; a crescent-shaped area of the outer shell surface adjacent to the columella margin may be redissolved. Operculum paucispiral to mesospiral, horny, brown. Radula with narrow central tooth, whose marginal cusps rise above the central one. Pelagic egg capsule is a circular disc, one side flat, the other one convex with spiral ridges, each capsule containing one egg. Penis with open spermiduct; presence and configuration of accessory organs are utilised and described in the subgenus diagnoses.

As discussed above, at present it is not justified to separate on a subgenus level spirally striated species from those with a granose or nodulose sculpture. The relationships between *Nodilittorina* as defined herein, and other nodulose taxa as well as the genus *Littorina* are shown in Table 1. The non-nodulose species of *Nodilittorina* used to be classified in *Littorina;* however, the low degree of relationship can easily be seen. In Table 1, the opportunity is seized to propose a new definition of the genus *Littorina* in its accustomed sense, splitting the genus as understood in current literature into the four genera *Littorina s. str., Littoraria, Fossarilittorina,* and *Melarhaphe,* the rationale of which is considered to be obvious.

Three subgenera of *Nodilittorina* are recognised:

Nodilittorina (Nodilittorina): Penis with one (rarely none or 2) penial glands, at a variable degree in contact with the basal enlargement; this subgenus comprises the bulk of the species, *i.e.,* with nodulose, granose and spiral sculpture; opercula type A and B; radula types "moderate," "pick" and "vestigial" of Rosewater, 1980.

Nodilittorina (Tectininus) Clench & Abbott, 1942: One penial gland widely apart from basal enlargement and surrounded by papillae; operculum mesospiral (type C); radula extremely vestigial. Only one species: *N. (T.) antoni* (Philippi) (= *Echininus nodulosus* Auct.)

Nodilittorina (Liralittorina) Rosewater, 1981: Penis without appendages; shell, radula and operculum characters within range of *N. (Nodilittorina).* Only one species: *N. (L.) striata* (King & Broderip).

Key to Shell Identification (Figure 5)

(including *Nodilittorina helenae*)

1. Shell with nodulose sculpture 2
   Shell spirally sculptured only; 6-8 primary spirals on visible part of whorls 6
2. Operculum mesospiral, 5-6 volutions; shell top-shaped, not conical due to convex and nodose whorls; aperture relatively small; nodes strongly developed, 2nd and 3rd row (counted from adapical row) distant from each other .... *N. antoni,* p. 34
   Operculum with maximal 4.5 volutions, paucispiral; shell shape more regularly conical 3
3. The two primary rows of nodules distant from each other, strongly unequal 4
   The two primary rows of nodules closer together, subequal ... 5
4. Apical angle about 45°; light bands at the suture, the periphery and the umbilical side seen externally ..... *N. helenae,* p. 37
   Apical angle 50-60°; no white external bands except on the umbilical side, but nodules white .... *N. vermeiji,* p. 31
5. Columella abapically often dilated, sometimes a pseudoumbilicus; nodules rounded to spinose .... *N. dilatata,* p. 29
   Columella not dilated; nodules rounded .... *N. tuberculata,* p. 33
6. Primary spirals distinctly incised; no or sporadic intercalations of secondary spirals 7
   Primary spirals more or less regularly doubling, primary and secondary spirals becoming equal, on last whorl often disappearing; interior with 2nd light band near the suture 8
7. Shell shape strictly conical; whorls gradually increasing, contours straight; height of aperture less than half of shell height; occasionally 2nd light interior band; operculum type B .... *N. angustior,* p. 25
   Shell shape ovate-conical; whorls more rapidly increasing, slightly convex; height of aperture more than half of shell height; operculum type A .... *N. riisei,* p. 26; *N. glaucocincta,* p. 27; and *N. mordax,* p. 28
   To be distinguished by radula characters only
8. Last whorls with 15-20 very fine spirals above the suture, often extinguishing; keel reduced; narrow ziczac lines, not confluent .... *N. ziczac,* p. 19
   Last whorls with 7-17 spirals above the suture, more incised than at *ziczac;* keel somewhat more pronounced; colouration more extensive 9
9. Shell up to 10mm long, slender, conical; dark brown median zone on whorls variable, absent to conspicuous; 2nd interior light-coloured band absent to present ..... *N. lineolata,* p. 21

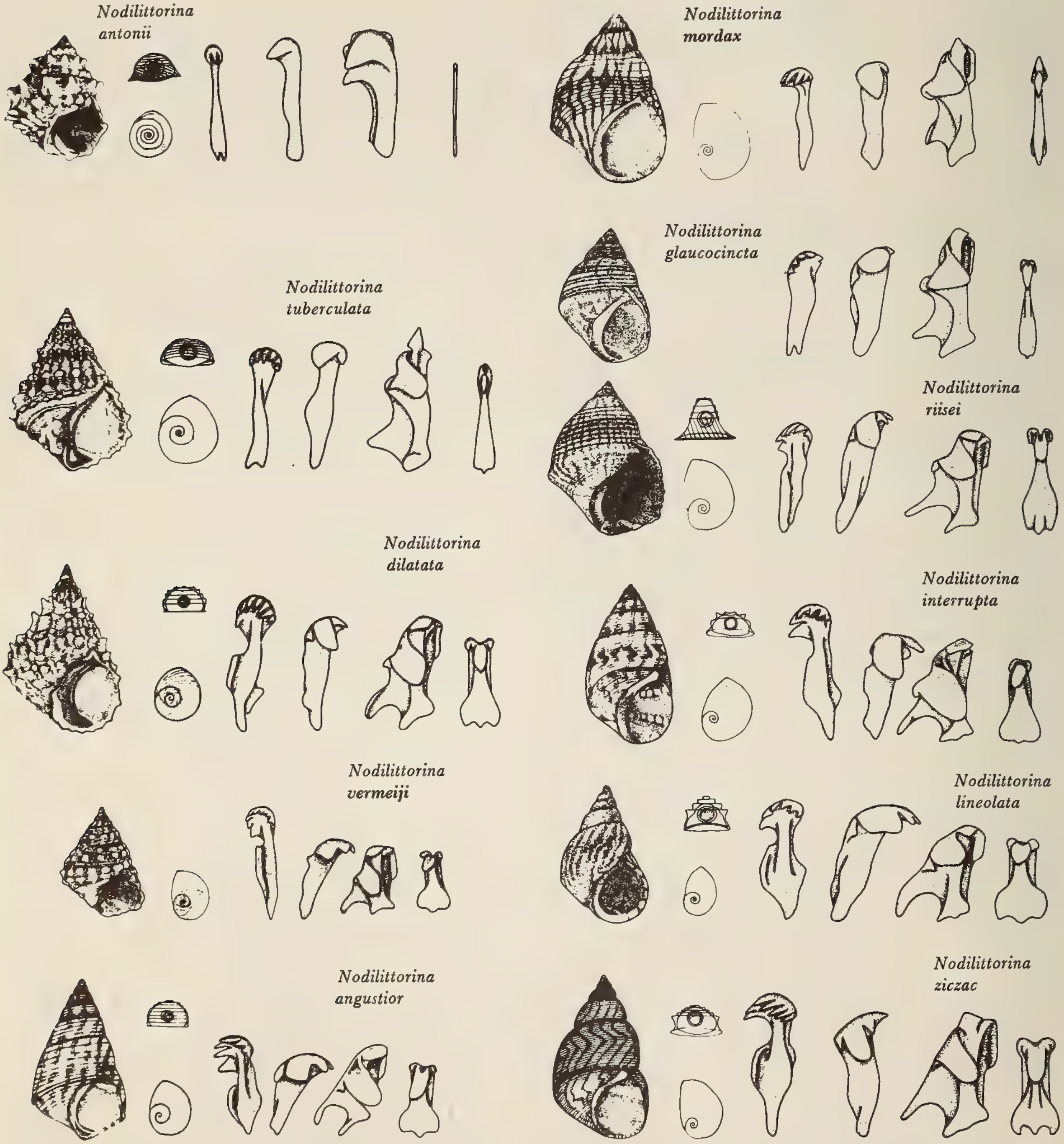


Figure 5

The West Atlantic species of *Nodilittorina*

Compilation of shell, radula, egg capsule and operculum morphological features. Arrangement of species according to similarity of characters does not necessarily imply phylogenetic relationships. In the vertical direction, the array follows the radula characters: at the bottom species with a primitive *Nodilittorina*-type radula *(e.g., N. ziczac)* are to be found, while towards the top radula characters approach those of *Nodilittorina (Tectininus) antoni;* (after Abbott, 1954a; Bandel, 1974; Borkowski, 1971; Borkowski & Borkowski, 1969; Marcus & Marcus, 1963; and new)

Shell about 15mm long (average), broader conical; dark brown median zone on whorls always broad and strongly developed; interior always with two light bands ..... *N. interrupta,* p. 23

Key to Radula Identification (Figure 5)

(including *Nodilittorina helenae)*

1. Teeth of moderate ("normal") size, inner marginal with 4 cusps, outer marginal with 7-9 cusps 2
   Central tooth more or less reduced; cusp number of remaining teeth reduced, *i.e.,* inner marginal with 1-3 cusps, outer marginal with 3-6 cusps; one cusp of both lateral and inner marginal tooth greatly enlarged 9
2. Basal platform of central tooth wide 3
   Basal platform of central tooth narrow 6
3. Margins of basal platform convex, thus largest width of basal platform remote from its posterior end ...... *N. ziczac,* p. 19 and *N. helenae,* p. 37
   Margins of basal platform straight 5
5. Transition from the posterior portion of the basal platform to its anterior portion in the central tooth rounded .... *N. angustior,* p. 25
   Transition angulate .... *N. lineolata,* p. 21
6. Largest width of the central tooth near the posterior edge of the basal platform; length/width ratio of central tooth 1.7-2.2 *N. interrupta,* p. 23
   Largest width of central tooth remote from the posterior edge of the basal platform; or basal platform rectangular 7
7. Outer marginal tooth with 8 cusps; length/width ratio of central tooth not exceeding 2.5 8
   Outer marginal with 7 cusps; length/width ratio of central tooth 2.5-2.8 .... *N. riisei,* p. 26
8. Length/width ratio of central tooth 2.1-2.3 .... *N. dilatata,* p. 29
   Length/width ratio of central tooth 2.3-2.5 .... *N. vermeiji,* p. 31
9. Lateral tooth with 4 cusps 10
   Lateral tooth with 1-3 cusps 11
10. Outer marginal tooth with 6 cusps; length/width ratio of central tooth 5-6 .... *N. glaucocincta,* p. 27
    Outer marginal tooth with 7 cusps; length/width ratio of central tooth 5.6-6.5; third cusp of lateral tooth very large .... *N. tuberculata,* p. 33
11. Lateral and inner marginal teeth with 3 cusps each, outer marginal tooth with 5-6 cusps; central tooth 6-12 times longer than wide .... *N. mordax,* p. 28
    Lateral and inner marginal teeth with one very large, massive cusp each, outer marginal tooth with 3 cusps; central tooth tiny, with one cusp .... *N. antoni,* p. 34

Subgenus *Nodilittorina (Nodilittorina)* Martens, 1897

* *Nodilittorina* Martens, 1897: 204. Type species: *Littorina pyramidalis* Quoy & Gaimard, 1833 (SD/Abbott, 1954a: 451).

* *Echinolittorina* Habe, 1956a: 96, 98-. Type species by M: *Litorina tuberculata* Menke, 1828.

* *Granulilittorina* Habe & Kosuge, 1966: 313, 328. Type species by M: *Granulilittorina philippiana* Habe & Kosuge, 1966 (= *Litorina millegrana* Philippi, 1848).

* *Austrolittorina* Rosewater, 1970: 467. Type species by OD: *Littorina unifasciata* Gray, 1827.

Nodilittorina (Nodilittorina) ziczac (Gmelin, 1791)

(Figures 5, 6, *14, 15, 18, 19, 45*)

- *Trochus ziczac* Chemnitz, 1781: plt. 166, figs. 1599a-b (here reproduced Figure *45*) ("Sugar Islands" in the West Indies; rejected work, not binominal).

* *Trochus ziczac* Gmelin, 1791: 3587, no. 122 (Type locality des. Bequaert, 1943): Barbados. Types probably lost; **lectotype** (herein): original of Chemnitz, 1781, plt. 166, fig. 1599b).

* *Littorina zigzag* "Chemnitz" Orbigny in Ramon de la Ságra, 1842: 210-, plt. 15, figs. 5, 8 (emendation of *ziczac* Gmelin, 1791) (here Figure *18*).

* *Littorina debilis* Philippi, 1846: 140 (no locality given; **lectotype** herein: BMNH 1968.222, here Figure *19*). Philippi, 1847: 47, plt. *Litorina* 6, fig. 7. Reeve, 1857: no. 70, plt. 14, fig. 70. Küster, 1856: 22-, plt. 3, figs. 9-11.

* *Litorina d'Orbignyana* Philippi, 1847: 162, plt. *Litorina* 3, fig. 12 (includes *zigzag* Orbigny, 1842; therefore Orbigny's original, BMNH 1854.10.4.130, is hereby designated **lectotype**, Figure *18* herein; type locality: Martinique).

- *Litorina ziczac,* Philippi, 1847: 162-, plt. *Litorina* 3, figs. 13-14. Küster, 1856: 22-, plt. 3, figs. 6-8. Weinkauff, 1882: 32 (part).
- *Littorina ziczac,* Reeve, 1857: no. 57, plt. 11, fig. 57. Abbott 1954b: 132, plt. 19, fig. E. ?Lewis, 1960: 415- (part), figs. 11G, H (spawn). Abbott, 1968: 82, ?fig. 81 (penis, spawn), fig. 83.3 (shell). Kaufmann & Götting, 1970: 348-; fig. 34. Borkowski & Borkowski, 1969: 408-413; fig. 4c (spawn), plt. 66, figs. 5-6 (shell). Borkowski 1971: 827-836, fig. 2 (spawn). Bandel, 1974: 93-113, figs. 8 (shell); 15A-B, 17 (spawn), 18-21, 45-46 (radula). Flores, 1973a: 13-, plt. 2, figs. 1-5. Borkowski, 1975: 369-376; fig. 1C (radula). Bandel, 1975: 15; plt. 1, figs. 1-3 (embryonic shell).

* *Littorina (Melaraphe) zic-zac* "Chemnitz" Mörch, 1876: 137-, no. 321 (emendation of *ziczac* Gmelin, 1791).

- *Littorina (Melaraphe) ziczac,* Tryon, 1887: 251 (part), plt. 45, fig. 5 (copy Reeve, 1857).
- *Littorina (Melarhaphe) ziczac,* Martens, 1900: 577, 583 (part). Bequaert, 1943: 14-18; plt. 5, figs. 1-4 (part, most synonyms and remaining figures to be excluded). Abbott, 1954a: 450: ?fig. 55j (penis), fig. 55k (spawn)(part: all spirally sculptured Caribbean species included here). Abbott, 1964: 65 (part).

* *Littorina zigzac,* Lebour, 1945: 465; figs. 5a-d (spawn, veliger) (emendation of *ziczac* Gmelin, 1791).

- *Littorina (Littorina) ziczac,* Rosewater, 1970: 423. Abbott, 1974: 68; fig. 556.

Description: Shell ovate-conical, 15-20mm long, with slightly convex, regularly increasing whorls, the last bluntly angular at the periphery; no umbilicus. **Embryonic shell:** one planispiral whorl, with finely granulose sculpture and growth lines; diameter 0.15mm; aperture slightly

Figure 6

Distribution of *Nodilittorina (N.) ziczac* (Gmelin, 1791)

higher than wide. Larval shell not observed. **Teleoconch:** sculpture commences with 5-6 visible, incised spiral lines separated by flattened ridges; after approximately 2 whorls the number doubles; later more spirals may intercalate, bringing the number of spirals above the suture up to 15-20. Umbilical side with similar, but more closely spaced spirals. Blunt angle at the periphery made up by thickening of the shell wall. **Colour** at first brown, then gradually becoming whitish with thin axial and ziczac markings always at angles to the growth lines; interior of shell brown except a light band around the umbilicus and another, less sharply defined one near the suture; exterior pigmentation may be largely reduced, producing a nearly white shell. **Aperture** ovate, angulate adapically; columellar edge moderately broad, slightly concave, more or less brown, adapically thickening, smoothing the transition to the parietal wall by a callus with a straight interior edge. Parietal wall with thin brown shell layer. Outer lip simple. External shell surface adjacent to columella not redissolved. Operculum horny, brown, paucispiral, last whorl broader than half of operculum length.

Radula: basic *Nodilittorina* type (Figure *18,* also B DEL, 1974).

Spawn: LEBOUR, 1945; ?LEWIS, 1960 (figs. 11G-H only, however slightly different from the figures of other authors); BORKOWSKI & BORKOWSKI, 1969; BORKOWSKI, 1971; BANDEL, 1974; see Figure *5.*

Penis: ABBOTT (1954a) figured a penis of *"Littorina ziczac"* from the Bahamas. As at that time all spirally sculptured *Nodilittorina* species were united under the name of *ziczac,* this might be a penis of *N. angustior* or *N. mordax* as well.

Types: Gmelin's *Trochus ziczac* was founded on figures and description of Chemnitz only. Dr. Knudsen (København) kindly informed us that Chemnitz had three collections at his disposal: his own, Spengler's and that of Count Moltke. The two last-named are in the Universitets Zoologiske Museum of København, but the location of his own is not known. Chemnitz stated his specimens to be present in his collection, a fact being consistent with Dr. Knudsen's statement that there is no material in København. As the species is easily recognizable in Chemnitz' figures (here refigured), the designation of fig. 1599b (Figure *45*) to represent the **lectotype** is considered to be sufficient to stabilise nomenclature.

Philippi's *Littorina debilis* proved to be a half-grown specimen of *Nodilittorina ziczac* with a reduced colour pattern. The hereby designated **lectotype** had parts of the radula preserved.

In 1847 Philippi distinguished a more distinctly sculptured *Littorina d'Orbignyana* and a "true" *L. ziczac* with reduced sculpture and more pronounced axial colour lines. Such differences are often encountered in populations and are of intrasepcific rank; the radula exhibits no differences. Philippi's types may be in Berlin (East), but as he included

Explanation of Figures *30* to *36*

Nodilittorina (N.) riisei (Mörch, 1876)

Figure *30:* Cuba. ZMK. Lectotype. Shell: 9.6×7.0mm, Radula: × 680 FN 1394/43

Figure *31:* Cuba. SMF. Shell: 7.5×5.6mm, Radula: × 370 FN 1615/1

Nodilittorina (N.) glaucocincta (Mörch, 1876)

Figure *32:* Lesser Antilles, St. Jean. ZMK. Holotype of *Littorina (Melaraphe) floccosa* var. *glaucocincta* Mörch, 1876. Shell: 13.1×8.4mm, Radula: a) × 350 FN 1382/19
b) (inner and outer marginal teeth) × 570 FN 1382/20

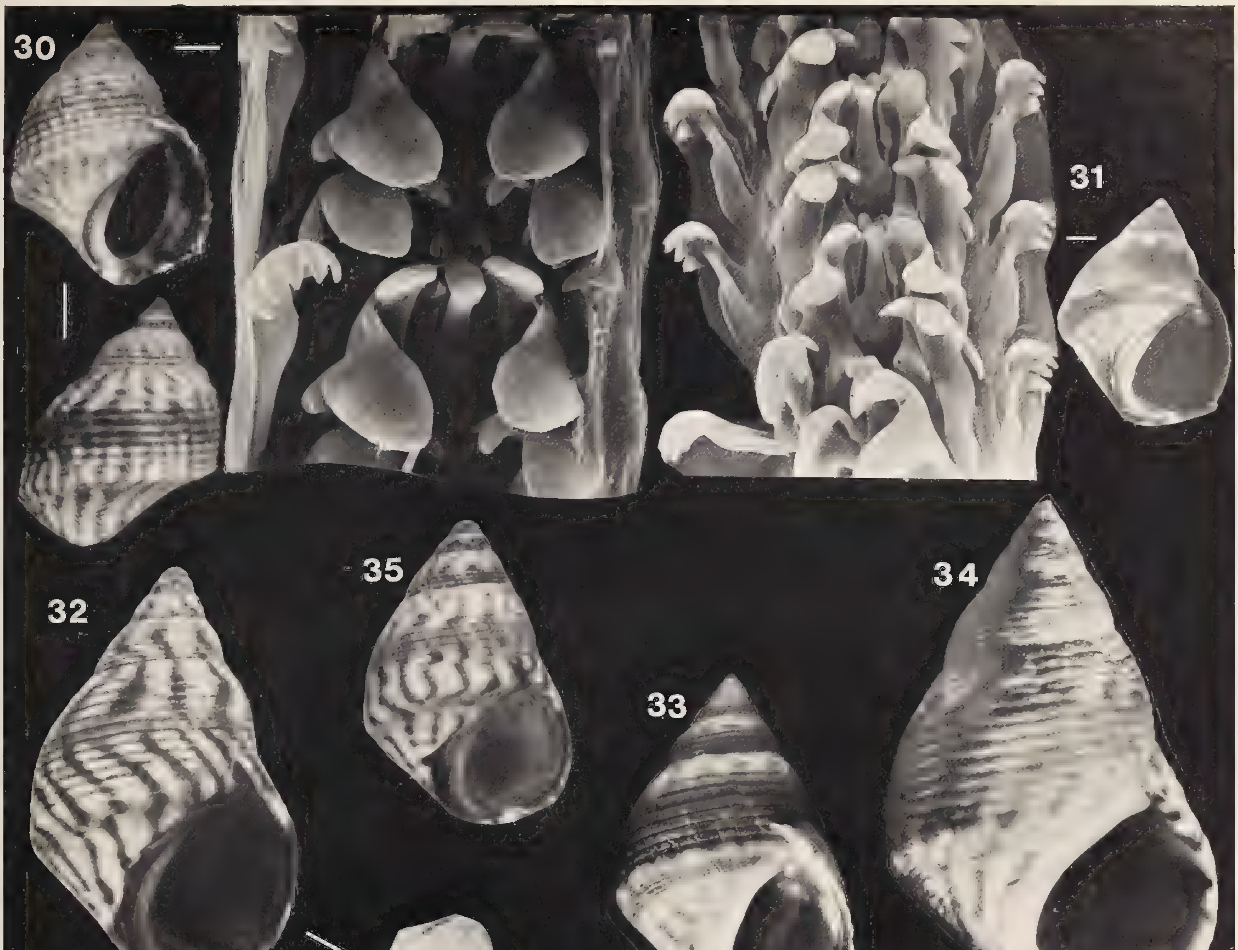
Figure *33:* Jamaica. MCZ 156162. Paratype of *Littorina jamaicensis* C.B. Adams, 1850. Shell: 11.5×7.4mm, Radula: × 370 FN 1599/4

Doubtful species, possibly *Nodilittorina glaucocincta* (Mörch, 1876)

Figure *34:* Jamaica. MCZ 186133. Lectotype of *Littorina jamaicensis* C. B. Adams, 1850. 16.9×10.6mm

Figure *35:* Antilles. ZMK, labelled *"Littorina glaucocincta* Beck." 10.1×6.8mm (compare Figure *32*)

Figure *36:* Martinique. BMNH 1854.10.4.139. Lectotype of *Littorina (Melaraphe) angustior* var. *fasciata* Mörch, 1876; original of ORBIGNY, 1842, plt. 14, fig. 25. Shell: 14.3×8.7mm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the *"zigzag"* of Orbigny, 1842, in his *L. d'Orbignyana*, this original specimen was the only available one and is designated to be the **lectotype** of *L. orbignyana* Philippi, 1847.

Relationships. *Nodilittorina lineolata* and *N. interrupta* are closely allied, but differ in the slightly lower number of more pronounced spirals, a more pronounced angulation at the periphery; the egg capsule of both *N. interrupta* and *N. lineolata* has four spiral ridges instead of 5. *Nodilittorina lineolata* also is smaller, more slender; both species have more intensive colour markings and the tendency towards a dark brown median zone on the whorls. *Nodilittorina ziczac* and *N. interrupta* are sympatric in the Southern Caribbean, where *N. interrupta* inhabits a higher supratidal zone than *N. ziczac; N. lineolata* is geographically separated from both *N. ziczac* and *N. interrupta* and could be regarded as a geographical race of, preferably, *N. interrupta.*

Range. Bermuda, Florida, all Caribbean islands, Colombia, Venezuela; occurrence on the coast of Middle America mainland probable, but no material available.

Material examined. Bermuda (Lebour, 1945, (spawn); BMNH (shells)). Florida: Miami; Boca Raton; Key Biscayne (no radula). Bahamas: S. Bimini; San Salvador (USNM 749794 through 749797). Cuba (SMF). Hispaniola: Port-au-Prince, Cacique Island (USNM 749798). Antilles: Martinique (**lectotype** of *L. d'orbignyana* Philippi, 1847, BMNH 1854.10.4.130); Barbados (type locality, no material seen) untypical spawn figures by Lewis, 1960, fig. 11G-H; Curaçao, Cornelisbaai (USNM 749799). Colombia: Santa Marta (USNM 749800, 749801). Venezuela: La Guaira (RMNHL); Carupano (SMF 209798). No locality: SMF 196010 (coll. Helm, 1817, with preserved radula); **lectotype** *L. debilis* (BMNH 1968.222).

Nodilittorina (Nodilittorina) lineolata (Orbigny, 1840)

(Figures 1A, 3A, 5, 7, *20-22*)

✱ *Littorina lineolata* Orbigny, 1840: 392- (Port of Rio de Janeiro; **lectotype** BMNH 1854.12.4.363, Figure *20* herein) (part, synonyms excluded).

• *Littorina lineata,* Orbigny, 1842: 208; no. 120 (part, excl. figs. and synonyms). Borkowski, 1975: 369, 371 (part, only synonym *"brazilensis"* = misspelling for *brasiliensis* Vermeij & Porter, 1971) (not *Phasianella lineata* Lamarck, 1822).

✱ *Litorina pusilla* Philippi, 1847: 164; plt. *Litorina* 3, fig. 23 ("Brasilia or Sandwich Islands" type locality restricted to Brasilia herein; types not available, might be in Berlin (East)) (not *Littorina pusilla* M'Coy, 1844: 32, pl. 5 fig. 26). Küster, 1856: 11; plt. 1, figs. 20-22.

• *Littorina (Melaraphe) lineolata,* Mörch, 1876: 138, no. 323.

• *Littorina (Melaraphe) pusilla,* Mörch, 1876: 140, no. 328. Tryon, 1887: 251; plt. 45, fig. 8 (copy Küster, 1856).

• *Littorina (Melaraphe)* sp.n (or *pusilla* var.?), Mörch, 1876: 140-, no. 329.

• *Littorina (Melaraphe) ziczac,* Bequaert, 1943: 15, 17 (part, figs. excl.). Matthews, 1968: 184, fig. 1. Rios, 1970: 33 (not *Trochus ziczac* Gmelin, 1791).

• *Littorina ziczac,* Marcus & Marcus, 1963: 7-33, figs. 1 (shell), 3 (radula), 9 (osphradium), 15-16 (penis), 24-25 (female genitalia), 28-29 (spawn), 30 (young shell).

✱ *Littorina ziczac brasiliensis* Vermeij & Porter, 1971: 448 (new name for *Litorina pusilla* Philippi, 1847, not M'Coy, 1844). Vermeij, 1973: 324.

Description: Shell ovate conical, about 10 mm long, with slightly convex, regularly increasing whorls, the last angular at the periphery; no umbilicus. Apex very often heavily corroded by algae.

Teleoconch: Sculpture commences with 7 visible incised spiral lines separated by flattened ridges; this number may double later. Umbilical side with similar, but more closely spaced spirals. Angle at the periphery of variable strength, made up by thickening of the shell. Colour at apex brown, then gradually becoming whitish with axial and, in large specimens, ziczac markings always at angles to the growth lines; a conspicuous dark brown median band is rarely seen on the whorls; shell interior dark brown with a light band on the umbilical side and occasionally (in about half of specimens) a second, less distinct light band near the suture. Aperture ovate, angled adapically; columellar margin broad, very slightly concave, dark brown, adapically thickening, smoothing the transition to the parietal wall by a callus with straight interior edge. Parietal wall with brown shell layer. Outer lip simple. External shell surface adjacent to columella sometimes slightly redissolved.

Operculum: horny, paucispiral, width of its last whorl more than half of the remainder of the operculum.

Radula: is of the basic *Nodilittorina* type, with the transition from the posterior portion of the basal platform of the central tooth to its anterior portion angulate.

Spawn: (Marcus & Marcus, 1963) a cupola-shaped capsule with one egg, one side flat, opposite side convex with 4 spiral ridges, separated from flat side by a steep-sloped smooth zone.

Relationships: *Nodilittorina ziczac* is larger than *N. lineolata,* its spiral sculpture is weaker and commences with 5-6 spirals which may double twice; always two light bands in the interior; egg capsule with 5 ridges. *N. interrupta* is also larger, but always has a conspicuous dark brown median zone on whorls and two light interior bands, and shells of equal size are generally broader in *N. interrupta. N. interrupta* and *N. lineolata* are probably most closely related, but they are geographically widely separated. The shell of *N. angustior* may be very similar to *N. lineolata,* but this is regarded as homoeomorphous as both species are sufficiently distinguished by their spawn and operculum characteristics to be regarded as not closely related.

Figure 7

Distribution of *Nodilittorina (N.) lineolata* (Orbigny, 1840) and *N. (N.) interrupta* (C. B. Adams *in* Philippi, 1947)

Nomenclature. In recent years, the name *lineolata* Orbigny has been applied to a mixture of species encompassing *Nodilittorina interrupta, N. glaucocincta, N. riisei* and *N. mordax.* However, from Orbigny's original diagnosis it is obvious that he considered *lineolata* to be a mere variety of *"Littorina lineata* Lamarck" (= *N. angustior* according to his 1842 figures, but probably *N. interrupta* of his intention), demonstrating that he did not confuse the names *lineata* and *lineolata:*

> "Cette espèce, que nous considérons comme une variété de la *Littorina lineata* des Antilles, est beaucoup plus petite. Avec les mêmes couleurs, elle est quelquefois moins anguleuse, mais ne nous paraît pas en différer spécifiquement."

The 1840 publication of Orbigny is considered to be the original publication of the name *Littorina lineolata,* although the author cited another publication of the name *lineolata* in a paper entitled "Mollusques des Antilles." No work with such a title has been published; and as the numbers allocated to *Littorina lineolata* and to *L. columellaris* in the synonymy citations of 1840 are the same as published for *L. lineata* and *L columellaris* in 1842, it is assumed that "Mollusques des Antilles" is a manuscript title subsequently dropped when the actual manuscript was published in Ramon de la Sagra's account of the Isle of Cuba (Orbigny, 1842).

By its type locality and by its preserved type specimens the identification of this species is beyond doubt. Orbigny himself, in a later study (1842) contributed further to the confusion about *Nodilittorina lineolata,* in that he included his *lineolata* in *"Littorina lineata,"* even citing it as *"lineata."* Since 1847, the name *pusilla* Philippi, 1847 came into more frequent use; it was proposed for individuals with a heavily corroded spire. Although it is preoccupied, the substitution name *brasiliensis* Vermeij & Porter, 1971 is unnecessary as the name *lineolata* is without doubt available for the Brazilian species. Bequaert (1943: 17) selected "Barbados," one of the two so-called "Sugar Islands" cited in Chemnitz' references as type locality for both *N. ziczac* and *N. lineolata;* this selection is rejected for *N. lineolata* because it is based on Orbigny's reference to Chemnitz (1781: plt. 166, figs. 1600a-b (refigured Figure *45* herein)) only, which is not conspecific with the material Orbigny actually described; the selection of a **lectotype** (herein) supersedes this and any possible other restriction of the use of the name *lineolata* (Art. 74 a(ii) IRZN).

Distribution. South America: Brazil and Uruguay.

Material studies. Brazil: Desterro (SMF, no radula), Pernambuco (BMNH), São Vicente near Santos (USNM 749802); Prov. Rio de Janeiro, Prainha (IRSNB); Rio de Janeiro (Lectotype, BMNH 1854.12.4.363; SMF), São Paulo (SMF, no radula). Uruguay: Cabo Polonia, Rocha (SMF).

Nodilittorina (Nodilittorina) interrupta
(C. B. Adams in Philippi, 1847)
(Figures 5, 7, *16, 17, 23-26)*

- *Phasianella lineata* Lamarck, 1822: 54 (Antilles; part, not the lectotype which is *Littoraria tesselata* (Philippi, 1847); 3 paratypes in MHNG 1096/87/2-4, Figure *23* herein) (not *Buccinum lineatum* Gmelin, 1791, which is *Littoraria (Littorinopsis) scabra* (Linnaeus, 1758)).
- *Littorina marnat* Potiez & Michaud, 1838: 279 (part); plt. 28, figs. 9-10 (St. Thomas; synonymy excluded is *N. punctata* (Gmelin, 1791): **lectotype** hereby designated: original of *Trochus marnat* Adanson, 1757 (plt. 12, fig. 1) = holotype of *Trochus punctatus* Gmelin, 1791, refigured by Fischer-Piette, 1942: plt. 10, figs. 2a-b, from Senegal).
- *Littorina lineata,* Orbigny, 1842: 208 (part, excl. figs.)
- *Litorina lineata,* Philippi, 1847: 163-; plt. *Litorina* 3, fig. 18. Küster, 1856: 23-; plt. 3, figs. 12-13.
* *Litorina ziczac* var. *interrupta* C. B. Adams in Philippi, 1847: 164 (sub *Litorina lineata*) (no locality given; material in the C. B. Adams collection from Jamaica, MCZ 186124, here Figure *24*).
* *Littorina jamaicensis* C. B. Adams, 1850: 71 (lectotype design. by Clench & Turner, 1950: 296-, 380; plt. 38, fig. 19, herein refigured Figure *34; nomen dubium* due to lack of radula; paratypes are *N. interrupta* (Figure *24*) and *N. glaucocincta* (Figure *33*)).
- *Litorina lineata* var. *interrupta,* Küster, 1856: 24; plt. 3, figs. 14-15.
* *Littorina (Melaraphe) floccosa* Mörch, 1876: 138, no. 322 (Lesser Antilles, St. Thomas; **lectotype** ZMK, Figure *25* herein).
* *Littorina (Melaraphe) angustior* var. a *fasciata* Mörch, 1876: 139, no. 324a (refers to *Littorina lineata* Orbigny, 1842: plt. 14, fig. 25; Martinique; **holotype,** BMNH 1854.10.4.139, herein Figure *36.* Species identification doubtful due to lack of radula, thus *nomen dubium;* not *Littorina fasciata* Gray, 1839).
- *Littorina lineata* var. *interrupta,* Clench & Turner, 1950: 294, 380; plt. 38, fig. 18 (invalid paratype designation, fig. 18, MCZ 186 123; invalid lectotype designation, p. 294).
- *Littorina lineolata,* Kaufmann & Götting, 1970: 349; fig. 35 (not of Orbigny, 1840).
- *Littorina* sp. Bandel, 1974: 93-113; figs. 9 (shell), 16A, 17 (spawn), 18-21, 46-47 (radula). Bandel, 1975: 14-, plt. 1, figs. 4-6 (embryonic shell).

Description. Shell elongate ovate-conical, about 15mm long; whorls slightly convex, slowly and regularly increasing, the last bluntly angular at the periphery; no umbilicus. **Embryonic shell:** one whorl, planispiral, finely granulated, with growth lines; shell diameter 0.13mm; aperture slightly higher than wide, its margin with shallow sinuses at their sides. Larval shell 2.5 whorls sculptured with approx. 7 spirally arranged rows of granules mostly fusing to ziczac ridges; growth lines present and a terminal varix with a deep adapical sinus (Figures *16, 17*).

Teleoconch: Earliest sculpture not preserved; on later whorls sculpture consists of 10 incised spiral lines above the suture, separated by flattened ridges; three more spirals below suture; only on last whorl spirals may double and simultaneously become obsolete; umbilical side with similar, but more closely spaced spirals. Blunt angle at the periphery made up by thickening of the shell. Colour of apex brown; a broad brown median zone on the visible parts of the whorls and another narrow brown zone abapical to the peripheral angle persist throughout growth; width and intensity of these zones vary, they may be less intense than axial and ziczac markings being at angle with the growth lines. Interior brown but for narrow light bands near the suture, on the umbilical side and at the peripheral angle, the latter being the least distinct and most narrow one. Aperture ovate, angled adapically; columellar edge broad, very slightly concave, more or less brown, adapically thickening, smoothing the transition to the parietal wall by a callus with straight interior edge. Parietal wall with light brownish shell layer. Outer lip simple. External shell surface adjacent to columella sometimes very slightly redissolved. Operculum horny, paucispiral, last whorl broader than half of operculum length.

Radula: Basic *Nodilittorina* type; central tooth slightly narrowed, the sides of the basal platform are rounded.

Spawn (Bandel, 1974): Cupola-shaped egg capsule with four ridges on top of the convex side and smooth, slightly concave steep-sloped flank.

Relationships: *Nodilittorina ziczac* differs in size, sculpture, and colour pattern, and the central tooth of the radula has a broader basal platform with strongly convex lateral edges. *N. lineolata* has sometimes a similar colour pattern, but is also different in size, sculpture, details of the central tooth and also in the operculum. *Nodilittorina glaucocincta,* also living in Jamaica, and its allies *N. riisei* and *N. mordax* usually have broader shells with a larger aperture, stronger spiral sculpture and without the adapical light-coloured interior band. However there may be shell varieties which are more slender, less intensely sculptured and showing a weak adapical interior band; these shells cannot be distinguished from some individuals of *N. interrupta* with an equally strongly sculptured shell (*e.g.,* Figure *26*) without studying the radula and the spawn. The radula of *N. interrupta* is similar only to the one of *N. riisei,* but the egg capsules are very different.

Nomenclature: *Phasianella lineata* Lamarck: The type sample is composed of this species and *Littoraria tesselata* (Philippi, 1847); Bequaert (1943: 13) selected the only individual belonging to the latter species to be the lectotype. For fuller discussion see appendix.

Littorina marnat Potiez & Michaud: The figured specimen, said to be from St. Thomas, can be determined as *N. interrupta* because additional material from this locality, constituting the lectotype and paratypes of *floccosa* Mörch, 1876, proved the specific identity with *N. interrupta.* The species name of Potiez & Michaud, being that of Adanson, 1757, for the West African form known as *N. punctata* (Gmelin, 1791), is taken as an indication of the authors' intent as to which populations they considered to be typical of their nominal species, and the lectotype is designated accordingly.

Littorina interrupta: Philippi (1847) mentioned and defined the specific name *"interrupta* C. B. Adams" the first time; however, he considered this a colour variety of his *"Litorina lineata"* not worthy of a name even on the variety level; *i. e.,* the name *interrupta* is published as a synonym here. Subsequently the name has been accepted for a taxon only once (Küster, 1856), but this should satisfy the requirements of availability of names published primarily in synonymy (Art. 11 (d), IRZN). In case this interpretation should be rejected, the species dealt with here would retain the specific name *"interrupta,"* but the authorship had to be credited to Küster, 1856. As Philippi himself did not intend to publish this name validly, he should not be cited as the author, but C. B. Adams instead.

The type of the nominal species *"interrupta"* has to be selected from the published specimens; *i. e.,* from those Philippi had at hand; thus the selection of paratypes from the C. B. Adams collection (Museum of Comparative Zoology, Cambridge, Mass.) and of the figs. 14-15 of plt. 3 of Küster (1856) as lectotype is invalid. Also the citation of the name as of "Philippi, 1856" is incorrect. Nevertheless, the specimens of the C. B. Adams collection, exhibit-

Explanation of Figures *37* to *41*

Nodilittorina (N.) ***mordax*** Bandel & Kadolsky, spec. nov.

Figure *37:* Bahamas, Nassau, Paradise Island, Holotype. USNM 749813. Shell: 11.8×8.9 mm, Radula: × 410 FN 931/1

Figure *38:* Curaçao, Cornelisbaai. Paratype. USNM 749816. Shell: 10.9×7.6 mm, Radula (figured by Bandel, 1974 (figs. 50-51, as *jamaicensis*)) × 290 FN 1903/19

Figure *39:* S. Bimini, Sunshine Inn. Paratype. USNM 749815. Shell: 7.6×5.6 mm, Radula: a) × 710 FN 1427/13
b) × 710 FN 1427/15

Littoraria tesselata (Philippi, 1847)

Figure *40:* Antilles. MHNG 1096/87/1. Lectotype of *Phasianella lineata* Lamarck, 1822, and of *Littorina tesselata* Philippi, 1847. Shell: 16.6×11.0 mm. Paratype figure see Figure *23*

Figure *41:* Haiti, Port-au-Prince, Cacique Isl., Ibo Beach. USNM 749825. Shell: 14.9×10.5 mm, Radula: × 440

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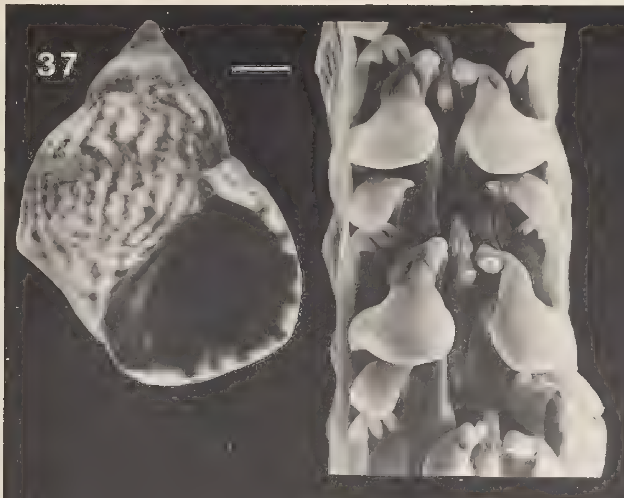

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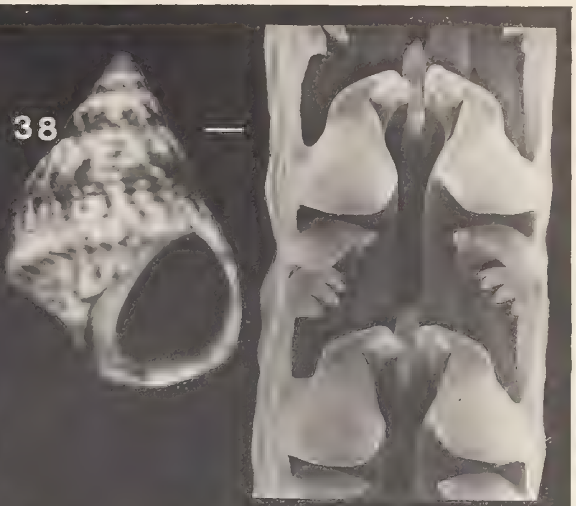

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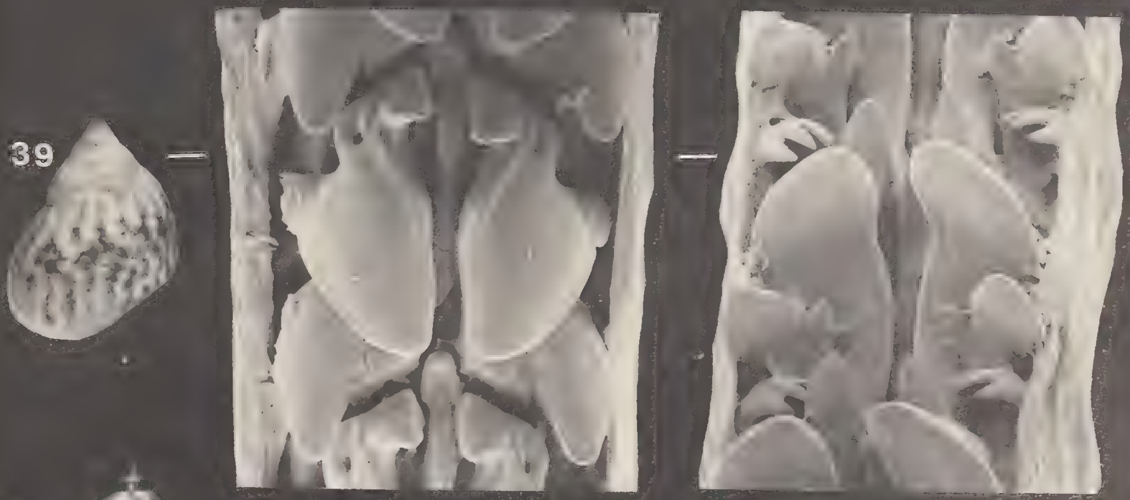

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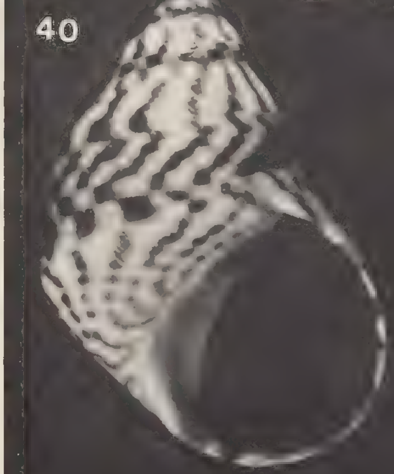

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ing the colour variety described by Philippi (1847) (see Figure *24*), were very useful to identify the name *"interrupta."*

Littorina jamaicensis C. B. Adams, 1850, has to be considered as a doubtful name, as the lectotype, designated by Clench & Turner, 1950, no longer contained the radula. Paratypes proved to be *N. interrupta* and *N. glaucocincta*, which can securely only be separated by their radula (and probably spawn) properties. The lectotype is a slender shell with a small aperture and strong spiral sculpture; the two first-named characters are more typical for *N. interrupta*, while the latter occurs more frequently in *N. glaucocincta*.

Distribution: Southern Caribbean Sea, from Jamaica and Hispaniola to Columbia.

Material examined. Jamaica (paratypes of *L. jamaicensis* C. B. Adams, 1850, MCZ 186123, 186124; other material, SMF); Hispaniola, Haiti, St. Marc (SMF). Lesser Antilles: St. Thomas (lectotype and 50 paratypes of *L. floccosa* Mörch, 1876, ZMK); St. Vincent (BMNH); St. Croix (1 paratype of *floccosa*, ZMK). Costa Rica: Limón (SMF). Columbia: Santa Marta (USNM 749803). Locality unknown: 3 paratypes of *Phasianella lineata* Lamarck, 1822, MHNG 1096/87/2-4. **Doubtful material** (no radula): Martinique (lectotype of *Littorina angustior fasciata* Mörch, 1876, (BMNH 1854.10.4.139).

Nodilittorina (Nodilittorina) angustior

(Mörch, 1876)

(Figures 5, 8, *27-29*)

- *Littorina lineata*, Orbigny, 1842: 208; plt. 14, figs. 24, 26, 27 (not fig. 25, not *Phasianella lineata* Lamarck, 1822). Borkowski & Borkowski, 1969: 409-414; fig. 4B (spawn), plt. 66, figs. 1-2 (shell). Borkowski, 1971: 827-836; fig. 2 (spawn). Flores, 1973: 14-; plt. 2, figs. 6-10. Borkowski, 1975: 369-376; fig. 1A (radula).
* *Littorina carinata* Orbigny, 1842: 209; plt. 15, figs. 1-4 (Cuba; **lectotype** (BMNH 1854.10.4.128, here Figure *28*) (not *Delphinula carinata* Woodward, 1833 nor *Turbo carinatus* Woodward, 1833, which are both forms of *Littorina littorea* (Linnaeus, 1758)). Reeve, 1857: no. 50, plt. 8, fig. 50.
- *Litorina carinata*, Philippi, 1847: 163; plt. *Litorina* 3, fig. 19. Küster, 1856: 19; plt. 2, figs. 28-29.
* *Littorina (Melaraphe) angustior* Mörch, 1876: 139, no. 32 (type locality (hereby designated): Havana, Cuba; **lectotype** (hereby designated): Mörch collection, ZMK, herein Figure *27*).
- *Littorina (Melaraphe) carinata*, Mörch, 1876: 139, no. 325.
- *Litorina ziczac*, Weinkauff, 1882: 32 (part, not figs.; not of Gmelin, 1791).
- *Litorina angustior*, Weinkauff, 1882: 67-, plt. 8, fig. 15 (paratype).
- *Littorina (Melarhaphe) lineata*, Martens, 1900: 577, 583 (not of Lamarck, 1822).
- *Littorina (Melarhaphe) ziczac*, Bequaert, 1943: 15; plt. 5, fig. 5 (part, not of Gmelin, 1791). Warmke & Abbott, 1962: 52- (part), plt. 9, fig. L.
- *Littorina lineolata*, Abbott, 1964: 65 (part, not of Orbigny, 1840). Abbott, 1968: 82; fig. 83.1.? Flores, 1973: 15-, plt. 2, figs. 11-15.

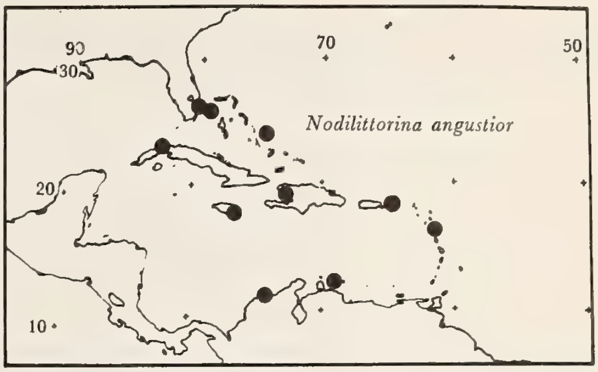


Figure 8

Distribution of *Nodilittorina (N.) angustior* (Mörch, 1876)

- *Littorina (Austrolittorina) lineata*, Rosewater, 1970: 423.
- *Littorina jamaicensis*, Bandel, 1974: 95, 99, 103; figs. 10 (shell), 17 (spawn) (not the radula which is from *Nodilittorina mordax spec. nov.*; not *jamaicensis* C. B. Adams, 1850).
- *Littorina (Austrolittorina) angustior*, Abbott, 1974: 68-; fig. 560.

Description: Shell conical, about 10-15 mm long, with nearly straight but stepped contours of the whorls, the last angular to bluntly keeled at the periphery; no umbilicus.

Protoconch: About 3 whorls, brown, worn.

Teleoconch: Sculpture consists of 6-7 incised spiral lines separated by flattened ridges; no or only sporadic intercalations of secondary spirals. Umbilical side with similar but weaker spirals. Angle or keel at periphery made up by shell material.

Colour: On early whorls a light zone at the adapical suture and a brown zone abapically of it; this brown zone mostly disappears during growth but may sometimes persist; oblique, closely spaced brown axial markings cover all whorls. Interior brown except two narrow bands near the suture and on the umbilical side; a third band at the peripheral angle is blurred, narrower and often obsolete.

Aperture: Small, ovate, angled adapically. Columellar edge broad, slightly concave, brown, passing without an angle to the parietal wall which is covered by a brown shell layer. Outer lip simple. Sometimes faint indications of redissolving of the external shell surface adjacent to the columellar margin.

Operculum: Horny, paucispiral, its last whorl narrower than its spiral part.

Radula: Of basic *Nodilittorina* type; in the central tooth the lateral edges are rounded at the transition from the posterior to the anterior portion of the basal platform.

Spawn (Borkowski & Borkowski, 1969; Borkowski, 1971): Capsule cupola-shaped, with spiral ridges over the whole convex side down to the edge of the flat side.

Relationships: By its slender conical form, the relatively small aperture, the shape of the egg capsule and the narrowly coiled operculum, this species appears to be isolated amongst the Western Atlantic spirally sculptured species of *Nodilittorina.*

Nomenclature: Many authors credited the specific name *"lineata"* to Orbigny, 1842. However, Orbigny referred to *Phasianella lineata* Lamarck, 1822 which is not conspecific: the lectotype is *Littoraria tesselata* (Philippi, 1847) while the three paratypes belong to *Nodilittorina interrupta* (C. B. Adams in Philippi, 1847). Possibly Orbigny (1842) considered his *Littorina lineata* to be *N. interrupta* but his figures show *N. angustior* and *N.* cf. *interrupta,* and his reference to Rio de Janeiro specimens includes *N. lineolata.*

The name *"carinata* Orbigny, 1842" was rejected by Bequaert (1943), Borkowski & Borkowski (1969) and others as a presumed homonym of *Turbo carinatus* J. Sowerby, 1819. As this species does not belong to the Littorinidae, it is neither a primary nor a secondary homonym of *Littorina carinata* Orbigny. However, two aberrant fossil varieties of *Littorina littorea* (Linnaeus), described by Woodward (1833) as *Delphinula carinata* and *Turbo carinatus,* make *L. carinata,* Orbigny, 1842 really after all a secondary junior homonym.

The distinction of *"lineata* Orb." (= *angustior* Mörch *s. str.*) and *carinata* Orb. is based on the existence of an angulate or keeled periphery, respectively. This character, however, is variable within the species. *"L. lineata"* was sometimes identified with *N. interrupta, e.g.,* by Philippi, 1847 and Küster, 1856.

Range: The whole Caribbean Sea, as far south as Venezuela, as far north as Florida.

Material examined: Florida: Key Biscayne (no radula); Miami (USNM 749804); Boca Raton (749805); Bahamas: S. Bimini (749806); San Salvador (749807). Cuba: Lectotype and paratypes of *Littorina carinata* Orbigny, 1842, (BMNH 1854.10.4.128); Havana (lectotype and 1 paratype of *L. angustior* Mörch, 1876, ZMK); dto. (SMF). Jamaica (SMF). Hispaniola Haiti, St. Marc (SMF). Antilles: St. Thomas (ZMK: 6 paratypes of *L. angustior* Mörch, no radula); St. Thomas, near Buck Island (ZMK: 6 paratypes of *L. angustior* Mörch); St. Martin (ZMK: 5 paratypes of *L. angustior* Mörch, no radula); Guadeloupe, E. tip of Grande Terre, Pointe des Châteaux (749808); Curaçao, Cornelisbaai (749809). Colombia: Santa Marta ((749810).

Nodilittorina (Nodilittorina) riisei

(Mörch, 1876)

(Figures 5, 9, *30, 31*)

* *Littorina (Melaraphe) Riisei* Mörch, 1876: 140, no. 327 (Cuba; **lectotype** (hereby): ZMK, Fig. *30* herein).

• *Littorina lineolata,* Borkowski & Borkowski, 1969: 408-414; fig. 4A (spawn), plt. 66, figs. 3-4 (shell). Borkowski, 1971: 826-840; figs. 1A, B (nurse cells), 2 (spawn). Bandel, 1974: fig. 17 (spawn) (part). Borkowski, 1975: 369-376; fig. 1B (radula). (Not *lineolata* Orbigny, 1840).

Description: Shell ovate-conical to conical-ovate, up to 17 mm long, with slightly convex, regularly increasing whorls, the last bluntly keeled at the periphery.

Protoconch: Probably paucispiral, brown (only worn parts preserved).

Teleoconch: Sculpture consists of 6 narrow spiral furrows separated by flattened elevated ridges; in large specimens this number may rise to 9 by intercalation of a few more furrows of equal size; further, small spiral ridges of second rank may show up in these furrows. Peripheral keel made up by thickening of the shell; umbilical side with numerous closely spaced incised spiral lines.

Colour: At first brown, then development of a light zone at the adapical suture; brown middle zone persists on all whorls in variable width and intensity; another narrow brown zone abapically of the peripheral keel. Interior dark brown except a narrow band on the umbilical side; near the suture a less intensely pigmented zone.

Aperture: Ovate, angled adapically; columellar margin broad, slightly concave, brown, passing without forming an angle into the parietal margin by a callus with straight interior margin; parietal wall with thin brown shell layer; outer lip simple. A small part of the external shell surface adjacent to the columellar margin is regularly redissolved.

Operculum: Horny, brown, paucispiral, width of last whorl larger than width of the spiral part.

Radula: Close to the basic *Nodilittorina* type, but central tooth fairly narrow, and outer marginal with 7 cusps only (instead of 8 as in many species).

Spawn: (Borkowski & Borkowski, 1969; Borkowski, 1971): a high cupola-shaped capsule with spiral ridges on the convex side, and oblique striae on the steep and slightly concave sides.

Relationships: *Nodilittorina glaucocincta* and *N. mordax* have virtually identical shells and are only to be distinguished by their radula characters: in *N. mordax* the central tooth is much narrower than in *N. glaucocincta,* and the other teeth reduce their cusp numbers, while one cusp in the lateral and in the inner marginal tooth increases in size. *Nodilittorina interrupta, N. angustior* and *N. lineolata* may have similar colour patterns, but differ in other shell characters, including the presence of a second light-coloured band in the interior, as well as by their primitive radula and different egg capsules.

Range: Florida and Cuba.

Material examined: Florida: Miami (USNM 749811); Boca Raton (USNM 749812); Key Biscayne (B/K). Cuba (lectotype and 1 paratype, ZMK; other material, SMF).

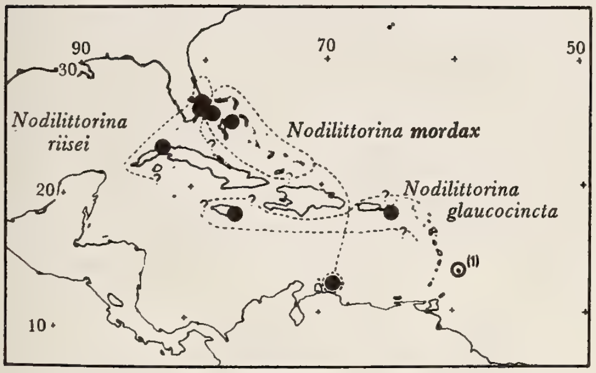


Figure 9

Distribution of *Nodilittorina (N.) riisei* (Mörch, 1876), *glaucocincta* (Mörch, 1876) and ***mordax*** spec. nov. From Barbados (locality marked (1)) spawn similar to that of *N. riisei* was described (Lewis, 1960)

Nodilittorina (Nodilittorina) glaucocincta

(Mörch, 1876)

(Figures 5, 9, *32, 33*)

* *Littorina jamaicensis* C. B. Adams, 1850: 71 (Jamaica; lectotype S.D., by Clench & Turner, 1950; 296-, 380; plt. 38, fig. 19; MCZ 186 133; of doubtful species identity due to lack of radula, refigured herein Figure *34;* paratypes with radula partly conspecific with *L. glaucocincta* (Figure *33*), and partly with *L. interrupta* (Figure *24*). *Nomen dubium*).

* *Littorina (Melaraphe) floccosa* var. a (*Littorina glaucocincta* Beck), Mörch, 1876; 138, no. 322a (St. Jean; **holotype** ZMK, Figure *32* herein).

Description: The shell is essentially the same as that described for *Nodilittorina riisei* and that of *N. mordax.* The radula is characterised by a very narrow central tooth, a lateral tooth with the second cusp (counted from the centre of the radula) enlarged, the inner marginal tooth with three cusps the central of which is enlarged, and the outer marginal with 6 cusps only.

Relationships: *Nodilittorina glaucocincta* can be distinguished from *N. riisei* and *N. mordax* by its radula characters only. A full discussion is given under *N. mordax.* The shell of *N. interrupta* usually is more slender, the spiral sculpture weaker and the adapical light-coloured zone in the aperture is more pronounced, but some individuals may be indistinguishable by shell characters alone.

Remarks: Many literature references cannot be allocated with certainty to the synonymy lists of either *Nodilittorina riisei, N. glaucocincta, N. mordax* or *N. interrupta,* due to lack of data on the radula and spawn characters. Amongst them is the lectotype of *Littorina jamaicensis* C. B. Adams, 1850, while paratypes proved to belong to *N. interrupta* and to *N. glaucocincta.* Another one is the nominal taxon *"Littorina angustior fasciata* Mörch, 1876," which is tentatively included in *N. interrupta,* as the shell resembles this species slightly more than *N. glaucocincta.* Lewis depicts an egg capsule from Barbados (1960: figs. 11E-F, as *"Littorina ziczac"*) very similar to those of *N. riisei.* If the assumed close relationship between *N. riisei, N. glaucocincta* and *N. mordax* is correctly assumed, it might be the egg capsule of either *N. glaucocincta* or *N. mordax* whose proven distribution is closer to Barbados than that of *N. riisei.*

Types: The lectotype and paratypes of *Littorina jamaicensis* C. B. Adams are preserved in the C. B. Adams collection in the MCZ. The radula of a paratype could be examined.

The holotype of *Littorina floccosa glaucocincta* Mörch is kept in the Mörch collection in the ZMK; it still contained the radula. The type designation was somewhat difficult, as in the original publication Mörch named only one locality, St. Jean. In the collection, however, the only sample from St. Jean was labelled *"Littorina..."* while another sample without a proper locality ("inter testas minutas ex Ins. Antill.") was determined as *"Littorina glaucocincta* Beck." The two samples contained rather similar shells (Figures *32* and *35*). Probably the specimens without exact locality were the original *"Littorina glaucocincta"* of Beck, a manuscript name before Mörch, 1876, who identified with this the St. Jean specimen he had received from Unger. He probably failed to note this determination on the label, and he did not mention the Beck specimens because of their vague locality. As only the St. Jean specimen was included in the original description, it becomes automatically the holotype.

Range: Jamaica; Virgin Islands.

Material examined: Jamaica (paratypes of *L. jamaicensis,* MCZ 186133). Virgin Islands, St. Jean (holotype of *glaucocincta,* ZMK). Doubtful material (no radula): "Antilles" (ZMK, labelled *Littorina glaucocincta* Beck). Jamaica (lectotype *L. jamaicensis,* MCZ 186133).

Nodilittorina (Nodilittorina) ***mordax***

Bandel & Kadolsky, spec. nov.

(Figures 5, 9, *37-39*)

- *Littorina jamaicensis,* Bandel, 1974a: 95-108 (part); figs. 18-21, 50-51 (radula) (not the shell description and figure which is *N. angustior;* not *jamaicensis* C. B. Adams, 1850).
- *Littorina lineolata,* Bandel, 1974a: 95-108; figs. 11 (shell), 36-38 (radula) (part, not *lineolata* Orbigny, 1840). Bandel, 1974b: 13; fig. 6D (faeces).

Holotype: B/K (USNM 749813), Fig. 37 (shell, radula).

Paratypes: B/K (USNM 749814 through 749816).

Type locality: Bahamas, Nassau, Paradise Island; Bandel collected 1970.

Etymology: *mordax* (Lat.): biting, because of the large lateral teeth.

Diagnosis: A species of *Nodilittorina* with a spirally sculptured shell identical with those of *N. riisei* (Mörch, 1876) and *N. glaucocincta* (Mörch, 1876), but characterized by radula properties: The central tooth is so much reduced that it has lost its function; the third cusp of both the lateral and, to a lesser extent, the inner marginal tooth (counted from the centre of the radula) are extremely large, while the remaining cusps are very small, the marginal ones being obsolete or nearly so. This radula is very similar to the one of *Nodilittorina tuberculata* (Menke, 1828), in which however, the outer marginal tooth has 7 cusps instead of 5-6 in *N.* ***mordax.***

Description of the shell: Compare *Nodilittorina riisei* (Mörch, 1876); see also Bandel, 1974, p. 99f, as *"Littorina lineolata";* for the description of the radula see Bandel, 1974 p. 108 (as *"L. jamaicensis"* from Curaçao and *"L. lineolata"* from Paradise Island, Bahamas). Operculum paucispiral, width of its last whorl larger than that of the spiral part.

Relationships: The indistinguishable shells found in *Nodilittorina riisei, N. glaucocincta* and *N.* ***mordax*** suggest very close relationships; *i. e.,* evolution from a common ancestor probably by geographical separation, as these species are now allopatric. *N. interrupta* has very similar shell characters, but mostly a weaker sculpture and a second light-coloured band in the interior; the shape of the egg capsule and the radula demonstrate that this species is not particularly closely related to any species of the *N. glaucocincta* group. *N. tuberculata* has a radula very similar to that of *N.* ***mordax,*** but differs in every other character. Some radula properties of the species mentioned above may be compiled in Table 2:

Table 2

Radula characters of some *Nodilittorina* species.

	Length/width ratio	Cusp number of		
	Central tooth	Lateral tooth	Inner marginal	Outer marginal
N. interrupta	1.7 - 2.2	4	4	7 - 8
N. riisei	2.5 - 2.8	4 (5)	4	7
N. glaucocincta	3.7 - 5	4	4	6
N. ***mordax***	7 - 8	3 - 4	2 - 3	5 - 6
N. tuberculata	6.9 - 7.5	3	3	7
N. antoni	(reduced)	1	1	3

Explanation of Figures *42* to *45*

Nodilittorina (N.) dilatata (Orbigny, 1842)

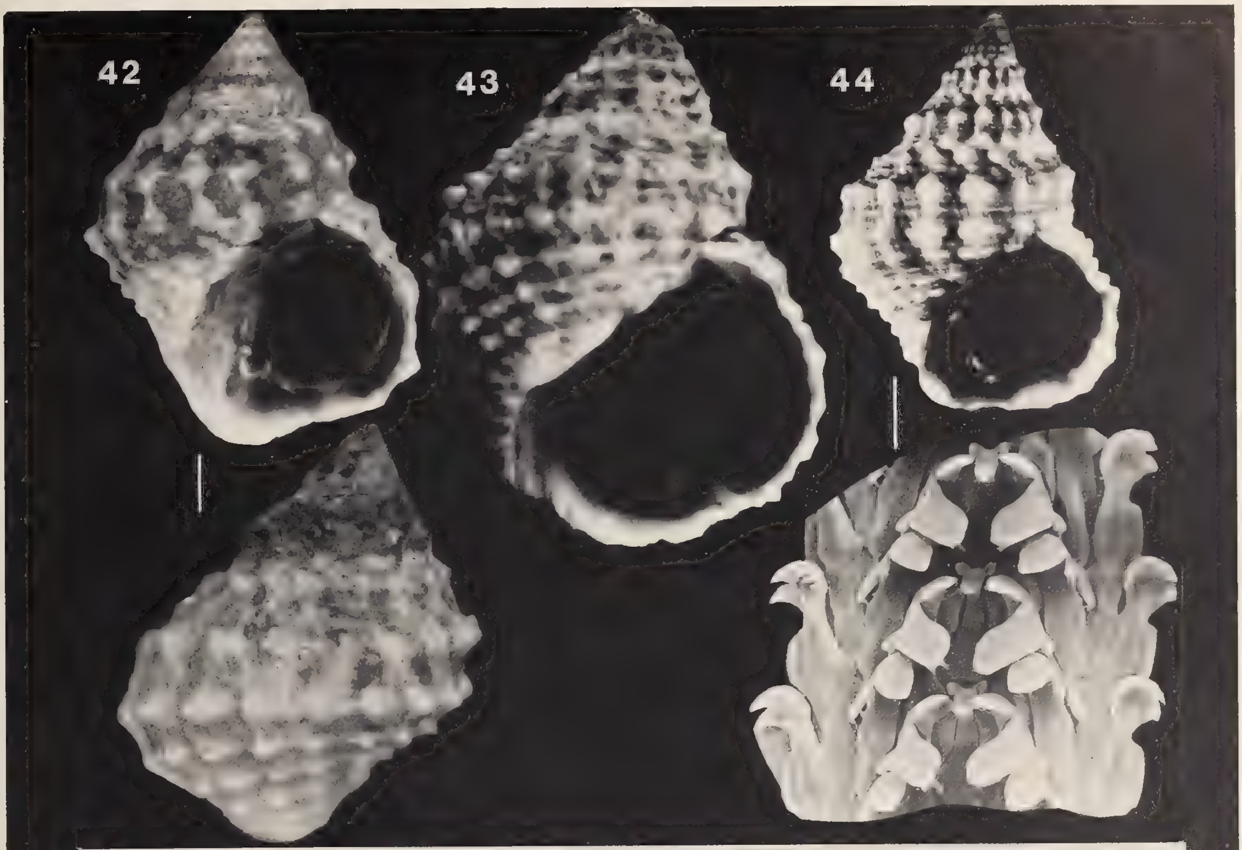
Figure *42:* Cuba, Havana. BMNH 1845.10.4.126. Lectotype. 13.9 ×10.7 mm

Figure *43:* Bahamas, Nassau, Paradise Island. USNM. Radula figured by Bandel, 1974 (figs. *48, 49*)

Figure *44:* Miami. USNM 749817. Shell: 13.1×9.4 mm, Radula: ×290 FN 1406/4

Figure *45: Nodilittorina* species figured by Chemnitz, 1781. Plt. 166, figs. 1599 a, b: Lectotype figure of *Trochus ziczac* Gmelin, 1791 (= *Nodilittorina ziczac* (Gmelin, 1791)). Presumably from Barbados (Bequaert, 1943). Height of original figures: a) 16 mm, b) 15 mm. Plt. 166, figs. 1600 a, b: Individual cited in the original publication of *Trochus ziczac* Gmelin, 1791 (var. *β*), *Phasianella lineata* Lamarck, 1822, and *Littorina lineolata* Orbigny, 1840. Presumably from Barbados (Bequaert, 1943); does not constitute a type figure; doubtful species identity, might be either *Nodilittorina interrupta* (C. B. Adams *in* Philippi, 1847), *N. jamaicensis* (C. B. Adams, 1850), *N. glaucocincta* (Mörch, 1876), *N. riisei* (Mörch, 1876) or *N.* ***mordax*** spec. nov. Height of original figures: a) 12 mm, b) 13 mm

Plt. 163, figs. 1545-1546: Lectotype figure of *Trochus nodulosus* Gmelin, 1791 (designated by Clench & Abbott, 1942: 3) from the Pacific. Height of original figure: 18 mm. The Caribbean *"Littorina" tuberculata* Menke, 1828, was established by comparison to this figure and accompanying description, being differentiated by its smaller size only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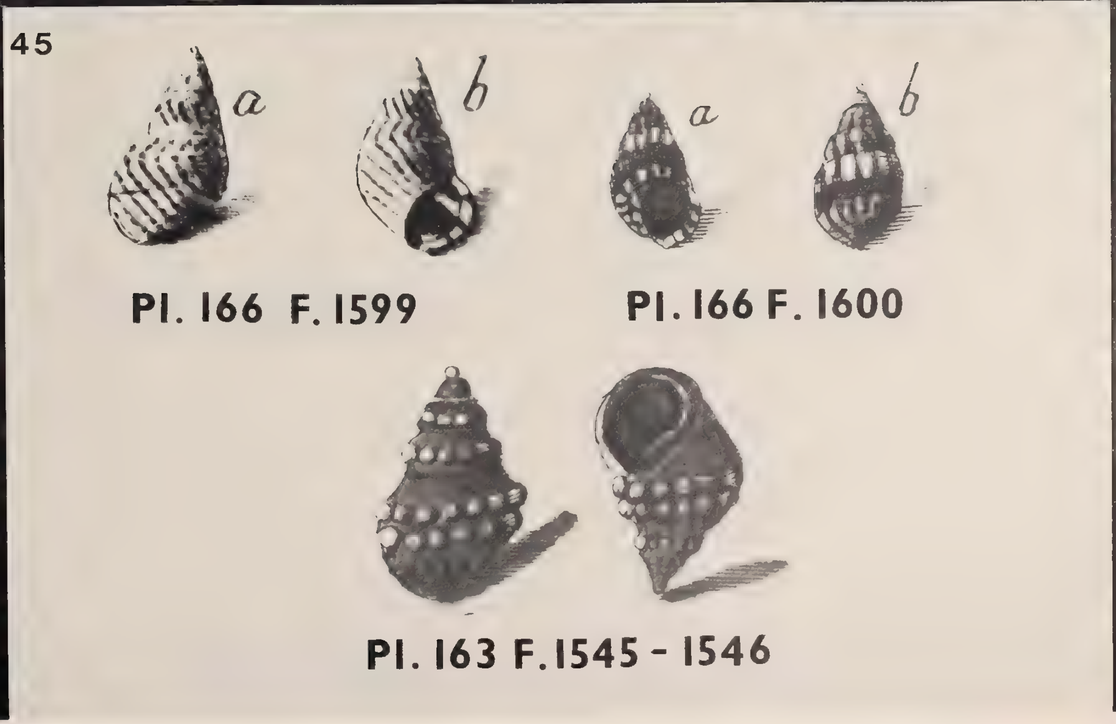

45
a
b
Pl. 166 F. 1599
a
b
Pl. 166 F. 1600
Pl. 163 F. 1545 - 1546

Obviously, the radulae of *Nodilittorina riisei, N. glaucocincta* and *N. **mordax*** represent three stages of increasing modification of the basic *Nodilittorina*-type radula as exemplified by *N. interrupta.* The radula of *N. tuberculata* is indeed very similar to that of *N. **mordax,*** but a close relationship is highly improbable: it would imply that during the whole process of radula differentiation in the *N. glaucocincta* group the shell and operculum characters had remained constant, until the properties of *N. **mordax*** had developed, and then all of a sudden the shell and operculum characters turned into those of *N. tuberculata.* The egg capsule of *N. tuberculata* is also very different from that of *N. riisei,* while the egg capsules of *N. glaucocincta* and *N. **mordax*** are not yet known. Interestingly, the egg capsule of *N. antoni,* where the process of radula modification is most advanced, shows some resemblance to the one of *N. riisei,* particularly the oblique striations on the deep flank of the cupola. Shell and operculum of *N. antoni,* however, are extremely different from *N. riisei* or *N. **mordax.*** More anatomical data are required to trace possible relationships in more detail; it emerges already now that several properties, in particular the radular modifications towards a reduced central tooth and the remaining teeth having one very large cusp, have developed repeatedly in the West Atlantic. The subgenus *Echinolittorina* Habe, 1956, based only on the radula characters of *N. tuberculata,* is of no use in classification, as it would have to include *N. **mordax,*** a species certainly not closely related to *N. tuberculata,* but to *N. glaucocincta* and *N. riisei.* A subgenus *Echinolittorina* thus would have to comprise the two last-mentioned species, plus *N. **mordax*** and *N. tuberculata;* but no reasonable definition of a group so composed could be made.

Range: Bahamas and Curaçao.

Material examined: Bahamas: S. Bimini, Sunshine Inn (C. Edwards *leg.;* USNM 749815) (3 paratypes); Nassau, Paradise Island (K. Bandel *leg.* 1970; USNM 749813-749814; holotype and 30 paratypes. Curaçao, Cornelisbaai (K. Bandel *leg.* 1971; USNM 749816; 22 paratypes).

Nodilittorina (Nodilittorina) dilatata

(Orbigny, 1842)

(Figures 5, 10, *42-44*)

- ∗ *Littorina dilatata* (Orbigny, 1842: 207; plt. 14, figs. 20-23 (type locality: Cuba, Havana; **lectotype:** BMNH 1854.10.4.126, Fig. *42* herein). Reeve, 1857: no. 9, plt. 2, fig. 9.
- • *Litorina dilatata,* Philippi, 1846: 145; plt. *Litorina* 2, fig. 13.
- • *Littorina (Tectus) dilatata,* Mörch, 1876: 133-, no. 312.
- • *Litorina (Tectarius) dilatata,* Weinkauff, 1882: 47; plt. 5, figs. 17-19; plt. 12, figs. 1, 4.
- • *Tectarius nodulosus,* Tryon, 1887: 258 (part); plt. 47, fig. 60 (copy Reeve, 1857), plt. 48, fig. 74 (copy Orbigny, 1842: fig. 21) (not of Gmelin, 1791).
- ∗ *Echinella nodulosa* var. *matanzensis* Richards, 1935: 257; plt. 25, figs. 26, 30, 31 (type locality: Cuba, Matanzas Province, 6.5 km NE Sabanilla in Matanzas Bay; stratum typicum: lowest marine terrace of Matanzas Bay, up to 7.6 m elevation, Quaternary; holotype: original of Richards' fig. 30, 13:11 mm, Carnegie Museum, Pittsburgh, Pennsylvania).
- • *Tectarius (Nodilittorina) tuberculata* "Wood," Clench & Abbott, 1942: 2- (part), plt. 2, figs. 1-2 (not of Wood, 1828 nor of Menke, 1828).
- • *Echinella trochiformis,* Lebour, 1945: 466; fig. 7 (spawn, veliger) (not of Dillwyn, 1817).
- • *Nodilittorina tuberculata,* Abbott, 1954a: 451- (part); figs. 551 (spawn, after Lebour, 1945), 56a (distribution, partly). Abbott, 1954b: 134; plt. 19, fig. J. Borkowski, 1971: 827-836; fig. 2 (spawn). Borkowski, 1975: 369-376; fig. 2B (radula) (not *Litorina tuberculata* Menke, 1828).
- •. *Nodilittorina (Echinolittorina) tuberculata,* Abbott, 1974: 70 (part), fig. 570 (shell, operculum) (not of Menke, 1828).
- • *Nodilittorina dilatata,* Bandel, 1974: 95-113; figs. 12 (shell), 17 (spawn), 18-21, 48-49 (radula).
- • *Nodilittorina (Granulilittorina) dilatata,* Rosewater, 1981: 33.

Description: Shell broadly conical, up to 18 mm long, with slightly convex, regularly increasing whorls; outline of shell controlled by nodose sculpture; sometimes a pseudumbilicus.

Protoconch: Probably paucispiral, light brown (worn parts only preserved). Diameter of embryonic shell 0.10-0.13 mm (Lebour, 1945).

Teleoconch: Sculpture commences with three spiral rows of nodes; the adapical one is the smallest, the two other ones are of about equal strength, with a small part of the abapical one covered by the succeeding whorl. The entire surface is from an early stage on covered with subequal spiral threads (spiral elements of 2nd order); delicate spirals of 3rd order are preserved only on later whorls, where the spirals of 2nd order becomes nodulose; umbilical side with 2-3 smaller node rows, and spirals of 2nd and 3rd order as on the apical side; growth lines reduced in number and strength, the stronger ones squamose, but never prevailing over 3rd order spirals. Main nodes with more or less rhombic base, acute, often tending to channelled spines when their aperture-wards flank is not completely filled with shell material.

Colour: Brown pigment distributed throughout shell, lacking in nodes, 2nd order spirals and in the narrow band in the umbilical side; exterior appears bluish grey with white sculpture, interior brown.

Aperture: Roundish, angled adapically; columella margin very broad, brown, but in the abapical tip plane;

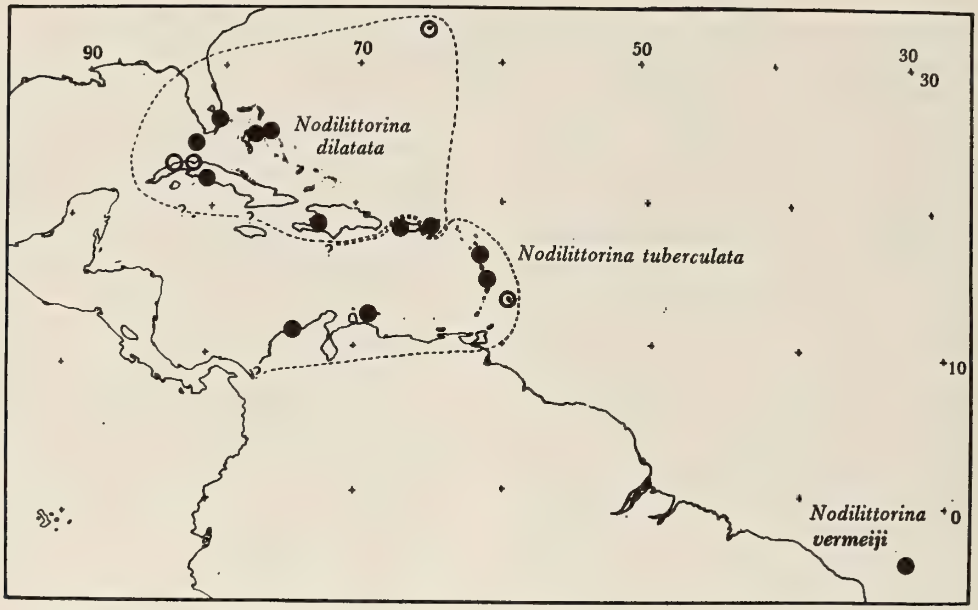


Figure 10

Distribution of *Nodilittorina (N.) dilatata* (Orbigny, 1842), *vermeiji* spec. nov., and *tuberculata* (Menke, 1828)

abapically concave, expanded, slightly recessed and protruded abapical-wards (this character intensifies with age); plane of columella margin receded against external shell surface, forming in adults a pseudumbilicus of variable size, sometimes very large and deep; columella margin passes into a thick brown parietal callus, both forming a single, gently curved arc. Outer lip simple, with channelled tips where nodes are accreted, as the accretion proceeds from the exterior to the interior. Shell surface adjacent to the pseudumbilicus sporadically redissolved, nodes of umbilical side adjacent to parietal wall regularly redissolved.

Operculum: Horny, paucispiral, width of last whorl less than half of operculum length.

Radula: Basic *Nodilittorina* type; central tooth narrow (see key p. 19).

The pelagic **egg capsule** is cupola-shaped, it bears five spiral ridges on its convex side and has a smooth zone adjacent to its flat side.

Synonymy: The form described by Orbigny is quite easily identified by its pseudumbilicus and its locality, which is remote from the area of the similar *Nodilittorina tuberculata.* Therefore, no uncertainty arises because of the lack of the radula of the lectotype.

The form named by Richards (1935) is certainly conspecific as judged from the figures and the locality which is inside the established distribution area of *N. dilatata* and far away from that of other species; *e.g., N. tuberculata.* Richard's diagnosis, however, contradicts his figures; besides, it is not clear what he understood to be *"Echinella nodulosa"* (cited without author); 4 species can be hidden under this name:

(1) *Nodilittorina (Nodilittorina) pyramidalis* (Quoy & Gaimard, 1833), synonymous with *Trochus nodulosus* Gmelin, 1791 (preoccupied by Solander, 1766).

(2) *Nodilittorina (Tectininus) antoni* (Philippi, 1846), misidentified by Pfeiffer (1839) as *"Litorina nodulosa"* of Gmelin, this misinterpreted subsequently to constitute the introduction of a new species *"Litorina nodulosa* L. Pfeiffer, 1839." For a detailed explanation of synonymy and nomenclature see below.

(3) *Nodilittorina (Nodilittorina) tuberculata* (Menke, 1828), which was included in or confused with *N. nodulosa* (Gmelin) (= *N. pyramidalis*) by some authors (see synonymy below).

(4) *Nodilittorina (Nodilittorina) dilatata* (Orbigny, 1842), as included in *N. tuberculata* and with this species in *N. pyramidalis.*

In each case, the "carinae" are not more pronounced, the remaining carinae not reduced, the lip is not "smaller" than that of any one of the 4 species, judging from Richard's figures.

Relationships: The shell is quite similar to that of *Nodilittorina tuberculata;* however, in *N. dilatata* the tubercles are often more acute, the shape is slightly broader, the last whorl larger, and the columella abapically more strongly dilated in adult specimens; in addition a pseudumbilicus encircled by a ledge may appear; the most important difference is found in the radula, while minor differences occur in spawn morphology, too. For discussion of other species see under *N. tuberculata.*

Range: From Bermuda and Florida in the North to the northern Lesser Antilles (St. Thomas) in the South.

Material examined: Bermuda (BMNH; spawn figured by LEBOUR, 1945). Florida: Miami (USNM 749817); Long Key, Key West (SMF 189493); Cuba: Havana (lectotype, BMNH 1854.10,4,126, shell only); Matanzas Bay, Quaternary (*Echinella nodulosa matanzensis* of RICHARDS, 1935); Cienfuegos (SMF 167803). Bahamas: Nassau, Paradise Islands (USNM 749818); Cat Isl., Arthur's Town (RMNHL). Hispaniola: Haiti (SMF). Jamaica (SMF). Lesser Antilles: St. Thomas (SMF 209754).

Nodilittorina (Nodilittorina) vermeiji

Bandel & Kadolsky, spec. nov.

(Figures 5, 10, *46-48*)

- *Nodilittorina (Echinolittorina) tuberculata helenae,* MATTHEWS, 1968: 185; fig. 4 (not *tuberculata* Menke, 1828, nor *helenae* E. A. Smith, 1890). RIOS, 1970: 33; plt. 6.
- *Nodilittorina helenae* ssp., VERMEIJ, 1973: 325 (not *helenae* E. A. Smith, 1890).
- *Nodilittorina (Granulilittorina) miliaris,* ROSEWATER, 1975: 10-. ROSEWATER, 1981: 34-35 (part, locality Fernando de Noronha only; not *miliaris* Quoy & Gaimard, 1833).

Holotype: B/K (USNM 749819) Figure *46;* length 9.7 mm, width 7.5 mm.

Type locality: Isla Fernando de Noronha, Baia de Sueste (540 km NE Recife, NE. Brazil).

Etymology: G. J. Vermeij provided us with 27 specimens.

Diagnosis: A new species of *Nodilittorina s. str.* with a shell of more or less broadly conical shape, intensively brown pigmented with white, large, rounded nodules and a spiral angle of about 50-60°; the two main rows of nodules become distant and unequal during ontogenesis, the abapical row being stronger and sometimes bipartite; radula similar to that of *N. dilatata* (Orbigny, 1842); a difference from *N. helenae* and *N. miliaris* is found in the central tooth, where the transition between basal platform and the "neck" supporting the central cusp is angular in *N. vermeiji,* and rounded in *N. miliaris* and *helenae.* Operculum coiled narrowly paucispiral.

Description: Shell more or less broadly conical, solid, 14.3 mm high at maximum; whorls slightly convex, aperture less than half of shell height. Colour intensive brown exteriorly and interiorly except for a yellow band on the umbilical side and the white nodules.

Sculpture: Apex ca. 2.5 brown whorls; then 3 primary spirals originate, the strongest situated in the middle of the not overlapped part of the whorls, the abapical one is half overlapped by the succeeding whorl. These spirals are at first uniformly brown; nodules develop first on the middle row and only later on the other spirals; they are opaque-white. Probably simultaneously with the primary spirals secondary spirals develop, but they could not be observed before the third whorl due to corrosion. The first and second primary row (counted from the apex) remain closely together and may attain equal strength on the last whorl; the third primary row, which is ½ to ¾ overlapped by spiral whorls, remains free only in the last whorl where it is situated at the periphery, its nodules being now larger than those of the adapical rows; sometimes this peripheral row may split in two rows of nodules, which can be seen only on the last whorl. On the umbilical side, three irregular rows of weaker nodules, separated by a broader interval without nodules or granules from the main row of nodules, are developed. If the spiral main rows are classified as spirals of first order, spirals of second and third order are present, too: the spirals of second order cover tubercles and interstices, without forming nodules, and are themselves covered by spirals of third order; the latter are only visible at at least 20 × magnification; they are undulate and form a fine shagreen with the growth lines which are of the same width. The aperture is roundish with four blunt angles at (1) the junction outer lip/parietal wall, (2) at the junction parietal wall/columella margin, (3) at the transition columella/outer lip, (4) at the outer lip, where the abapical primary row of nodules meets it. The outer lip is simple and sharp, with faint tips where nodules are accreted, the columella is broad and somewhat deepened, concave, and slightly inclined inward, and at the base slightly pronounced abapicalwards, concave and receded.

Radula: A "normal" *Nodilittorina* radula: the central tooth is narrow but not reduced and its lateral cusps overtop the central cusp; the lateral and inner marginal teeth have four cusps each, the third (counted from the centre) being the largest; the outer marginal has eight cusps.

Operculum: Horny, brown, narrowly coiled, paucispiral, width of last whorl equals that of the spiral part; entire margin thin and flexible.

Spawn: Not known.

Relationships: *Nodilittorina vermeiji* belongs possibly to the Southern Atlantic *Nodilittorina miliaris* group, which is characterised by its sculpture: the second and third primary row of nodules are markedly distant and in most cases unequal (unlike *N. dilatata, N. tuberculata, N. pyramidalis* etc.), the abapical one being strongest and frequently bipartite; there is also a tendency to develop additional beads. The radula is the "normal" *Nodilittorina* radula. Within this group, *N. helenae* (E. A. Smith, 1890) is more slender (apical angle about 45°), the nodules are coloured with brown and the adapical ones are much smaller. *Nodilittorina miliaris* (Quoy & Gaimard, 1833) from Ascension Island has smaller, more numerous and more elevated nodules; the abapical primary row is regularly bipartite, and secondary rows of nodules are common. *Nodilittorina vermeiji*, however, differs from both *N. miliaris* and *N. helenae* apart from sculpture and shape also by the operculum, whose last whorl is more narrowly coiled (cf. Figure 5; for *N. miliaris* and *N. helenae* see ROSEWATER, 1981: plt. 3, figs. F, I) and by details of the central tooth of the radula: the transition from the basal platform to the "neck" supporting the central cusp is angular in *N. vermeiji* (Figure *47*), while it is rounded in *N. miliaris* (Fig. *49*) and in *N. helenae* (Rosewater, 1981: plt. 4, fig. E).

Range: Restricted to Fernando de Noronha, off the coast of Brazil.

Material examined: Fernando de Noronha (BMNH: 11 paratypes, nos. 1889.2.21.63-6, 88.6.27.52-5, 87.2.9.1831-3); ditto, Baia de Sueste (Vermeij *leg.* 27.6.1969 at high watermark; holotype and 6 paratypes, (USNM 749819-749820); ditto, Praia da Atalaia (Vermeij *leg.* 28.6.1969, 20 paratypes; USNM 749821).

Nodilittorina (Nodilittorina) tuberculata (Menke, 1828)

Figures 1C, 3B, 5, 10, *13, 52-55*

- Der kleinknotige Kräusel CHEMNITZ, 1781: 42 (part, only the smaller "species").
- *Trochus nodulosus* [var.] Gmelin, 1791: 3582, no. 98 ("...mari Americam meridionalem alluente"; based on CHEMNITZ, 1781).
* *Litorina tuberculata* Menke, 1828: 25 (based on GMELIN, 1791 only; types of Chemnitz probably lost. **Neotype** hereby designated: Fig. *52*, from Guadeloupe, deposited in USNM 749822). Menke, 1830: 44 (not MENKE, 1829: 10, which is based on *Trochus nodulosus* GMELIN, 1791 (= *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833)).
* *Litorina thiarella* ANTON, [1838]: 53, no. 1922 (no locality given, types probably lost).
- *Littorina nodulosa,* ORBIGNY, 1842: 205; plt. 14, figs. 11-14 (BMNH 1854.10.4.124, here Figure *53*) (not of GMELIN, 1791).
- *Litorina trochiformis,* PHILIPPI, 1846b: 143; plt. *Litorina* 2, figs. 12, 14 (part, not fig. 15; not *Turbo trochiformis* Dillwyn, 1817).
* *Litorina trochiformis* var. *minor* PHILIPPI, 1846b: 143 (based on reference to *Litorina thiarella* Anton, [1838] only).
- *?Litorina trochoides,* PHILIPPI, 1847: 159; plt. *Litorina* 3, fig. 3 (not *Littorina trochoides* Gray, 1839).
- *Littorina (Tectus) tuberculata,* MÖRCH, 1876: 133.
- *Littorina (Tectus) tuberculata,* var. *minor,* MÖRCH, 1876: 133 (reference to *Litorina thiarella* Anton, [1838]).
- *Litorina (Tectarius) thiarella,* WEINKAUFF, 1882: 45-; plt. 5, figs. 9-11 (Guadaloupe).
- *Tectarius (Nodilittorina) tuberculatus* "Wood," CLENCH & ABBOTT, 1942: 2-; ?plt. 2, figs. 3-5 (part, *Nodilittorina dilatata* (Orbigny, 1842) included in this species; not *Turbo tuberculatus* Wood, 1828).
- *Nodilittorina tuberculata,* ABBOTT, 1954a: 451-; figs. ?55b (shell), 55d (foot), 55f (operculum), 55h (faeces), 55n (penis), 56a (distribution in part), 57b (radula). ABBOTT, 1954b: 134 (part, not fig.). ABBOTT, 1968: 82; figs. 81 (penis), ? 83.10 (shell). KAUFMANN & GÖTTING, 1970: 350; fig. 38. FLORES, 1973a: 10-, plt. 1, figs. 1-4. BANDEL, 1974a: 93-113; figs. 13 (shell), 16B, 17 (spawn), 18-21, 39-41 (radula). BANDEL, 1974b: 13; fig. 6E (faeces). BANDEL, 1975: 17-; plt. 2, figs. 3, 5 (embryonic shell).
- *Nodilittorina (Echinolittorina) tuberculata,* HABE, 1956a: 98-. WARMKE & ABBOTT, 1962: 54; fig. 12a (operculum), plt. 9, fig. R (shell). ? ROSEWATER, 1970: 424; plt. 326, figs. 10, 12. ABBOTT, 1974: 70 (part; figs. and syn. *dilatata* = *Nodilittorina dilatata* (Orbigny, 1842); syn. *trochiformis* Dillwyn = *N. pyramidalis* (Quoy & Gaimard, 1833)).
- *Tectarius tuberculatus* "Wood," LEWIS, 1960: 414-; figs. 10A, B (spawn), 10D (veliger) (not *Turbo tuberculatus* Wood, 1828, not fig. 10C).

Explanation of Figures *46* to *51*

Nodilittorina (N.) vermeiji Bandel & Kadolsky, spec. nov.

Figure *46:* Isla Fernando de Noronha, Baia de Sueste, 540 km N.E. Recife, N.E. Brazil. Holotype 9.7×7.5 mm. USNM 749820

Figure *47:* dito. Paratype. USNM. Shell: 7.0×5.3 mm, Radula: × 370 FN 1901/7

Figure *48:* dito. Paratype. BMNH 1889.2.21.63. H. 8.9 mm

Nodilittorina (N.) miliaris (Quoy & Gaimard, 1833)

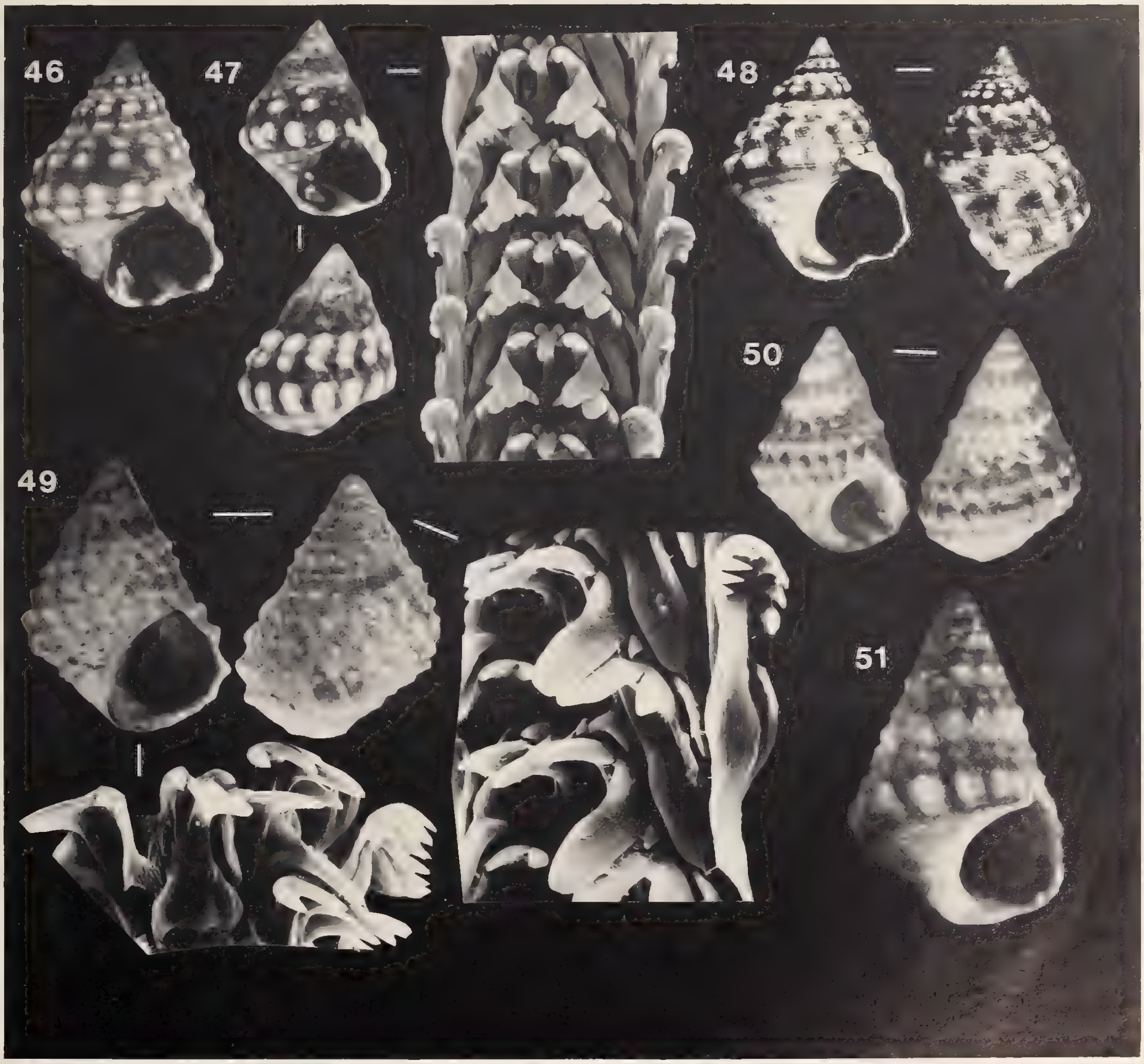
Figure *49:* Ascension Island, Mac-Arthur Point. J. ROSEWATER leg. 10.7.1976 USNM 749825. Shell: 9.5×6.9 mm. Radula: a) × 800 b) × 930

FN University Erlangen-Nürnberg 4926, 4918

Figure *50:* Lectotype of *Littorina lemniscata* Philippi, 1846. BMNH 1968.216. Shell: 8.4×5.7 mm. Erroneously reported from Cuba

Nodilittorina (N.) helenae (E. A. Smith, 1890)

Figure *51:* St. Helena. BMNH 1889.10.1.2546. Paratype 11.6×7.0 mm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Description: Shell conical, 13-18 mm long, with slightly convex, regularly inceasing whorls; outline of shell dominated by nodose sculpture; no umbilicus. **Embryonic shell:** one slightly conispiral whorl, colourless except the red umbilicus, coarsely granulated, growth lines in its distal part; diameter 0.11 mm. **Larval shell:** about 2.5 conispiral whorls sculptured with approx. 7 spirally arranged rows of granules, often fusing to ziczac lines (Figure *13*).

Teleoconch: Sculpture of earliest whorls not preserved; earliest preserved sculpture consists of three spirally arranged rows of prominent nodes of which the adapical one is smaller than and more distant from the two middle rows of nodes. Nodes and interstices are covered by subequal spiral threads; in late whorls one thread in each interstice between the three rows of nodes becomes stronger, indistinctly nodulose and rarely grows into nodes of equal strength as the main nodes. The nodes are elevated but more or less rounded and circular to elongated in the spiral direction. Where only faint growth lines and no attack of cyanophyceans occur, a third order sculpture of delicate spiral threads is seen, covering the main nodes and spirals of 2nd order. The umbilical side is covered by three rows of smaller nodes, and spiral threads of 2nd and 3rd order as in the remainder of the shell.

Colour: A brown pigment is present throughout the shell but in the most elevated elements of the sculpture, *i.e.*, the nodes and in later whorls in the second order spirals; interior uniformly brown but for a light band in the umbilical side.

Aperture: Roundish, angled adapically; columella margin broad, brown, straight, abapically strongly expanded, concave (this obsolete in juveniles), recessing; adapically passing without angle into the parietal margin; parietal and protruding abapical wall with brown shell layer; outer lip simple, but in juveniles with channeled tips where the nodes are accreted (the external part of a node before the inner part being secreted). External shell surface adjacent to the columella regularly redissolved.

Operculum: Horny, paucispiral, width of last whorl about ⅓ of length of operculum.

Nomenclature and types: The name *tuberculata* Menke, 1828, which has been in general use only since 1954 (Abbott) for the species here dealt with, and for *Nodilittorina dilatata* (Orbigny), which was re-recognized as a distinct species only in 1974 (Bandel), is based on a rather dubious literature reference: Menke (1828) referred to *Trochus nodulosus,* var. "minor" of Gmelin, 1791, which is entirely based on Chemnitz', 1781 unfigured variety of his plt. 163, figs. 1545-1546, here refigured Figure *43*. These are the lectotype figures of *Trochus nodulosus* Gmelin, 1791 (non Solander, 1766) (designated by Clench & Abbott, 1942: 3; invalid) type locality: Cuba, Havana; Chemnitz: "kömmt durch die Cookische Seereisen aus den Südländern" (comes by Cook's expeditions from the southern countries, [*i. e.*, the Pacific])), which can easily be identified with *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833) (P. H. Fischer, 1967b; Rosewater, 1970). The expression used by Gmelin, *"Trochus nodulosus* ... Habitat in oceano australo, et (minor) mari Americam meridionalem alluente...," is interpreted not as the introduction of a variety named "minor" but as a descriptive term without nomenclatorial status. Chemnitz differentiated his "kleinere Art... aus Westindien" (smaller "species" from the West Indies) only by its smaller size. This "diagnosis" contains not the least factual substance to recognise any particular *Nodilittorina* species: Chemnitz' figure is 18 mm high, but *Nodilittorina pyramidalis* varies between 5 and 24 mm shell height (Rosewater, 1970), while *N. tuberculata* in its accustomed sense is usually between 11 and 16 mm high. Further, *N. tuberculata* has a well developed row of nodules adjacent to the suture which is—as Chemnitz' figures clearly show—absent or very weak in *N. pyramidalis.* If considered a *nomen nudum, N. tuberculata* would gain nomenclatorial status not before Mörch, 1876; the name would then be unavailable because of subjective homonymy with *Turbo tuberculatus* Wood, 1828 (= *Nodilittorina (Tectininus) antoni* (Philippi)) and the species dealt with here would have to be named *N. thiarella* (Anton, [1838]). Although in the original diagnosis of *"Litorina" thiarella* no locality is given and the types are lost, the description is sufficient to recognize *N. tuberculata* (diagnosis translated from the German):

> "Ovate-conical, spire acute, five whorls with strongly stepped contours, each with a double row of closely spaced nodes separated by a shallow furrow, base finely granulated; bluish grey, nodes white; non-umbilicate; columella fairly narrow, overtopping the base and dilated; aperture roundish. Width 2.5‴, height 3‴."

As the name *thiarella,* however, has not been used in the more recent literature, as opposed to *tuberculata,* it is proposed to maintain the name *tuberculata* Menke, 1828, in its accustomed sense and as described here. The original publication is construed as follows: the reference to Chemnitz' publication is regarded as a reference to a formal diagnosis, indicating that the West Indian species is smaller than the lectotype figure of *nodulosus; i. e.*, smaller than 18 mm. The provenance allows a choice between *Nodilittorina dilatata* and *N. tuberculata* auct. Individuals similar to Chemnitz' figures of *nodulosus* are found only amongst *N. tuberculata* auct., although the subsutural row of nodules is still more prominent than in *N. pyramidalis.* Such an individual from Guadeloupe (Figure *52*) is proposed to be the **neotype** of *"Litorina" tuberculata* Menke, 1828.

Relationships: Radula and spawn characteristics allow a convincing distinction between *Nodilittorina dilatata* and *N. tuberculata;* shell properties are less useful, although

N. dilatata proved often to develop a spiny sculpture and a relatively broad shell, and the abapical row of nodules is more frequently covered by the succeeding whorl; also, in *N. dilatata* the columella often is more dilated, developing a groove in the umbilical region (pseudumbilicus). It is remarkable that the radula is extremely different from the one of *N. dilatata*, and almost identical with the one of *N. mordax;* it is outlined under this species, that the radula features in common are most likely homoeomorphs. Consequently, the subgenus *Echinolittorina* Habe, 1956, based solely on these radula characters, in *N. tuberculata*, is rejected. The true relationships of *N. tuberculata* are difficult to assess; the Galapagian *N. galapagiensis* (Stearns, 1893) is similar in shell properties, but radula and spawn are not known. The Indo-Pacific *N. pyramidalis* (Quoy & Gaimard) has a radula more similar to the one of *N. dilatata*, while the shell differs from both *N. dilatata* and *N. tuberculata* in that the beads of nodules are largely reduced except the two main peripheral ones; and the egg capsule is insufficiently described (Habe, 1956b). In the Southern Atlantic, several closely related species, collectively named the *Nodilittorina miliaris* group, show no particular relationship to *N. tuberculata* or *N. dilatata*.

Range: Caribbean Sea, from Puerto Rico to Colombia and Venezuela.

Material examined: Puerto Rico: Rincon Lighthouse (Abbott, 1954a, radula fig'd). Antilles: Martinique, Sta. Lucia (BMNH 1854.10.4.124, original of Orbigny, 1842); Barbados (Lewis, 1960, spawn fig'd); Guadeloupe, E. tip of Grande Terre, Pointe des Châteaux (USNM 749822, Vermeij *leg.;* **neotype**); Curaçao, Cornelisbaai (USNM 749823). Colombia: Sta. Marta (USNM 749824).

Subgenus *Nodilittorina (Tectininus)* Clench & Abbott, 1942

• *Tectinius* Clench & Abbott, 1942: 4. Type species by monotypy: *Echininus (Tectininus) nodulosus* "Pfeiffer" Clench & Abbott, 1942 (= *Litorina antoni* Philippi, 1846; non *Trochus nodulosus* Gmelin, 1791 which is *N. (N.) pyramidalis).*

Nodilittorina (Tectininus) antoni (Philippi, 1846)

(Figures 1D, 3C, 5, 11, *56-59*)

* *Turbo tuberculatus* Wood, 1828: 57; plt. 6, fig. 30 (no locality given; **lectotype** BMNH 1887.4.26.13, Figure *56* herein) (not *Turbo tuberculatus* Pennant, 1777, nor *Litorina tuberculata* Menke, 1828).

* *Litorina scabra* Anton, [1838]: 53, no. 1920 (no locality given; types unknown) (not *Helix scabra* Linnaeus, 1758).

• *Litorina nodulosa*, L. Pfeiffer, 1839: 537- (not of Gmelin, 1791; not intended as the introduction of a new species, but of a new combination ex *Trochus nodulosus* Gmelin). Philippi, 1846: 144; plt. *Litorina* 2, fig. 11 (cites Pfeiffer as author of the species name; not of Gmelin, 1791). Philippi, 1847: 159; plt. *Litorina* 3, fig. 2 (copy Orbigny, 1842).

• *Littorina tuberculata*, Orbigny, 1842: 206; plt. 14, figs. 15-19 (Cuba, Havana; BMNH 1854.10.4.125, Figure *57* herein. **Lectotype** (hereby) of *Litorina Pfeifferiana* Weinkauff, 1882 and **holotype** of *Echininus (Tectininus) nodulosus* Clench & Abbott, 1942). Philippi, 1847: 159; plt. *Litorina* 3, fig. 1 (copy Wood, 1828).

* *Litorina Antonii* Philippi, 1846: 145; plt. *Litorina* 2, fig. 18 (*Litorina scabra* Anton, [1838] included in synonymy, but not expressly proposed as a substitution name. Locality: Antilles; types unknown.).

• *Nina tuberculata*, Mörch, 1876: 132-, no. 310 (not Menke, 1828).

* *Litorina (Tectarius) Pfeifferianus* Weinkauff, 1882: 46; plt. 5, figs. 15-16 (based on reference to L. Pfeiffer (1839), Philippi (1846: *Litorina nodulosa*) and Orbigny (1842) only; **lectotype** hereby: original of Orbigny, 1842, figs. 16-17, BMNH 1854.10.4.125, Figure *57* herein. Type locality: Cuba, Havana).

• *Litorina (Nina) Antoni*, Weinkauff, 1882: 89-; plt. 5, figs. 13-14. Weinkauff, 1883: 227 (in syn.: *pfeifferiana* Weinkauff, 1882).

• *Echinella nodulosa*, Dall, 1889: 146-147 (not Gmelin, 1791).

* *Echininus (Tectininus) nodulosus* "L. Pfeiffer," Clench & Abbott, 1942: 4; plt. *3*, figs. 1-5 (holotype: original of Orbigny, 1842, plt. 14, fig. 17, BMNH 1854.10.4.125, here Figure *57;* type locality: Cuba, Havana) (not *Trochus nodulosus* Gmelin, 1791, which is *Nodilittorina (N.) pyramidalis* (Quoy & Gaimard, 1833)). Abbott, 1954a: 458-; figs. 55a (shell), 55c (foot), 55e (operculum),55g (faeces), 55p-q (penis), 56b (distribution), 57a (radula). Abbott, 1954b: 135; plt. 19, fig. H. Warmke & Abbott, 1962: 54; fig. 12B (operculum), plt. 9, fig. O (shell). Rosewater, 1972: 510; plt. 388, figs. 18-20, plt. 390, figs. 13-15. Abbott, 1974: 70; fig. 572.

• *Echininus nodulosus*, Abbott, 1968: 82; fig. 83.9 Borkowski, 1971: 827-836; fig. 2 (spawn). Vermeij, 1973: 321. Bandel, 1974a: 95-113; figs. 17 (spawn), 18-21, 42-44 (radula). Borkowski, 1975: 371-; fig. 2D (radula).

• *Echininus (Tectininus) antoni*, Kadolsky, 1971: 192.

Description: Shell broadly conical, up to 20 mm long with slightly convex, regularly increasing whorls; outline controlled by nodose sculpture; no umbilicus.

Protoconch: Probably paucispiral, brown (only worn parts preserved).

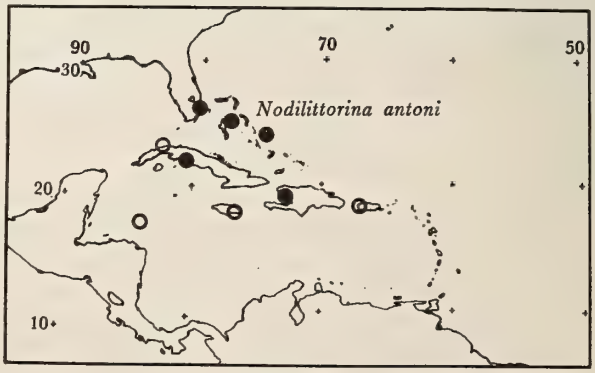


Figure 11

Distribution of *Nodilittorina (Tectininus) antoni* (Philippi, 1846)

Teleoconch: Sculpture commences with three rows of nodes, of which the adapical one is small, the middle one is large and spiny, and the abapical one is largely covered by the succeeding whorl. Spiral elements of 2nd order only preserved on later whorls: numerous subequal spiral ridges covering nodes and interstices, becoming themselves nodulose on the latest whorls. A cover of delicate spiral threads of third order is developed where growth lines are faint; otherwise the surface is densely covered by thread-shaped to squamose growth lines. The sequence of increasing width of sculpture elements is: spirals of 3rd order - growth lines - spirals of 2nd order - node rows. Umbilical side with 2-3 smaller node rows, spirals of 2nd order and growth lines as on the apical side of the shell; spirals of 3rd order only near the periphery.

Colour: Brown shell pigment uniformly distributed, lacking only in the nodes, nodules and in a band on the umbilical side; exterior surface appears in greenish grey to bluish grey.

Aperture: Subcircular, angled adapically. Columella margin moderately broad, expanded abapically, concave, recessing and slightly protruded abapically; outer edge of columella passes with an angle, inner edge with a wide arc into the parietal margin. Parietal wall with thin brown shell layer. A crescent-shaped portion of the external shell surface centred at the junction of the columellar and parietal edge is redissolved. Outer lip simple but for channelled tips where nodes are accreted as the nodes are accreted from the exterior to the interior.

Operculum: Subcircular, horny, brown, mesospiral; thicker than in other *Nodilittorina* species; external side concave, internal side convex.

The **radula** has 7 teeth in a transverse row, which are extremely modified: the central tooth is a very narrow rudiment without any function; the lateral tooth is very large, bearing one large and massive cusp and a smaller one on its exterior side; the inner marginal is small and narrow, bearing only one relatively large and massive cusp; the outer marginal is small, narrow and has three small cusps.

The pelagic **egg capsule** is cupola-shaped and bears wavy spiral ridges on the convex top and wavy oblique lines on the steep sides. (Borkowski, 1971).

The **penis** is large and shows a basal enlargement and on its distal part a penis gland surrounded by small papillae (Abbott, 1954a).

Relationships: The penis gland being very distant from the basal enlargement, the presence of papillae on the penis and the mesospiral operculum demonstrate this species to be unrelated to other *Nodilittorina* species. The retention of the subgenus *Tectininus* Clench & Abbott, 1942, defined by these characters, is certainly justified. The sculpture pattern, the abapical columella expansion and the pigmentation pattern are identical to that of other nodose *Nodilittorina* species; the egg capsule contains morphological elements observed in *N. riisei. Tectininus* has been attributed subgenerically to the Indo-Pacific *Echininus* only by its operculum characters. However, *Echininus* opercula are calcified and more narrowly coiled (true multispiral type): The width of the last whorl is 10% of the operculum length, while in *N. antoni* it is 20%. This compares better with the operculum of *Tectarius,* where the figure is 18-27%. Such opercula are named mesospiral by Rosewater (1972). There are sufficient differences between *Echininus, Tectarius* and *Tectininus* in a shell, penis and radula characters to exclude close relationships.

Nomenclature and types: Kadolsky (1971) pointed out that L. Pfeiffer (1839) (cited as author of *"Echininus nodulosus"* as constantly as erroneously), who misidentified specimens of the species dealt with here with the Pacific *Trochus nodulosus* Gmelin, 1791 (now *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833)), considered himself as author only of the combination *"Litorina nodulosa."* As a new species name, the name *"nodulosa"* has not been validly established until 1942, when Clench & Abbott named *"Litorina nodulosa* L. Pfeiffer" as the type species of their newly proposed subgenus *Echininus (Tectininus).* These authors expressly excluded from their synonymy list the synonyms associated by L. Pfeiffer with his *"Litorina nodulosa."* Thus, they have intentionally used L. Pfeiffer's misidentification as a name for a type species of a new subgenus. According to article 70(b) of the IRZN this constitutes the introduction of a new nominal species, *Echininus (Tectininus) nodulosus* Clench & Abbott, 1942. Their designation of a lectotype for *"Litorina nodulosa* L. Pfeiffer" has to be interpreted as a holotype designation for *Echininus (Tectininus) nodulosus* Clench & Abbott, 1942. The holotype is figured by Orbigny, 1842 on plt. 14, figs. 16 and 17, but not 19 which shows the operculum.

Although widely used, the name *nodulosa* Clench & Abbott cannot be maintained for this species, because of two available senior synonyms: *antoni* Philippi, 1846 and *pfeifferiana* Weinkauff, 1882. In addition, *Nodilittorina (Tectininus) nodulosus* (Clench & Abbott, 1942) would be a junior secondary homonym of *Trochus nodulosus* Gmelin, 1791, which is now classified as *Nodilittorina (Nodilittorina) pyramidalis* (Quoy & Gaimard, 1833).

An older name proposed for this species, *scabra* Anton [1838] is not available because of secondary homonymy with *Helix scabra* Linnaeus, 1758. Philippi (1846) seemingly introduced *Litorina Antonii* as a replacement name for *scabra* Anton, as he included both *scabra* Linnaeus and *scabra* Anton in the genus *"Litorina."* Although a homonymy no longer exists, since *scabra* Anton is attributed to *Nodilittorina (Tectininus)*, while *scabra* Linnaeus is a *Littoraria (Littorinopsis)*, names rejected as secondary homonyms prior to 1961 cannot be reinstated. Types of *scabra* Anton and *antoni* Philippi are not known, but the diagnoses and Philippi's figure agree well with this species. The type of *pfeifferiana* Weinkauff was selected from the original material of Orbigny as Weinkauff referred to literature only; thus *pfeifferiana* Weinkauff and *nodulosa* Clench & Abbott are absolute synonyms as based on the same type specimen.

Range: Between Florida in the North and Hispaniola and Jamaica in the South.

Material examined: Florida: Miami (USNM 749826). Bahamas: San Salvador (USNM 749827); Nassau, Paradise Island (USNM 749828). Cuba: Havana (Orbigny, 1842, lectotype of *pfeifferiana* Weinkauff, 1882 and holotype of *nodulosa* Clench & Abbott, 1942; BMNH 1854.10.4.125); Cienfuegos (SMF 167803). Hispaniola: Haiti, St. Marc (SMF). Jamaica (Clench & Abbott, 1942). Puerto Rico: Rincon Lighthouse (Abbott, 1954a; penis and radula fig'd). Bay of Honduras: Swan Island (Clench & Abbott, 1942). No locality: lectotype of *Turbo tuberculatus* Wood, 1828 (BMNH 1887.4.26.13 (no radula)).

APPENDIX

Species incorrectly associated with Western Atlantic *Nodilittorina* species

Nodilittorina species erroneously recorded from the Western Atlantic

Nodilittorina (Nodilittorina) miliaris (Quoy & Gaimard, 1833)

(Figures *49, 50*)

* *Littorina miliaris* Quoy & Gaimard, 1833: 484; plt. 33, figs. 16-19 (Ascension Island; holotype MHNP, figured by Rosewater, 1970: 494-; plt. 381, figs. 1-2; and Rosewater, 1981: plt. 2, fig. J).
* *Litorina echinata* Anton, [1838]: 53 (no locality given; types unknown; placed in synonymy of *Nodilittorina miliaris* by Philippi, 1847: 160; plt. *Litorina* 3, fig. 5).
* *Littorina granularis* Gray, 1839: 140 (no locality given; holotype BMNH 87.4.26.9, refigured by Rosewater, 1970: 494; plt. 381; figs. 3-4, "eastern Atlantic").
* *Littorina lemniscata* Philippi, 1846a: 139 ("Cuba," erroneous locality; **lectotype** BMNH 1968.216, Figure *50* herein). Reeve, 1857: no. 6, plt. 2, fig. 6. Weinkauff, 1882: 91-; plt. 13, figs. 5, 8.

Remarks: Present knowledge of this species suggests its restriction to Ascension Island in the South Atlantic. The form living on the coasts of Fernando de Noronha, 300 km off the Brazilian coast and 2000 km W of Ascension, has been identified with *Nodilittorina miliaris* by Rosewater, 1975 and 1981 and with the *N. helenae* by Matthews, 1968 and Vermeij, 1973. The differences are outlined under *N. vermeiji*, spec. nov.

Littorina lemniscata Philippi, 1846, was originally recorded from Cuba, but has not been rediscovered there or anywhere else in the world. Examination of the lectotype, preserved without the radula, led to the conclusion to place this form into the synonymy of *Nodilittorina miliaris.* Available data on the form of Ascension Island (Rosewater, 1970, 1975 and 1981, and specimens received by courtesy of J. Rosewater) indicate that *N. lemniscata* is somewhat more slender and lacks secondary rows of nodules; but these differences are slight, and even if one objects to regarding them as being conspecific, *N. miliaris* would be the most closely related species to *N. lemniscata,* so far known. Particularly the numerous, small but prominent, rounded nodules seen in *N. lemniscata* distinguish also *N. miliaris* from related species, such as *N. vermeiji* spec. nov., *N. helenae* (E. A. Smith, 1890) and *N. natalensis* (Philippi, 1847).

The opportunity is seized to propose also the synonymy of *Litorina echinata* Anton, [1838 and *Littorina miliaris* Quoy & Gaimard, 1833, although the first-named had never been considered as a West Atlantic species. Philippi (1847) already identified it with *Nodilittorina miliaris,* but later

Explanation of Figures *52* to *59*

Nodilittorina (N.) tuberculata (Menke, 1828)

Figure *52:* Guadeloupe, E. tip of Grand Terre, Pointe des Châteaux. Neotype. USNM 749822. Shell: 13.0×9.5 mm, Radula: × 210 FN 1641/7A

Figure *53:* Martinique. BMNH. 1854.10.4.124. Original of Orbigny, 1842 (plt. 14, figs. 11-13). Shell: 14.1×11.2 mm

Figure *54:* Martinique. BMNH 1854.10.4.124. Orbigny collection. Shell: 13.0×9.3 mm, Radula: × 265 FN 1599/23

Figure *55:* Colombia, Santa Marta. USNM 749824. Shell: 13.0× 9.5 mm, Radula: × 205 FN 956/14

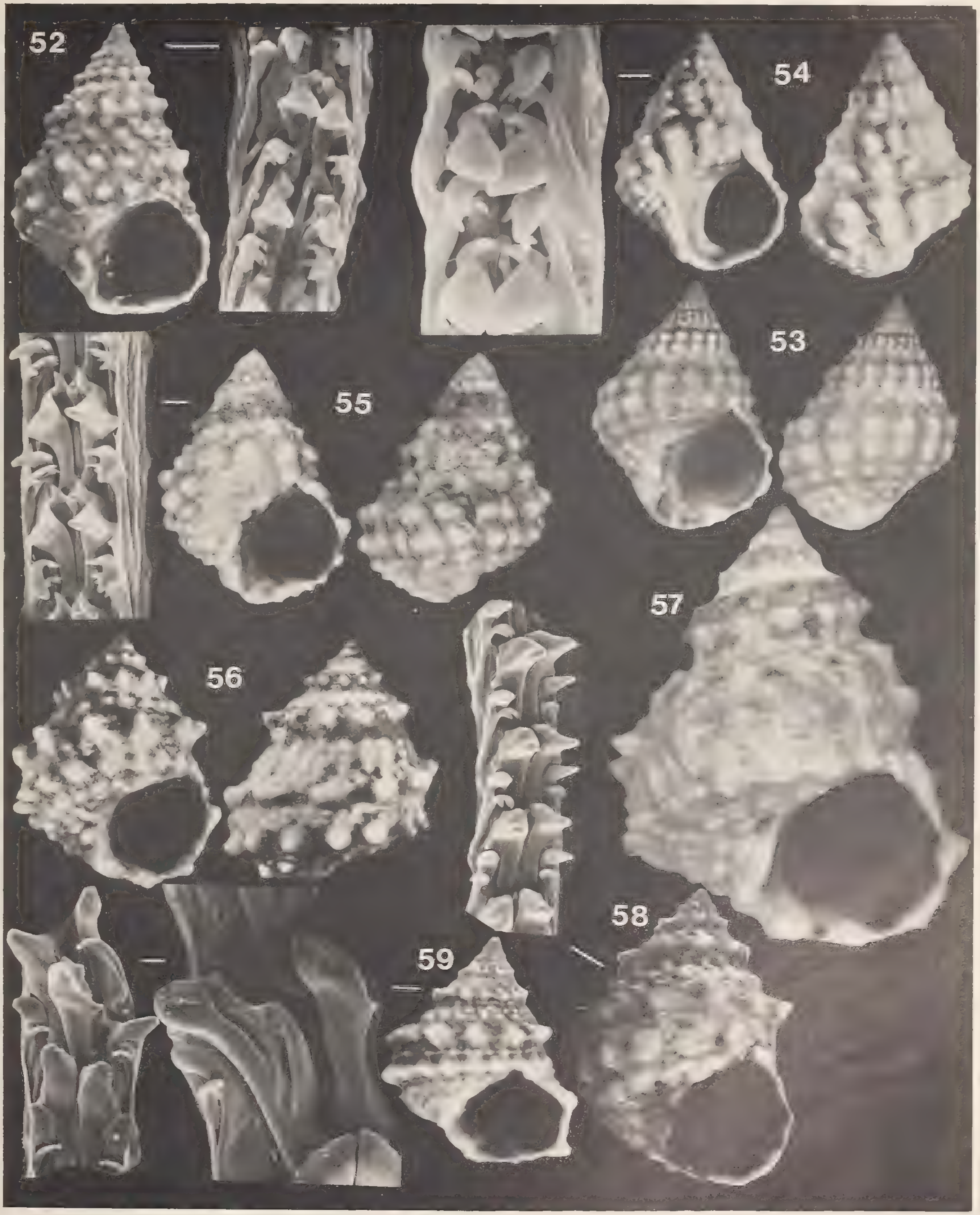
Nodilittorina (Tectininus) antoni (Philippi, 1846)

Figure *56:* Locality unknown. BMNH 1887.4.26.13. Lectotype of *Turbo tuberculatus* W. Wood, 1828. 13.0×10.8 mm

Figure *57:* Cuba, Havana. BMNH 1854.10.4.125. Probably original of Orbigny, 1842 (plt. 14, figs. 16-17, as *tuberculata*); lectotype of *Litorina Pfeifferiana* Weinkauff, 1882; holotype of *Echininus (Tectininus) nodulosus* "Pfeiffer" Clench & Abbott, 1942. 23.1×14.4 mm

Figure *58:* Bahamas, San Salvador. USNM 749827. Shell: 15.7× 11.1 mm, Radula: × 130 FN 1920/6

Figure *59:* Same as Figure *58:* USNM 749827. Shell: 11.9×10.1 mm, Radula: × 212 FN 1465/7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Litorina echinata Anton was forgotten. The original diagnosis may be cited in translation from the German original:

> "Obliquely conical-pyramidate, five whorls, the last fairly bulgy, 3/5 of the whole, with nine rows of fairly distantly placed spines (Stacheln); in the middle of the whorl with a thread-shaped brown circlet, greyish white, spines white, the ones of the base brown; columella broad, curved; non-umbilicate; aperture long-oval, brown, with two white stripes. One [specimen].
>
> Variety: much narrower, last whorl half the size of the whole, less bulgy. Unicolored red-brown, with a yellow stripe. Width 4.5''', height 7'''. One [specimen]." [9.8 : 15.3mm].

Analysis of the diagnosis shows that in fact it corresponds best with *Nodilittorina miliaris:* Nine rows of "spines" on the last whorl indicate that beads of 2nd order are present, and that the nodules cannot be as large as, say, in *N. dilatata;* the expression used, "Stacheln," indicates that they must be elongated and pointed; the colour pattern is peculiar, but externally visible light-coloured zones are seen in the lectotype of *Littorina lemniscata* and in the closely related *N. helenae,* thus it is conceivable that in an extreme colour variation only a narrow dark circlet is left in the middle of the whorls.

Nodilittorina (Nodilittorina) helenae (E. A. Smith, 1890)

(Figure *51*)

* *Littorina helenae* E. A. Smith, 1890: 283; plt. 21, fig. 19 (St. Helena; lectotype BMNH 1889.10.1.2546-54, refigured by Rosewater, 1981: plt. 2, fig. L; paratype Figure *51* herein).

Vermeij (1973) identified the *Nodilittorina* population of Fernando de Noronha with this endemic form of St. Helena. The differences are outlined under *N. vermeiji* spec. nov. *Nodilittorina helenae, N. vermeiji* and *N. miliaris* are certainly closely allied but distinct enough to distinguish them as separate species. The distinguishing characters of *Nodilittorina helenae* are the slender conical shell, the lack of convexity of the whorls, the weak, nodulose sculpture, the presence of two externally visible yellowish bands, one at the periphery, the other on the umbilical side, this one forming the internal light band known in all *Nodilittorina* species; nodules pigmented yellowish, not white, the two adapical primary rows very weak, the abapical one strong and bipartite, thus the 2nd and 3rd row being extremely unequal. Radula, penis and operculum were described and figured by Rosewater, 1981.

Nodilittorina (Nodilittorina) unifasciata unifasciata

(Gray, 1827)

* *Litorina mauritiana* var. *crassior* Philippi, 1847, Abb. Beschr. Conchyl. 2: 165; plt. *Litorina* 3, figs. 15, 17a (type locality: "Cuba" (fig. 15 only) is erroneous, corrected by Rosewater (1970) to Australia).
* *Litorina cubana* Weinkauff, 1882, Syst. Conch.-Cab. 2 (140): 68; plt. 9, figs. 2-3 (type locality: "Cuba" is erroneous, corrected hereby to Australia; types not known).
• *Littorina (Melarhaphe) ziczac,* Bequaert, 1943, Johnsonia 1 (7): 15 (part, only the synonyms *crassior* Philippi and *cubana* Weinkauff).
• *Littorina (Austrolittorina) unifasciata unifasciata,* Rosewater 1970, Indo-Pacific Moll. 2 (11): 467-480; plt. 325, fig. 17-18; plt. 326, fig. 5; plt. 259, figs. 1-5; plt. 360, figs. 1-4; plt. 361, figs. 1A (radula), 1C (penis).

Remarks: The names *crassior* Philippi and *cubana* Weinkauff refer to shells of *Nodilittorina* with spiral sculpture and without colour markings except of a broad and blurred, slightly darker zone adapically of the periphery. No western Atlantic form has this colour pattern; they are typical, however, of the Australian *N. unifasciata unifasciata.*

Nodilittorina (Nodilittorina) knysnaensis (Philippi, 1847)

* *?Turbo dispar* Montagu, 1815, Trans. Linnean Soc. London 11(2): 195; plt. 13, fig. 4 (type locality Poole, England, is erroneous; types not found in the Exeter Museum nor in the British Museum (Natural History); *nomen dubium et oblitum,* included in synonymy of *"Littorina ziczac* (Gmelin)" by Bequaert, 1943 (Johnsonia 1(7): 15) and Abbott, 1964 (Nautilus N.S. 78:65)). Brown 1844, Illustr. recent conchol. Great Britain and Ireland...(2nd edition): 16; plt. 10, fig. 22.
* *?Littorina dispar,* Brown, 1844, Illustrations of the Recent Conchology of Great Britain and Ireland...(2nd edit.): 128. Jeffreys 1865, British Conchology...3:376.
* *Litorina knysnaensis* Philippi, 1847, Abb. Beschr. Conchyl. 2: 196; plt. Litorina 4, fig. 4 (South Africa: Caput Bonae Spei ad regionem fluminis Knysna). Krauss 1848, Die südafrik. Mollusken: 102.
* *Littorina picea* Reeve, 1857, Conch. icon. 10: no. 83, plt. 15, fig. 83 (no locality given; lectotype: Rosewater 1970, plt. 364, figs. 19-20, BMNH 1968.320).
• *Littorina (Austrolittorina) knysnaensis,* Rosewater, 1970, Indo-Pacific Moll. 2(11): 478-; plt. 364, figs. 17-23 (shell), plt. 365, fig. D (penis), plt. 369 (distribution).

Bequaert (1943) and Abbott (1964) included *Turbo dispar* Montagu, 1815, in *Nodilittorina ziczac (sensu lato).* The original description and figure, however, show a shell broader than *N. ziczac,* intensively dark pigmented, with a white band near the columella, and spiral furrows. This proves the species belongs to *Nodilittorina,* but the dark colour pattern without perceptible markings is quite anomalous for a Western Atlantic species. *Turbo dispar* is more likely synonymous with *Litorina knysnaensis* Philippi, 1847, as there is a particular similarity to the specimen which constitutes the lectotype of *L. picea* Reeve, 1857; the numerous small light-coloured dots reported for *N. knysnaensis* might have been obsolete or overlooked in *Turbo dispar.* As types are not preserved, the identity of *Turbo dispar* Montagu, 1815 cannot be established with certainty; thus it is preferred to consider it a doubtful and forgotten name.

West Atlantic species
erroneously attributed to *Nodilittorina*

Littoraria tesselata (Philippi, 1847)

(Figures 40-41)

* *Phasianella lineata* Lamarck, 1822: 54, no. 6 (Antilles; lectotype SD Bequaert, 1943: 13: original of Delessert, 1841: plt. 37, figs. 11a-b; MHNG 1096/87/1, here Figure *40*) (not *Buccinum lineatum* Gmelin, 1791, which is *Littoraria scabra* (Linnaeus, 1758)).
* *Littorina undulata* Orbigny, 1842: 212; plt. 15, figs. 12-14 (Martinique) (not *Littorina undulata* Gray, 1839).
• *Littorina lineata,* Deshayes in Lamarck, 1843: 243-.
* *Litorina* [*ziczac* var.] *undulata* "Menke" Philippi, 1847: 163 (no locality given; not of Gray, 1839).
* *Litorina tesselata* Philippi, 1847: 226; plt. *Litorina* 5, fig. 26 (Martinique; new name for *Littorina undulata* Orbigny, 1842).
• *Littorina (Melarhaphe) nebulosa tesselata,* Bequaert, 1943: 13; plt. 4, figs. 8-10.
• *Littorina (Austrolittorina) tesselata,* Rosewater, 1970: 423.
• *Littorina (Littoraria) tesselata,* Rosewater, 1981: 26.

Lamarck (1822) possibly intended to describe *Nodilittorina interrupta* (C. B. Adams in Philippi, 1847) under the name of *Phasianella lineata,* as the three paratypes belong to that species (see Figure *23*). However the only specimen of *Littoraria tesselata* in the type lot has been figured by Delessert (1841); Deshayes (1843) restricted Lamarck's species to that figured by Delessert; and eventually, Bequaert (1943) designated this figure as lectotype. The original is refigured (Figure *40*) herein and clearly shows its identity with *L. tesselata* Philippi. Other authors confused Lamarck's *lineata* with *N. interrupta, N. angustior* and *N. glaucocincta* group (see the synonymy lists of these species).

The attribution of *Littoraria tesselata* to *Austrolittorina* by Rosewater (1970) is certainly incorrect, as *L. tesselata* shows no interior of the shell pigmented with brown, no light-coloured basal band, and the central tooth of the radula is not narrowed, its lateral cusps are on the same level with the central cusp (Figure *41*). Further the penis has a basal "flap" without glands (Rosewater, 1981). Judging from shell and radula characters alone, *L. tesselata* appears to be most closely related to *L. undulata* (Gray, 1839) from the Pacific. The identity of the specific names *undulata* of Gray (1839), Orbigny (1842) and Philippi (1847) is by coincidence.

CONCLUSION

Evolution of the genus *Nodilittorina*
in the Western Atlantic

FOSSIL RECORD:

No suitable evidence to shed light on the evolutionary history of the genus *Nodilittorina* in the West Atlantic has emerged so far. Richards (1935) reports *N. ziczac* (or perhaps any other "smooth" species) and *N. dilatata* (under the name of *Echinella nodulosa matanzensis* n. var.) from a Pleistocene raised beach (25′) of Matanzas Bay, Cuba. From the Paraná Formation of Argentina, Borchert (1901) describes *"Littorina" paranensis* and *"Littorina" unicostalis.* The first-named he compares with *Nodilittorina angustior* (Mörch) and *Nodilittorina ariesensis* (Fontannes, 1879/82), the latter with *"Littorina" paranensis* only. Although probably belonging to *Nodilittorina,* the descriptions and figures are not detailed enough to ascertain the relationships of these species.

RECENT EVIDENCE:

The properties of the living Western Atlantic species of the genus *Nodilittorina* are visualised in Figure 5. Analysis of the properties so far known has revealed that two major features in the evolution of the *Nodilittorina* species can be recognized: speciation by geographical separation and homoeomorphology.

The speciation by (or during?) geographical isolation is shown in three species groups:

1) *Nodilittorina interrupta* (S. Caribbean) and *N. lineolata* (Brazil);

2) *Nodilittorina riisei* (Florida, Cuba), *N. glaucocincta* (Jamaica, Lesser Antilles), and *N. mordax* (Bahamas, Curaçao);

3) *Nodilittorina vermeiji* (Fernando de Noronha), *N. miliaris* (Ascension), *N. helenae* (St. Helena), *N. natalensis* (S.

and E. Africa) (the three last-named are not included in Figure 5 as being not Western Atlantic).

As negative evidence of the above, less closely related species overlap more or less in their geographical distribution: *Nodilittorina ziczac* and *N. interrupta* in the Southern Caribbean; *N. angustior* and *N. ziczac* in the entire Caribbean Sea; possibly *N. tuberculata* and *N. dilatata* at their northern, respectively, southern areal boundaries in the area of Puerto Rico/St. Thomas.

Homoeomorphologies occur worldwide in the family Littorinidae and are dealt with in the chapters on the taxonomic importance of the different organs. Homoeomorphologies in Western Atlantic species may be compiled here:

1) operculum type B (paucispiral, narrowly coiled) in (a) *Nodilittorina angustior,* (b) the conical, strongly nodulose *Nodilittorina* species like *N. tuberculata, N. dilatata* etc.

2) (possible homoeomorphs:) strongly nodulose species widely differing in anatomy: (a) *Nodilittorina dilatata, N. pyramidalis, N. miliaris* group etc., (b) *N. tuberculata,* (c) *N. antoni* (a common origin of all these species is still possible, but not well conceivable with the evidence at hand).

3) egg capsule: cupola-shaped, entire convex side covered by spiral ridges: (a) *Nodilittorina angustior,* (b) *N. tuberculata.*

4) egg capsule: only top portion of the convex side covered by spiral ridges, and steep flanks with oblique striae: (a) *Nodilittorina riisei* (and probably also the closely related *N. glaucocincta* and *N. mordax*), (b) *N. antoni.*

5) Radula with reduced central tooth, other teeth with reduced number of cusps, one cusp in both the lateral and the inner marginal teeth very large: (a) *Nodilittorina glaucocincta* and *N. mordax,* (b) *N. tuberculata,* (c) *N. antoni.*

Strangely enough, double homoeomorphologies occur repeatedly in the West Atlantic nodilittorines: *Nodilittorina angustior* and *N. tuberculata* (items 1 and 3), *N. tuberculata* and *N. antoni* (2 and 5), *N. mordax* and *N. antoni* (4 and 5). This circumstance would cast doubt as to whether the pertinent properties are really homoeomorphologies instead of homologies, if not the sum of all their characters would dismiss any close relationship. Apparently, when interpreting the relationship and evolution of this group of animals, one is faced with the problem of recognising numerous and repeated homoeomorphologies evolving from a repertoire of characters limited enough to not allow a further separation of the pertinent species into several genera. The problem is at present intensified by the limited knowledge of anatomical data.

For example, the available data on the penis morphology suggest that *Nodilittorina tuberculata, N. lineolata* and *N. ziczac* auct. (*i. e.,* either *N. ziczac s. str., N. angustior* or *N. mordax*) have characters in common which distinguish them from both spirally sculptured and nodulose species of the Indo-Pacific area. If these differences prove to be consistent in the species not yet investigated, the conclusion would be possible that all Caribbean Nodilittorinae had evolved from a common source different from the ancestors of the Indo-Pacific species, thus demonstrating any characters they may share with the Indo-Pacific species to be homoeomorphologies. On the other hand, there must be close affinities between Atlantic and Pacific Middle American species, as the Atlantic and Pacific Ocean were disconnected in this area only in geologically fairly recent time.

In summary, the genus *Nodilittorina* seems to have undergone a rapid evolution in recent times (approximately since the beginning of the Miocene). One driving mechanism of this evolution is obviously geographic isolation; another one may be ecological separation as shown in the two morphs of *N. hawaiiensis* Rosewater & Kadolsky. In the species dealt with here, the first-named mechanism can be demonstrated in several species groups. The origin of these species groups, their historical development and possible migration paths, however, cannot yet be traced due to the limited amount of anatomical data of the living species and the extremely poor fossil record.

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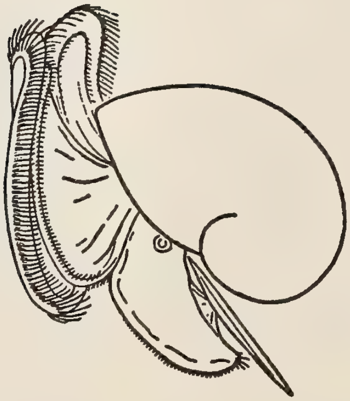

Taxonomic Notes on *Chiton carmichaelis* Gray, 1828, Type Species of *Plaxiphora* Gray, 1847

(Mollusca : Polyplacophora)

BY

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(3 Plates)

INTRODUCTION

Pilsbry (1893) raised some serious questions concerning the identity of *Chiton carmichaelis* Gray, 1828, type species of *Plaxiphora* Gray, 1847a, described from Cape of Good Hope, and the *C. carmichaelis* later reported by Gray (1847a) from South America. In addition to the discrepancy in localities, Pilsbry (1893, 14:318) pointed out that the original *carmichaelis* (1828), described as one-half inch long and scarcely keeled, did not seem to correspond to the large and strongly carinate South American specimens. Pilsbry *(loc. cit.)* surmised that *C. carmichaelis* Gray, 1828 and *C. carmichaelis* Gray, 1847a, are distinct biological entities, and that it had been "sheer piracy on Gray's part to shift his name from some poor little half-inch Cape of Good Hope specimen to this fine form from Cape Horn." Thus, Pilsbry *(loc. cit.)* adopted the name *Plaxiphora setiger* (King & Broderip, 1831) for the "fine large form from Cape Horn," with *C. carmichaelis* Gray, 1847a (not Gray, 1828), as junior synonym. Subsequently, Pilsbry (1911) stated that *Chiton auratus* Spalowsky, 1795 [erroneously cited by Pilsbry as *"Chiton aureus"*] was the oldest available name for the common South American *Plaxiphora*. Sykes (1894), having seen the type of *C. carmichaelis* [Gray, 1828] thought it identical with *C. setiger* and concluded that *C. carmichaelis* was "a South American species, and the Cape [of Good Hope] a locality...in error" (*op. cit:* 135). Although Sykes' opinion was accepted by Haddon (1886) and Ashby (1913), Pilsbry's view has prevailed and the South American *Plaxiphora* has been treated uncritically by most chiton workers as *P. aurata.*

The purpose of this paper is to ascertain the taxonomic status of *Chiton carmichaelis* Gray 1828, and *C. auratus* Spalowsky, 1795, and inquire into the nomenclatural questions raised by Pilsbry (1893) concerning the South American *Plaxiphora.* To this end, I was fortunate to meet with the generosity of the Trustees of the British Museum (Natural History) [BMNH], Muséum National d'Histoire Naturelle, Paris [MNHN], and U.S. National Museum of Natural History, Washington, D.C. [USNM], who made it possible to study the pertinent types and other historically relevant material in their repositories. In the process, a review of the nominal species involved in the taxonomy of the South American *Plaxiphora* was undertaken.

SYSTEMATIC TREATMENT

Polyplacophora Gray, 1821

Remarks: Persistently, the name Polyplacophora has been incorrectly attributed to Blainville by authors since Pilsbry (1893, 14: vi). Blainville (1816) was the first taxonomist to group chitons under a single name, Polyplaxiphora; but nowhere in Blainville's writings on chitons (1816, 1824, 1825, 1826) does the term "polyplacophores" or its equivalent appear. The name Polyplacophora was introduced by Gray (1821: 234), not as a correction of "polyplacophores" [as mistakenly stated by A. G. Smith (1960: 49)], but quite clearly as his own replacement for Blainville's Polyplaxiphora.

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Through the years, Gray's Polyplacophora has gained favor over Blainville's Polyplaxiphora [judged *"mal formé"* by Fischer (1885: 870), and emended to Polyplaciphora by Dall (1879: 301)] as well as over earlier proposed names for the group, such as Loricata (Schumacher, 1817) and Crepipoda (Goldfuss, 1820). Thus, recognizing its wide acceptance, Cox (1958) recommended that, since the nomenclature of higher taxonomy categories is not bound by considerations of priority, Polyplacophora Gray, 1821, be accepted as valid and placed on the Official List of Names in the Order/Class Group of the International Commission of Zoological Nomenclature. Thus far, the Commission has taken no action on the proposal.

Neoloricata Bergenhayn, 1955

Mopaliidae Dall, 1889

Plaxiphora Gray, 1847a

[**Type species,** *Chiton carmichaelis* Gray, 1828, by OD]

Plaxiphora carmichaelis (Gray, 1828)

(Figures *1* to *7*)

Main Synonymy:

Chiton carmichaelis Gray, 1828: 6; 1847a: 68; 1847b: 169; 1857: 186.
Chiton setiger King & Broderip, 1831: 338.
Chiton frembleii Broderip *in* Broderip & Sowerby, 1832: 28.
Choetopleura savatieri Rochebrune, 1881b: 119; 1889: 135-136, plt. 9, fig. 3 (as *Chaetopleura*).
Choetopleura ahnni Rochebrune, 1884: 34.
Chaetopleura hahni Rochebrune, 1889: 136-137, plt. 9, fig. 4.
Chaetopleura frigida Rochebrune, 1889: 137-138, plt. 9, fig. 5.
"*Chiton aureus* Spalowsky" Pilsbry, 1911: 36 [*nomen nullum*].
Mopalia (Semimopalia) grisea Dall, 1919: 514-515.

Type Material:

Chiton carmichaelis Gray, 1828: **Lectotype** and **paralectotype,** (BMNH 1951.1.25.1-2), herein designated.

Chiton setiger King & Broderip, 1831: **Lectotype** (BMNH 1978143), and **paralectotypes** (BMNH 1859.9.23.44; BMNH 1859.9.23.45; BMNH 1859.9.23.43+51; BMNH 1978143; BMNH 1978144; BMNH 1978145; BMNH 1978146; BMNH 1859.9.23.62), herein designated; locality, *"ad oras insulae* Tierra del Fuego *et in freto* Magellanico" (King & Broderip, 1831: 338).

Chiton frembleii Broderip, 1832: **Lectotype** (BMNH 198024) and **paralectotype** (BMNH 198025), herein designated; locality, "Sinu Valparaiso," Chile [33°02′ S, 71°38′ W].

Choetopleura savatieri Rochebrune, 1881: **Lectotype** (MNHN), herein designated; locality "Détroit de Magellan" [54° S, 71° W].

Choetopleura ahnni Rochebrune, 1884: Type material not found at MNHN; locality, "Pounta-Arenas" Patagonia [55°09′ S, 70° 55′ W].

Chaetopleura hahni Rochebrune, 1889: **Lectotype** (MNHN), herein designated; locality, "Baie Orange, Punta Arenas," here restricted to Bay of Orange, Chile [55°30′ S, 68°02′ W].

Chaetopleura frigida Rochebrune, 1889: Type material not found at MNHN (A. Tillier, *in litt.,* 14 June 1979); locality, "Baie Orange," Chile [55°30′ S, 68°02″ W].

Mopalia (Semimopalia) grisea Dall, 1919: Holotype (USNM 218734); locality, "Between Cape Pillar and Cape Horn, Tierra del Fuego."

Type Locality: Tierra del Fuego, Chile [54°30′ S; 67°00′ W], as designated by Gray (1847a: 68).

Remarks: The type lot of *Chiton carmichaelis* (BMNH 1951.1.25.1-2) consists of two specimens preserved dried. They are accompanied by a Museum label which reads, in part, "... *Chiton carmichaelis* Gray / SYNTYPES / Cape of Good Hope / Capt. Carmichael / 2 specs. Acc. no. / *Specil. Zool.* 1828: 6 / smaller spec. (disarticulated spec.) appears to be Wood's figure & Gray's measured specimen." On a wood tablet to which the two specimens were at one time glued, the following has been written on a pasted label: "Type / carmichaelis, Gray / S. Africa / Capt. Carmichael."

The larger of the two specimens measures 21mm in length; it is intact except for the removal of the soft parts. The specimen is dark brown with longitudinal creamy streaks; carinate; smooth tegmentum; anterior valve with 10 well formed radial ribs, granulose towards the apex, separated by smooth surface about 2-3 times width of ribs; lateral areas of intermediate valves with 2 similar radial

Explanation of Figures *1* to *3*

Figure *1: Chiton carmichaelis* Gray, 1828. Lectotype (BMNH 1951.1.25.1)

Figure *2: Chiton carmichaelis* Gray, 1828. Paralectotype (BMNH 1951.1.25.2). Close-up side view

Figure *3: Plaxiphora carmichaelis* (Gray, 1828). Lectotype of *Chiton setiger* King & Broderip, 1831 (BMNH 1978143)

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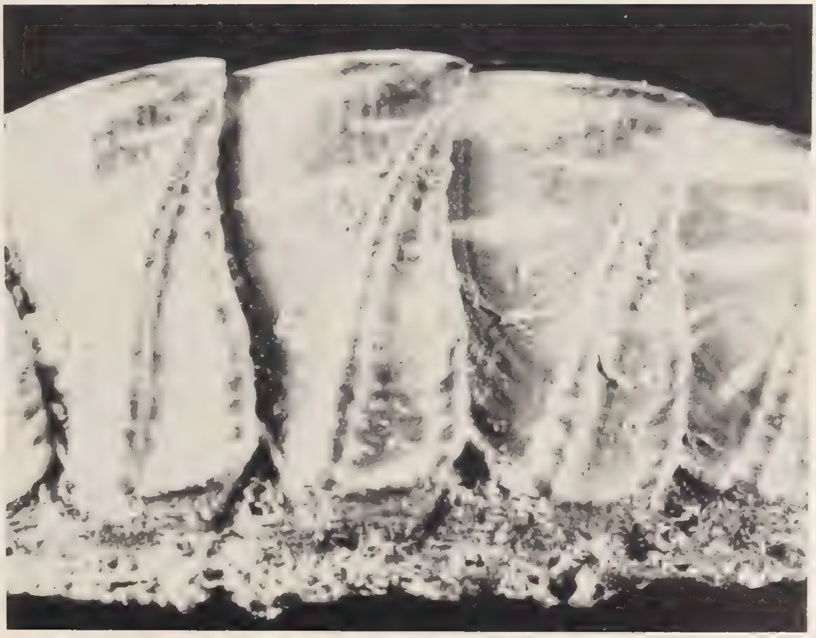

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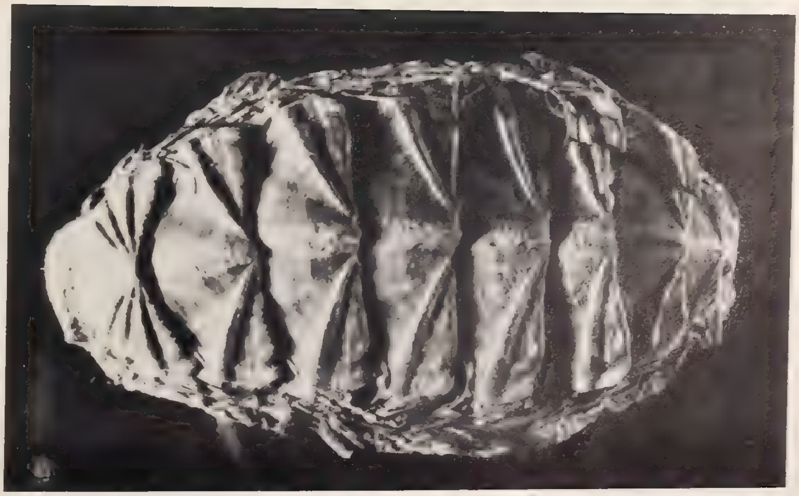

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ribs separated by smooth surface; central areas smooth; posterior valve subtriangular with mucro posterior, almost at edge of valve; girdle with sparse, long, simple hairlike formations (mostly broken); articulamentum white.

The smaller specimen, here designated **Lectotype**, is partly disarticulated; estimated length, 14mm; features very similar to larger specimen; intermediate valves with uni-slit insertion plates; insertion plate of anterior valve not accessible for study. Posterior valve with no slits but a transverse callus; width of sinus / width of sutural lamina = 0.66mm/1.66mm = 0.40. Width of valve i / width of valve viii = 5.1mm/3.7mm = 1.38. From the dimensions and characteristics, it is apparent that this is Gray's described specimen in *Spicilegia Zoologica* (1828: 6). The species is illustrated here for the first time (Figures *1, 2*). The two type specimens of *Chiton carmichaelis* were compared, with specimens of the common South American *Plaxiphora*, collected at Isla Chiloé, Chile, as well as to the types of *Chiton setiger* King & Broderip, 1831, and found to be conspecific.

It must be added that since Gray's original description there have been no reports of *Plaxiphora carmichaelis* in South Africa (Krauss, 1848; Martens, 1874; Sykes, 1894; Sowerby, 1903; E. A. Smith, 1910; Bartsch, 1915; Ashby, 1931; Barnard, 1963; Day, 1963). *Chiton wahlbergi* Krauss, 1848, allocated by Pilsbry (1893: 322) to *Plaxiphora* has been shown to be a synonym of *Onithochiton literatus* (Krauss, 1848) instead (Ashby, 1931). The only *Plaxiphora* recognized in Africa is *P. parva*, Nierstrasz, 1906, known solely from Nierstrasz's original description, and a single specimen referred to by Barnard (1963: 332-333; figs. 29c-e). The examination of this specimen, available through the generosity of Elizabeth K. Giles, South African Museum, as reported elsewhere (Ferreira & Bertsch, 1979), demonstrated it to be very different from, the type specimens or the description of *Chiton carmichaelis*, Gray, 1828.

The type material of *Chiton setiger* King & Broderip, 1831, consists of four lots marked "Syntypes," and four lots of "Probable Syntypes." Three of the lots of "Syntypes" are from Captain P. P. King collection; they are from "Port Gallant, S. America," and bear BMNH reg. nos. 18959.9.23.44 [2 incomplete specimens, disarticulated], 1859.9.23.45 [1 specimen], and 1859.9.23.43+51 [4 specimens]. The fourth lot of "Syntypes" has no locality indicated; it bears BMNH reg. no. 1978 143, and consists of 10 specimens. The Museum label indicates that the specimens were presented by Capt. P. P. King, explaining that "As these specimens were not originally registered they were prob.[ably] presented prior to 1837 and are probably the specimens King [& Broderip, 1831: 338] refers to as being in the Mus. Brit." In fact, among the four lots of "Syntypes," this lot contains the only specimen large enough [65mm long] to correspond to the size [2⅜ inches] given in the original description of the species. A specimen from this lot is here designated **lectotype**; the specimen, well preserved, flat, not eroded or encrusted, measures 39mm in length (including girdle); the girdle still bears many intact hairs (Figure *3*).

Of the four lots of *Chiton setiger* labeled "Probable Syntypes," three are from the Broderip Collection, BMNH 1978144 [1 specimen], BMNH 1978145 [2 specimens], and BMNH 1978146 [2 specimens]; they have no indication of locality. The fourth lot of "Probable Syntypes," BMNH 1859.9.23.62, consists of a single specimen from Capt. King Colln., and "? S. America" locality. All of these 23 specimens in 8 lots correspond in every respect to King & Broderip (1831) description of *Chiton setiger;* the entire group is here regarded as a syntype series, with one specimen, as mentioned above, here designated **lectotype**, the others **paralectotypes**.

The syntype series of *Chiton frembleii* consists of three specimens, well preserved, dry, flat, soft parts removed, measuring 25mm, 38mm, and 45mm in length. They are accompanied by a Museum label which reads, *"Chiton frembleii* Broderip / SYNTYPES / Loc. data lost / H. Cuming colln. / 3 specs. / Acc. no: 1829 / P.Z.S. Lond. 1832: 28." The specimens are mottled cream and brown; they correspond well to Broderip's (1832: 28) description of the species. The medium sized specimen, 38mm long, 26mm wide (at valve iv), is here designated **lectotype** (BMNH 198024) (Figure *4*), the other two, **paralectotypes** (BMNH 198025).

Choetopleura [sic] *savatieri* Rochebrune, 1881, was described from a specimen collected by Dr. Savatier at the Strait of Magellan during the Magicienne expedition. The specimen, preserved dry in the MNHN collection, here designated **lectotype** and illustrated (Figure *5*), corresponds in every respect to Rochebrune's (1881: 119) description and to the current concept of *Plaxiphora carmichaelis*. It is accompanied by a museum label which reads, in part, "Mr. le Dr. Savatier XIV. 317. / Type [on red background] / Plaxiphora savatieri Rochbr. 1881 / Dt. de Magellan..." An older label states "(Type) Dr. Savatier / Camp.ᵉ de la Magicienne." Specimen fairly well preserved, flat; valves vi and vii intact but loose; all other valves in place but broken longitudinally; right half of valve ii, loose. Specimen's dimensions correspond exactly to those given by Rochebrune (1881), 30mm long, 22mm wide (including girdle); but, originally, the specimen must have been longer by at least 10mm, considering that valves vi and vii are now detached. Seven specimens, part of a lot of 12 specimens in the MNHN collection, preserved in alcohol, varying in length from 40mm to 70mm approximately, were also examined, and regarded conspecific with the **lectotype** here designated. They[?] are accompanied by a green-framed museum label reading *"Acanthopleura Savatieri*, Roch. / *Plaxiphora setiger*, King / Punta Arenas / Mr. Lebrun no. 25 1883," and likely part of the material obtained during the Cape Horn Expedition of 1882-1883, later referred to *Chaetopleura savatieri* by ROCHEBRUNE (1889: 135-136; plt. 9, fig. 3).

The type material of *Choetopleura* [*sic*] *ahnni* Rochebrune, 1884 has not been found at the Muséum National d'Histoire Naturelle, Paris. A specimen purported to be of *C. ahnni* at MNHN, is accompanied by an old museum label, bordered with green, reading *"Chaetopleura hahni* Roch. / = *Plaxiphora setigera* / Exp. Cap Horn Baie Orange." Fairly well preserved in alcohol, the specimen measures 38mm in length; a bit of white string is attached to the front part of the girdle; it corresponds well to ROCHEBRUNE'S (1884) original description of *ahnni*, but it is almost identical [same length, very similar markings and encrustations] to the lectotype of *Chaetopleura hahni* Rochebrune, 1889 [see ahead]. Given the accompanying label, similarities of morphology and the manner in which it was tagged [with a white string perforating the anterior part of the girdle as in the lectotype of *C. hahni*], the specimen may be safely regarded as part of the type lot of *C. hahni*, and not the original material upon which *C. ahnni* was described. KAAS & VAN BELLE (1980) stated that the name *hahni* 1891 is an emendation of *ahnni* 1884; this is likely the case for, except for the localities, the respective descriptions are virtually identical. However, there is no way of deciding whether Rochebrune intended *hahni* to supersede *ahnni*, or the name was misspelled in 1884 or in 1889. According to the rules of the International Code of Zoological Nomenclature (London, 1964) the two names represent two nominal species, and each one must be treated on its own merits; since the two names quite obviously refer to the same biological species, *hahni* must be regarded as a junior synonym of *ahnni*.

Prior to the finding of the specimen above mentioned [as purported type of *ahnni*], the type material of *Chaetopleura hahni* Rochebrune, 1891, was known from a single specimen here designated **lectotype** and illustrated (Figure *6*). The specimen, preserved in alcohol, somewhat curled, has an estimated length of 38mm; it is attached to a small glass ball by a white string perforating the anterior part of the girdle. It is labeled "Type," and accompanied by a locality label "Baie Orange / Exp. du Cap Horn." It conforms in all respects to ROCHEBRUNE'S (1891: 136-137; plt. 9, fig. 4) description.

The type material of *Chaeotopleura frigida*, reported by IREDALE & HULL (1932) at the Paris Museum, could not be found (A. Tillier, *in litt.*, 14 June 1979). But from Rochebrune's figure and description (1891: 137-138; plt. 9, fig. 5) it is apparent that *frigida* is conspecific with *Plaxiphora carmichaelis* from the same locality, an opinion already expressed by PILSBRY (1893, 14: 317), IREDALE & HULL (1932), and LELOUP (1942, 1956).

"Chiton aureus Spalowsky" Pilsbry, 1911, obviously an incorrect citation of *Chiton auratus* Spalowsky, 1795, is here cast aside as *nomen nullum*. Under the name *"Plaxiphora aurea* Spalowsky" HEDLEY (1916) recorded the presence of *Plaxiphora carmichaelis* at Macquarie Island and Garden Bay in the Antarctic.

The holotype of *Mopalia (Semimopalia) grisea* Dall, 1919 in the repository of the U.S. National Museum of Natural History (USNM 218734) consists of a single specimen, preserved dry, 20mm long (including girdle), here illustrated for the first time (Figure *7*). Although A. G. SMITH (1977) did not question the validity of the species, the reexamination of the photographs of the holotype (CASIZ Color Slides Series Nos. 3301-3304, and AJF Nos. 375/6-18, 395/1-3) revealed its conspecificity with *Plaxiphora carmichaelis* (Gray, 1828). Accordingly, the subgenus *Semi-*

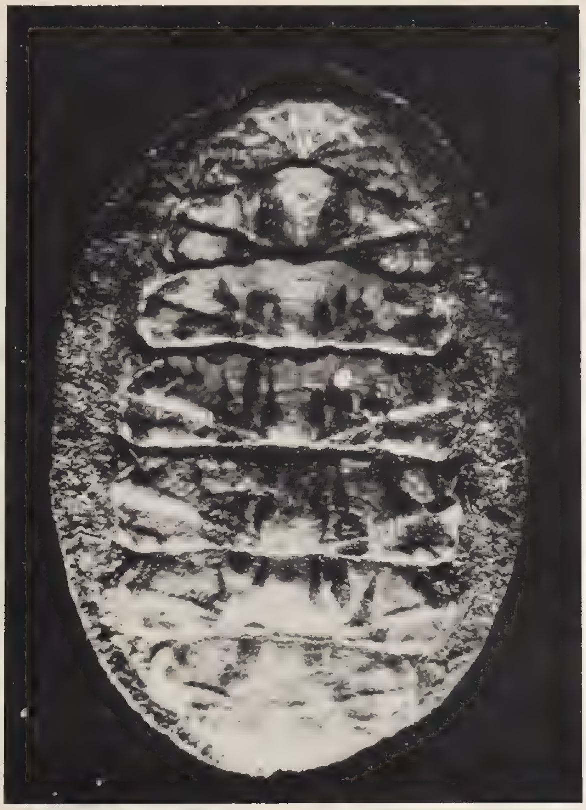
Explanation of Figures *4* to *7*

Figure *4: Plaxiphora carmichaelis* (Gray, 1828). Lectotype of *Chiton frembleii* Broderip, 1832 (BMNH 198024)

Figure *5: Plaxiphora carmichaelis* (Gray, 1828). Lectotype of *Choetopleura savatieri* Rochebrune, 1881 (MNHN, Paris)

Figure *6: Plaxiphora carmichaelis* (Gray, 1828). Lectotype of *Chaetopleura hahni* Rochebrune, 1889 (MNHN, Paris)

Figure *7: Plaxiphora carmichaelis* (Gray, 1828). Holotype of *Mopalia (Semimopalia) grisea* Dall, 1919 (USNM 218734)



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mopalia Dall, 1919 [type species, *M. (S.) grisea*] becomes a synonym of *Plaxiphora* Gray, 1847.

Choetopleura [*sic*] *veneris* Rochebrune, 1884, [type locality: "Pounta-Arenas (mission Lebrun, Patagonie)"] is, from the description, a probable synonym of *Plaxiphora carmichaelis.* However, its type material has not been found so far at the Muséum National d'Histoire Naturelle, Paris (Dr. P. Bouchet, *in litt.,* 18 August 1980), and must for the moment, as suggested already by Kaas & Van Belle (1980), be left as a *nomen inquirendum.*

The question of *Chiton auratus* Spalowsky, 1795, generally accepted since Pilsbry (1911) as senior synonym of *P. carmichaelis,* was investigated at first through the good efforts of Melanie Miller, Academy of Natural Sciences, Philadelphia, who checked the description and illustrations of the species in the very rare *Prodromus in Systema Historicum Testaceorum,* and confirmed the fact that Pilsbry's citation [1911: 36] was incorrect for "...the true name is *auratus...*, and not *aureus*" (M. Miller, *in litt.,* 7 November 1978). M. Miller also established that *C. auratus* is the only chiton cited by Spalowsky in the *Prodromus.* Subsequently, Aileen Blake and Solene Whybrow, British Museum (Natural History), generously arranged for photographic copies of the description and illustration of *C. auratus* Spalowsky in the *Prodromus,* which, for their great historical interest, are here reproduced with their permission (Figure *8*). As it may be appreciated, both description and illustration are far from adequate to identify the species with *Plaxiphora carmichaelis* as Pilsbry (1911) had suggested. The stated locality of *C. auratus, "Mare australe (ad ins.* Otaheiti ?)," leaves too much room for uncertainty. In addition, warm-water Tahiti [modern name for Otaheiti] is outside of the known range of cold-water *Plaxiphora carmichaelis;* and the only known *Plaxiphora, P. kamehamehae* Ferreira & Bertsch, 1979, described from Hawaii, is a very small-sized species with a definite tegmental sculpture which could not have been confused with the large *P. carmichaelis.* No type material of *C. auratus* has been found at the British Museum (Natural History) (A. Blake, *in litt.,* 7 May 1980). So, *Chiton auratus* Spalowsky, 1795 emerges from this investigation as a name not applicable with certainty to any known taxon; it is here recommended that it be suppressed as a *nomen dubium.*

The observations made in the course of this investigation firmly establish *Chiton carmichaelis* Gray, 1828 as conspecific with the South American *Chiton setiger* King & Broderip, 1831, Pilsbry's question about Gray's proper use of the name *carmichaelis* for the Magellan species is thus laid to rest. It is clear, now, that Gray's (1828) type specimens of *Chiton carmichaelis* were originally attributed to Cape of Good Hope in error, as also suggested by the fact that, in later publications, Gray (1847a, 1847b, 1857) made no further reference to Cape of Good Hope but, instead, spoke of *carmichaelis* as a species of Tierra del Fuego. It can be surmised, albeit on subjective grounds, that Gray having become aware of his error in the original type locality of *carmichaelis* (1828) simply "corrected" it in later references (1847a, 1857), without explanation, and unaware of the taxonomic turmoil that his action would cause. In what manner Gray came to realize the error in locality remains a matter of conjecture. The type specimens were apparently brought to Gray's attention by "Capt. Carmichael," after whom the species is named. But attempts to learn about Capt. Carmichael, his voyages, and possible collecting sites, as indirect clues to the provenance of the specimens have proved futile (A. Blake, *in litt.,* 21 September 1979) so far.

Since there remains no doubt that the type locality of *Chiton carmichaelis* Gray, 1828 was erroneously designated in the original reference, in conformity with Recommendation 72E of the International Code of Zoological Nomenclature (London, 1964), the **type locality** is here corrected to Tierra del Fuego as subsequently indicated by Gray (1847a).

In addition to the examination of the type material of *Chiton carmichaelis,* several other lots also labelled *carmichaelis* in the repository of the Mollusca Section, British Museum (Natural History) were studied thanks to the generosity of Aileen Blake. Some of these lots proved to be of great interest. Two of the lots demonstrate the presence of the species at the Falkland Islands (BMNH 1842.2.21.3; BMNH Acc. No. 2287 [from British Antarctic Survey]).

Most valuable, for biogeographic reasons, was the opportunity to study the lot labelled *Plaxiphora carmichaelis* (Gray) from the *H.M.S. Challenger* Expedition of 1873-1876, Station 306A, and referred to in the *Report on the Polyplacophora* (Haddon, 1886: 32-33). The lot (BMNH 1289.11.9.23) consists of loose chiton valves which are found to belong to specimens of two different species. Five whole valves (including an anterior and a posterior valve) and two fragments of valves are of *P. carmichaelis;* but four other valves (also including an anterior and a posterior valve) are of the tropical Indo-Pacific *Acanthopleura gemmata* (Blainville, 1825). The specimen(s) of *P. carmichaelis* are reported to have been collected at "Station 306A. January 2, 1876. Lat. 48°27′ S., Long. 74°30′ W. South Chili, 345 fathoms..." (Haddon, *loc. cit.*). Obviously, the admixture of valves of *A. gemmata* is an unfortunate misplace-

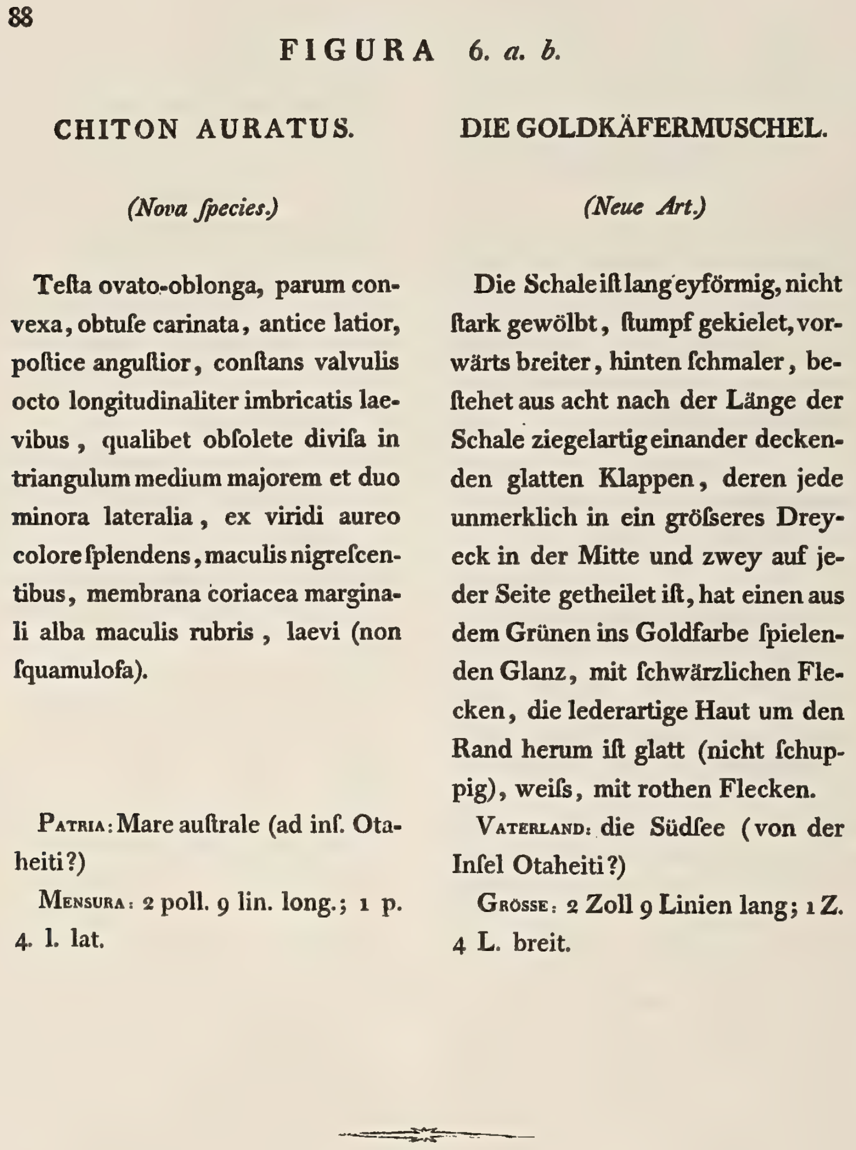

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FIGURA *6. a. b.*

CHITON AURATUS.

(Nova ſpecies.)

Teſta ovato-oblonga, parum convexa, obtuſe carinata, antice latior, poſtice anguſtior, conſtans valvulis octo longitudinaliter imbricatis laevibus, qualibet obſolete diviſa in triangulum medium majorem et duo minora lateralia, ex viridi aureo colore ſplendens, maculis nigreſcentibus, membrana coriacea marginali alba maculis rubris, laevi (non ſquamuloſa).

Patria: Mare auſtrale (ad inſ. Otaheiti?)

Mensura: 2 poll. 9 lin. long.; 1 p. 4. l. lat.

DIE GOLDKÄFERMUSCHEL.

(Neue Art.)

Die Schale iſt lang eyförmig, nicht ſtark gewölbt, ſtumpf gekielet, vorwärts breiter, hinten ſchmaler, beſtehet aus acht nach der Länge der Schale ziegelartig einander deckenden glatten Klappen, deren jede unmerklich in ein gröſseres Dreyeck in der Mitte und zwey auf jeder Seite getheilet iſt, hat einen aus dem Grünen ins Goldfarbe ſpielenden Glanz, mit ſchwärzlichen Flecken, die lederartige Haut um den Rand herum iſt glatt (nicht ſchuppig), weiſs, mit rothen Flecken.

Vaterland: die Südſee (von der Inſel Otaheiti?)

Grösse: 2 Zoll 9 Linien lang; 1 Z. 4 L. breit.

Figure *8*

Chiton auratus Spalowsky, 1795. Photographs of the original description and illustrations of the species in *Prodromus in Systema historicum Testaceorum,* 1795, p. 88, figs. 6a and 6b, kindly provided by the British Museum (Natural History)

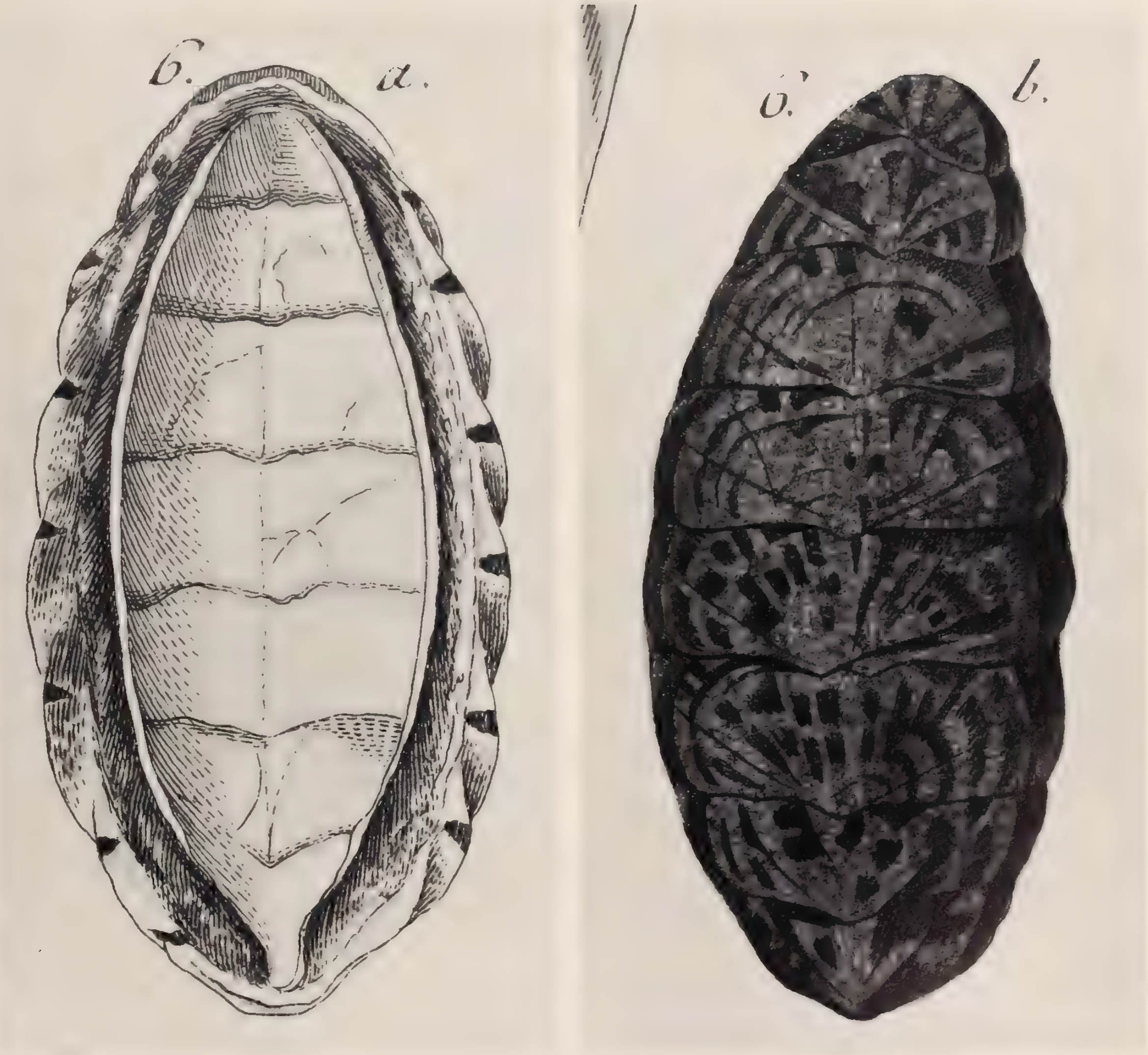

Figure *8*

ment of material; but a more grievous error is the report of *P. carmichaelis,* an intertidal species, from a depth of "345 fathoms [631m]." In the *Narrative of the Cruise* it is indicated that on that particular day, January 2, 1876, the ship stopped off Middle Island, and landed surveying and exploring parties; the latitude obtained on the west extremity of the island was 48°28′03″ S, and "Whilst the exploring parties were on shore the ship sounded, trawled, and took temperatures in 345 fathoms..." (Tizard *et al.,* 1885: 863). The account reveals, therefore, that on that day there were two possible sources of collections, the trawled material from 345 fathoms [? Station 306], and the land and intertidal material collected by the exploring party on the shores of Middle Island [? Station 306A]. Thus it may be surmised that the specimens of *P. carmichaelis* [but not those of *A. gemmata,* a species which is not known to inhabit such cold waters] collected at the *H.M.S. Challenger* Station 306A, very likely came from the intertidal zone of Middle Island, South Chile, at a latitude of 48°28′ S approximately, and not from the depth and latitude reported by Haddon *(loc. cit.).*

The distribution of *Plaxiphora carmichaelis* is not known with precision. This investigation suggests that *P. carmichaelis* is confined to the Magellan Province, from Chiloé Island, Chile [43° S; 73° W] on the Pacific side, to the Falkland Islands [52° S; 60° W] on the Atlantic side, and the adjacent Sub-Antarctic Region. Leloup (1956), following Iredale & Hull (1932), added a number of other nominal species of *Plaxiphora,* described from Australia and New Zealand, to the synonymy of *P. carmichaelis* on the assumption of conspecificity. And although such an assumption is quite credible, the possible circumantiboreal distribution of *Plaxiphora carmichaelis* remains to be investigated.

ACKNOWLEDGMENTS

I wish to express my deep appreciation to Aileen Blake, Kathie Way, Solene Morris, and the Trustees of the British Museum (Natural History); Dr. Philippe Bouchet, Muséum National d'Histoire Naturelle, Paris; and Dr. Joseph Rosewater, U.S. National Museum of Natural History, Washington, D.C., who generously provided the opportunity to examine and photograph precious specimens in their custody. Many thanks are also due to Melanie Miller of the Academy of Natural Sciences, Philadelphia, and to the staff of the Departments of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco. I am particularly grateful to Drs. Barry Roth and Peter U. Rodda for their advice and critical reading of the manuscript.

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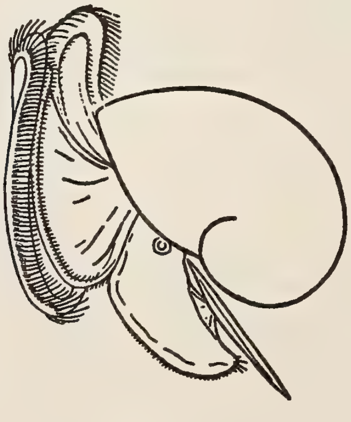

A Study of the Biology of *Diplodon delodontus* (Lamarck, 1819)

(Bivalvia : Hyriidae)

I—Ecological Aspects and Anatomy of the Digestive Tract

BY

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(1 Plate; 7 Text Figures)

INTRODUCTION

THIS IS A PRELIMINARY STUDY OF *Diplodon delodontus* (Lamarck 1819) (Unionacea, Hyriidae). In the synonymy of *Diplodon delodontus,* several names were also included by CASTELLANOS (1959):

1819—*Unio delodonta* Lamarck;
1834—*Unio lacteolus* Lea;
1834—*Unio divaricatus* Lea;
1853—*Unio fokesi* Dunker;
1856—*Unio browni* Lea;
1859—*Unio rudus* Lea;
1866—*Unio paraguayensis* Lea.

This mollusc has been found in a neotropical area restricted to South America: Paraná river, Paraguay river, La Plata River and their tributaries in southern Brazil (CASTELLANOS, 1959). They are bentonic organisms living in lenetic and lotic systems.

The purpose of the present report is to carry out a preliminary study of the internal morphology of *Diplodon delodontus,* with special mention of its digestive tract. Determinations *in vivo* of ciliary currents as well as other physioecological characteristics have also been described.

The anatomic studies were based on the works of GRAHAM (1948/49), PURCHON (1956, 1958), FRANC *in* GRASSÉ (1960) and MORTON (1956).

MATERIALS AND METHODS

The molluscs were collected monthly from April 1980 to April 1981 from a bank of *Diplodon delodontus* in La Plata River (34° 53′ S; 57° 50′ W), Berisso, Buenos Aires province, Argentina, at 1.5 m depth. Forty adult animals of both sexes from 70 to 110 mm long were collected on each occasion. The temperature and pH of the water were also measured. The animals were maintained in aquaria with aerated tap water at 22° C. The bottom of the aquaria was covered with sand and mud from the river to reproduce natural conditions.

The taxonomic determination was done following PARODIZ' (1973) criteria and the description of the internal structures is the result of our direct observations.

The digestive tract was studied by a plastic injection. Four mL of an acetonic solution of 15 g percent of Rodophax AX-85-15 (Roche Lab., France) were injected per animal. The shell valves were opened at the level of the adductor muscle with a Swann-Morton bistoury. The shell was cut forming an U-shaped hole to display the mouth. The digestive tract was then canalized, washed with distilled water and acetone and the plastic solution injected. The animals were immersed in running water for 24 hrs and then disintegrated for 24 hrs in a 1% solution of HCl acid.

The stomach was studied after the dissection at different planes. The ciliary currents were investigated "in vivo."

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KEY TO LETTERING ON FIGURES

Key to Lettering on Figures

A:	Pigment area
AA:	Anterior adductor
AI:	Ascending intestine
Am:	Amebocyte
AOG:	Anterior oral groove
C:	Crest
CE:	Ciliated epithelium
CI:	Cilia
CS:	Crystalline style
CT:	Cardinal teeth
DD:	Digestive diverticula
DDu:	Opening of stomach into the digestive diverticula (1-2-3-4)
DI:	Descending intestine
DOG:	Dorsal oral groove
DW:	Dorsal wall
E:	Minor typhlosole
EE:	External epithelium
EN:	Epithelium
ES:	Exhalant siphon
F:	Fold
Fo:	Foot
Fu:	Furrow
FPM:	Mantle fusion point
G:	Marginal groove of inner demibranch
H:	Heart
ID:	Inner demibranch
IFPL:	Inner fold of labial palps
IG:	Intestinal groove
IS:	Inhalant siphon
L:	Ligament
LILP:	Left inner labial palps
LOLP:	Left outer labial palps
LLP:	Left labial palps
LP:	Labial palps
M:	Mantle
MB:	Mantle bridles
Mo:	Mouth
O:	Oesophagus
OD:	Outer demibranch
P:	Pericardium
Pa:	Particle
PA:	Posterior adductor muscle
PL:	Pallial line
POG:	Proximal oral groove
PR:	Posterior retractor muscle
R:	Rectum
RG:	Rejection groove
Ro:	Rotation
S:	Septum
Sa:	Sagitta
SA SA_3 SA_7 SA_8	Sorting areas
SI:	Sigmoid intestine
SS:	Style sac
SP:	Sensory papilla
St:	Stomach
T:	Tentacle
TY:	Major typhlosole
U:	Umbo
V:	Valve
VM:	Visceral mass

The animals were previously anesthetized by an injection of sodium pentobarbital (6mg/100g body weight). Then, few milligrams of carmine red or carborundum were suspended in the water of a small aquarium where the animals were maintained during 6 to 12 hrs. The movement of the particles of different size was checked under the stereoscopic microscope.

RESULTS AND DISCUSSION

Habitat and ecology:

From our data, *Diplodon delodontus* (Figure *1*) prefers well oxygenated bodies of fresh water and temperatures that vary from 12 to 24°C. Generally, we found them between 1.30 and 1.50m deep. The pH of water was between 7.1 and 7.2. In the aquarium, temperatures higher than 30°C killed them quickly in spite of rapid water circulation and good aeration. However, they were easily adapted at lower temperatures to aquarium conditions. The animals required approximately 5 days for their complete adaptation. During this period, they moved actively in different directions.

They lie on one of the shells, in a horizontal position and they move extending the robust foot. They bury slowly into the sand, using the foot as a digging element and helping it by closing the posterior portion of the valves, thus producing a current of water and sand.

A rapid microscopic observation of the gastric content showed the predominance of phytoplankton and abundant organic detritus of vegetal origin as well as amoebae and flagellates. The importance of colloidal detritus stuck to sand particles as nutrients for bentonic filtering invertebrates has already been shown by TSUCHUYA & KURIHARA (1979). A quick analysis of the plankton showed the presence of diatoms, chlorophyta and cyanophyta in variable proportions depending on the season, amoebae, bacteria and spores.

Although the *Diplodon delodontus* is a fresh-water species, it normally feeds for periods from 4 to 6 hrs during the high tide as has been observed by MORTON (1956) in *Lasaea rubra.*

SYSTEMATIC REVIEW

Phylum: Mollusca
Class: Pelecypoda
Sub-class: Polysyringia
Order: Lamellibranchia
Sub-order: Heterodonta
Super family: Unionacea
Family: Hyriidae
Genera: *Diplodon* Spix (1827)
Species: *Diplodon delodontus* (Lamarck 1819)

Digestive system

The siphons: There are two separate short siphons (Figures 2-3) which are formed from the fused inner lobes of the mantle margins. The inhalant siphon projects not far from the substratum, the orifice being held near the surface of the sand. The inhalant activity of the siphon was generally produced twice a day during 4 to 6 hrs, but this cycle may be affected by different factors. The first food selection is done by the inhalant siphon, which is very efficient in sorting particulate material according to size, by using tentacles of different length.

The mouth: The mouth (Figures 2-4) is laterally delimited by a pair of labial palps. They are well-developed, semicircular in shape and covered with a large number of delicate parallel ciliated folds (Figures 4 A-D). The second food selection is carried out in the palps. Water that enters through the inhalant siphon (IS) reaches the pallial cavity and contacts the gills. In the gills, the ciliary currents originate and they remove the material to the palps and then to the mouth. These ciliary currents were investigated under the stereoscopic microscope, by the addition of small quantities of finely-powdered carborundum or carmine red. It was observed that palp cilia vibrate displacing the material in the direction of the mouth (Figures 5 A-B). The movement of the cilia in the folded surfaces of the inner side of the palps imitates the characteristics of a transporting strip. This movement is provoked by a cytosolic current and not by a nervous stimulus (DE ROBERTIS, 1977) (Figures 6 A-B).

In this species, the inner gills are closely attached to the corresponding internal palp faces (Figure 4 A) and are provided with an alimentary canal (G) (Figures 4 B-C). The alimentary canal is placed on the inferior margin and transports alimentary particles onto the edges of the inner palp faces as already described. The apices of these edges transport the particles that have been accepted according to size, towards the mouth as well as along the dorsal oral groove (DOG) and the anterior oral groove (AOG) (Figures 4-5).

Coarse material is covered with mucus and follows the opposite direction to the acceptance currents, being then ejected via the inhalant siphon (IS). To reach the inhalant siphon, they pass first into the troughs and then contact

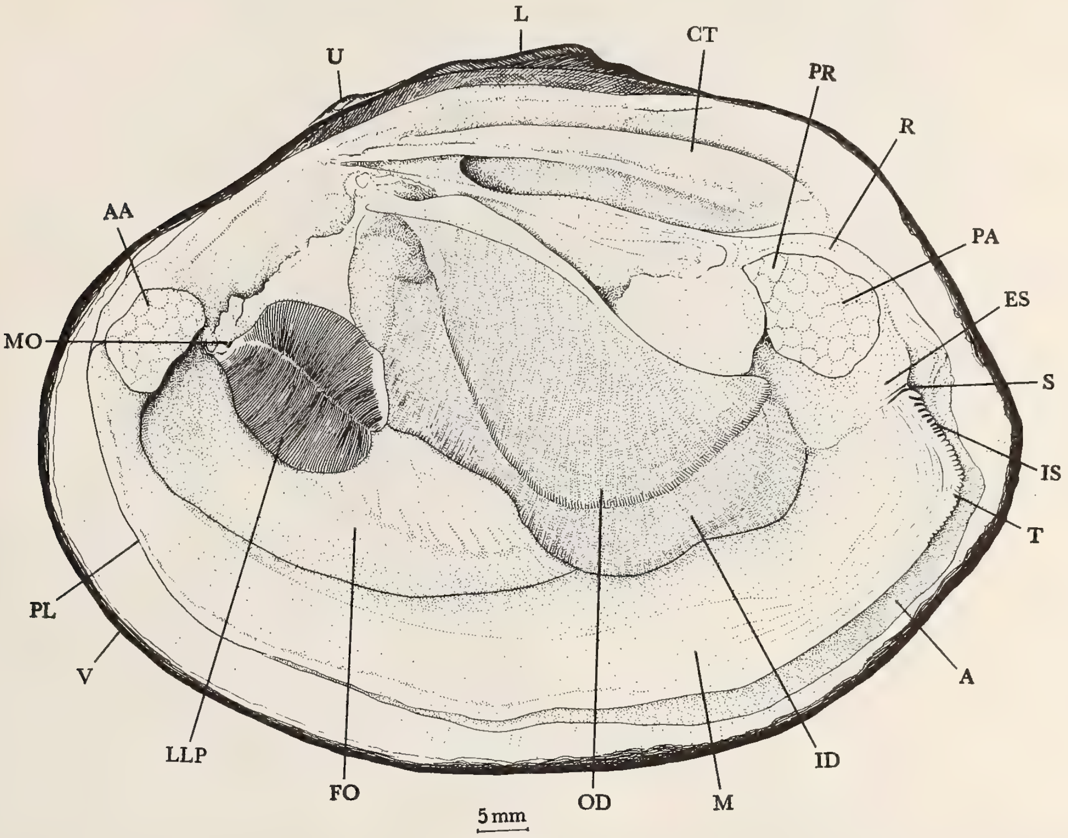

Figure 2

General aspect of *Diplodon delodontus.* The shell and left mantle were removed.

the lateral edges (RG) of the palps. They are eliminated as pseudofaeces by the inhalant siphon.

The stomach: The mouth is followed by a short oesophagus that turns to the right to reach the stomach (Figure 7). The stomach is located in an antero-dorsal position, being easily recognized by its gelatinous appearance.

The pH of the stomach content is around 6.5. The stomach performs an efficient mechanical sorting of specific nutrients and shows the different areas of selection, typical of the Hyriidae family.

At the stomach cavity (Figure 8) there is a system of shorter cilia that produces slow ciliary currents. The particles are kept there for a longer time in order to facilitate the digestion, before the major typhlosole sends those particles towards the ducts of the digestive diverticula (D.D.).

This undulate minor typhlosole (TME) of whitish colour was observed in the interior of the stomach (Figure 8). The zone of particle admission is parallel. The alimentary particles are carried to the left and right blind sacs by the major typhlosole (TMA). They enter both sacs and move to the right and left digestive ducts located in the

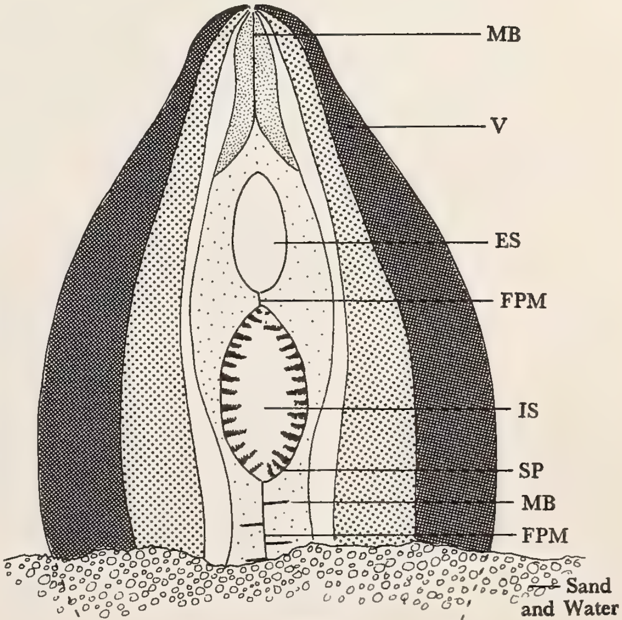

Figure 3

Drawing of the siphons when the animal is actively siphoning clean water taken from the aquarium. The animal has not buried itself completely into the sand, yet.

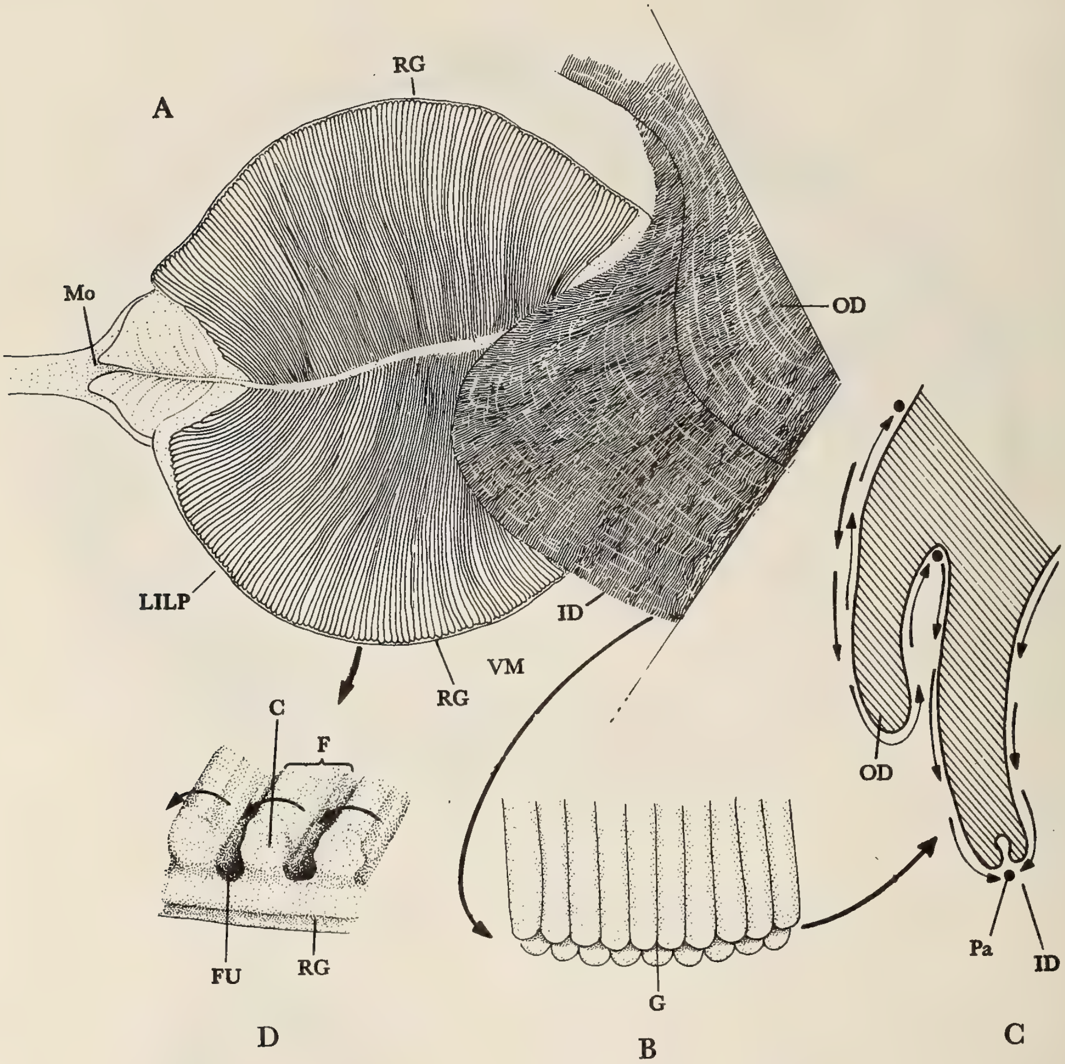

Figure 4

A: Inner faces of left palps related to internal gill position; B: Alimentary canal of internal gill; C: Scheme of gills, showing displacement of alimentary particles; D: Labial palp folds.

Explanation of Figures *1, 9* and *10*

Figure *1:* Right shell of *Diplodon delodontus* with growth edges and rings.
Figure *9:* Digestive tube in Rodophax Ax-85-15. Left and right digestive ducts are indicated.
Figure *10:* Digestive and circulatory systems in Rodophax Ax-85-15.

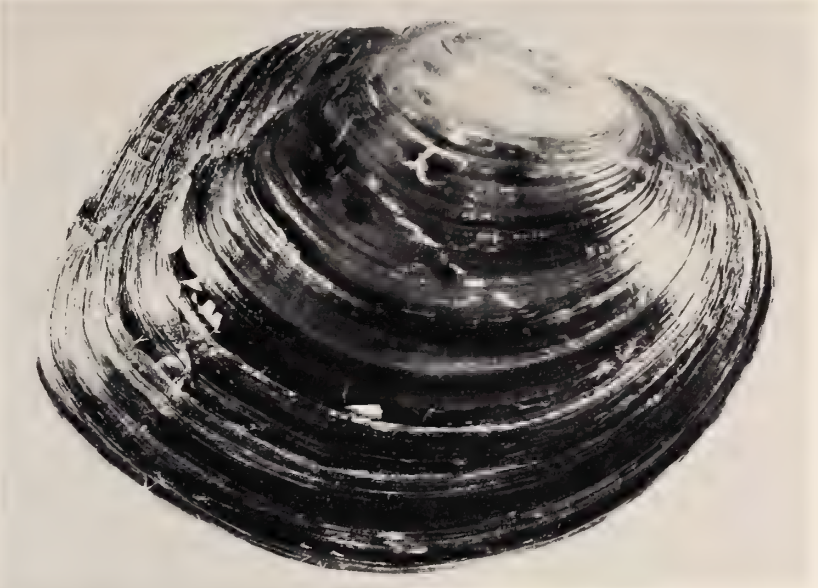

Figure *1*

Figure *9*

Figure *10*

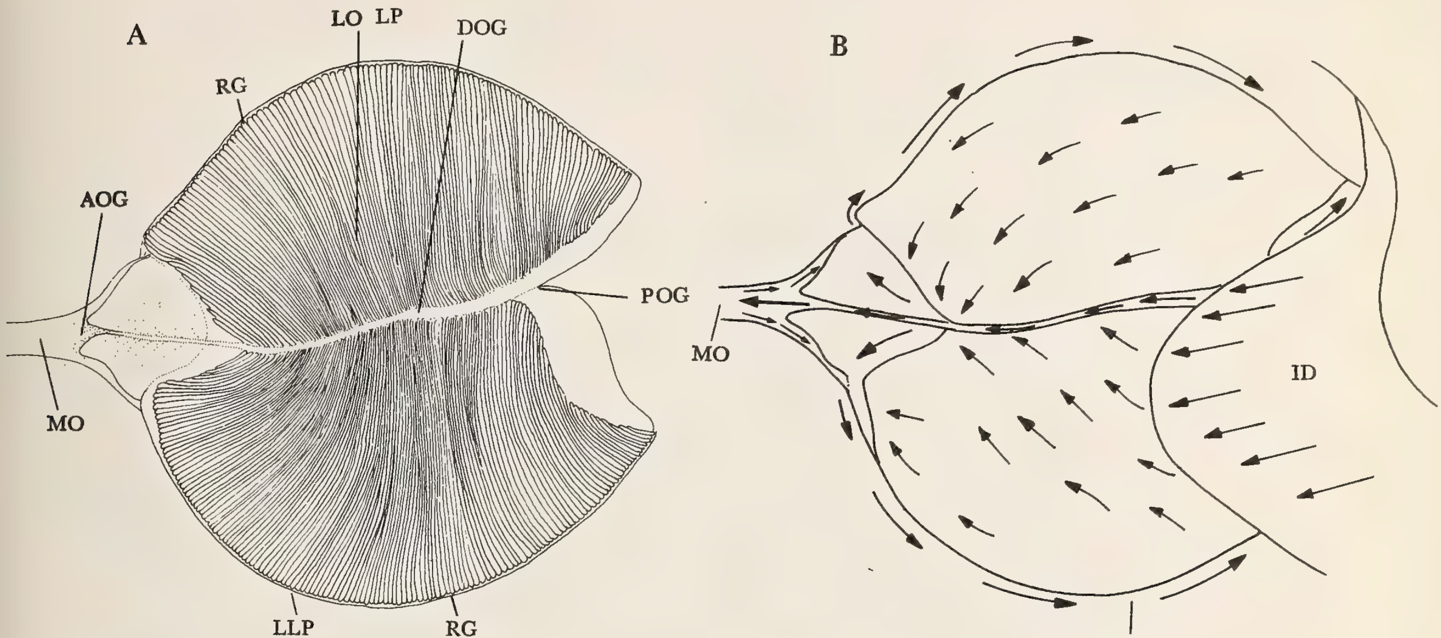

Figure 5

A: Labial palp; B: Arrows indicate particle movement.

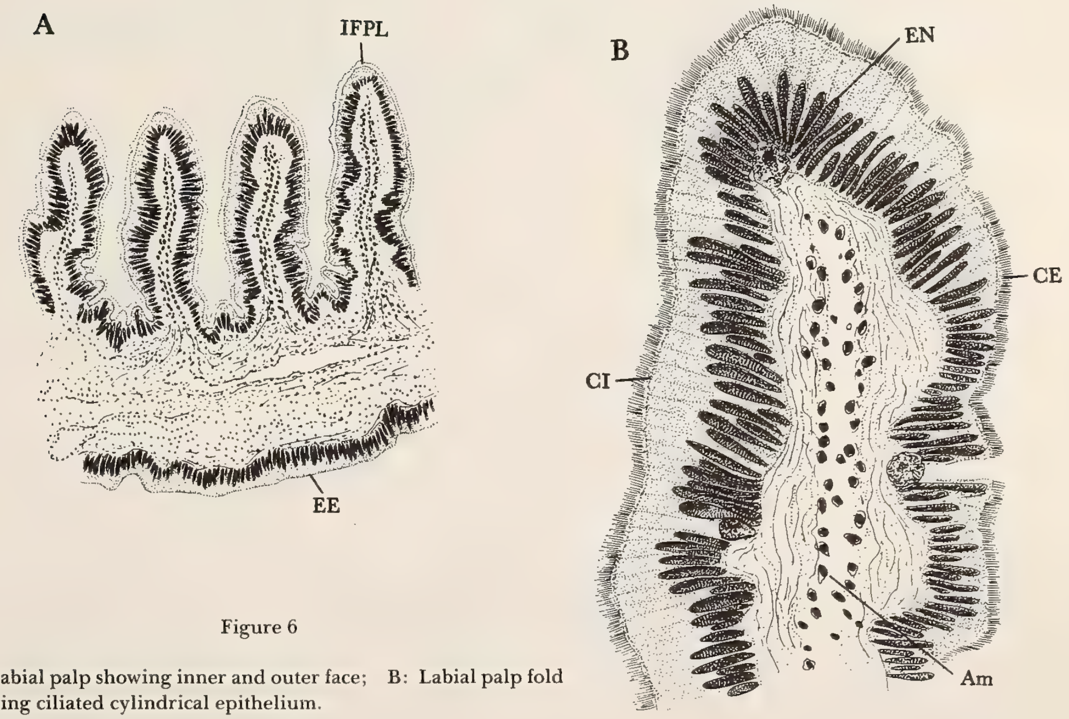

Figure 6

A: Labial palp showing inner and outer face; B: Labial palp fold showing ciliated cylindrical epithelium.

lateral portion of the sac bottoms. The stomach is of type IV. The areas of selection show ridges and grooves, semicircular folds, similar to the aortic valves of vertebrates. The area S_3 of the right lateral wall of the stomach and the area S_7 under the oesophagus orifice are directly visible after sectioning the stomach.

The crystalline style is located in the style-sac, ventrally to the floor of the stomach and rotates clockwise (Figure 8). It periodically contacts the sagitta when rotating. The crystalline style showed different lengths (30 to 70mm) depending on the stage of the digestion. It is absent at the beginning of the filtration period during the high tide.

The digestive diverticulum surrounds the stomach ventrally and laterally. It is easily differentiated by its reddish colour. Its weight varies between 2.50 to 2.55g in this species.

The intestine: The intestine begins by a descendant part followed by a sigmoidal section. The sigmoidal intestine forms a series of curves located in the posterior portion of the animal, between the gonadal organs and the posterior portion of the foot. It is followed by an ascendant section that changes to horizontal and crosses the heart (Figure 7) surrounded by the ventricle. The solidification of the faeces occurs probably in this part as it was described by Narain & Singh (1974) for other species of bivalves.

The anus is located a little above the site of the posterior adductor muscle.

The Rodophax technique (Niveiro, 1978) as is shown in Figures *9-10* clearly determines the position of *Diplodon delodontus* in the sub-class of Polysyringia since it proves that several ducts at left and right sides of the stomach reach the digestive diverticulum.

CONCLUSIONS

1. *Diplodon delodontus* is a neotropical mollusc that prefers freshwater rivers 1.5 to 6m deep and of 12 to 24°C, rich in fine substrate and vegetal detritus in uncontaminated areas. The preferential diet is phytoplankton and vegetal detritus.
2. The first food selection occurs in the siphon by means of tentacles of different length. Normally, it filters for periods of 4 to 6 hrs during the high tide.
3. The ciliary currents of the ctenidia are so designed as to allow only the smallest particles access to the selective sorting mechanisms of the labial palps. The oral groove determines the amount and quality of the particles to enter the mouth.
4. The third food selection occurs in the stomach by means of microcilia. By the Rodophax technique, it was proved that the *Diplodon delodontus* is a Polysyringia and the stomach corresponds to the Type IV of Purchon.
5. It is worth to add that some cyanophyta cross the selection barriers, but they were found afterwards undigested in the faeces.
6. They are easily adapted to artificial habitats as is shown by their capacity to reproduce and produce living glochidia in aquaria.

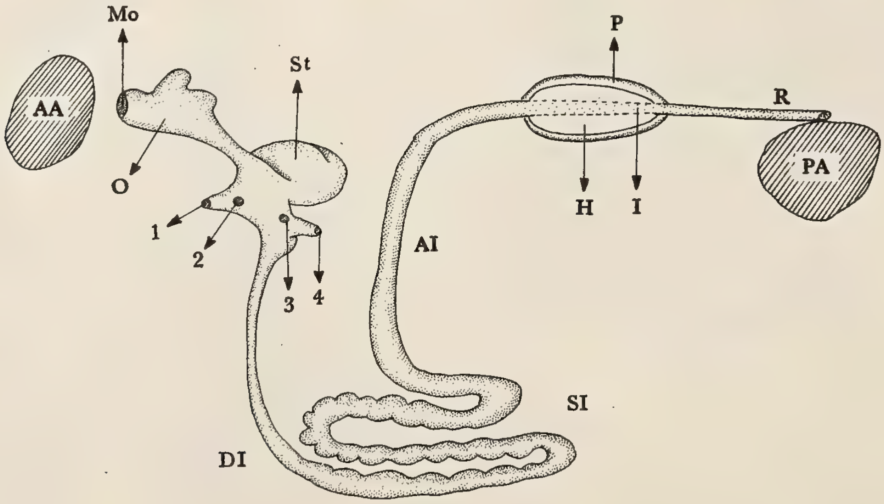

Figure 7

Digestive system scheme.

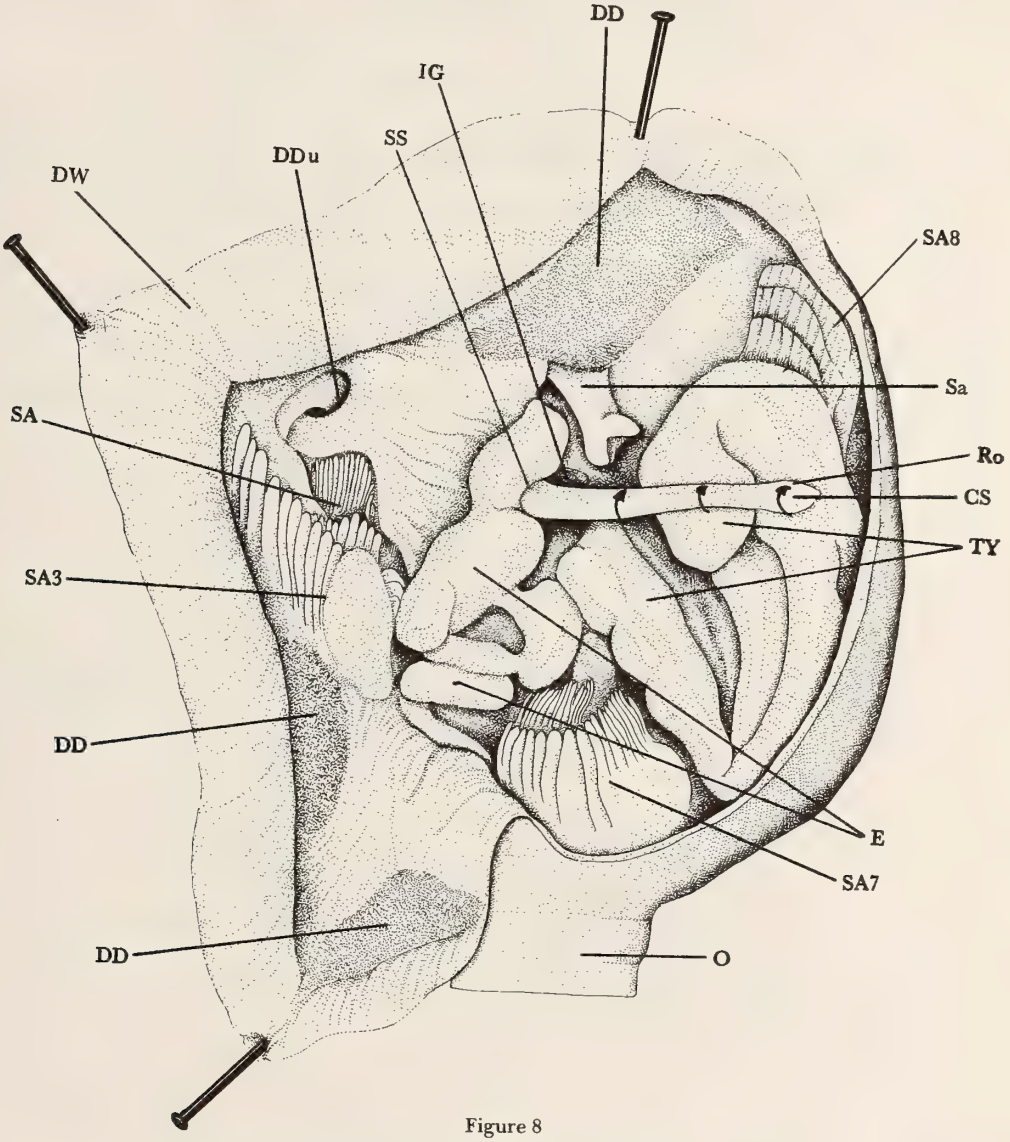

Figure 8

Dorsal inner portion of stomach. Dorsal wall turned to left. Clockwise rotation of crystalline style.

7. The species is dioecious and the period of reproduction corresponds to September-October. During this period, the inoculation of particles under the mantle evokes an abortive spawning of mature eggs between 12 to 24 hrs after the stimulus.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the scientific assistance of Dr. César Gómez Dumm and the advice of Dr. Zulma Ageitos de Castellanos and Dr. R. Ronderos.

Mrs. María C. Estivariz's drawings, skillfully done, are acknowledged.

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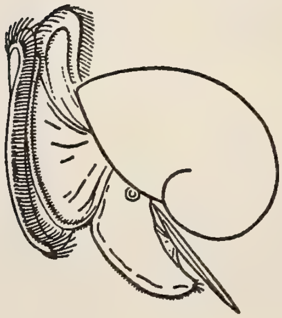

A Study of the Biology of *Diplodon delodontus* (Lamarck, 1819)

(Bivalvia : Hyriidae)

II—Structure of the Digestive Diverticula of *Diplodon delodontus*. A Light and Electron Microscopic Study

BY

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(4 Plates)

INTRODUCTION

In the first part of this series (Huca, submitted) the internal morphology of the digestive tract of *Diplodon delodontus* was presented. In the present work, the structure of the digestive diverticula was studied by light and electron microscopy.

MATERIALS AND METHODS

Adult specimens of *Diplodon delodontus* from 8 to 12 cm in length were obtained in La Plata River, Berisso, Buenos Aires Province, Argentina, from April 1980 to May 1981.

Specimens were maintained in large tanks with aerated tap water. While still alive, the animals were opened and small pieces from the digestive diverticula were obtained. For light microscopic studies, the material was fixed in Bouin's solution and embedded in paraffin. Sections were stained with hematoxylin-eosin. For electron microscopy, the specimens were fixed for 3 hrs in a phosphate buffered p-formaldehyde-glutaraldehyde solution (Karnovsky, 1965) at room temperature, post-fixed in 1% phosphate buffered osmium tetroxide and embedded in araldite. Sections 1 μm thick were stained with toluidine blue and observed through the light microscope in order to detect areas for a later ultrastructural study. Blocks were cut in a LKB Ultratome III-microtome. Ultrathin sections were stained with uranium-lead and observed in a Siemens Elmiskop I electron microscope operated at 60 KV.

RESULTS

Light microscopy:

The digestive diverticula of *Diplodon delodontus* has the general aspect of a compound branched tubular gland. It is formed by numerous blind-ending tubules connected with an arborescent system of primary and secondary ducts which opens in the stomach through four short main ducts.

The tubules appeared either round or oval in cross sections and were composed of a non-ciliated pseudostratified epithelium (Figure *1*). In some tubules, the outline of the lumen was undulated owing to variation in the height of the lining cells.

At least two main types of cells were observed in the epithelium of the tubules. The more numerous type consisted of columnar or tall prismatic cells with clear, lightly acidophilic cytoplasm and round oval nuclei. Abundant vacuoles of different sizes as well as gross inclusions were frequently found in the cytoplasm (Figures *3*, *4*). The free surface of the columnar cells was well defined and seemed to possess a striated border. However, in some tubules the apical border appeared irregular and diffuse. In these zones,

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columnar cells showed masses of cytoplasm apparently projecting and releasing into the lumen (Figure *2*).

The other type of epithelial cells consisted of basal pyramidal shaped elements which also maintained a connection with the underlying tissue (Figures *3, 4*). The free poles of these cells looked narrow and they were not easy to detect in the lumen of the tubules. The basal cells were intercalated between the columnar cells and presented intense cytoplasmic basophilia. A number of cells showed a strongly basophilic cytoplasm, but contained vacuoles characteristic of the columnar cells. These elements could be considered as intermediate cells.

The primary ducts of the digestive diverticula (Figure *5*) presented a wide lumen and were composed of simple ciliated columnar epithelium. The nuclei were oval and basally located. Some clear vacuoles could be found in the apical pole of these cells.

The secondary ducts (Figure *6*) showed a simple columnar epithelium with a well-defined striated border in the free surface.

The tubules and the ducts were surrounded by abundant loose connective tissue (Figures *1* to *6*) and smooth muscle cells. Numerous blood lacunae with discontinuous endothelium and free blood cells were seen in the intertubular space. A number of free cells, which can be considered as amoebocytes, were found inside the blood lacunae, in the connective strands and also between the epithelial cells of the tubules.

Electron microscopy:

The electron microscopic studies of the digestive diverticula corroborated the histological structure observed with the light microscope and added interesting ultrastructural features.

The tall prismatic cells of the tubular epithelium (Figures *9, 11*) showed a clear cytoplasmic matrix containing moderately developed organelles. Mitochondria were dense and granular endoplasmic reticulum appeared as scattered long cisternae, which sometimes were arranged in groups. The most striking feature of these cells was the presence of numerous large vacuoles which occupied an extensive part of the cytoplasm in the apical half of the cell. The vacuoles were of variable size and shape and contained a heterogeneous material. They were frequently seen fused with each other. Some of these vacuoles enclosed either fine granular material of moderate electron density or lipid-like content. In others, the material was predominantly membranous and consisted of small vesicles, filaments and concentric parallel lamellae. The outer membranes of the vacuoles were frequently discontinuous or absent. In this case, the heterogeneous content came into contact with the cytoplasmic matrix. In some prismatic cells, round or oval membrane-bounded bodies could also be found. They contained a dense matrix and some dark bands with a crystalloid aspect (Figure *12*).

Explanation of Figures *1* to *6*

Figure *1:* Digestive tubules and interstitial space. Hematoxylin-eosin. × 250

Figure *2:* Digestive tubules. The arrow indicates shedding of cytoplasmic masses. Hematoxylin-eosin. × 300

Figure *3:* Digestive tubules showing columnar cells (C) containing numerous vacuoles, and basal cells (B) with basophilic cytoplasm. Fixed in Karnovsky's solution and stained with toluidine blue. × 950

Figure *4:* Digestive tubules. Basophilic cells (B) and columnar cells with dark inclusions (C) are indicated. Numerous vacuoles (V) accumulated in the lumen. Fixed in Karnovsky's solution and stained with toluidine blue. × 950

Figure *5:* Secondary duct. Hematoxylin-eosin. × 320

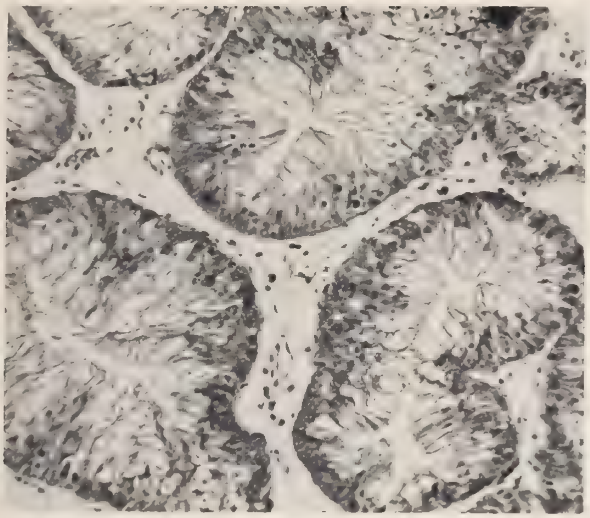
Figure *6:* Primary duct containing abundant material in the lumen. Hematoxylin-eosin. × 250

Explanation of Figures *7* to *9*

Figure *7:* Basophilic pyramidal cell showing a great development of its organelles. A clear columnar cell is shown in the upper-right corner. × 9000

Figure *8:* Secretory-like granules in basophilic cells. A lipid droplet (L) and mitochondria (M) are indicated. × 15000

Figure *9:* Columnar cells showing the nucleus (N) and granular endoplasmic reticulum profiles (ER). The heterogeneous content of the vacuoles occupies most of the cytoplasm. × 12000



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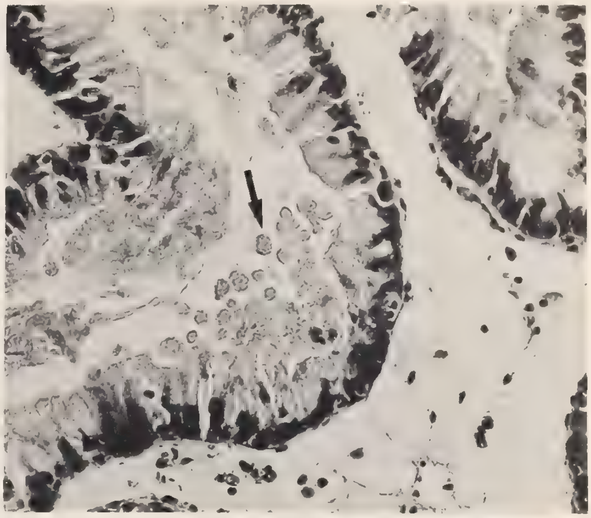

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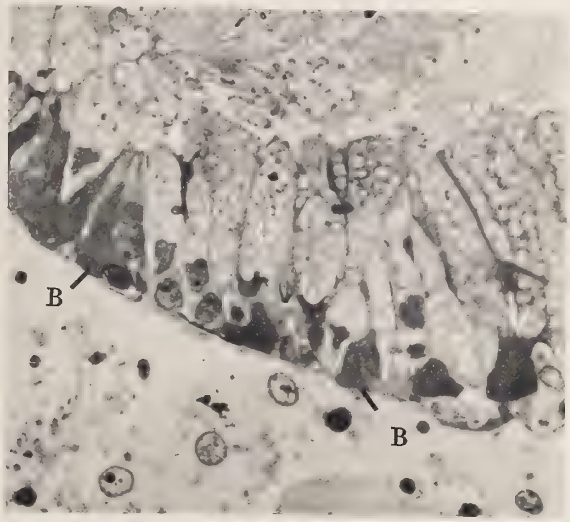

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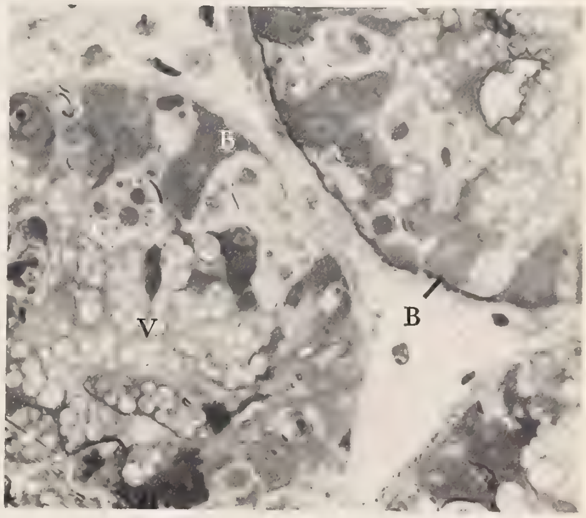

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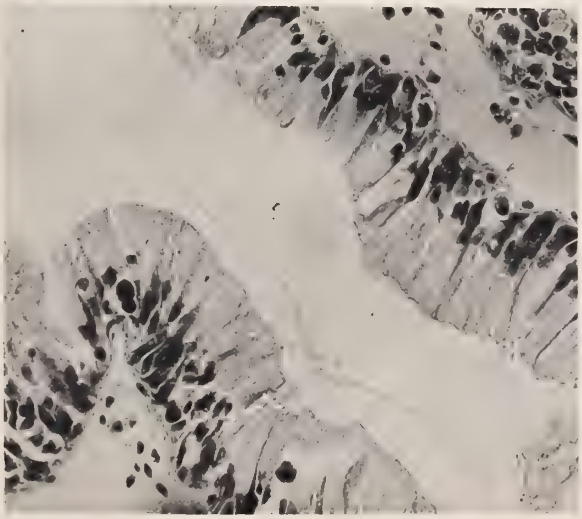

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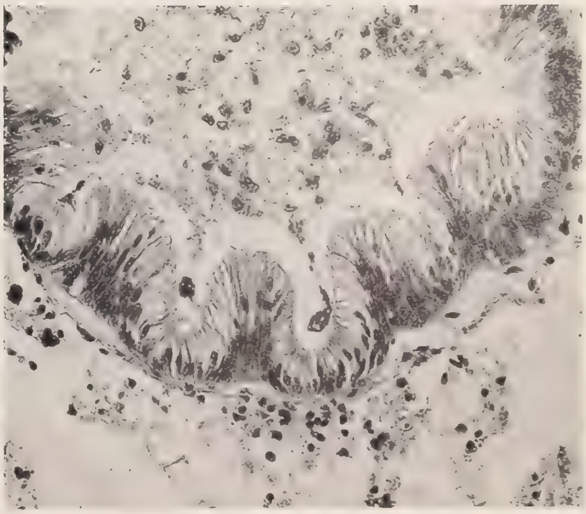

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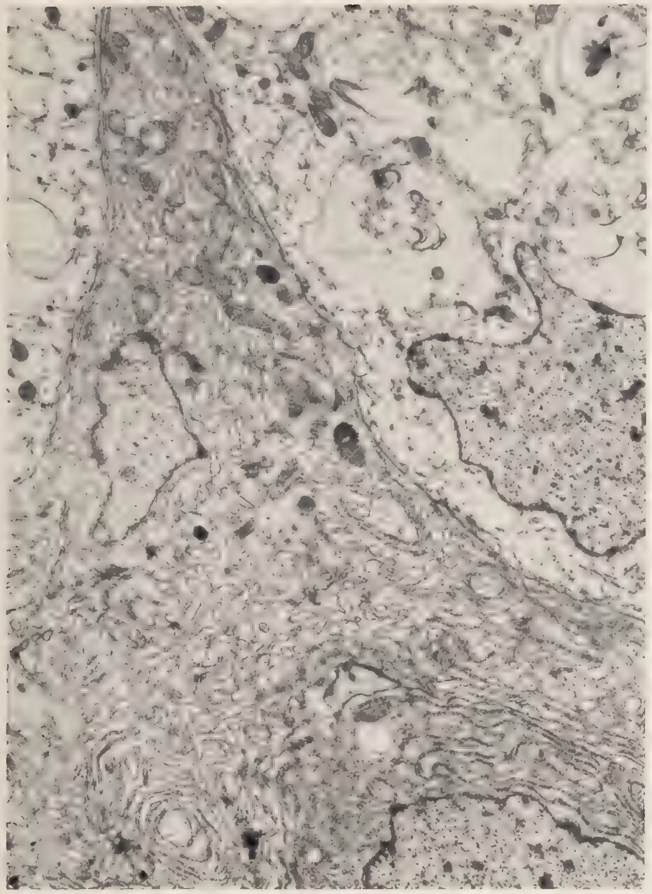

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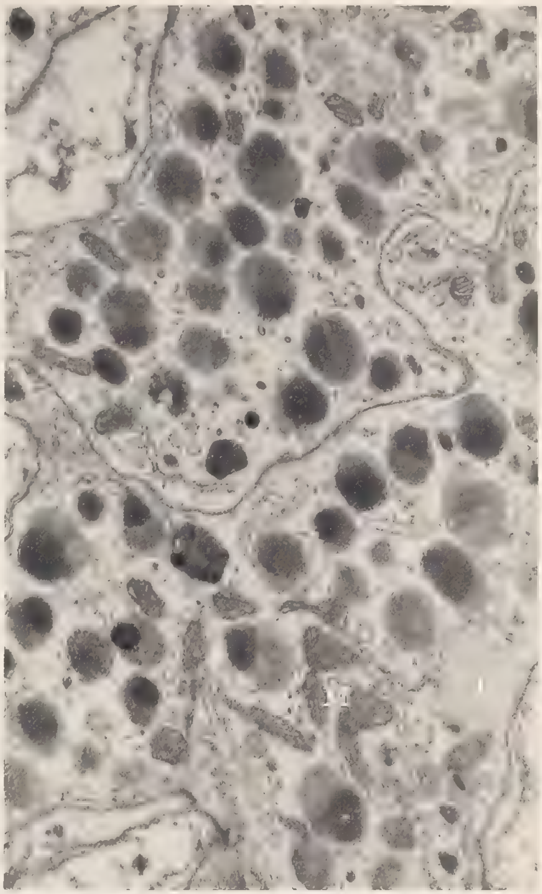

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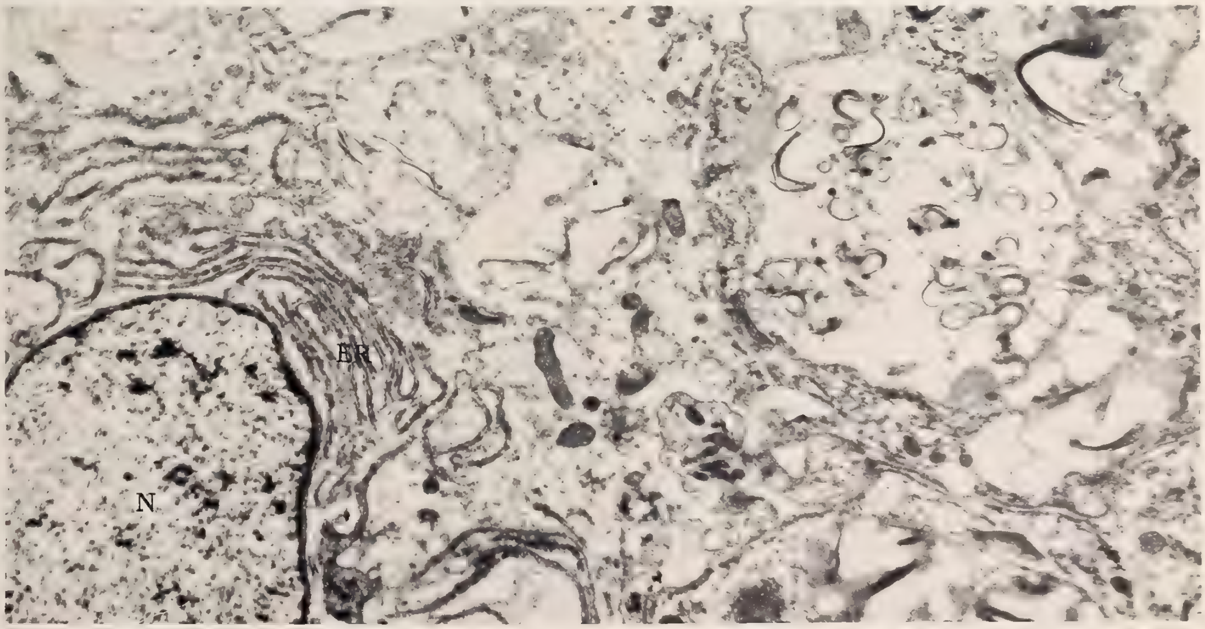

9

The apical surface of the columnar cells exhibited numerous long microvilli. In some digestive tubules, rounded or irregular cytoplasmic masses appeared to pinch off the distal pole of the cells (Figure *11*). These fragments contained either vacuoles similar to the ones described above, or their content was dispersed over the cell matrix.

When observed through the electron microscope, the basal basophilic cells showed well-developed cytoplasmic organelles (Figures *7,10*). The granular endoplasmic reticulum was specially conspicuous and occupied an extensive area. It displayed two different aspects: numerous sparse vesicles, and groups of flat parallel cisternae, sometimes adopting the picture of "Nebenkerne." The Golgi complex was well developed and included a large number of microvesicles. Dense granular material was visible in the Golgi zone or near it. Furthermore, in some basal cells, abundant round membrane-bounded granules with secretory appearance could also be observed in the cytoplasm. They showed a dense content with a darker core and coexisted with lipid-like droplets (Figure *8*). Columnar and basal cells possessed tight junctions near the apical poles.

Intermediate epithelial cells could not be easily identified. However, some columnar cells presented more developed cytoplasmic organelles, especially the granular endoplasmic reticulum.

The electron microscopy of the epithelial ducts revealed tall slender cells with basal nuclei and the regular number of usual organelles (Figures *13, 14*). Desmosomes and zonula occludens were seen near the apical poles. In the free surface, the plasma membrane showed numerous microvilli regularly arranged. Occasional cilia could be observed in the secondary ducts, but they were quite abundant in the epithelial cells of primary ducts (Figure *14*).

DISCUSSION

The light and electron microscopy of the digestive diverticula of *Diplodon delodontus* is described for the first time in the present study. Although the general features are coincident with those previously reported in other lamellibranchiate bivalves (Yonge, 1926; Mansour & Zari, 1946; Morton, J. E., 1956; Morton, B., 1969; McQuiston, 1969; Owen, 1970; Pal, 1971/1972; Mathers, 1972; Palmer, 1979), special differences can be emphasized.

The histophysiology of the digestive tubules and ducts has been a matter of numerous publications. However, after over 50 years of study, the function of the epithelial cells from the digestive diverticula in bivalves remains controversial (Palmer, 1979).

As in other bivalves, the epithelium of the digestive tubules in *Diplodon delodontus* is composed of two basic cell types: 1) columnar clear cells or digestive cells with many cytoplasmic vacuoles containing heterogeneous material; 2) pyramidal basal cells, or basophilic cells. In our species, this second type does not occupy epithelial crypts as it does in most of the bivalves, but they are intercalated between the columnar cells.

The digestive cells have similar characteristics as those of some absorptive elements of other invertebrate species. Their ultrastructure has been studied in several reports (Sumner, 1966; McQuiston, 1969; Owen, 1970; Pal, 1972). It is thought that, despite many structural similarities, there exist differences in the electron microscopy of the digestive cells, depending on the ecological niches from which the bivalves were obtained (Pal, 1972). Thus, our own description may contribute to the subject in new aspects.

The vacuoles with heterogeneous material have been named digestive spheres and they were considered to represent different types of lysosomes (Reid, 1966; McQuiston, 1969; Pal, 1972; Palmer, 1979). In *Diplodon delodontus,* digestive spheres are particularly abundant and resemble those described in *Lasaea rubra* by McQuiston (1969). In our case, the outer membrane frequently disappears and the content could be observed free in the cytoplasmic matrix.

It is known that in some species such as *Lasaea rubra* (Morton, 1956; McQuiston, 1969), *Ostrea edulis* (Mathers, 1972) and *Arctica islandica* (Palmer, 1979) the digestive cells eliminate the distal portion of the cytoplasm, or else the entire cell may be shed. This could be the way of releasing the residual products and enzymes like esterases, endopeptidases and acid phosphatases, which would play a role in the extra-cellular digestion in the stomach (Palmer, 1979). In *Mya arenaria,* instead, the mechanism of elimination of post-digestive materials is not clear and the synthesis of hydrolysis products within the intravacuolar digestive pathway has been proposed (Pal, 1972). In *Diplodon delodontus,* the shedding mechanism was quite evident and it was demonstrated by both the light and the electron microscope.

With regard to the cytoplasmic bodies containing electron dense crystalloid structures, it can be suggested that they are peroxisomes (De Duve & Baudhuin, 1966). These organelles are known to participate in extramitochondrial oxidative processes and to be connected with glyconeogenesis. Bodies resembling peroxisomes have been previously described by Pal (1972) in digestive cells of *Mya arenaria.* However, these organelles seem to be much more developed in *Diplodon delodontus.*

The ultrastructure of the basophilic cells has also been shown in several species of bivalves (McQuiston, 1969; Owen, 1970; Pal, 1971). The development of an extensive granular endoplasmic reticulum and a conspicuous Golgi complex, as well as the presence of secretory-like granules have been considered consistent with protein secretory activity (McQuiston, 1969; Owen, 1970; Palmer, 1979). However, histochemical studies have not provided enough information about the nature of the apical granulation of these cells (Palmer, 1979). It is also thought that immature basophilic cells serve to replace both digestive and mature secretory cells (McQuiston, 1969; Owen, 1970). Furthermore, in digestive diverticula of *Arctica islandica,* Palmer (1979) found mitosis only in "basophilic A" cells, which would represent the first step of a series of phases in the life of one basic cell type.

According to our material, the granular endoplasmic reticulum of basophilic cells has an extraordinary development and its appearance is consistent with an active function in the elaboration of proteins to be "exported" out of the cell. This fact, together with an extensive Golgi complex and the existence of numerous secretory-like granules support the view that in *Diplodon delodontus* basophilic cells play an important role in production and release of proteinic material. Pal (1971) assumed that most of the apical granules of *Mya arenaria* basophilic cells are not released but autodigested by means of the lysosomal system. In our case, only scarce lysosomes were found in this type of cell. On the other hand, regarding the lack of exocytosis, it is possible that a releasing mechanism other than granular extrusion might exist for basophilic cells of digestive diverticula in bivalves.

Histochemical studies carried out in *Ostrea edulis* and *Crassostrea angulata* (Mathers, 1972) indicated that the ducts of digestive diverticula produce digestive enzymes. Moreover, Palmer (1979) found exopeptidase-inactivity in epithelial cells of primary and secondary ducts of digestive diverticula in *Arctica islandica.* This author suggested that some of those enzymes are either utilized as extracellular hydrolytic ones or involved in secretion of other hydrolytic enzymes at the plasma membrane level.

The fine characteristics of the duct epithelium in *Diplodon delodontus* did not reveal an important function connected with the elaboration of secretory products. As judged by the ultrastructure of the apical pole, duct cells would reflect the well-known role in the absorptive process rather than a secretory function (Mathers, 1972). In *Arctica islandica,* the absorptive role is supported by the presence of an intense alkaline phosphatase in the distal border of primary and secondary ducts (Palmer, 1979).

ACKNOWLEDGMENTS

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Explanation of Figures *10* to *12*

Figure *10:* Basophilic cell containing largely developed endoplasmic reticulum consisting of concentric flat cisternae or "nebenkern" (ER) and dispersed rough vesicles. The Golgi zone (G) includes dense bodies and numerous microvesicles. × 15000

Figure *11:* Apical pole of a columnar cell. Cytoplasmic masses are being released. Vacuoles of variable content are shown in both the cell and the shedding portions. Microvilli (arrows) are also observed. × 4000

Figure *12:* Dense bodies containing crystalloids appear in a columnar cell. Mitochondria (M) and endoplasmic reticulum (ER) are indicated. × 30000

Explanation of Figures *13* and *14*

Figure *13:* Epithelial cells of a secondary duct. × 6000

Figure *14:* Apical pole of a primary duct cell. Brush border and cilia are present in the free surface. Mitochondria (M) and junctional complexes (asterisk) are also shown. × 20000

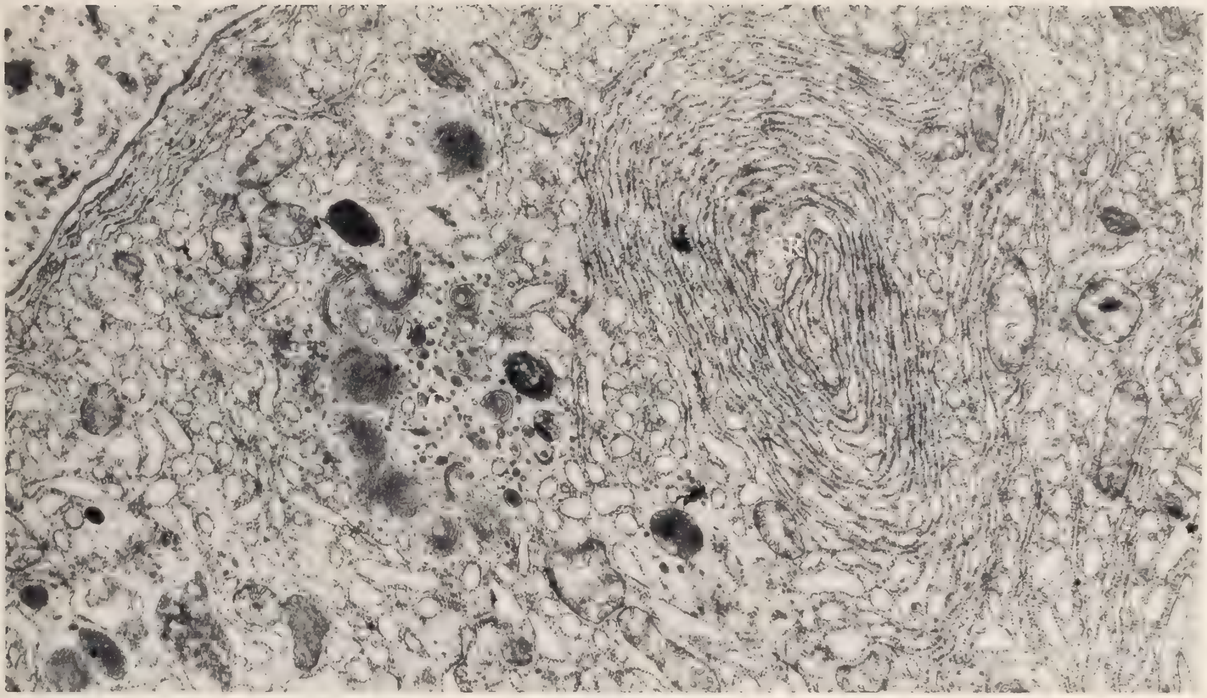

Figure *10*

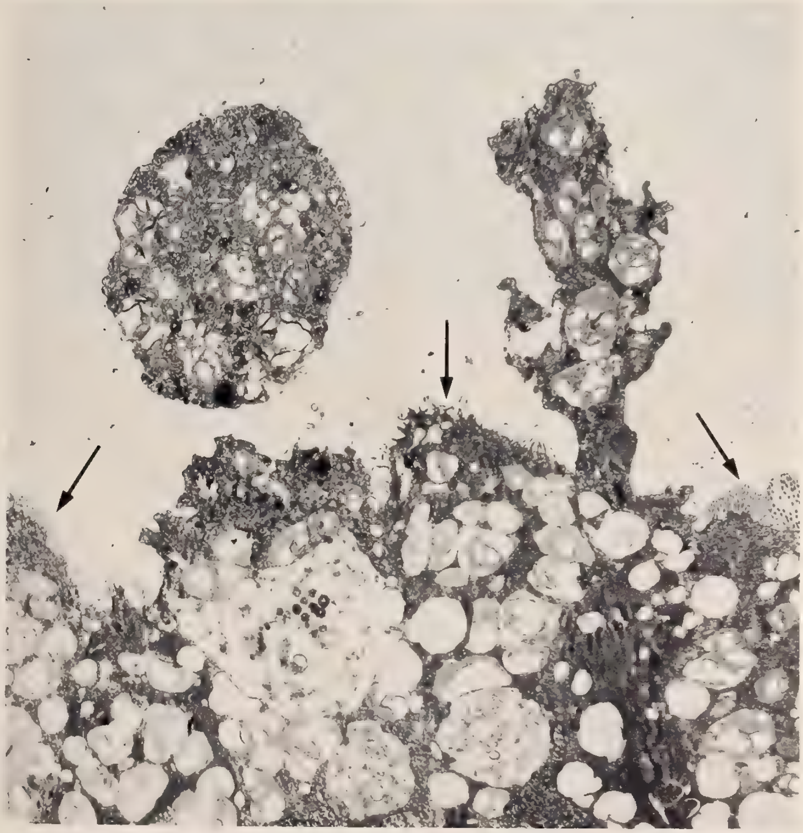

Figure *11*

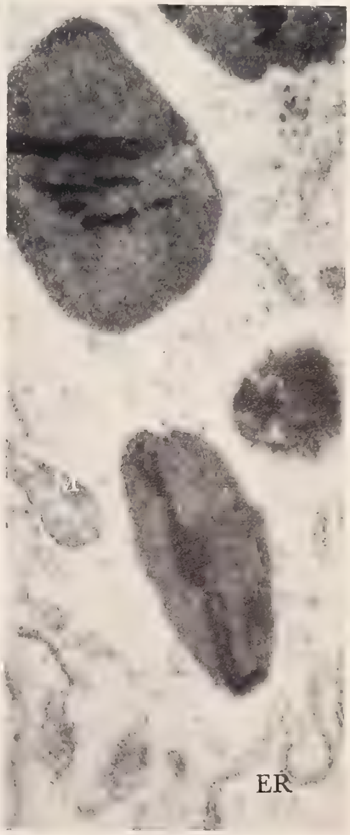

Figure *12*

Figure *13*

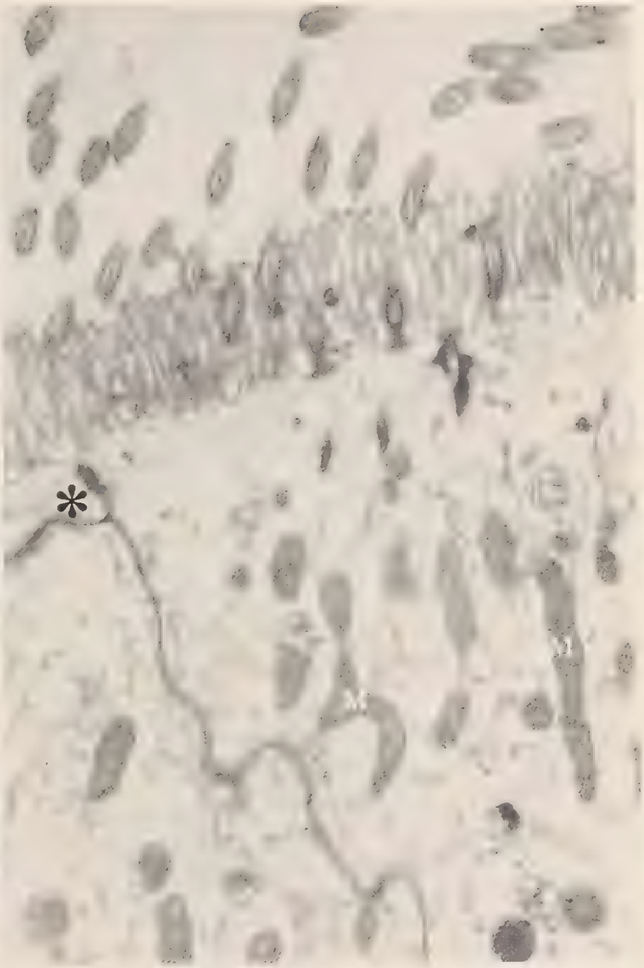

Figure *14*

Light and Electron Microscopy of a Muscle from *Diplodon variabilis* Maton

BY

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(2 Plates)

INTRODUCTION

The ultrastructure of mollusc muscle has been described by Cohen *et al.* (1971), McKenna *et al.* (1973), Richardot *et al.* (1971), Szent-Gyorgyi *et al.* (1971), Wilson (1969), Zs-Nagy *et al.* (1971), Plesh (1977). Although there exist many papers that study muscle ultrastructure in other invertebrates [Dewey *et al.* (1973), Jensen *et al.* (1975), Kryvi (1971, 1973), Rosenbluth (1968) and Smith *et al.* (1973)] to our knowledge, no investigations have been made on *Diplodon variabilis,* which is an autochthonic species of Argentina.

This paper presents new findings of the structure of the muscle of two organs of the bivalve *Diplodon variabilis* at the light and electron microscopic levels. For our study we chose the musculature of the foot and the muscle tissue of the mantle, both showing the same features.

MATERIAL AND METHODS

Young and adult *Diplodon variabilis* clams were collected from the rivulet Miguelin-Punta Lara, Buenos Aires and were immediately dissected, after making a gonadal puncture in order to determine the sex. For light microscopic study, pieces of the foot and mantle were separated from the living animal and fixed in Bouin's and Carnoy's fluids. The material was dehydrated in ethanol, embedded in paraffin and sections (6μm) were stained with hematoxylin-eosin and iron-hematoxylin. For electron microscopic study, small pieces of the foot and mantle were fixed in Millonig's fluid for 120 minutes at 0°C. Specimens were dehydrated in ethanol and embedded in araldite. Ultrathin sections were stained with uranyl-acetate and lead citrate and examined with an Elmiskop I electron microscope operated at 60 KV.

RESULTS

No structural or ultrastructural differences were observed between the foot and mantle muscular tissue. The muscular fibres are disposed in bundles. They are present in both faces of the mantle, valvar and pallial (Figure *1*) and the bundles penetrate into the "roundlet" [the distal part of the ventral border of the mantle]. In the foot, the sections of the muscle are always organized in bundles (Figure *2*, *4*).

The muscular cells have large multiple peripheric nuclei (Figure *3*). With the iron-hematoxylin technique, as well as with the phase contrast microscopy, we have observed longitudinal striation (Figure *4*).

At the ultrastructural level, the muscle cells are seen as somewhat irregular in shape and show flattened peripheral nuclei which contain dense masses of chromatin condensed along the nuclear membrane. (Figure *5*). A thin basement membrane surrounds each muscle cell.

Most of the cytoplasm is occupied by myofilaments, which are arranged parallel to the axis of the cell (Figure *6*). The myofilaments are variable in diameter—thick and thin ones can be seen without any constant relationship occurring between them (Figure *7*). It should be remarked that it is possible to observe myofilaments of intermediate thickness. All the myofilaments show an oblique striation,

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[1] Part of this work was submitted in partial fulfillment of the requirements for the degree of Doctor of Natural Sciences at the Instituto de Biología, Histología and Embriología, Facultad de Ciencias Médicas, Universidad Nacional de La Plata, Buenos Aires, Argentina.

due to the presence of alternating light and dark bands (Figure *8*). The clear bands are approximately twice as wide as the dark ones. Electron opaque material seems to radiate from the border of the dark bands into the cytoplasmic matrix (Figure *9*). Myofilaments are embedded in a somewhat lighter matrix, containing variable amounts of alpha and beta glycogen granules (Figure *7*).

The periphery of the fiber presents vesicles of granular endoplasmic reticulum and numerous free ribosomes. Round mitochondria are located close to the cell membrane. The mitochondrial matrix is dense and the cristae, often dilated, are irregularly arranged (Figure *5*). Collagen fibrils and unmyelinated axons are found between muscle cells (Figure *10*).

DISCUSSION

In the last several years the fine structure of the muscle of numerous invertebrates has been the focus of widespread interest. In this respect, there is a vast bibliography on the subject. Dewey (1968; 1973), Jensen *et al.* (1975), Kryvi (1971), Rosenbluth (1972).

The perfect symmetry of the mammalian muscle does not exist in molluscs, although in some species of molluscs there is some degree of symmetry.

Studying the mantle ultrastructure of the pelecypod *Spisula solidissima,* Wilson (1969) describes only thick filaments in the "non striated" muscle. The figures that the author shows much resemble those we have obtained in *Diplodon variabilis,* but he presents low magnification photographs which do not reveal transversal striation.

McKenna & Rosenbluth (1973) have studied the electron microscopy of the retractor muscle of the "byssus" of two bivalve molluscs: *Mytilus edulis* and *Brachidontes comissus.* Although this work is mainly concerned with the myoneural and intermuscular joints, the pictures very clearly revealed the existence of a transversal striation in the myofilaments. Cohen *et al.* (1971), taking into account the 145 Å periodicity described in the "non striated" mollusc muscle, which is repeated at 925 Å, had fractionated the paramyosin. They found that aggregates of this substance have a 725 Å periodicity and concluded that paramyosin would form an axis covered with myosin.

Jensen & Myklebust (1975) have reported differences between the muscle of "body and vessels" from a pogonophore, *Siboglinum fiordicum.* Both muscle types have thick and thin filaments of variable diameter, but only the thick filaments of the body myocells show a clear periodicity. The authors assumed that in the muscle of the blood vessels, among the thick filaments, those which are smaller in diameter and without striation, would be similar to

Explanation of Figures *1* to *5*

Figure *1:* Light micrograph of mantle muscle fibers. Hematoxylin-eosyn × 250

v—valvar face, p—pallial face, r—roundlet

Figure *2:* Light micrograph of the foot: basal region. Hematoxylin-eosyn × 630

b—muscle bundles

Figure *3:* Light micrograph of foot muscular cells. Iron-hematoxylin × 400

n—nucleus

Figure *4:* Light micrograph of foot muscle bundles. Iron-hematoxylin × 1000

l—longitudinal striation

Figure *5:* Longitudinal section through mantle muscle cell, showing: × 10000

n—peripheral nucleus, M—mitochondria
bm—basement membrane, myofilaments (arrows)

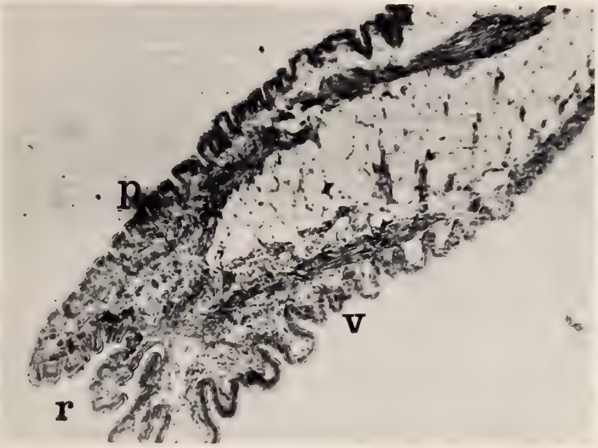

Figure *1*

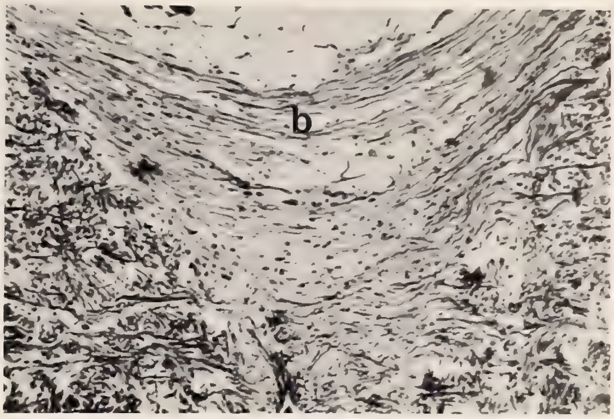

Figure *2*

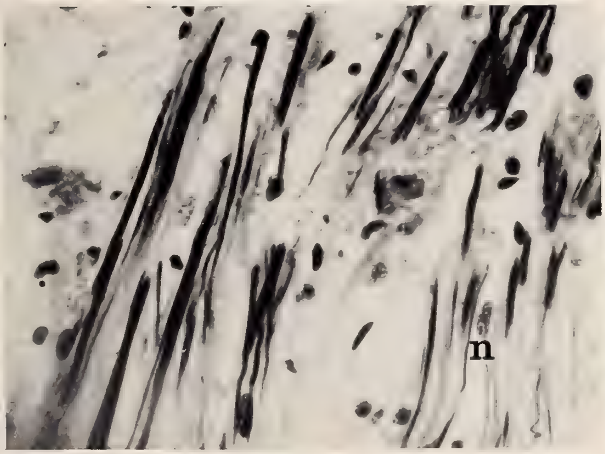

Figure *3*

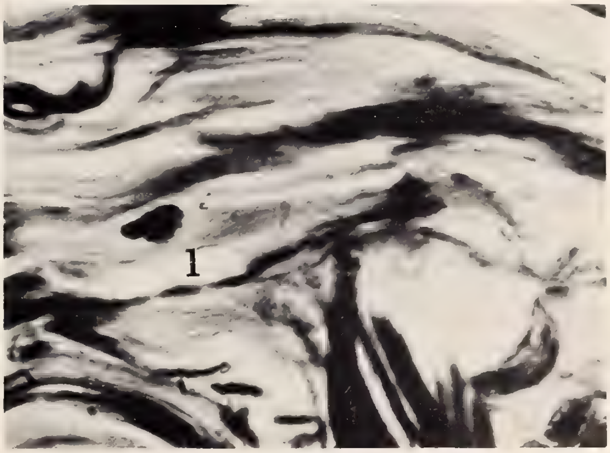

Figure *4*

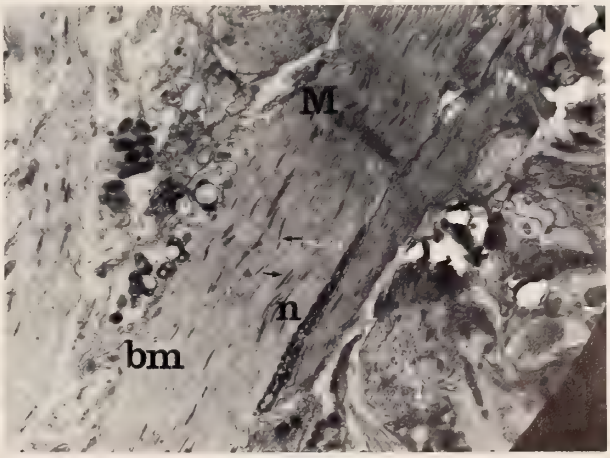

Figure *5*

those of the heart and blood vessels from molluscs and annelids.

In the buccal bulb muscle of the mollusc *Ferrisia wantieri* (Richardot *et al.,* 1971) fibers have been described which are intermediate between striated and smooth type. These fibers resemble those of the embryonic myocardium of vertebrates. The figures that the authors show are similar in several aspects to the ones obtained by us from *Diplodon variabilis.* However, in *Ferrisia wantieri* discontinuous Z bands connecting myofibrils are present.

Paramyosin, thick striated myofilaments have been found in epithelial cells from annelids, where muscle could be considered as striated (Smith *et al.,* 1973). Other authors have described an "obliquely striated" muscle in annelids (Kryvi, 1971; Rosenbluth, 1968) and crab (Dewey, 1973; Rhea *et al.,* 1973) which seems to be a complex muscular tissue with a particular oblique striation, showing light and dark disks, presence of Z bands, and a well developed sarcoplasmic reticulum. It is interesting to note that in annelids (Kryvi, 1971) with "obliquely striated" muscle, images are shown where the filaments present an irregular distribution, similar to the one we have observed in some muscular cells of *Diplodon variabilis.*

Whether the sliding theory is acceptable or not for mollusc muscle has been a matter of discussion. Zs-Nagy *et al.* (1971) thoroughly discussed this subject and termed "polymorphous" the muscle that they consider to be neither striated nor smooth. This author studied the adductor muscle of the mollusc *Anodonta cygnea,* which is similar in many aspects to the *Diplodon variabilis* muscle, and accepts the independent contraction theory for this kind of tissue.

It can be concluded that the muscle from the *Diplodon variabilis* foot and mantle represents a particular muscular tissue which is rather similar to the one described in the adductor muscle of the *Anodonta cygnea.* As in that case, the denominations "striated" or "smooth" would not be suitable. In accordance with Zs-Nagy, (1971) we propose to name this type of muscle "polymorphous" and suggest that it, too, may contract by the mechanism of independent contraction.

SUMMARY

The histomorphology of the muscle of the mantle and foot of the nacreous clam *Diplodon variabilis* was studied by means of light and electron microscopy. The musculature of these organs shows a special muscle tissue, which is intermediate between the smooth and the striated type. Ultrastructural observation reveals two kinds of myofilaments, thick and thin, which show an irregular distribution. Both types of filaments have an oblique striation and present a regular periodicity. The results of our observation led us to consider this muscle as a "polymorphous" type.

ACKNOWLEDGMENTS

The author is greatly indebted to Prof. Dr. C. L. Gómez Dumm for his stimulating interest and valuable comments during this study and preparation of the manuscript and to Dr. M. Restelli for advice in histological techniques. Thanks are also due to Prof. Dr. J. M. Echave-Llanos for providing facilities in the course of this work, to Mrs. M. Lagomarsino, F. Bustos and G. Neira for technical assistance and to Dr. Arthur Lampert for correction of the English.

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Explanation of Figures *6* to *10*

Figure *6:* Foot muscle cell showing numerous myofilaments (mf) × 15000

Figure *7:* Mantle cell muscle, showing thick myofilaments (T), thin myofilaments (t), and glycogen granules (G) × 45000

Figure *8:* Myofilaments showing an oblique striation × 80000

Figure *9:* Cross-section through thick (T) and thin (t) myofilaments × 80000

Figure *10:* Interstitial space between muscle cells (m) × 13000
c—collagen, a—unmyelinated axon

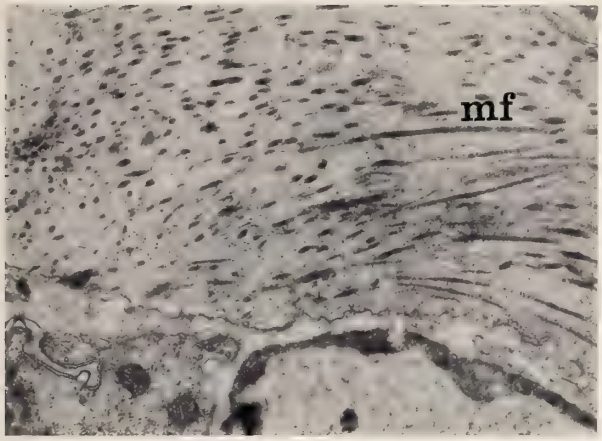

Figure *6*

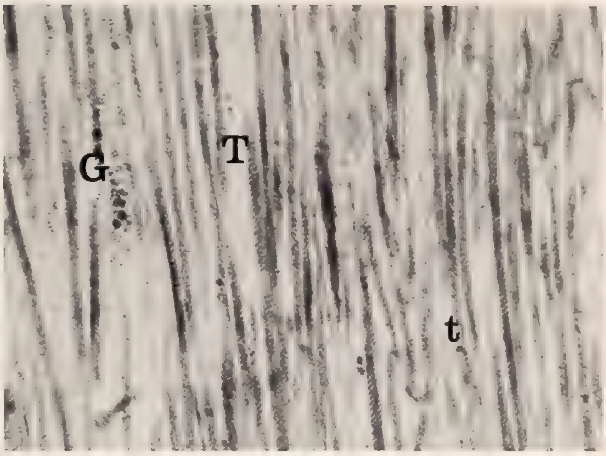

Figure *7*

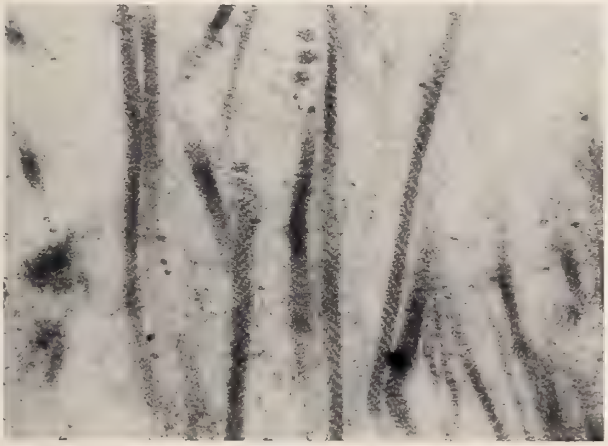

Figure *8*

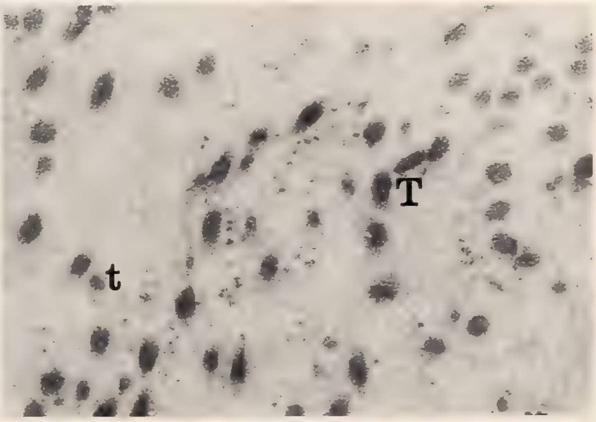

Figure *9*

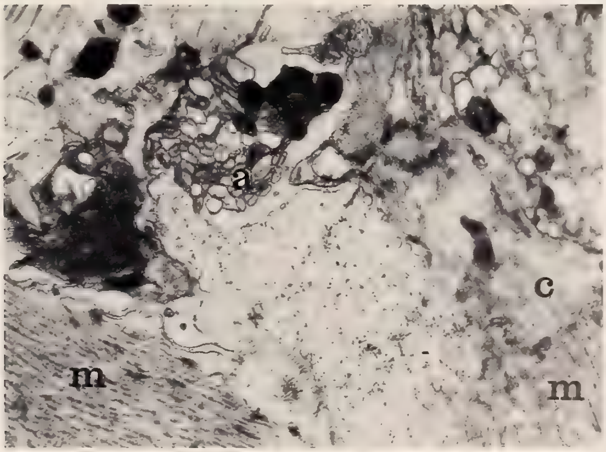

Figure *10*

Review of the Muricid Genus *Attiliosa*

(Mollusca : Gastropoda)

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(1 Plate; 1 Text figure)

THE GENUS *Attiliosa* is a small muricine group containing but a few species, each one of which has had a more than usually complicated nomenclatural history. In the eastern Pacific the only species, which was selected by EMERSON (1968: 380) as type of the genus, was originally described as *"Coralliophila" incompta* Berry. Subsequently, BULLOCK (1976: 133) showed it to be a junior synonym of *"Peristernia" nodulosa* named by A. ADAMS (1855: 313) as coming from Australia!

In the western Atlantic there are just two species referable to the genus. The first to be recognized as an *Attiliosa* was *A. aldridgei*, originally described as *"Vasum" aldridgei* by NOWELL-USTICKE (1969: 18) but soon changed to *Attiliosa* in a revised edition of his work (1971: 11). Because of lack of communication this same species was later described from Cuba as *"Muricopsis" poeyi* by SARASUA & ESPINOSA (1979: 2).

The history of the second western Atlantic form is extremely complex. Named as *"Muricidea" philippiana* by DALL (1889: 213), the type lot contained two specimens. One, subsequently designated as lectotype (VOKES, 1976: 122), is an *Attiliosa;* the other not only is not the same species, it is not even in the same subfamily. As RADWIN & D'ATTILIO (1978: 131) demonstrated, the second specimen is a member of the muricopsine genus *Acanthotrophon.*

In a monograph on *Attiliosa* in the western Atlantic (VOKES, 1976: 120) the latter was considered to be the same as the Pliocene *"Muricidea" striata* Gabb but additional material disproved this identity and the Recent form was subsequently named *Acanthotrophon striatoides* (VOKES, 1980: 13).

Thus, to date there are but three species, one eastern Pacific and two western Atlantic, recognized as being referable to *Attiliosa.* Between them they have been variously referred to *Peristernia, Coralliophila, Muricidea, Muricopsis* and *Vasum.*

This paper is occasioned by the recognition of yet another member of the genus. *"Murex" noduliferus* Sowerby, 1841, certainly has a history sufficiently convoluted to admit it to the ranks of this collection of confused taxa. Over the years this species has been named three times *(Murex noduliferus, Muricidea caledonica,* and *Murex fruticosus).* It has been placed in *Murex, Phyllonotus, Muricidea, Trophon, Typhis, Ocenebra, Drupa, Morula, Poirieria, Muricopsis,* and *Marchia.* The complete synonymy given below will document the odyssey of this misunderstood species.

The person to come closest to the present assignment was CERNOHORSKY (1967: 125), who cited it as *Poirieria.* At first glance the presence of several small denticles at the anterior end of the columellar lip would seem to negate this placement but the subgenera *Poirieria (Panamurex)* and *P. (Pazinotus)* do possess such denticles. However, the short body, high spire, and very ornamented spinose shell of *"M." noduliferus* seemed to Vokes to indicate placement in *Muricopsis* (VOKES, 1970b: 186).

A reappraisal of the generic assignment was called for when D'Attilio had the opportunity to examine the radula and it proved to be unquestionably muricine (see Figure 11) in contrast to the muricopsine type it was assumed to have. Armed with this new information we began a search for a proper place for the once again homeless species.

Good specimens of *"Murex" noduliferus* are extremely

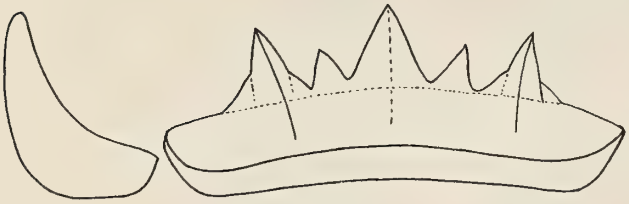


Figure 11

Radula of *Attiliosa nodulifera* (Sowerby). Tres Reyes Isle, Dawis Gasan, Marinduque, Philippine Islands. SDNHM 78081, slide: G. E. Radwin; drawing: Anthony D'Attilio; specimen from R. Lumawig

rare, most are encrusted with a coating of calcareous algae (Figures *3*, *4*). It was this fact that provided a clue to the present placement; in *Attiliosa* there seems to be a generic propensity toward this limy coating. The Atlantic species are more often than not completely camouflaged by lime (Figure *6*); only rarely (Figures *7*, *10*) can the nature of the external ornamentation be seen. The pictures provided by Emerson in his original discussion of the genus (1968: plt. 53, figs. 1-5) show that the eastern Pacific species is equally prone to this overgrowth.

Although *Attiliosa nodulifera* is more spinose than the other members of the group, comparison with an unworn example of *A. aldridgei* shows that the tendency to spines is there, especially in the young stages (Figure *9*), and the spines seen in *A. nodulifera* are simply an exaggeration of the small spinelets seen in *A. aldridgei.*

Although it has been suggested the species named *Muricidea caledonica* by Jousseaume is a synonym of *M. noduliferus,* the two forms do seem to be consistently different in one small detail. In *M. caledonica* there are four sharply pointed spines on the body-whorl portion of each varix. In *M. noduliferus* the two uppermost and two lowermost sets of spines tend to fuse into two massive knobs. But this is not always the case, as seen in Figure *2*. Ponder (1972: plt. 22, fig. 2) figured a good example of the *"caledonica"* form and, comparing it with *A. nodulifera,* he noted that "careful examination of typical *nodulifera* shows that the knobs are formed by the fusion of 2 rows of spines and in some specimens they remain separate, especially in the basal row." He also figured the radula of this specimen and noted that it differed from typical *Muricopsis* in having the rachidian tooth flat, as in *Murex,* rather than curved as in *Muricopsis.* His illustration shows a radula identical to that given here for *Attiliosa nodulifera* (Figure 11) but for us the connection was not made until working on this paper.

Recognition of *"Murex" noduliferus* as an Indo-Pacific member of the genus *Attiliosa* led to the re-examination of other species of Indo-Pacific *"Muricopsis"* and *M. orri,* only recently named by Cernohorsky, is yet another member of *Attiliosa.* Although there has been no radula figured for this species the shell morphology is very close to that of *A. nodulifera,* especially the form *"caledonica."*

Although it is obvious from the confusion of the two groups that *Muricopsis* and *Attiliosa* do have a similar shell morphology, being another of the many confusing examples of convergence in the Muricidae *(e.g., Pterynotus* and *Pteropurpura),* there is one usual difference between the two. The shell of *Muricopsis* has four or five equi-sized spiral cords on the body-whorl portion of the varices, which are also equi-spaced over the body. In *Attiliosa* (at least the spinose forms) there are four spiral cords, two upper and two lower ones, separated by a gap.

In addition to the spines there is also a difference in the nature of the columellar denticles. In *Muricopsis,* as Ponder pointed out (1972: 244), there are one or two, relatively weak, denticles on the columella. In the spinose members of *Attiliosa,* those that would be likely to be confused with *Muricopsis,* there are two to four, strong, denticles. However, in the non-spinose forms of *Attiliosa* the denticles are as evanescent as in *Muricopsis.*

In overall shell characters it appears that *Attiliosa nodulosa* and *A. philippiana* are one cognate species pair, sharing the nodose shell form with lirations on the inner side of the outer lip; *A. aldridgei* and the two (or three, if *caledonica* is indeed different) Indo-Pacific species are another set of cognates, with denticles rather than lirations on the inner side of the lip and a more ornamented shell externally. In addition, they also are the only members that have color on the shell, having orangey-brown tips to the spines (see Radwin & D'Attilio, 1976: plt. 28, fig. 5, for the color pattern in *A. aldridgei)* and a bright yellow aperture.

Recognition of *Attiliosa nodulifera* and *A. orri* as *Attiliosa* extends the geographic range of the group into the Indo-Pacific province. Presumably the line originated in the western Atlantic as a branch of the *Poirieria* clan. As noted above, two subgenera of *Poiriera*—*Panamurex* and *Pazinotus,* do have columellar denticles. The general shell morphology is compatible, especially with some of the species referred to *Panamurex,* such as *P. mauryae* Vokes and *P. velero* Vokes, the principal differences being the stronger spiral cords and longer siphonal canal in *Panamurex* (see Vokes, 1970a, for illustrations).

The geologic history of *Attiliosa* is very scant, with *A. aldridgei* first being recorded from the early Pliocene Gurabo Formation in the Dominican Republic. There are a number of species in the Dominican beds that seem to be most closely related to living Indo-Pacific forms and it is assumed that somehow the western Atlantic *A. aldridgei* is the ancestor of the Indo-Pacific *A. nodulifera* and *A. orri.* *Attiliosa philippiana* has no recorded fossil history in the western Atlantic but in the early Pliocene Esmeraldas Formation of Ecuador (TU 1399) we have a single specimen of *A. nodulosa,* so that both lineages have an ancestry at least that old.

However, the line may have European representatives that are not yet recognized. As Vokes noted (1970a: 6), in the Oligocene beds near Gaas, France, a species of *Panamurex,* originally described as *Fusus turbinelloides* Grateloup, is present. This form is morphologically very similar to *Panamurex lychnia* (Gardner) or *P. mauryae* Vokes from the lower Miocene Chipola Formation in Florida. In the middle Miocene (?Tortonian) of northern Italy, there is another species, which Bellardi (1872: 146; plt. 9, fig. 20) cites as *Fusus villae* Michelotti. Whether or not it is actually Michelotti's species is somewhat uncertain as the original illustration (1847: plt. 10, fig.11) seems to be a different form. Nevertheless, the shell figured by Bellardi is almost certainly an *Attiliosa,* having an appearance very like that of *A. aldridgei.* It is described by Bellardi as having two or, rarely, three "transverse costulae" on the angle of the whorl, and the anteriormost costula larger and cariniform. These costulae (or spiral cords) cross eight longitudinal nodes. His illustration shows clearly the appressed suture and the strong umbilicus of *Attiliosa.* Thus, the connection between the Caribbean *Attiliosa* species and the Indo-Pacific ones may have come through Europe much earlier than we now think possible.

Because the nomenclatural history of these few species is so extraordinarily complicated, below are more-or-less complete synonymies for the species involved.

Attiliosa nodulosa (Adams, 1855)

Peristernia nodulosa A. Adams, 1855, Zool. Soc. London, Proc., (1854), p. 313.

Coralliophila nodulosa (Adams). Melvill, 1891, Manchester Lit. Phil. Soc., Mem. Proc., (ser. 4) 4: 409-410.

Peristernia nodulosa Adams. Hedley, 1908, Linnean Soc. New South Wales, Proc., 33: 486; plt. 8, fig. 11 (syntype).

Coralliophila incompta Berry, 1960. Leaflets in Malac., 1(19): 119.

Coralliophila incompta Berry. DuShane & Sphon, 1968, The Veliger, 10(3): 242; plt. 35, fig. 11.

Attiliosa incompta (Berry). Emerson, 1968, The Veliger, 10(4): 380; plt. 53, figs. 1-5 (fig. 1 = holotype), text figs. 2-5.

Attiliosa incompta (Berry). Keen, 1971, Sea shells of tropical west America, 2nd Ed., 529, fig. 1021.

[*Calotrophon (Attiliosa)*] *incompta* (Berry). Vokes, 1971, Bulls. Amer. Paleontology, 61(268): 59.

Calotrophon (Attiliosa) incompta (Berry). Abbott, 1974, Amer. Seashells, 2nd Ed., p. 188.

Attiliosa incompta (Berry). Kaicher, 1974, Card catalogue of world-wide shells, pack no. 6; Muricidae, part 2, fig. 515.

Attiliosa incompta (Berry). Vokes, 1976, Tulane Stud. Geol. Paleont., 12(3): 111.

Attiliosa nodulosa (Adams). Bullock, 1976, Tulane Stud. Geol. Paleont., 12(3): 133; plt. 1, figs. 6-8 (syntypes-BMNH).

Attiliosa incompta (Berry). Radwin & D'Attilio, 1976, *Murex* Shells of the World, p. 26; plt. 3, fig. 1.

Attiliosa nodulosa (Adams). Radwin & D'Attilio, 1978, Tulane Stud. Geol Paleont., 14(3): 132; figs. 5, 5a (radula).

Attiliosa nodulosa (Adams). Kaicher, 1980, Card catalogue of world-wide shells, pack no. 25; Muricidae, part 5, fig. 2578 (type-BMNH).

Attiliosa philippiana (Dall, 1889)

Muricidea philippiana Dall, 1889, Harvard Mus. Comp. Zool., Bull. 18: 213 (in part, Cabo Catoche specimen only); 1902, U.S. Natl. Mus., Proc. 24: 504; plt. 29, fig. 5 (USNM 93337).

Not *Muricidea philippiana* Dall. Dall, 1889, U.S. Natl. Mus., Bull. 37: 120 [= *Acanthotrophon striatoides* Vokes].

Not *Coralliophila philippiana* (Dall). M. Smith, 1953, Illus. Cat. Recent Species Rock Shells, p. 33; plt. 20, fig. 20 [USNM 34642; = *Acanthotrophon striatoides* Vokes].

[*Calotrophon (Attiliosa)*] *philippiana* (Dall). Vokes, 1971, Bulls. Amer. Paleontology, 61(268): 81.

Calotrophon (Attiliosa) philippiana (Dall). Abbott, 1974, Amer. Seashells, 2nd Ed., p. 188.

Not *Muricopsis philippiana* (Dall). Humfrey, 1975, Sea Shells of the West Indies, p. 138; plt. 16, fig. 3 [= *A. aldridgei* (Nowell-Usticke)].

Attiliosa philippiana (Dall). Vokes, 1976 (Sept.), Tulane Stud. Geol. Paleont. 12(3): 120; plt. 8, figs. 12-14 (fig. 12 = lectotype, USNM 93337; there designated).

Not *Attiliosa philippiana* (Dall). Radwin & D'Attilio, 1976 (Dec.), *Murex* Shells of the World, p. 26; plt. 3, fig. 10 [USNM 34642; = *Acanthotrophon striatoides* Vokes].

Attiliosa philippiana (Dall). Radwin & D'Attilio, 1978, Tulane Stud. Geol. Paleont. 14(3): 132; figs. 6, 6a (radula).

Attiliosa philippiana (Dall). Vokes, 1980, The Veliger, 23(1): 10.

Not *Attiliosa philippiana* (Dall). Kaicher, 1980, Card catalogue of world-wide shells, pack no. 25; Muricidae, part 5, fig. 2574 [USNM 34642; = *Acanthotrophon striatoides* Vokes].

Attiliosa aldridgei (Nowell-Usticke, 1969)

(Figures *6-9*)

Vasum aldridgei Nowell-Usticke, 1969, Suppl. List New Shells St. Croix, p. 18; plt. 4, no. 834.

Attiliosa aldridgei (Nowell-Usticke). Nowell-Usticke, 1971, Suppl. Listing New Shells, Revised Edition, p. 11; plt. 2, no. 680.

Muricopsis philippiana (Dall). Humfrey, 1975, Sea Shells of the West Indies, p. 138; plt. 16, fig. 3. (*not* of Dall).

Attiliosa aldridgei (Nowell-Usticke). Vokes,1976, Tulane Stud. Geol. Paleont. 12(3): 124; plt. 8, figs. 9-11.

Attiliosa aldridgei (Nowell-Usticke). Radwin & D'Attilio, 1976, *Murex* Shells of the World, p. 25; plt. 28, fig. 5 (paratype-AMNH 168901).

Attiliosa aldridgei (Usticke). Fair, 1976, The *Murex* Book, p. 19.

Attiliosa aldridgei (Nowell-Usticke). Radwin & D'Attilio, 1978, Tulane Stud. Geol. Paleont. 14(3): 132; fig. 7 (radula).

Muricopsis poeyi Sarasua & Espinosa, 1979, Poeyana, 193: 2; text figs. 1a, 1b.

Attiliosa aldridgei (Nowell-Usticke). Kaicher, 1979, Card catalogue of world-wide shells, pack no. 20; Muricidae, part 4, fig. 1990 (paratype-AMNH 168901).

Attiliosa nodulifera (Sowerby, 1841)

(Figures *1-5*)

Murex noduliferus G. B. Sowerby, Jr., 1841, Conch. Illust., plt. 194, fig. 94; 1841, Zool. Soc. London, Proc., pt. 8: 147.

Not *Murex noduliferus* Sowerby. Reeve, 1845, Conch. Icon., 3, *Murex*, plt. 31, fig. 150 [= *Spinidrupa euracantha* (Adams)].

Murex (Trophon) fruticosus Gould, 1849, Boston Soc. Nat. Hist., Proc. 3: 143; 1852, U.S. Expl. Exped. Wilkes 12: 236; plt. 17, figs. 287, 287a.

Murex (Muricidea) noduliferus Sowerby. Adams & Adams, 1853, Gen. Rec. Moll. 1: 75.

Typhis fruticosus (Gould). Gould, 1862, Otia Conch., pp. 66, 245.

Murex (Phyllonotus) noduliferus (Sowerby). Tryon, 1880, Man. Conch., 2: 111; plt. 30, figs. 282 (= Conch. Ill., fig. 94), 288 (= Wilkes Exp., fig. 287).

Muricidea caledonica Jousseaume, 1881, Le Naturaliste, Année 3, (44): 349; 1882, Rev. et Mag. Zool., (Ser. 3) 7: 345.

Murex (Muricidea) caledonica (Jousseaume). Poirier, 1883, Nouv. Arch. Mus. Hist. Nat. Paris, (Ser. 2) 5: 110; plt. 5, fig. 3 (lectotype).

(?) Murex (Phyllonotus) caledonicus (Jousseaume). Adam & Leloup, 1938, Mus. Roy. Hist. Nat. Belg., Mém., (Hors Ser.) 2(19): 154; plt. 6, fig. 11.

Muricidea caledonicus Jousseaume. Fischer-Piette & Beigbeder, 1943, Mus. Hist. Nat. Paris., Bull., (Ser. 2) 15: 206.

(?) Ocenebra nodulifera (Sowerby). Kuroda & Habe, 1952. Check-list and Bibliog. Rec. Mar. Moll. Japan, p. 72 (including *M. fruticosus* in synonymy, p. 69).

Trophon fruticosus (Gould). M. Smith, 1953, Illus. Cat. Recent Species Rock Shells, p. 23; plt. 16, fig. 19 (holotype-USNM 5685).

Drupa (Morula) nodulifera (Sowerby). Shikama, 1963, Select. Shells World in Col., 1: plt. 59, fig. 1.

Murex (Trophon) fruticosus [*Typhis*] Gould. Johnson, 1964, U.S. Natl. Mus., Bull. 239: 79.

Poirieria nodulifera (Sowerby). Cernohorsky, 1967, The Veliger, 10(2): 125; plt. 15, fig. 17; 1967, Mar. Shells Pacific, 1: 128; plt. 27, fig. 166.

Muricopsis noduliferus (Sowerby). Vokes, 1970, The Veliger, 13(2): 186; 1971, Bulls. Amer. Paleontology 61(268): 75 (including *M. fruticosus* in synonymy, p. 51).

[*Muricopsis*] *caledonica* (Jousseaume). Vokes, 1971, Bulls. Amer. Paleontology 61(268): 27.

Muricopsis (Spinidrupa) cf. *nodulifera* (Sowerby). Ponder, 1972, Malac. Soc. Australia, Jour., 2(3): 243; plt. 22, fig. 2; text fig. 3:29 (radula).

Muricopsis noduliferus (Sowerby). Cernohorsky, 1976, Auckland Inst. Mus. Rec. 13: 119; figs. 22-26 (figs. 22, 23 syntypes-BMNH; including *M. fruticosus* in synonymy).

(?) Marchia nodulifera (Sowerby). Radwin & D'Attilio, 1976, *Murex* Shells of the World, p. 59; plt. 27, fig. 3 (including *M. caledonica* in synonymy).

Explanation of Figures *1* to *10*

Attiliosa nodulifera (Sowerby)

Figure *1:* Australian Museum C. 132210; height 26.7 mm, diameter 17.4 mm. Locality: Talasea, New Britain, Papua-New Guinea × 2

Figure *2:* SDNHM 78076a; height 29.0 mm, diameter 20.1 mm. Locality: Ata'a-Malaita, Solomon Islands × 2

Figure *3:* SDNHM 78076b; height 27.5 mm, diameter 16.8 mm. Locality: Ata'a-Malaita, Solomon Islands (Both coll. Van der Riet) × 2

Figure *4:* SDNHM 61723; height 28.2 mm, diameter 17.7 mm. Locality: Province of Ilocos Sur, Luzon Island, Philippines. (Coll. J. E. Norton) × 2

"Muricidea" caledonica Jousseaume

Figure *5:* **Lectotype** (here designated), Mus. Hist. Nat. Paris; height 30 mm (*fide* Fischer-Piette & Beigbeder, 1943, p. 206) Locality: New Caledonia (Photograph courtesy of Philippe Bouchet, Muséum d'Histoire Naturelle, Paris) × 1½

Attiliosa aldridgei (Nowell-Usticke)

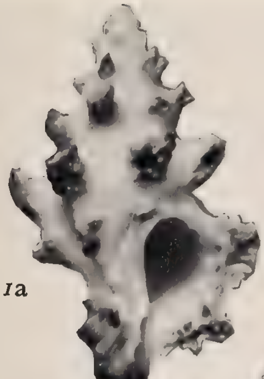
Figure *6:* FSBC I-11237; height 28.7 mm, diameter 18.2 mm. Locality: Andros Island, Bahamas × 2

Figure *7:* PRI 30012; height 20.2 mm, diameter 13.0 mm. Locality: TU 1215, Gurabo Formation, early Pliocene, Dominican Republic × 2½

Figure *8:* USNM 792393; height 12.3 mm, diameter 8.2 mm. Locality: Bimini Island, Bahamas × 10

Figure *9:* USNM 323924; height 10.8 mm, diameter 6.9 mm. Locality: TU 1240, Moín Formation, early Pleistocene, Costa Rica × 4

Figure *10:* Inst. Zoologia, Acad. Sci. Cuba, No. 67 (holotype-*Muricopsis poeyi* Sarasua and Espinosa); height 21.3 mm, diameter 13.2 mm. Locality: Marianao, Provincia Ciudad de La Habana, Cuba. (Photograph courtesy of Hortensia Sarasua, Instituto de Zoologia, Academia de Ciencias de Cuba) × 3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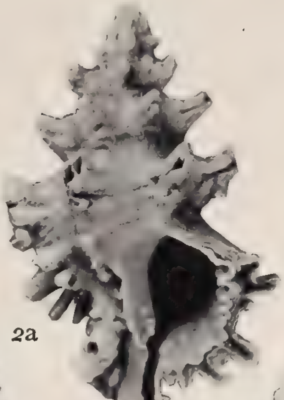
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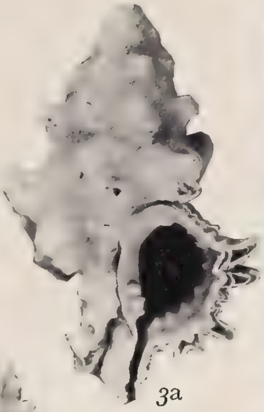
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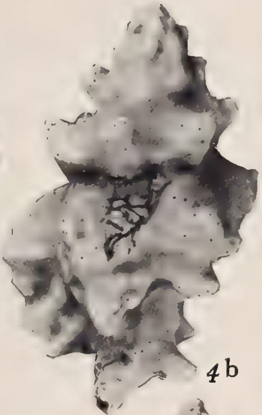
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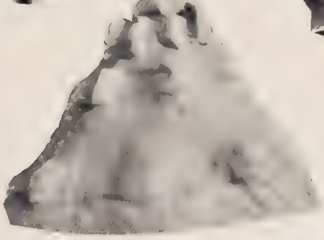
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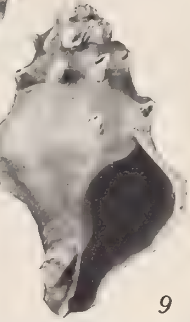
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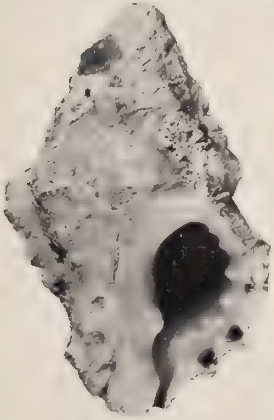
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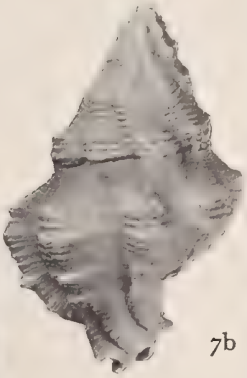
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Muricopsis caledonica (Jousseaume). **Fair**, 1976, The *Murex* Book,, p. 28; plt. 17, fig. 229 (lectotype).

Muricopsis noduliferus (Sowerby). **Fair**, 1976, The *Murex* Book, p. 62; plt. 17, fig. 230 (including *M. fruticosus* in synonymy).

Muricopsis nodulifera (Sowerby). **Kaicher**, 1980, Card catalogue of world-wide shells, pack no. 25; Muricidae, part 5, fig. 2554.

Attiliosa orri (Cernohorsky, 1976)

Muricopsis infans (E. A. Smith). **Radwin & D'Attilio**, 1976, *Murex* Shells of the World, p. 168; plt. 3, fig. 3 (*not* of Smith).

Muricopsis orri **Cernohorsky**, 1976, Auckland Inst. Mus., Rec. 13: 116; figs. 12-18.

Muricopsis orri Cernohorsky. **Kaicher**, 1979, Card catalogue of world-wide shells, pack no. 20; Muricidae, part 4, fig. 2062.

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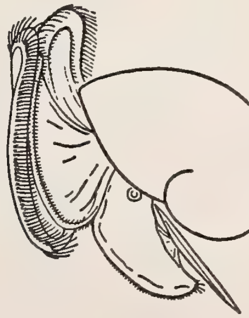

A New Eastern Pacific Species of *Eulimostraca*

(Gastropoda : Eulimidae)

BY

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(2 Plates; 3 Text figures)

INTRODUCTION

THIS PAPER DESCRIBES a new species of *Eulimostraca* from off La Jolla, California and transfers *Niso hipolitensis* Bartsch, 1917 to the genus *Eulimostraca* Bartsch, 1917. *Eulimostraca galapagensis* Bartsch, 1917 and *Eulimostraca bartschi* Strong and Hertlein, 1937 are also refigured and discussed.

BARTSCH (1917: 333) named the genus *Eulimostraca,* sole species, *E. galapagensis,* which was "dredged off Galapagos Island [sic], by the United States Bureau of Fisheries steamer Albatross, at station 2813, in 40 fathoms [73m] on coral sand bottom, bottom temperature 80° [27° C]." His distinguishing features for *Eulimostraca* are (1) inner lip not appressed to the attentuated basal portion of the preceding whorl, (2) whorls almost flattened, (3) outer lip of aperture not expanded, and (4) presence of color markings.

A second species of *Eulimostraca* was dredged in 22 meters about 8 kilometers west of Mazatlán, Sinaloa, Mexico by the Templeton Crocker Expedition. It was described by STRONG & HERTLEIN (1937: 170) and named *E. bartschi* in honor of Dr. Paul Bartsch.

A third species of *Eulimostraca* has recently been recognized from the western Atlantic. LYONS (1978) redescribed and transferred *Eulima subcarinata* Orbigny, 1842 to the genus *Eulimostraca.* This species occurs from the Caribbean and Yucatan to waters off Florida and North Carolina. LYONS (1978: 81) remarked that although no western Atlantic species had been previously assigned to *Eulimostraca,* several evidently belong there including *Eulima hemphilli* Dall, 1884 and several other species at present undescribed that occur in the Bahamas and off both Florida coasts.

SYSTEMATIC ACCOUNT

EULIMACEA H. & A. Adams, 1853
EULIMIDAE H. & A. Adams, 1853
Eulimostraca Bartsch, 1917
Type species: *Eulimostraca galapagensis* Bartsch, 1917 by M

Eulimostraca attilioi Hertz & Hertz, spec. nov.

(Holotype: Figures *1* to *3* — Paratype: Figures *4* to *6*)

Description: The shell of this species is extremely large for the genus, sturdy, and elongate-conic. With 10½ whorls

Explanation of Figures *1* to *6*

Eulimostraca ***attilioi*** Hertz & Hertz, spec. nov.

Figure *1:* Holotype (SDNHM 80762); length, 7.57mm; maximum diameter, 3.08mm; apertural view
Figure *2:* Same as in Figure *1;* profile view
Figure *3:* Same as in Figure *1;* dorsal view
Figure *4:* Paratype (Hertz collection); length, 8.90mm; maximum diameter, 3.17mm; apertural view
Figure *5:* Same as in Figure *4;* profile view
Figure *6:* Same as in Figure *4;* dorsal view


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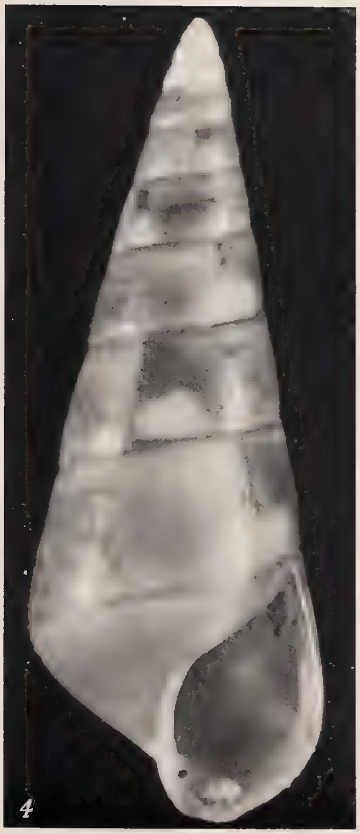
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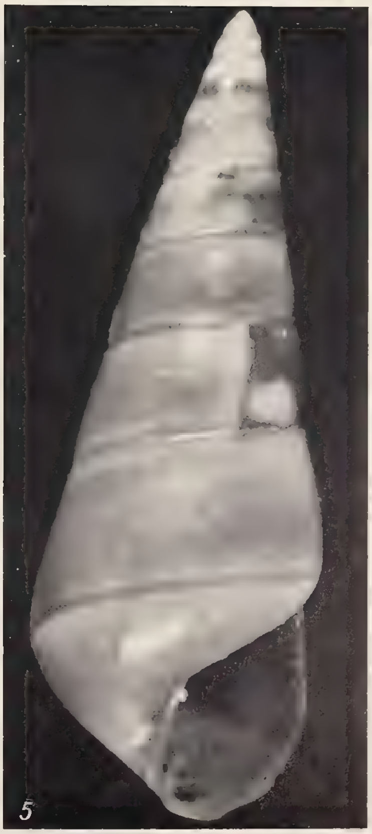
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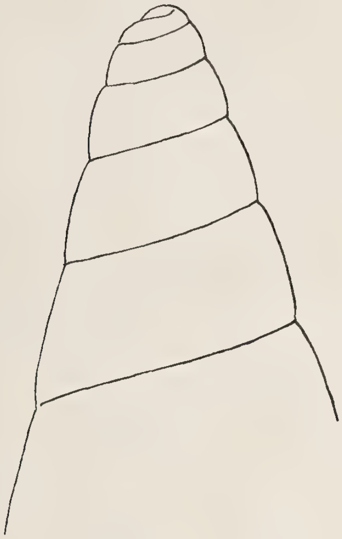

Figure 7

Detail of early whorls of *Eulimostraca attilioi* Hertz & Hertz, spec. nov.

Figure 8

Detail of *Eulimostraca attilioi* Hertz & Hertz, spec. nov. showing profile of sinuous outer lip

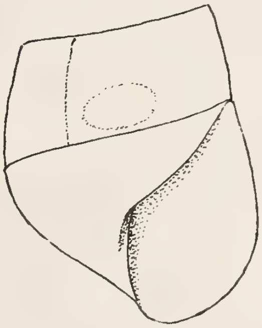

Figure 9

Detail of aperture of *Eulimostraca attilioi* Hertz & Hertz, spec. nov. showing umbilical depression

it shows no clear demarcation between protoconch and teleoconch (Figure 7). The earliest whorls are polished white, somewhat rounded, and the remaining ones highly polished, light brown, and flattened. The first half whorl is compressed and slightly convex. Occasional series of faint, scratch-like, incremental axial lines are visible under magnification (Figure *2*). The suture is weakly impressed, showing a darker brown line of color. Distinctive large circular white blotches appear behind the base of each varix-like resting place (Figures *1* to *6*). The body whorl is rounded at the base with a brown line extending to the aperture. The aperture is broadly oval and pointed at both ends; the outer lip thin, flattened above, bulging centrally, and somewhat convex below. When seen in profile, the outer lip appears sinuous or s-shaped (Figure 8). The inner lip is simple, not appressed.

The umbilical area is reduced to a chink (Figure 9). The operculum is corneous.

Type locality: South of La Jolla Trench, off San Diego, California in 90 to 140 meters.

Holotype: San Diego Natural History Museum Cat. no. 80762.

Dimensions of holotype: Length 7.57 mm; maximum diameter 3.08 mm.

Paratype: The paratype is in the Hertz collection. It is larger than the holotype, has 10½ whorls, is almost identical to the holotype but has a chipped outer lip. Length 8.90 mm; maximum diameter 3.17 mm.

Discussion: The holotype and paratype were obtained through the generosity of Loyal J. Bibbey. They were trawled in nets by Ronnie Nicols from January to June 1979. *Eulimostraca attilioi* is extremely large for the genus, being about 2½ times the size of the largest previously reported species. In size, shape, sturdiness, and coloration it is similar to species of the genus *Niso* Risso, 1826 (type species: *Niso eburnea* Risso, 1826), but lacks the true umbilicus of *Niso.* The circular white blotches of *E. attilioi* distinguish it from all other *Eulimostraca.* Similar spots, although differing in color, have been reported (Kuroda & Habe, 1950: 53, plt. 10, fig. 6) for *Amamibalcis kawamurai* Kuroda and Habe, 1950.

Eulimostraca attilioi is named for our friend and mentor, Anthony D'Attilio, who has shared with us his love and knowledge of the Mollusca.

Eulimostraca galapagensis Bartsch, 1917

(Holotype: Figures *10, 11*)

The type of *Eulimostraca galapagensis* and seven additional specimens were dredged by the Albatross in 75 m off the Galapagos Islands. The holotype, housed in the National Museum of Natural History, Smithsonian Institution (Cat. no. 251281), is a poorly preserved specimen of 11 whorls. It measures 3.8 mm in length and has a maximum diameter of 1.2 mm. The original Bartsch illustration (plt. 43, fig. 1) was retouched under Bartsch's supervision and gives no indication of the poor condition of the specimen.

The shallow, narrow, umbilical depression of the holotype is a distinguishing character of the genus *Eulimostraca.* The original description of *E. galapagensis* follows. "Shell broadly elongate-conic, thin, translucent, showing the internal structure through the substance of the shell. Whorls rather high between the sutures, moderately well rounded, appressed at the summit; polished, marked by exceedingly fine incremental lines only. Suture lightly impressed. Periphery of the last whorl somewhat inflated; strongly angulated, marked by a narrow brownish band. Base short, well rounded. Aperture very broadly oval; posterior angle acute; outer lip thin, tinged with brown on the posterior half, decidedly protracted in the middle, to form a claw-like element; inner lip strongly curved, slightly reflected, fusing only slightly, posteriorly, with the preceding whorl; parietal wall covered by a thin callus."

We have examined a lot of two well-preserved specimens (SDNHM 41228) from Corinto, Ecuador taken by the Crocker Expedition, as well as the figured type of *Eulimostraca galapagensis.* Dr. Joseph Rosewater (personal communication) of the National Museum of Natural History, Smithsonian Institution, advised that the seven additional specimens of the type lot could not be found. The reported distribution of this species is the Galapagos Islands and Ecuador.

Lyons (1978: 80-83) reassigned the western Atlantic species *Eulima subcarinata* Orbigny, 1842 to the genus *Eulimostraca* and remarked on its similarity to *E. galapagensis.*

Eulimostraca bartschi Strong & Hertlein, 1937

(Holotype: Figures *12, 13*)

The type of *Eulimostraca bartschi* and seven additional specimens were dredged by the Templeton Crocker Expedition about 8 km west of Mazatlán, Sinaloa, Mexico in 22 m. The holotype, in the California Academy of Sciences (Cat. no. 6986), measures 1.8 mm in length with a maximum diameter of 0.5 mm. Following is the original description. "Shell minute. elongate conic, translucent, the internal structure showing through and forming a distinct false suture, pale flesh color, with the base light brown, showing through as a darker line between the true and false sutures on the spire; whorls nine, the first three somewhat rounded, the latter whorls becoming flattened, sutures very indistinct; periphery subangulated, base short, rounded; aperture oval with the posterior angle acute; outer lip somewhat drawn forward in the middle; inner lip curved, raised,

Explanation of Figures *10* to *16*

Figure *10: Eulimostraca galapagensis* Bartsch, 1917. Holotype (USNM 251281); length, 3.8 mm; maximum diameter, 1.2 mm; apertural view

Figure *11:* Same as in Figure *10;* dorsal view

Figure *12: Eulimostraca bartschi* Strong & Hertlein, 1937. Holotype (CAS 6986); length, 1.8 mm; maximum diameter, 0.5 mm; apertural view

Figure *13:* Same as in Figure *12;* dorsal view

Figure *14: Eulimostraca hipolitensis* (Bartsch, 1917). Holotype (USNM 127544); length, 3.1 mm; maximum diameter, 1.2 mm; apertural view

Figure *15:* Same as in Figure *14;* dorsal view

Figure *16: Eulimostraca hipolitensis* (Bartsch, 1917). Hypotype (CAS 12744); length, approximately 3.4 mm; maximum diameter, approximately 1.2 mm; apertural view


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16

with behind it a shallow groove in the umbilical region; body with a thin, well defined callus."

Strong & Hertlein (1937: 171) state that this species differs from *Eulimostraca galapagensis* primarily in its much smaller size and less angulated periphery. In addition to the type, we have examined one other specimen of *E. bartschi* (SDNHM 41227) taken by the Crocker Expedition "off Corrientes, Mexico." The holotype of *E. bartschi,* shown in Figures *12* and *13*, and the specimen from Corrientes have a thickened lip edge not apparent in *E. galapagensis.*

Eulimostraca hipolitensis (Bartsch, 1917)

(Holotype: Figures *14, 15*—Hypotype: Figure *16*)

Niso hipolitensis Bartsch, 1917

After studying a number of lots of *Niso hipolitensis* Bartsch, 1917, we have reassigned this species to the genus *Eulimostraca* Bartsch, 1917. Two of the characters of the genus *Niso* Risso, 1826, clearly differentiate it from *Eulimostraca.* Risso (1826: 218-219) states that the suture in *Niso* is narrow and deep ("sutura angusta, profunda") and that the base has a deep umbilicus ("umbilicus profondus, conico-concavus"). In *Eulimostraca* the suture is only slightly impressed and there is no true umbilicus, merely a shallow, narrow depression behind the inner lip.

Bartsch's original description of *Niso hipolitensis* was based on a very poorly preserved specimen (Figures *14* and *15*) which was collected by Henry Hemphill in shell washings at San Hipolito Point, Baja California, Mexico. As noted in the original Bartsch description which follows, the suture is "feebly impressed" and the inner lip almost covers the "narrow umbilicus." "Shell very small, elongate-conic, narrowly umbilicated. Tip yellowish-white, base white with a broad median brown band; anterior half of aperture white. Surface polished, marked by fine lines of growth only. Suture feebly impressed. Periphery of the last whorl angulated. Base short, well rounded. Aperture broadly oval; posterior angle acute; outer lip thin, curved and slightly patulose; inner lip curved and revolute, almost covering the narrow umbilicus.... The type has 10 whorls and measures—length, 3.1mm; diameter, 1.2mm."

Our examination of the holotype revealed a specimen with a narrow depression behind the inner lip rather than a true umbilicus (holotype: USNM Cat. no. 127544).

Two additional specimens of *Eulimostraca hipolitensis* (CAS 12744 and 12745), previously figured by Emerson (1965: 7, fig. 10) from off the west coast of Isla Asunción, Baja California, Mexico (CAS Loc. no. 27245) were examined and the larger specimen (CAS 12744) is shown in Figure *16*. This is a specimen in fine condition and clearly shows the umbilical chink. The specimens in these two lots vary from other lots examined in the thread-like raised line posteriorly on the suture which gives the impression that the suture is wide and more deeply impressed.

Other material studied from the San Diego Natural History Museum, Los Angeles County Museum of Natural History (LACM), and the Hertz collection is listed as follows: SDNHM 34798, 6 specimens, San Hipolito, B.C., Mex.; LACM 67-66, 3 specimens, Isla Asunción, B.C., Mex. (27°06′N; 114°17′W), 8-21m; LACM 67-70, 1 specimen, northeast of Pta. Belcher, Magdalena Bay, B.C., Mex. (24°35′N; 112°05′W), 2-9m; LACM 66-16, 1 specimen, El Tule, Canelo Bay, B.C., Mex. (22°55′N; 109°50′W), 5-9m; LACM 71-14, 3 specimens, east side of Pta. Entrada at Sail Rock (north entrance to Magdalena Bay), B.C., Mex. (24°32.4′N; 112°04′W), 3-15m; Hertz collection, 1 specimen, off side of sea mount approx. 5km west of Isla Asunción, B.C., Mex., 9-30m.

Two unidentified lots from the Los Angeles County Museum (NH) appear to be *Eulimostraca hipolitensis.* They are LACM 71-151, 1 specimen, NE end of Cedros Is., B.C., Mex. (28°20′25″N; 115°11′20″W), 5-12m; LACM 72-42, 2 specimens with broken lips, E of Punta Ballena, Bahía Ballena, Puntarenas, Costa Rica (9°44′15″N; 84°33′45″W), 3-15m.

There is a degree of variability within the species. As previously noted, two specimens show a thread-like raised line posterior to the suture. In two specimens (LACM 67-66) the umbilical chink is somewhat deeper and the growth lines appear more pronounced. The largest specimen examined measured approximately 4.5mm in length.

The previously reported range (Emerson, 1965: 8) for *Eulimostraca hipolitensis* was from San Diego, California to San Hipolito Point, Baja California, Mexico (Bartsch, 1917); Los Angeles Bay, Baja California, Mexico (McLean, 1961).

Specimens of *Eulimostraca hipolitensis* and *E. galapagensis* studied show very little or no difference in shell morphology. Comparison of the original descriptions of both species also indicates the similarity in their shell characters. We have studied a specimen of *E. galapagensis* from Corinto, Ecuador and have tentatively identified a lot of *E. hipolitensis* from Costa Rica. Study of a large sampling of specimens from the southern portion of the range as well as anatomical studies may prove that *E. galapagensis* and *E. hipolitensis* are a single species with a widespread distribution. Should they prove to be the same species, then *E. hipolitensis* would fall in the synonymy of *E. galapagensis.*

ACKNOWLEDGMENTS

We are indebted to Loyal J. Bibbey for the lot of trawled material which yielded the holotype and paratype of *Eulimostraca attilioi.* Our special thanks go to David K. Mulliner for photographing the species illustrated and to Anthony D'Attilio who prepared the figure drawings and reviewed the manuscript. We are grateful to Dr. Barry Roth, California Academy of Sciences, and to Dr. James H. McLean and Gale G. Sphon, Los Angeles County Museum of Natural History, for the loan of type and study material and for making the collections of these institutions available to us. We are also grateful to Dr. Joseph Rosewater of the National Museum of Natural History, Smithsonian Institution, for the loan of type material. Spencer Luke, Scripps Institution of Oceanography, and Carey Resch Smith, Santa Barbara Museum of Natural History, were kind enough to provide access to the eulimid material in their respective institutions. William G. Lyons, Florida Department of Natural Resources, graciously provided information on Atlantic eulimids.

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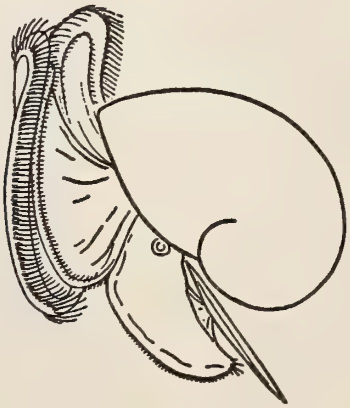

Excretory Concretions in the Sunray Venus Clam, *Macrocallista nimbosa*

(Bivalvia : Veneridae)[1]

BY

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(1 Plate)

INTRODUCTION

CONCRETIONS HAVE BEEN OBSERVED in the kidneys of *Macrocallista nimbosa* [Lightfoot, 1786] in the past but were only described as a "dark granular mass" (STOKES, *et al.*, 1968). Recent investigations have shown these concretions to be kidney stones formed of calcium phosphate in a mucopolysaccharide matrix (TIFFANY, 1979a; 1979b; TIFFANY, *et al.*, 1980). Although excretory concretions have been observed in other molluscs (*e.g.*, ANDREWS, 1976; 1979; BENSON & SUMMONS, 1981; BONGA & BOER, 1969; DELHAYE & BOUILLON, 1972; DOYLE, *et al.*, 1978; GEORGE, *et al.*, 1980; POTTS, 1967), *M. nimbosa* is unique in that kidney stones are present in all stages of its adult life history. In addition, kidney stones have been observed in every *M. nimbosa* sampled, regardless of geographical location (TIFFANY, 1979a).

The stones originate in the tubule cells of the nephridium in the form of stone precursors. It is believed that these stone precursors are eventually extruded into the lumen, where they continue to grow by epitaxy and aggregation (TIFFANY, *et al.*, 1980).

This report further describes the stones in the kidney of *Macrocallista nimbosa*. It also contains the first scanning electron micrographs of stones *in situ* as well as excised, cleaned stones.

MATERIALS AND METHODS

Clams were collected from sand bars in Sarasota Bay, Sarasota County, Florida.

Stones used for analysis were obtained by excising the nephridia from the animals and subsequently placing them in 5% sodium hypochlorite. This procedure resulted in digesting away the surrounding tissue, leaving the cleaned stones. It did not erode the surface of the stones *per se*. The stones were then washed several times in double distilled water and air dried on filter paper. These stones and pieces of undigested kidney tissue containing stones were fixed in 3% gluteraldehyde in 0.1M phosphate buffer for 3 hours at 24°C. After rinsing in phosphate buffer, tissue was transferred to specimen chambers and processed through a gradient flow of dilute through absolute acetone, followed by absolute amylacetate. The tissue was then dried in a critical point drier and mounted with carbon adhesive for viewing under a JEOL JSM-U3 scanning electron microscope.

Several thousand cleaned, unfixed stones were also observed and sized under a Nikon Biophot light microscope, equipped with reticle eye pieces.

RESULTS

Light microscopy of cleaned stones showed them to be irregular in shape, varying in size from 0.1mm to 2.5mm. SEM micrographs further demonstrated the surface topography of the stones to be highly convoluted and composed of microspherules (Figure *1*).

Scanning electron microscopy of tissue with stones *in situ* revealed strands of unknown composition connecting the stones with the kidney tubule walls (and apparently covering the stones and walls as well) (Figure *2*).

DISCUSSION AND SUMMARY

The irregular shape of the stones seen in Figure *1* may be the result of confined growth in which the stones take

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[1] Contribution No. 173 from the Tallahassee, Sopchoppy and Gulf Coast Marine Biological Association.

on the shape of the surrounding tubule. Previously published light micrographs of the stones *in situ* have shown them entirely filling the tubule lumen, taking the shape of the tubule cross-section (Tiffany, *et al.,* 1980). Andrews (1979) noted a similar condition in two species of *Viviparus.* The microspherules are reminiscent of those observed on the surface of developing molluscan shell or on the mineralized layer recently described by Carriker & Palmer (1979) in the oyster hinge. Further investigation will be required to clarify the nature of the convoluted stone surface.

The strands observed in Figure *2* suggest that the stones are attached to the tubule wall as opposed to existing freely in the tubule lumen. Andrews (1979) noted that excretory concretions, preserved in kidney tissue from *Viviparus* spp., were supported by processes from mucous cells. Histochemical tests showed the major constituent of apical vacuoles in these cells to be a mucopolysaccharide. The concretions also contained concentric layers of mucopolysaccharides. Tiffany, *et al.* (1980) have previously demonstrated concentric layering of mucopolysaccharides in the stones of *Macrocallista nimbosa;* however, connecting strands were not previously observed while using conventional light microscopic techniques. Although additional studies will be required to characterize these strands, a polysaccharide composition is likely.

In summary, this report contains the first scanning electron micrographs of excretory concretions (kidney stones) in *Macrocallista nimbosa.* The micrographs also illustrate, for the first time, the convoluted surface of the stones, composed of microspherules.

ACKNOWLEDGMENTS

I thank Drs. John B. Morrill and Michael J. Greenberg for their advice and assistance in this project and for their review of the manuscript. Special thanks are due to Dr. Art Allyn of the Allyn Museum of Entomology for the scanning electron micrographs contained herein. My students, Sharon Matola and Stephanie Gillespie were instrumental in all phases of this project. Dr. Al Beulig is graciously acknowledged for providing laboratory space.

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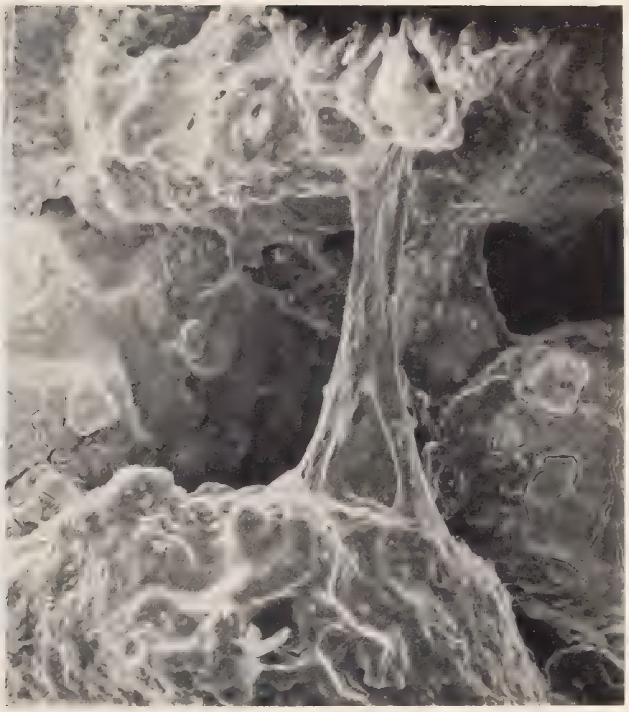
Explanation of Figures *1* and *2*

Figure *1:* Scanning electron micrographs of excretory concretions (kidney stones) removed from *Macrocallista nimbosa*
a. Varieties of stone shapes × 100
b. Fractured stone demonstrating surface topography and microspherules × 1000
Figure *2:* Scanning electron micrographs of *Macrocallista nimbosa* stones *in situ* demonstrating attachment of stones to tubule lumen
a. Stone in center of micrograph × 350
b. Stone to left, tubule wall to right, strands in center × 800


1b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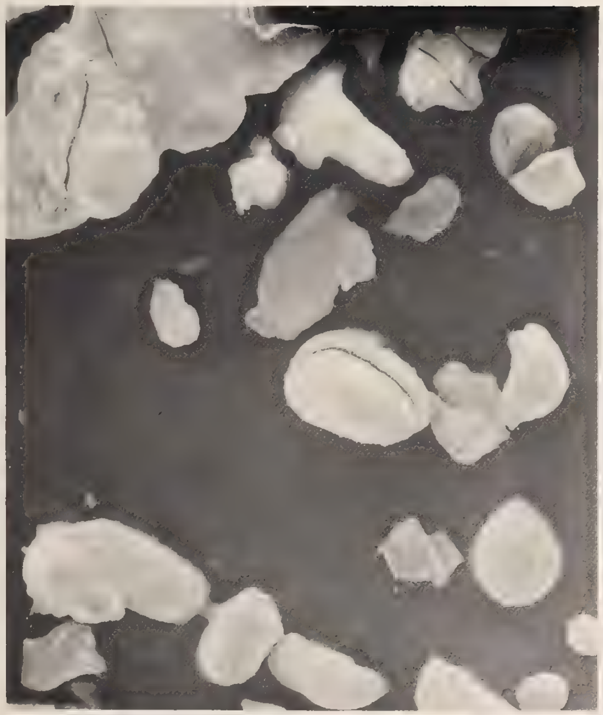
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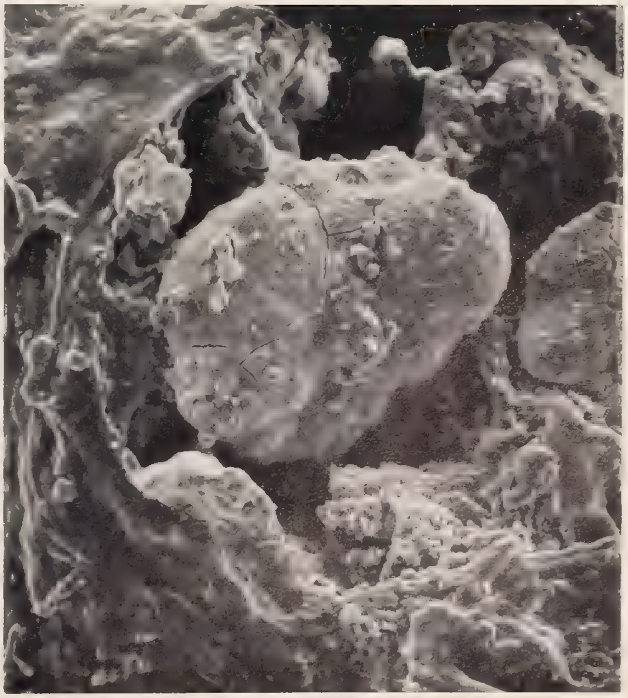
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Growth-Related Surficial Resorption of the Penultimate Whorl in *Terebra dimidiata* (Linnaeus, 1758) and Other Marine Prosobranch Gastropods

BY

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(1 Plate)

INTRODUCTION

IT HAS BEEN KNOWN for nearly one and a half centuries that many gastropods resorb previously deposited shell material. In a largely overlooked but perceptive and surprisingly current paper, GRAY (1833) observed that several intergrading forms of shell resorption occur in the Gastropoda. These include remodeling of the shell's interior, the formation of fissures in some limpets, removal of spines or other sculpture which would interfere with further growth and surficial resorption of the penultimate whorl. All but the latter form of resorption have received further attention by one or more later researchers (*e.g.*, WOODWARD, 1871; CROSSE & FISCHER, 1879; 1882a; 1882b; FISCHER, 1881; WOODWARD, 1892; LAMY, 1930; BERNER, 1942; MORTON, 1955; CARRIKER, 1972; VERMEIJ, 1973a; 1973b; KOHN *et al.*, 1979). The lack of attention given surficial resorption is unexpected as it apparently occurs in a wide range of prosobranch gastropods.

Authors have occasionally noted the occurrence of surficial resorption of the penultimate whorl (*e.g.*, HATHAWAY & WOODBURN, 1961; CARRIKER, 1972) but have not examined it in detail nor commented on the extent of its distribution among the Gastropoda. In the course of another study (SIGNOR, in press), I discovered that *Terebra dimidiata* (Linnaeus, 1758) resorbs the surface of the penultimate whorl prior to overgrowing the area with the body whorl. After inspecting the shells of other prosobranch species, it became obvious that surficial resorption, while generally overlooked and not well understood, is rather common. In this paper I describe the occurrence of surficial resorption in *T. dimidiata*, comment on the distribution of surficial resorption among the Prosobranchia and propose a hypothesis for the functional significance of the process.

ACKNOWLEDGMENTS

M. Colgan and members of the Guam Shell Club assisted in collecting specimens. Dr. A. Walker supplied access to S.E.M. facilities and Dr. P. Shipman provided technical assistance in all phases of the scanning electron microscopy. I thank P. Kat and J. G. Carter for discussions of various aspects of this study and for critically reading drafts of this paper. This project was funded in part by research grants from the Geological Society of America, Sigma Xi, the Scientific Research Society, a Harold T. Stearns Fellowship from the Geological Society of America and a Collo Murphy Memorial Scholarship from the National Capital Shell Club.

MATERIALS AND OBSERVATIONS

Live specimens of *Terebra dimidiata* were collected in Piti Bay, Guam, dried and returned to Johns Hopkins for further study. Three techniques were utilized to prepare the shells for inspection with a scanning electron microscope (S.E.M.). First, small individuals were mounted whole on S.E.M. stubs. Other specimens were fractured to allow study of cross-sections of the dissolved area. Lastly, specimens were cut with a rock saw, polished and etched with dilute hydrochloric acid. All specimens were cleaned in an ultrasonic bath, dried and coated with gold/palladium. S.E.M. examination of the prepared specimens was performed with an Itec Omniscan at the Department of Anatomy and Cell Biology of the Johns Hopkins University School of Medicine.

Macroscopically, the shell surface of *Terebra dimidiata* appears smooth with the exceptions of occasional pronounced growth lines, repaired injuries and a single spiral cuesta. Under S.E.M. a fine spiral pattern of pits, varying irregularly in diameter from 1-2 microns, can be observed (Figure *1*). The pits are linked in spiral rows by less pronounced incised grooves. Coeval grooves are subparallel, suggesting that deviations from a perfect spiral pattern reflect minor alterations in the direction of growth or positioning of the mantle edge.

The array of grooves and pits is a primary feature of the shell surface. The surface of newly deposited shell material, on the body whorl adjacent to the aperture, already bears clearly defined pits and grooves. This observation discounts the possibility that the pits and grooves result from abrasion or dissolution along weak areas of the shell and implies that areas lacking pits and grooves have been modified in some way. A similar, but larger feature apparently occurs in the closely related genus *Hastula*. For example, Marcus & Marcus (1960) and Morrison (1968) noted that the shell of *Hastula cinerea* (Born, 1778) is covered by spiral rows of minute "pricks" or pits which are visible under low optical magnification. The functional significance of these pits, if any, is unknown.

Pits and grooves occur over the entire surface of the shell except where older portions of the shell have been abraded, along a thin line above the suture (Figure *2*) and on the penultimate whorl adjacent to the aperture, in the parietal area (Figures *3*, *4*). In the latter cases, alteration of the shell surface was apparently accomplished by the animal itself. Individuals of all sizes bear identical resorption marks. As the animal grows and the aperture advances over the resorbed area on the penultimate whorl, additional resorption must take place in the parietal area at a rate equal to the rate of growth. The height of the body whorl is slightly less than the height of the resorbed area, leaving a narrow band of modified shell surface above the suture (Figure *2*). The boundary of the modified shell surface in the parietal area is coincident with the edge of the extended mantle when the animal is active, suggesting that resorption occurs at the mantle edge. This inference is supported by the observation that the total depth of resorption is reached within microns of the edge of the resorbed area (Figures *2*, *4*). *Terebra dimidiata* lacks a radula (Miller, 1975) and there are no rasp marks on the shell, hence there is no possibility that removal of the pits and grooves is accomplished by rasping. Total depth of dissolution is approximately 2 microns (Figure *5*). In cross-section (Figure *5*), the resorption appears to be a minor modification of the shell, removing only the pits and grooves, other foreign material attached to the shell and minor damage to the old shell surface.

The surficial resorption occurring on the shell of *Terebra dimidiata* is too fine to be observed with the naked eye or even under moderate magnification. Nevertheless, the area where resorption occurred can be differentiated from the surface still bearing pits and grooves by variations in the luster of the shell's surface, the resorbed area appearing brighter in reflected light.

Other terebrids (every species I have examined to date) also resorb part of the surface of the penultimate whorl during growth. In some species (*e.g.*, *Terebra cerithina* Hinds, 1844) evidence of resorption is concealed in larger individuals by development of a parietal callus. However, the resorbed area is clearly visible in juveniles. (Whether development of a parietal callus in *T. cerithina* is indicative of a terminal growth phase remains to be determined.) In most fresh terebrid specimens the resorbed area may be located without difficulty by its brighter luster.

Explanation of Figures *1* to *6*

Figure *1:* Shell surface of *Terebra dimidiata*. The pits lie in less pronounced grooves which are parallel to the direction of growth (left to right). There is no evidence of any periostracum in this species. Scanning Electron Micrograph. Scale bar = 10µm

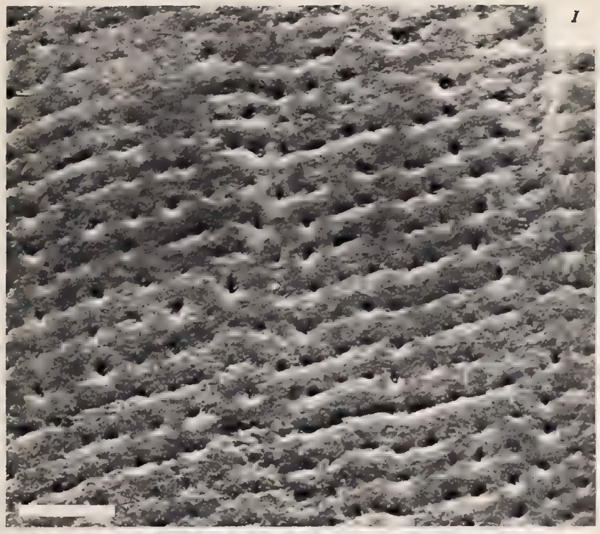
Figure *2:* Suture line of *T. dimidiata*. The pit and groove microsculpture is not present on the older whorl adjacent to the younger whorl. The shallow slope down into the smooth area suggests the snail has resorbed the pit and groove microsculpture, thus producing a secondarily smoothened shell surface. Scanning Electron Micrograph Scale Bar = 100µm Right side × 3

Figure *3:* Adapical edge of aperture, showing suture on penultimate whorl of *T. dimidiata*. The area immediately in front of the aperture is also secondarily smooth. Apex is to lower left. Scanning Electron Micrograph Scale Bar = 10µm

Figure *4:* Boundary between shell surface with pit and groove microsculpture and smooth shell surface in the parietal area. Apex is to lower left, aperture toward upper right. Scanning Electron Micrograph Scale Bar = 20µm

Figure *5:* Cross-section of resorbed area along suture line of *T. dimidiata*. Specimen was prepared by fracturing; there was no acid treatment. The shallow depth of resorption is evident in this figure; only the top few microns of shell material are removed. Apex is to lower left. Scanning Electron Micrograph Scale Bar = 10µm

Figure *6:* Surficial resorption in *Strombus alatus*. The moderately thick periostracum (left) is eroded away as the shell grows, revealing the surface of the shell which is subsequently resorbed. Scanning Electron Micrograph Scale bar = 10µm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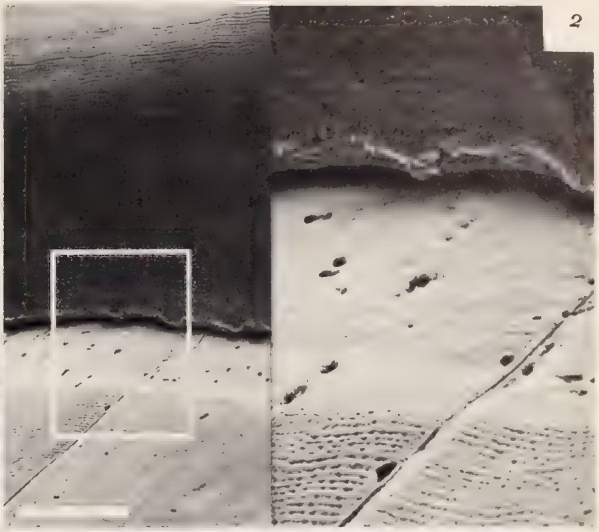
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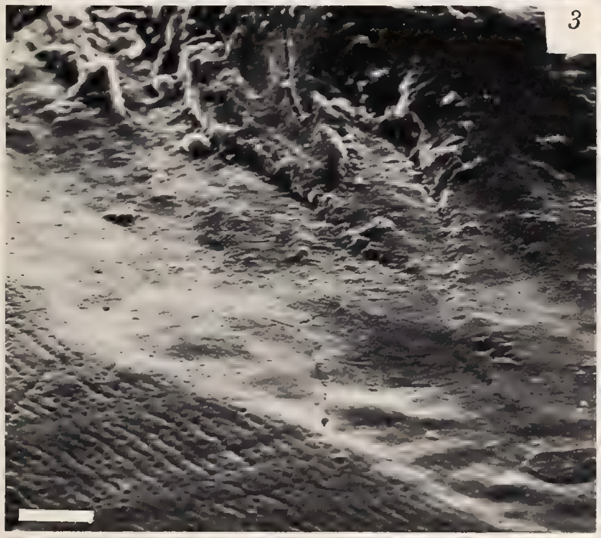
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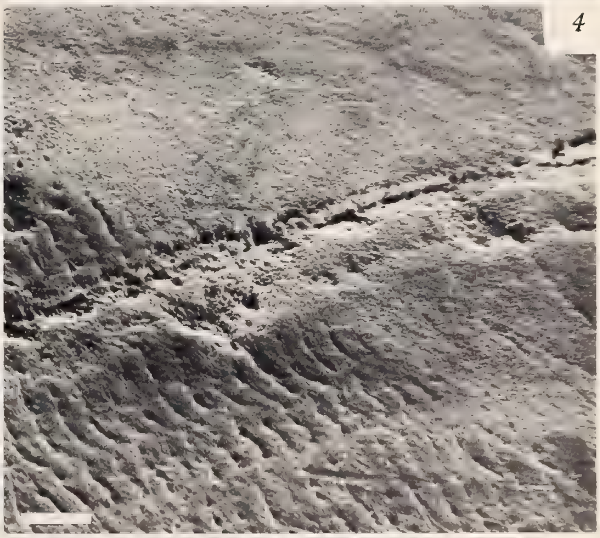
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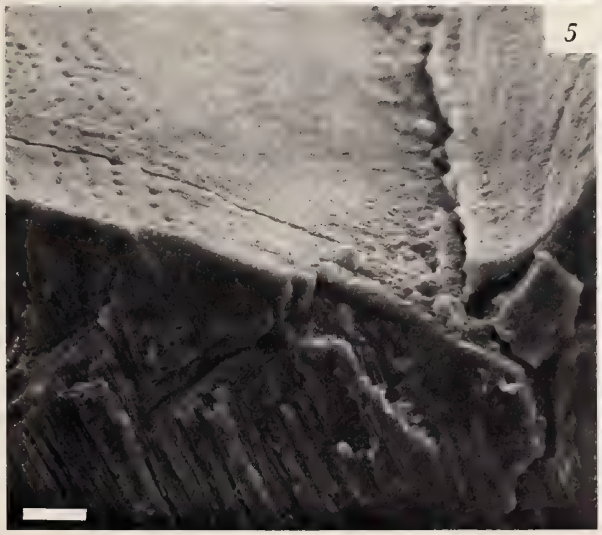
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SURFICIAL RESORPTION IN OTHER PROSOBRANCH SPECIES

Surficial resorption of the penultimate whorl occurs in many other species among the Archaeogastropoda, Mesogastropoda and Neogastropoda. In some archaeogastropods, the resorption is so profound that it may be easily observed without magnification (*e.g.*, *Mikadotrochus hirasei* (Pilsbry, 1903)). In *Trochus niloticus* Linnaeus, 1758, a species which possesses a well-developed periostracum, the periostracum on the base of the shell is progressively thinned near the aperture and is often completely removed, apparently by the mantle. Where some periostracum remains in the parietal area no surficial resorption can occur and the area under the remaining periostracum is preserved as a local elevation or topographic high, relative to areas where the periostracum was removed and shell resorption occurred. Later, both remaining periostracum and resorbed areas are overgrown by the advancing body whorl and are covered with newly deposited shell material.

Among the mesogastropods, *Strombus alatus* Gmelin, 1791, resorbs the periostracum and surface of the penultimate whorl; the narrow band of modified shell surface is parallel to the advancing edge of the parietal callus and is most obvious in juveniles (Figure 6). Juvenile *Rhinoclavis aspera* (Linnaeus, 1758) resorb part of the shell surface of the penultimate whorl prior to overgrowing the area with the body whorl. Evidence of the resorption is concealed in adult specimens by a parietal deposit. Other mesogastropods which resorb a portion of the penultimate whorl surface during growth include *Telescopium telescopium* (Linnaeus, 1758), and *Tonna canaliculata* Linnaeus, 1758.

Carriker (1972) observed that the neogastropods *Murex brevifrons* Lamark, 1822, and *M. fulvescens* Sowerby, 1834, erode the parietal area during periods of growth. He also noted that, when the advancing edge of the resorbed area meets a row of spines, the spines are eroded off at their bases (also see Gray, 1833). Other neogastropods which resorb a portion of the penultimate whorl surface during growth include *Melongena corona* (Gmelin, 1791) (Hathaway & Woodburn, 1961), *Mazatlania aciculata* (Lamark, 1822) and *Mitra mitra* (Linnaeus, 1758). In each case, the resorption is visible to the naked eye as an erosion or change in the luster of the shell at the edge of the parietal area.

Not all prosobranch gastropods resorb the penultimate whorl surface during growth. For example, *Neocancilla papilio* (Link, 1807) covers the preceding whorl with a thick parietal callus; I have not found any evidence of surficial resorption of the penultimate whorl in this species. I have found no evidence of surficial resorption in patelliform gastropods. Despite these and other exceptions, superficial resorption of the penultimate whorl is common and widely distributed among the Prosobranchia.

DISCUSSION

The functional significance, if any, of the pit and groove microsculpture and the surficial resorption of the penultimate whorl surface of *Terebra dimidiata* are unknown. It seems reasonable to surmise that, like other forms of shell dissolution found among the Gastropoda, surficial resorption of the penultimate whorl is intimately related to the process of growth. Surficial resorption cannot yield appreciable amounts of reusable calcium carbonate because so little shell material is resorbed, nor is the volume of the shell enlarged. One possible function of surficial resorption is that it provides a fresh surface upon which new shell material may be more easily deposited or more firmly attached. Certainly, attaching newly deposited shell material to the periostracum of the penultimate whorl or to a weathered or abraded shell surface would not enhance the structural integrity of the shell. Further evaluation of this hypothesis will have to await detailed analysis of how gastropods attach newly deposited portions of the body whorl to the penultimate whorl.

Surficial resorption of the penultimate whorl surface is distinct from other modes of shell resorption occurring in the Mollusca. The most thoroughly studied and widely discussed example of shell dissolution occurs in the bivalves during periods of anaerobic metabolism and possibly is the process responsible for the formation of growth lines (Lutz & Rhoads, 1977; 1980; Crenshaw, 1980 and references therein). In contrast, surficial resorption of the penultimate whorl must occur when the mantle is in an extended position and the animal, presumably, is active. Kohn *et al.* (1979) have shown that internal remodeling in *Conus* occurs over nearly half of the penultimate whorl, in a region already concealed by the body whorl. Similarly, internal resorption in the Neritidae (Gray, 1833; Woodward, 1892; Vermeij, 1973b), *Olivella* (Fischer, 1881; Crosse & Fischer, 1881), and Melampidae (Gray, 1833; Crosse & Fischer, 1879; 1881) is accomplished in the shell interior, apparently by the mantle surface. Surficial resorption occurs only in a narrow band, immediately in front of the advancing aperture. Occasional dissolution or resorption of spines and other sculpture (Gray, 1833; Carriker, 1972) or the formation of fissures is clearly distinct from surficial resorption of the penultimate whorl. In each case, the physiological and biochemical mechanisms of shell resorption may be similar but the pattern or program of resorption is quite different.

Most forms of gastropod shell resorption are in one way or another related to the unique shell forms, modes of growth, or ecologies of the shell-resorbing species. For example, internal resorption in *Conus* allows the genus to have shells with long, thin apertures but large volumes (Kohn *et al.*, 1979); if muricids were not able to remove previously deposited spines the snails would be forced to either avoid developing spines or drastically modify their geometry of coiling. In each case, shell resorption is one of a suite of adaptations which were evolved by different clades of snails in the course of adapting to their respective ecological circumstances. In contrast, the wide distribution of surficial resorption of the penultimate whorl among the Archaeogastropoda, Mesogastropoda and Neogastropoda indicates that the resorption is probably a primitive (or pleisiomorphic) character inherited from the group ancestral to the Gastropoda, presumably the cyclomyan monoplacophorans, or else developed very early in the evolutionary history of the snails. (Surficial resorption has not been documented in the Monoplacophora, but resorption of shell material has been described in the Bellerophontacea (Rollins, 1966), which are either cyclomyan monoplacophorans (Runnegar & Jell, 1976) or a polyphyletic group of monoplacophorans and primitive gastropods (Peel, 1980.) Other forms of shell resorption may have evolved earlier among the Monoplacophora but there is no evidence of other primitive, broadly distributed types of gastropod shell resorption. Therefore, surficial resorption probably preceded the evolution of other, more specialized, types of gastropod shell resorption and may consequently be of some interest in the analysis of the evolutionary history of the gastropods.

The capacity to resorb older shell material on the surface of the penultimate whorl in the course of growth may have been an adaptive precursor to other types of gastropod shell resorption. In turn, the ability to remodel the shell interior or remove preexisting sculpture, which would obstruct further growth, has facilitated evolution of a new suite of shell morphologies which are more resistant to post-Paleozoic durophagous predators (Carriker, 1972; Vermeij, 1977; 1978; Kohn *et al.*, 1979). The capabilities of gastropods to modify preexisting structures is likely responsible, in part, for the dramatic success of post-Paleozoic gastropods (Vermeij, 1977; 1978).

SUMMARY

Terebra dimidiata resorbs a thin layer of shell material, 1-2 μm in thickness, from the penultimate whorl surface as the aperture and body whorl advance during growth. The resorption removes the pit and groove micro-sculpture characteristic of the unmodified shell surface of *Terebra dimidiata.* The functional significance of the resorption remains to be determined; it is suggested here that surficial resorption of the penultimate whorl may enhance structural integrity of the shell by providing a surface better suited for deposition of new shell material.

Surficial resorption of the penultimate whorl occurs throughout the Prosobranchia but not in all species. The most reasonable explanation for the broad distribution of this feature is that it is a primitive character of the class. Superficial resorption could have been a preadaptation or evolutionary precursor to other forms of gastropod shell dissolution.

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On the Affinities of Septibranchia (Bivalvia)

BY

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(1 Text figure)

UNTIL RECENTLY the Poromyoidea and Cuspidarioidea were classified as Septibranchia, occasionally also including the Verticordioidea. According to the investigations by NAKAZIMA (1967), ALLEN & TURNER (1974), and BERNARD (1974), the Verticordioidea are clearly related to the Anomalodesmata (= Pholadomyina) and are therefore reclassified as a mere family group within the latter (*cf.* SALVINI-PLAWEN, 1980). Whereas the verticordioidean septa are viscerally innervated as are the bivalve gills, the septa in Septibranchia *s. str.* (= Poromyida) are directly innervated from the cerebral ganglia (*cf.* PLATE, 1897; BERNARD, 1974): Thus, with respect to the cerebrally-innervated septum, the origin of the Poromyoidea and Cuspidarioidea "up to now remains enigmatic" (SALVINI-PLAWEN, 1981: 270).

In connection with anatomical research we noticed the particular innervation of the gills in several Heterodonta, especially in *Mya* (Figure 1), as reported by PELSENEER (1891) as well as DAKIN (1910), and as summarized by STORK (1934): There is a fairly gradual separation of the branchial nerve from its wholly visceral origin towards a partially cerebral origin. As far as has been investigated, this progressive trend is represented by conditions in the genera *Mactra/Spisula—Venus/Tapes* or *Pholas/Teredo—Mya;* it is interesting to point out the fact that in this respect the Solenoidea *(Ensis)* show a conservative condition—as is typical for other bivalves (*cf.* PELSENEER, 1891; LIST, 1902; STORK, 1934). In Septibranchia *(s. str.),* the septum is innervated solely by a side branch of the cerebrovisceral connective since it separates from the latter fairly close to the cerebral ganglia; in addition, in *Cuspidaria obesa* there are two nerves each leading from the cerebropedal connective to the septum (PLATE, 1897). Owing to the fact that the branchial nerves in several Heterodonta, and especially in *Mya* spp. (Figure 1), take their origin in part from the cerebrovisceral connectives, the condition in Septibranchia might well represent a more advanced level of an identical

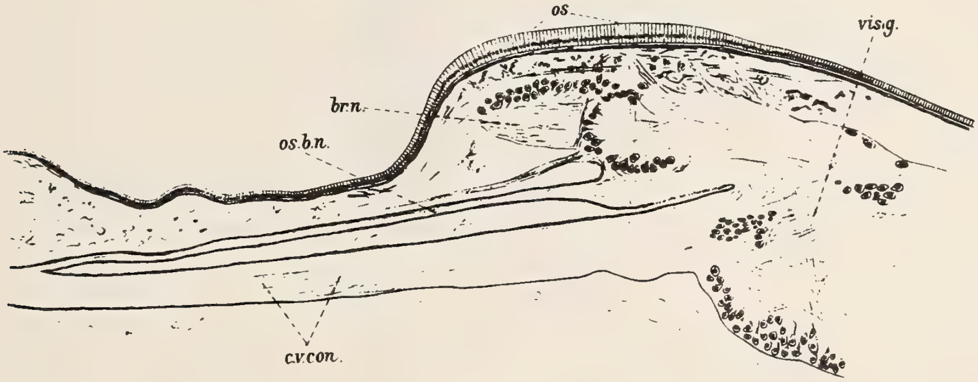

Figure 1

Sagittal section through the visceral and osphradio-branchial ganglion of *Mya truncata* (from DAKIN, 1910)
br. n.—branchial nerve, *c. v. con.*—cerebro-visceral connective, *os*—osphradial epithelium, *os. b. n.*—osphradio-branchial nerve/connective, *vis. g.*—visceral ganglion

trend being intensified by the differentiation of the septum (incorporating some portions of the foot?).

Purchon (1963) suggested a possible relationship of the septibranch and protobranch stomach, the similarities of which, however, are probably due to the correlation with food (*cf.* Allen & Turner, 1974: 516 f; Salvini-Plawen, 1980: 263); an autobranch-eulamellibranch origin of the septibranchs, therefore, is not contradicted—as indeed later accepted by Purchon himself (1978: 432). The classification of the Septibranchia (Poromyida) within the Anomalodesmata (Newell, 1969; Runnegar, 1974) refers mainly to the relationship of the Verticordioidea to the Pholadomyina, but not to the Poromyida which are fairly different (*cf.* Bernard, 1974). Moreover, Yonge (1957) and Runnegar (1974) underline the differences between the Poromyidae and Cuspidariidae, thus suggesting diphyletic origin; the respective characters include the structure of the inner shell layer (nacreous to homogeneous in Cuspidariidae), the elaboration of the siphons (with sheath in Cuspidariidae), and the structure of the septum. Accordingly, the conformities in Cuspidariidae and Poromyidae and/or Verticordiidae would be the result of convergence—which condition depreciates all mentioned characters as being phylogenetically unreliable. More recently, however, Yonge (1978: 245) pleads for a monophyletic origin of the special ligament condition with a lithodesma in Anomalodesmata as well as in Septibranchia (Poromyida). If so, the similarities existing between Septibranchia and Heterodonta in the innervation of the gills and septa, respectively, (as well as in the labial palps, etc.) would be set aside and would then likewise express mere analogies.

With respect to the high degree of convergences in structures of Bivalvia, no classification at the present state of knowledge will remain undisputed and wholly satisfactory in terms of evolutionary pathways (*cf.* Newell, 1969; Salvini-Plawen, 1980). The present communication, however, points to a character overlooked so far which strongly supports the diphyletic origin of at least the pseudo-septibranch Verticordioidea and the (eu-)septibranch Poromyida. Yet there is no consensus on whether or not the Poromyida took their origin in the Anomalodesmata (as independently did the Verticordioidea), or if they are derived from some stock within the Heterodonta.

SUMMARY

The partially cerebral innervation of the gills in some Heterodonta suggests an intermediate condition between the visceral supply of the gills in most other bivalves and the solely cerebral innervation of the septa in Poromyida (Septibranchia *s. str.*). This condition supports the diphyletic state of pseudo-septibranch Verticordioidea (Anomalodesmata) and (eu-)septibranch Poromyida—be it due to a convergent differentiation within the Anomalodesmata or due to an analogous origin from Anomalodesmata and Heterodonta, respectively.

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NOTES & NEWS

A. S. Z.

The 1982 Meeting of the American Society of Zoologists and American Microscopical Society, Animal Behavior Society, Crustacean Society, International Association of Astacology, and Society of Systematic Zoology will be held at the Galt House in Louisville, Kentucky from December 27 to December 30, 1982. A call for papers went out in April and the deadline for abstracts is August 27, 1982.

There are 14 symposia tentatively planned.

For detailed information contact Mary Wiley, Business Manager, American Soceity of Zoologists, Box 2739 California Lutheran College, Thousand Oaks, California 91360. Telephone: 805 492-3585

U. M. E.

The Eighth International Malacological Congress, sponsored by the Unitas Malacologica, will be held in Budapest, Hungary, in 1983, in the period from August 29 to September 3. Detailed information may be obtained by writing to László Pintér, Natural History Museum, Baross u. 13, H–1088 Budapest, Hungary.

Subscription Rates and Membership Dues

At its regular meeting on October 27, 1981, the Executive Board of the California Malacozoological Society decided, in spite of inflationary pressures, to maintain the same dues and subscription schedules as are in effect at present. This means that membership dues (which include a subscription to the Veliger) will remain at US$ 18.50 plus mailing charges of US$ 1.50 for domestic addresses and US$ 5.00 for all foreign addresses (including Canada and Mexico). The initiation fee for new members remains at US$ 2.00; reinstatement fee, due if membership renewals are not made to reach the Society on or before April 15 preceding the start of the new volume, will also remain at the old level of US$ 1.00. Further, the need for a new application for membership and the payment of a new initiation fee, if membership has been permitted to lapse through non-payment of dues for 11 months after the original deadline was reaffirmed. Similarly, the need to require the inclusion of a self-addressed, stamped envelope, if a receipt is required, was re-affirmed.

In view of the deplorable fact that the postal services throughout the world seem to become ever more expensive and also more unreliable, members are urged to lodge complaints for intolerable delays in deliveries of their journals with their local postmasters. Most likely, this will not result in better service, at least not immediately, but it may be hoped that in the long run it will lead to some improvement. Complaints to the Society cannot lead to any improvement, since we already do more than the requirements of the postal service in respect to second class mailings stipulate.

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.

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$25.00 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.

We think it important to bring to the notice of all our actual and potential correspondents that the postal fee for registered articles is the highest in the world: $3.25, regardless of destination. Further, to certain countries it is not possible to have mail pieces insured or registered. In the cases where the prospective recipient desires our communications sent as registered article, we must expect advance payment of that fee. We are unable to return manuscripts (either for reworking or with the recommendation that they be submitted elsewhere) other than by ordinary surface mail. In view of the ever more deteriorating postal services in most countries, we can obviously not assume any responsibility for the safe delivery of any items we must dispatch. Our responsibility must and does end with our delivery to the post office of any item.

Sale of C. M. S. Publications:

Effective September 1, 1981, all back volumes still in print, both paper covered and cloth bound, will be available only from "Seashell Treasures Books," 646 30th Street, San Diego, California 92102. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Pisor at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from "Seashell Treasures Books" are as follows:
Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:
[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]
Supplement to Volume 6: out of print.
Supplement to Volume 7: available again; see announcement elsewhere in this issue.
Supplement to Volume 11:
[The Biology of *Acmaea* by Prof. D. P. Abbott *et al.*, ed.]
Supplement to Volume 14:
[The Northwest American Tellinidae by Dr. E. V. Coan]
Supplement to Volume 16:
[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]
[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]
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.

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 through Volume 6: $9.00 each.
Volume 7 through Volume 12: $12.00 each.
Supplement to Volume 6: $3.00; to Volume 18: $6.00
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, 359 Roycroft Avenue, Long Beach, California 90814.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from "Seashell Treasures Books," 646 30th Street, San Diego, CA 92102. Orders should be sent directly there.

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 may be obtained by sending a self-addressed, stamped envelope to the Veliger, 1584 Milvia Street, Berkeley, CA(lifornia) 94709. Foreign correspondents should enclose one international postal reply coupon. Requests for the list, for which return postage is not provided, will be ignored.

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.

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.

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 First Interstate Bank (formerly United California Bank). This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable, except as indicated elsewhere in this section.

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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.- 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.

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. The following charges must be made:

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.

Policy Regarding Reprints

It seems necessary to bring the following points to the notice of prospective authors:

All manuscripts submitted for inclusion in The Veliger are subject to review by at least two scientists; acceptance is entirely on the basis of merit of the manuscript. Although many scientific journals assess page charges, the Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought.

Similarly, while it was hoped at the "birth" of The Veliger, that a modest number of reprints could be supplied to authors free of charge, this has not as yet become possible. We supply reprints at cost. Unfortunately, in recent years it has become "fashionable" for some authors and some institutions to ignore paying for reprints ordered and supplied in good faith or to delay payment for a year or more. This causes financial losses to the Society since our debts are paid promptly. Since the Society is in fact not making any profit, it is necessary to introduce a policy which, it is hoped, will protect us against negligence or possible dishonesty. In the case of manuscripts from sources outside of the United States, if a manuscript is accepted, we will inform the author of the estimated cost of reprints and require a deposit in U. S. funds to cover these costs. If such a deposit is not made, we will not supply any reprints. In the case of non-payment by domestic authors or institutions, we will pursue legal recourses.

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 $400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, $400.-). 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.

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.

BOOKS, PERIODICALS, PAMPHLETS

James Graham Cooper — Pioneer Western Naturalist

by EUGENE COAN. University Press of Idaho: Moscow, Idaho. 255 pp.; 31 figs. in text; portrait frontispiece. Title page dated 1981, but issued February 1982. $12.95, soft cover.

Although Cooper was an active collector in the heyday of western exploration, little has been written about him and his work. Coan has remedied this by searching out his journals and letters, now scattered in a dozen libraries, and letting excerpts from these tell the story. Born in New York, Cooper trained as a medical doctor. He was employed by several expeditions as surgeon-naturalist, and he collected for the Smithsonian Institution. He was with the Pacific Railroad Survey in Washington Territory in 1853-54, with a party that was trying to find a pass through the Cascades. His extensive marine collecting, however, did not begin until 1861, after he was with a military expedition that crossed the continent, reaching the coast, again, in Washington. Transferred to California, he soon met members of the California Geological Survey and by 1861 was offered employment on a program to review the natural resources of the state. He went first to Monterey, dredging and shore-collecting. The survey had a precarious existence for several years, but he continued work, submitting several reports on shells and fossils, even after the survey formally was dissolved. He then went into private medical practice but kept a lively interest in malacology, continuing to publish on both marine and land shells. In his later years he became especially interested in the fauna of Baja California. He died in Hayward, California, in 1902.

Coan's account provides not only a complete bibliography of works by and about Cooper but also a list of his zoological taxa, with location of type material and notes on taxonomic status for each of the species. Although Cooper published most on Mollusca, he also described a number of vertebrates (several kinds of fish, reptiles, birds, and mammals), one insect, and two fossil brachiopods.

It is ironic that 80 years had to elapse before a competent review was published on this interesting life and on the very real contribution that Cooper made to West American science. From now on his name as authority on a species-label should have more meaning to us, for his story, told in his own words, evokes for us the image of an engaging personality.

A. Myra Keen

Maryland's Oysters: Research and Management

by VICTOR S. KENNEDY and LINDA L. BREISCH. University of Maryland Sea Grant Program Number UM-SG-TS-81-04. 286 pp. Available at $8.00 from the Communications Program, Maryland Sea Grant Program, University of Maryland, College Park, MD 20742. 1981

Maryland's Oysters: An Annotated Bibliography

by VICTOR S. KENNEDY and LINDA L. BREISCH. University of Maryland Sea Grant Program Number UM-SG-TS-81-05. 51 pp. Available at $3.00 from the same address. 1981

Profusely illustrated with text figures, charts, maps and photographs, the paper on research and management is also a well written review of the important literature with critical comments and recommendations for future work. Although the orientation is entirely toward more efficient production of marketable oysters, there is much basic information of broader scientific interest. It is especially useful as a survey of the literature of the 18 years since Galtsoff's monumental work on the "American Oyster." There are 53 pages of references cited, some from regions beyond Maryland. The paper ends with an additional 56 page bibliography of papers dealing directly with Maryland oysters. There is much overlap, of course, but the latter list has a summary paragraph for each entry.

The second paper cited above is merely a reprint of the last 56 pages of the first paper, with changes of pagination. An earlier, more extensive annotated bibliography of world-wide references on oysters was published by the Maryland Sea Grant Program and reviewed by STOHLER (1981, The Veliger **23** (4): 382). Neither of these papers bears a date of publication as such; the date is hidden in the "Publication Number," a disruptive innovation of Sea Grant Program Publications in general. The first letters indicate the university, the SG means 'Sea Grant,' TS means 'Technical Series;' the first numbers indicate the last two numbers of the year of publication; the last two numbers are the actual publication number, which may start with one each year, or may not, according to the university.

Harold W. Harry

Acmaeidae: Gastropoda, Mollusca

by David R. Lindberg. xii + 122 pp. Boxwood Press, Pacific Grove, California. $12.50 1981

(The second volume in the series *Invertebrates of the San Francisco Bay Estuary System,* Welton Lee, Editor)

While still in graduate school, David Lindberg established himself as a world authority on acmaeid limpets and set new, uncompromising standards for the integration of detailed anatomical and ecological data into traditional taxonomy and systematics. His book on the acmaeid limpets of San Francisco Bay transcends the local geographic focus of the series and provides an excellent overview of the morphology, anatomy, systematics, distribution, and ecology of this taxonomically difficult group of common intertidal gastropods.

Techniques for study and identification of limpets are carefully described. A pictorial glossary provides an unusually fine clarification of terminology; and taxonomic by photographs of at least three views; and drawings of both the radular teeth and the configuration of the basal by photographs of at least tree views; and drawings of both the radular teeth and the configuration om the basal plates are presented in a style that facilitates comparison. One of the most helpful contributions of the book is the careful clarification of the range of ecological forms of a species that can develop on different substrata.

This is a thoroughly scholarly as well as eminently usable reference. Its value is augmented by a bibliography of Pacific Coast acmaeid literature by James T. Carlton.

Carole S. Hickman
Department of Paleontology
University of California

The Audubon Society Field Guide to North American Seashore Creatures

by Norman A. Meinkoth. 799 pp.; illust. Alfred A. Knopf, New York. $12.50 1981

Although the Audubon Society's Field Guide to Seashore Creatures does not deal exclusively with mollusks, Norman Meinkoth provides the finest set of photographs of living North American marine mollusks of which I am aware. It also provides an excellent companion to Harald Rehder's Field Guide to North American Seashells (see review by Stohler, The Veliger 24 (4): 384). While Rehder's guide emphasizes the shell, Meinkoth's guide focuses on the animals and their habits. More than 200 species are illustrated in color. Although some of the photographs have been necessarily "posed" (you can't photograph an infaunal clam while it is buried in the sand), many are captured in typical postures and behaviors in their natural habitats, crawling on or attached to natural substrata. Mantle edges, photoreceptors, tentacles, incurrent and excurrent siphons, and beautifully pigmented feet are displayed in action. Epibionts and cryptic encrustations have all been left intact.

One might fault the fact that the spirally coiled worm tube of *Spirorbis* is illustrated with the snails, and brachiopods appear among the cockles. But this is simply an attempt to group animals according to the most obvious shapes and colors one sees in the field. The text is arranged taxonomically and clarifies morphological distinctions as well as providing a wealth of ecological information.

Carole S. Hickman
Department of Paleontology
University of California

Gastropoda Romaniae – Ordo Stylommatophora 3 Suprafamiliile Clausiliacea Achatinacea

by Alexandru V. Grossu. 269 pp.; 140 text figs. Univ. din Bucuresti, Facultatea de Biologie. 1 October 1981

This extensive work is printed in the Rumanian language. Although a three-page summary in German is given, the complexity of the family of the Clausiliidae is too great to allow a succinct review. It must be noted, however, that many taxonomic units are used which are not generally accepted as valid "name bearers." Thus, there is a large number of "frm." [forma] and "mut." [mutant]. The Clausiliidae seem to include dextral as well as sinistral species and matings between such divergent species are reported as having been observed. in the process of mating; it is postulated that some "resulting hybrids" may have been described in the past as species and it is also suggested that such hybridization may indeed lead to species formation. However, the drawings may be unreservedly called adequate.

R. Stohler

Type Specimens of Molluscs in the National Museum of Natural Sciences, National Museums of Canada Ottawa, Canada

by Muriel F. I. Smith. 36 pp. National Museums of Canada Publications in Zoology, No. 15. 1981

This is an important source of information about the holdings of primary type material in the collection of the Museum of Natural Sciences in Ottawa. For each species the name is given, followed by bibliographic citation of original description, what kind of type, locality, collector and remarks. There are 216 primary and secondary types listed.

R. Stohler

La Fauna Malacologica Panameña. I. Punta Paitilla.
Parte 1. – Gasteropodos.
Parte 2. – Bivalvia y Polyplacophoros

by Miguel C. Avilés E. Thais Publicaciones Diversas de la Sociedad Panameña de Malacologia No. 1; 28 pp. 29 June 1981

The author provides a list of 87 species of gastropods, 36 species of bivalves and 3 of polyplacophorans. Each entry is followed by the synonyms applicable. It should be stressed that this list is based exclusively on the collection of the author. A brief list is also given of taxa reported by other workers (10 species of gastropods). It should be stressed that the collections are restricted to Punta Paitilla at the east end of the Bay of Panama.

It appears that Thais is a new journal, published by the Sociedad Panameña de Malacologia. Information on the Society and its publication is, no doubt, obtainable from Professor Miguel C. Aviles E, Apartado 6-593, Zona Postal El Dorado, Panamá, Republic de Panamá.

R. Stohler

Lista Preliminar de Referencias Bibliográficas Sobre la Fauna Malacológica Panameña

by Miguel C. Avilés E. Thais Publicaciones Diversas de la Sociedad Panameña de Malacologia No. 2; 59 pp. 21 August 1981

This is a list of publications dealing with the malacofauna of the Republic of Panama and with related subjects.

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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Address all other correspondence to Dr. R. STOHLER, *Editor*, Department of Zoology University of California, Berkeley, California 94720, U. S. A.

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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

The Family Lepidochitonidae Iredale, 1914 (Mollusca : Polyplacophora) in the Eastern Pacific

BY

ANTONIO J. FERREIRA

2060 Clarmar Way, San Jose, California 95128

(8 Plates; 40 Text figures)

The study of the chiton fauna of the eastern Pacific has revealed that a number of genera heretofore allocated to different families should, for their similarities, be brought together under a single family for which the family name Lepidochitonidae properly applies.

This paper presents a review of the genera and species of eastern Pacific chitons deemed to belong in Lepidochitonidae. The work is based upon the examination of material in the California Academy of Sciences, Department of Invertebrate Zoology (CASIZ), and Department of Geology (CASG), the U.S. National Museum of Natural History (USNM), the Natural History Museum of Los Angeles County (LACM), the Allan Hancock Foundation (AHF) [at LACM], Stanford University (SU) [at CASG], the San Diego Museum of Natural History (SDNH), the Academy of Natural Sciences of Philadelphia (ANSP), and the private collections of Glenn and Laura Burghardt, Salle Crittenden, George A. Hanselman, and Antonio J. Ferreira (AJF).

The following abbreviations for type-designations are used: M = monotypy; OD = original designation; SD = subsequent designation.

History of the Family Lepidochitonidae

1914. Iredale introduced the family-name Lepidochitonidae for the taxon theretofore known as Callochitonidae Plate, 1899. Thiele (1910) had divided the Callochitonidae into two subfamilies, Trachydermoninae (including *Trachydermon* Carpenter [with section *Craspedochilus* Sars], *Tonicella* Carpenter, *Schizoplax* Dall, *Middendorffia* Carpenter, *Nuttallina* Carpenter, *Mopaliella* Thiele, *Nuttallochiton* Plate, and *Notochiton* Thiele) and Callochitoninae (including *Callochiton* Gray [with subgenera *Icoplax* Thiele and *Trachyradsia* Carpenter] and *Eudoxochiton* Shuttleworth). Iredale pointed out that *Lepidochitona* Gray, 1821, superseded, as senior objective synonym, *Craspedochilus* Sars, 1878, which Pilsbry (1893, 15:63) had equated with *Trachydermon* Carpenter, 1864. Since the List of British Marine Mollusca of the London Conchological Society (1901) had given *Craspedochilus* full generic rank, independent of *Trachydermon*, Iredale concluded that "the acceptance of Thiele's classification and the recognition of *Lepidochitona*" (p. 127) would require that [in accordance with the then operative nomenclatural rule that the name of a family be based on the name of the oldest genus in it] Thiele's proposed family and subfamily names be repealed in favor of Lepidochitonidae (for Callochitonidae) and Lepidochitoninae (for Trachydermoninae).

1917b. Berry referred *Tonicella* and *Schizoplax* to Callochitonidae.

1918. Dall regarded *Trachydermon* a junior synonym of *Lepidochitona* with two sections, *Tonicella* and *Cyanoplax*, and one subgenus, *Spongioradsia.*

1921. Dall included *Lepidochitona, Tonicella, Basiliochiton, Cyanoplax, Spongioradsia, Schizoplax,* and *Nuttallina* in Lepidochitonidae.

1922. Berry accepted Lepidochitoninae (as a subfamily of Callochitonidae) to cover *Lepidochitona, Tonicella, Cyanoplax, Nuttallina,* and *Oligochiton* (fossil).

1925. Iredale & Hull defined Lepidochitonidae based on species now allocated to Callochitonidae Plate, 1899.

1929. Thiele defined Lepidochitonidae on the basis of "Shell surface uniformly granular, rarely with weak radial or longitudinal riblets, or even more exceptionally with ordered strong granules. Anterior and posterior valves with a variable number of slits. Eaves spongy. Girdle with small elongated scales or spicules on the upper surface, which may be arranged in groups. Radula second lateral tooth with a tricuspid head." [translation] (p. 7), dividing it into Lepidochitoninae (shell without eyes; sutural plates separated by a sinus; radula's *Seitenplatte* with pectinated blade), and Callochitoninae (shell with eyes; sutural plates merging and continuous; radula's *Seitenplatte* with the edge entire, or without shaft and blade). Lepidochitoninae included *Lepidochitona, Spongioradsia, Cyanoplax, Basiliochiton, ? Subterenochiton, Tonicella, Mopaliella, Middendorffia, Nuttallina, Nuttallochiton* and *Notochiton.*

1933. **Bergenhayn** considered Callochitoninae a subfamily of Ischnochitonidae, making no mention of *Lepidochitona* Gray.

1947a,b. **Smith** included *Lepidochitona, Tonicella, Schizoplax, Spongioradsia, Cyanoplax,* and *Nuttallina* in Lepidochitonidae.

1952. **Jakovleva** treated *Tonicella, Schizoplax* and *Lepidochiton* [sic] Gray, 1821 in Lepidochitonidae.

1955. **Bergenhayn** revised the classification of chitons and reverted to the use of *Trachydermon* placed, together with *Tonicella,* in Ischnochitonidae. *Nuttallochiton, Nuttallina, Notochiton,* and *Middendorffia* were placed in Callistoplacidae; *Schizoplax* became the basis for a new family, Schizoplaxidae; *Callochiton* and *Eudoxochiton* were grouped under Callochitonidae. Again, he made no mention of *Lepidochitona* Gray.

1956. **Leloup** included *Tonicella, Nuttallina, Nuttallochiton,* and *Callochiton* in Lepidochitonidae.

1960. **Fischer-Piette & Franc** recognized *Lepidochitona* Gray (as senior synonym of *Trachydermon*), together with *Tonicella,* under Ischnochitonidae.

1960. **Smith** adopted **Bergenhayn's** (1955) classification, and suppressed Lepidochitonidae as synonym of Ischnochitonidae. *Lepidochitona, Tonicella, Cyanoplax,* and *Basiliochiton* were included in Ischnochitonidae; *Nuttallina, Middendorffia* and *Nuttallochiton* in Callistoplacidae; *Schizoplax* remained the only representative of Schizoplacidae [name corrected therein].

1971. **Thorpe** (*in* Keen) placed *Mopaliella* and *Nuttallina* in Lepidochitonidae.

1972. **Kaas** recognized Lepidochitonidae for *Lepidochitona.*

1974. **Abbott** omitted Lepidochitonidae, placing *Lepidochitona, Tonicella,* and *Cyanoplax* in Ischnochitonidae.

1977. **Van Belle** considered Lepidochitoninae a subfamily of Ischnochitonidae with *Lepidochitona* (with *Spongioradsia,* and *Mopaliella* as subgenera), *Nuttallina, Tonicella* (with *Tonicina* as subgenus), *Ceratozona,* and *Middendorffia. Basiliochiton* and *Dendrochiton* were regarded synonyms of *Mopaliella. Schizoplax* was allocated to Schizoplacinae, and *Nuttalochiton* to Chaetopleurinae, both subfamilies of Ischnochitonidae.

1977. **Sirenko & Starobogatov** proposed a new classification of chitons with no mention of Lepidochitonidae.

1978. **McLean** included *Lepidochitona, Cyanoplax,* and *Nuttallina* in Lepidochitonidae.

1978. **Van Belle** changed his (1977) composition of Lepidochitoninae by removing *Ceratozona* (referred to Callistoplacinae), adding *Juvenichiton* Sirenko, 1975, and lowering *Middendorffia* and *Dendrochiton* (with *Basiliochiton* as synonym) to subgenera of *Lepidochitona.*

SYSTEMATIC ACCOUNT

Polyplacophora Gray, 1821

Neoloricata Bergenhayn, 1955

Ischnochitonina Bergenhayn, 1930

Lepidochitonidae Iredale, 1914

Definition: Relatively small chitons, with tendency to have brilliant colors. Tegmentum's sculpture simple or absent. Lateral areas weakly defined. Posterior valve frequently smaller than anterior valve. Girdle's upper surface paved with simple, small scales, round to oval in cross section, juxtaposed rather than imbricated, and, often hyaline spicules, or hair-like corneous formations interspersed or somewhat bunched at the sutures. Eaves spongy. Sutural laminae usually small, often triangular, separated by a well defined sinus. Insertion teeth about 8 in the anterior and posterior valves, 1 (sometimes 2) in the intermediate valves. Radula with tricuspid major lateral teeth.

Type-genus: *Lepidochitona* Gray, 1821

Synonyms: Tonicelloidea Simroth, 1894 (in part)
Trachydermoninae Thiele, 1910

Remarks: The family Lepidochitonidae Iredale, 1914, was erected to cover mostly Australian and Neozelanic species ("the majority of [its] species live in the southern hemisphere," **Iredale & Hull,** 1925: 347) but as here defined it seems to be confined to the northern hemisphere, instead. The "lepidochitonids" cited by **Iredale & Hull** (1925; 1927; 1929; 1930) in Australia and New Zealand waters are now regarded as members of the family Callochitonidae Plate, 1899, a more evolutionarily advanced group of chitons having no immediate connection with the lepidochitonids of the northern hemisphere.

As currently understood, the taxon Lepidochitonidae corresponds very closely to **Thiele's** (1910) subfamily Trachydermoninae which name was replaced by **Iredale's** (1914) Lepidochitoninae. In part, it corresponds also to Tonicelloidea Simroth, 1894, a "tribus" of the family Ischnochitonidae containing the genera *Schizoplax, Tonicella, Callochiton* and *Trachydermon.* Simroth's name (in the amended form, Tonicellidae) has been cited only in synonymy (**Smith** 1960; **Van Belle,** 1977), and its use in a classification scheme (such as that of **Sirenko & Staro-**

BOGATOV, 1977) is contrary to nomenclatural stability. Despite varying interpretations, the family name Lepidochitonidae has had general acceptance, and in the spirit of the International Code of Zoological Nomenclature (1964) [ICZN] (Preamble and Article 40-a) there seems to be no compelling reason to alter a conservative stand.

As here understood, Lepidochitonidae differs from Ischnochitonidae Dall, 1889 (as defined by Smith, 1960) in several significant features: 1) the essentially sculptureless tegmentum with weakly defined lateral areas, 2) the girdle with minute, simple, juxtaposed scales, often with interspersed hairs or glassy spicules (instead of the larger, imbricated, usually striated scales of ischnochitonids), 3) the small posterior valve, 4) the small sutural laminae and 5) the spongy eaves. It differs from Callochitonidae Plate, 1899 in 1) absence of shell eyes, 2) sutural laminae clearly separated by a sinus (connected or continuous in callochitonids), 3) intermediate valves with 1, or rarely 2 slits (with 3 or more slits in callochitonids) and 4) end valves with about 8 slits (with more than 12 slits in callochitonids).

Table 1

Length of the gill row in several species of Lepidochitonidae, as percentages of the length of foot.

Species	Gills % of foot
Lepidochitona	
cinerea (Linnaeus, 1767)	70
corrugata (Reeve, 1847)	80
liozonis (Dall & Simpson, 1901)	70
rosea Kaas, 1972	80
dentiens (Gould, 1846)	80
hartwegii (Carpenter, 1855)	100
beanii (Carpenter, 1857)	80
flectens (Carpenter, 1864)	80
lowei (Pilsbry, 1918)	100
keepiana Berry, 1948	90
Dendrochiton	
gothicus (Carpenter, 1864)	60
thamnoporus (Berry, 1911)	70
semiliratus Berry, 1927	70
lirulatus Berry, 1963	70
Tonicella	
marmorea (Fabricius, 1780)	80
rubra (Linnaeus, 1767)	70
lineata (Wood, 1815)	80
insignis (Reeve, 1847)	90
Nuttallina	
californica (Reeve, 1847)	60
crossota Berry, 1956	60
Schizoplax brandtii (Middendorff, 1847)	90
Spongioradsia aleutica (Dall, 1879)	60

The lepidochitonids, with their simple body-plan, featureless tegmentum, rudimentary girdle elements, short sutural laminae, and merobranchial gills (Table 1) should be regarded as relatively primitive in the evolution of chitons. Already PILSBRY (1893, 15:63), referring to *Trachydermon,* observed that "The genus is one of great antiquity, being the least differentiated of the Ischnochitonidae." In evolutionary terms, the lepidochitonids appear to occupy a place between the much simpler lepidopleurids on one side, and the more advanced ischnochitonids and mopaliids on the other.

At current count there are 23 species of lepidochitonids in the north Pacific (of which 18, in 6 genera, are members of the eastern Pacific fauna), and some 10 species (in 2 genera) in the north Atlantic. Only 2 genera, *Lepidochitona* and *Tonicella,* and 2 species, *T. marmorea* and *T. rubra,* are common to both oceans.

The distribution of the species and genera of Lepidochitonidae suggests that an ancestral lepidochitonid-stem was divided by the closure of the Tethyan seaway with the emergence of the Panamic isthmus; in the Pacific, the parental population of *Lepidochitona* evolved and gave rise to several other genera (such as *Schizoplax, Dendrochiton,* and *Spongioradsia*), while in the Atlantic it remained relatively static, at least at the generic level.

The following 6 genera are here recognized as members of the family Lepidochitonidae, all present in the eastern Pacific:

Lepidochitona Gray, 1821
Nuttallina Dall, 1871
Tonicella Carpenter, 1873
Schizoplax Dall, 1878
Spongioradsia Pilsbry, 1894a
Dendrochiton Berry, 1911

The geographic range of the species of Lepidochitonidae in the eastern Pacific is summarized in Figure 1.

The allocation of *Juvenichiton* Sirenko, 1975 (with *Micichiton* Sirenko, 1975, and *Nanichiton* Sirenko, 1975, as synonyms) to Lepidochitonidae was recommended by VAN BELLE (1978). But, although shell and girdle features of *Juvenichiton* have lepidochitonid-like features, the radula with only 11-13 teeth per row represents such a departure from all other known chitons (with 17 teeth per row) as to suggest a definite taxonomic distinction at the family level.

Lepidochitona Gray, 1821

Definition: Small in size. Tegmentum sculptureless, smooth or microgranular. Lateral areas weakly defined. Sutural laminae often triangular; sinus wide. Girdle with juxtaposed (i.e., not imbricated) simple, small round to oval scales, and, in some species, also with hyaline spicules or corneous bristles ("hairs") interspersed.

Figure 1

Geographical range of species of Lepidochitonidae in the eastern Pacific

Type-species: *Chiton marginatus* Pennant, 1777 [= *Chiton cinereus* Linnaeus, 1767] by M.

Synonyms:

Trachydermon Carpenter, 1864
  Type: *Ischnochiton (Trachydermon) flectens* Carpenter, 1864, by SD, Pilsbry, 1893.
Craspedochilus Sars, 1878
  Type: *Chiton marginatus* Pennant, 1777 [= *Chiton cinereus* Linnaeus, 1767], by M.
Middendorffia Dall, 1882a [*nomen correctum* Fischer, 1885 (*pro Middendorfia* Dall, 1882a)]
  Type: *Chiton polii* Philippi, 1836 (not Deshayes, 1833) [= *Chiton corrugatus* Reeve, 1847, *fide* Kaas, 1974] by OD.
Beanella Dall, 1882a *(nomen nudum)*
  Type: *"Chiton rissoi* Cuming" Dall, 1882, *nomen nudum* [not *Chiton rissoi* Payraudeau, 1827] replaced by *"C. pseudorissoi* Cpr. MS." Dall, 1882, also a *nomen nudum.*
Cyanoplax Pilsbry, 1892
  Type: *Chiton hartwegii* Carpenter, 1855, by SD, Pilsbry, 1893.

Adriella Thiele, 1893
  Type: *Chiton variegatus* Philippi, 1836 [= *Chiton cinereus* Linnaeus, 1767], by M.
Mopaliopsis Thiele, 1893
  Type: *Chiton cingillatus* Reeve, 1847 [= *Cyanoplax hartwegii* (Carpenter), *teste* Thiele, 1909] by M.
Mopaliella Thiele, 1909
  Type: *Chiton bipunctatus* Sowerby, 1832, by M.
Craspedochiton "Sars," Dall, 1918 [error for *Craspedochilus*] (not Shuttleworth, 1853)
Basiliochiton Berry, 1918
  Type: *Mopalia heathii* Pilsbry, 1898a, by OD.
Lophochiton Berry, 1925 (not Ashby, 1923)
  Type: *Basiliochiton lobium* Berry, 1925, by OD.
Ploiochiton Berry, 1926a (new name for *Lophochiton* Berry, 1925, not Ashby, 1923)
Lepidochiton "Gray, 1821" Thiele, 1929 (not Carpenter, 1857) [*nomen vanum*]
  Type: *Chiton marginatus* Pennant, 1777 [= *Chiton cinereus* Linnaeus, 1767] by M.

Remarks: *Lepidochitona cinerea* (Linnaeus, 1767), type-species of *Lepidochitona* Gray, 1821, is widely distributed in European waters, from Lofoten, Norway [68°30′ N; 15°00′ E] (*teste* Dall, 1879), through the western coast of Europe to the Mediterranean and Black Seas (Van Belle, 1978). Specimens up to 2 cm in length, carinate, varying in color from drab gray to green; valves slightly beaked, sculptureless except for minute granules mostly in quincunx; posterior valve narrower than anterior valve; eaves spongy; slit formula 9/11-1-9/12; girdle paved with minute scales oval to circular in section, not imbricated; gills extend along about 75% of foot. Jakovleva's (1952: 68) report of *Lepidochitona cinerea* [as *L. marginatus*] in the Pacific ocean is in error.

Carpenter (1864) established *Trachydermon* as a subgenus of *Ischnochiton* (and later, 1873, raised it to full generic rank), with 2 species (in one list on p. 612) *Ischnochiton (Trachydermon) pseudodentiens* Carpenter and *I. (Trachydermon) gothicus,* and 8 species (in another list on p. 649) *I. (Trachydermon) retiporosus* Carpenter, *I. (T.) interstinctus* Gould, *I. (T.) trifidus* Carpenter, *I. (T.) pseudodentiens* Carpenter, *I. (T.) gothicus* Carpenter, *I. (T.) hartwegii* Carpenter, *I. (T.) nuttalli* Carpenter, and *I. (T.) flectens* Carpenter. He did not designate a type-species.

Dall (1879) named *Chiton cinereus* Lowe as type-species of *Trachydermon* (an invalid designation, since *C. cinereus* Lowe is not in Carpenter's original list). In 1893, Pilsbry selected *Trachydermon flectens* (Carpenter, 1864) as type-species of *Trachydermon* ignoring the question whether Carpenter's (1864) "original list" consisted of only 2 or of 8 species. Since both lists are part of the same work,there seems to be no further reason to question the validity of Pilsbry's selection. In 1914, Iredale, recognizing *Lepidochitona* Gray as senior synonym of *Craspedochilus* Sars, substituted Lepidochitonidae for Callochitonidae, and Lepidochitoninae for Trachydermoninae; but he retained *Trachydermon* as subgenus of *Lepidochitona.* In 1918, Dall misinterpreted Iredale's (1914) action, and named *"C. pseudodentiens* Cpr. (= *dentiens* Gould)" as type of *Trachydermon* [on the assumption that Pilsbry, 1893, was not correct in accepting Carpenter's (1864: 649) eight species list]. In the same year, Berry (1918: 12) affirmed that the name *Trachydermon* was preoccupied and, as such, not available. But Palmer (1958: 285) pointed out that "although there are several uses of *Trachyderma*... the appellation of *Trachydermon* has not been used other than that of Carpenter," and quoted the consulted opinion of Prof. Henry Poirier to the effect that *Trachydermon* should not be rejected on account of its having the same origin and meaning as *Trachyderma.* This view is clearly in agreement with the current Code (ICZN, Article 56-a).

Middendorffia Dall, 1882a, was described as *"Lorica et zona extus ut in Acanthopleura; laminae acutae, extus rugosa, suffultae; sinus planatus haud laminatus*... Internally Ischnoid, externally Acanthopleuroid" (p. 287). In a tabular form, Dall (1882a: 289-290, tbls. 1-2) added: insertion plates regular, branching; slit formula 9-1-8; insertion teeth propped, smooth; eaves moderate, spongy; sinus simple; laminae separated; and girdle with "granular bristles." Its only representative, *Middendorffia corrugata* (Reeve, 1847), [often cited as *Middendorffia caprearum* (Scacchi, 1836), a *nomen dubium*], is essentially a Mediterranean species (Sabelli & Spada, 1971). My examination of specimens of *M. corrugata* from several localities in the Mediterranean demonstrated that the species belongs in *Lepidochitona,* since its distinguishing features (granulose tegmental surface, larger scale-like girdle elements, and forward directed insertion teeth in the posterior valve) are of less than subgeneric significance.

Pilsbry (1892) erected *Cyanoplax* as a subgenus of *Tonicella* Carpenter, 1873, to accommodate *Chiton hartwegii* Carpenter, 1855, and *Chiton bipunctatus* Sowerby, 1832. *Cyanoplax* was said to differ from *Tonicella s.s.* "in the long gills, different girdle, stumpy, bilobed anterior teeth, etc.," and from *Trachydermon* Carpenter, 1864, in "the peculiar blunt teeth, ambient gills and almost scaleless girdle" (Pilsbry, 1892: 44-45). Although *Cyanoplax,* often elevated to generic rank, has been accepted by most chiton workers, the distinctions are not enough to warrant segregating it from *Lepidochitona.* The relative length of the gills is a variable feature in *Lepidochitona* (Table 1), and the "stumpy, bilobed anterior teeth," only apparent in some larger specimens, does not seem to be a character of supraspecific importance. Van Belle (1977) apparently arrived at the same conclusion by placing *Cyanoplax* in the synonymy of *Lepidochitona.*

Thiele (1893) erected *Mopaliopsis* upon the radular characteristics of a specimen at first identified as *Chiton cingil-*

latus Reeve, 1847, but later (1909: 16) recognized as *Cyanoplax hartwegii* (Carpenter).

Mopaliella Thiele, 1909, was segregated from *Lepidochitona* solely for the presence of scattered hyaline spicules in the girdle, a distinction of less than generic or subgeneric relevance.

Basiliochiton Berry, 1918, was characterized by the presence of branching corneous bristles in the girdle. Since in all other respects (sculptureless tegmentum, small posterior valve, merobranchial gills, spongy eaves, tricuspid radula) the single species assigned to *Basiliochiton* conforms to the same body plan as that of *Lepidochitona*, the presence of girdle bristles seems to be of insufficient taxonomic significance to justify generic distinction.

Ploiochiton Berry, 1926 (new name for *Lophochiton* Berry, 1925, not Ashby, 1923), was erected as a subgenus of *Basiliochiton*. Smith (1960) placed *Ploiochiton* in the synonymy of *Basiliochiton*, whereas Thorpe (*in* Keen, 1971) and Van Belle (1977) regarded it as a synonym of *Mopaliella*. *Basiliochiton lobium* Berry, 1925, type species of *Ploiochiton*, has been recognized (Thorpe *in* Keen, 1971; Ferreira, herein) as conspecific with *Lepidochitona beanii* (Carpenter, 1857).

Lepidochitona, as here understood, is present in the eastern Pacific and in the Atlantic. It is represented by 3 species in the western Atlantic, *L. liozonis* (Dall & Simpson, 1901), *L. rosea* Kaas, 1972, and *L. montoucheti* Righi, 1973; 3 species described from the Canary Islands, *L. piceola* (Shuttleworth, 1853), *L. canariensis* (Thiele, 1909), and *L. stromfelti* (Bergenhayn, 1931); and 2 species in European waters, *L. cinerea* (Linnaeus, 1767), and *L. corrugata* (Reeve, 1847).

In the eastern Pacific, *Lepidochitona* is represented by 6 species:

Lepidochitona dentiens (Gould, 1846)
Lepidochitona hartwegii (Carpenter, 1855)
Lepidochitona beanii (Carpenter, 1857c)
Lepidochitona flectens (Carpenter, 1864)
Lepidochitona lowei (Pilsbry, 1918)
Lepidochitona keepiana Berry, 1948

The combined geographical range of the 6 different species of *Lepidochitona* in the eastern Pacific extends from Alaska to Peru, between latitudes 60° N and 5° S. (Figure 1).

Trachydermon sharpii Pilsbry, 1896, based on two specimens from Unalaska, Alaska, has been misassigned to *Lepidochitona* by authors following Dall (1921: 188). The extant syntype (ANSP 69140), here designated as lectotype (Figure *2*) is 15 mm long, dried, relatively flat; uniformly white; tegmentum microgranular, sculptureless except for vague concentric growth lines; lateral areas weakly defined; mucro central; articulamentum white; sutural laminae narrow; sinus shallow; insertion teeth small; slits 16-2(1)-13; girdle covered with imbricated, long, cylindrical scales. It corresponds in all of its features to *Stenosemus albus* (Linnaeus, 1767), as confirmed by direct comparison with specimens of *S. albus* from Alaska (LACM 73-23), and Norway (*ex* P. Kaas Colln.).

Lepidochitona dentiens (Gould, 1846)
(Figures *3*, *4*, 5, 6, *7*, *33*)

Chiton dentiens Gould, 1846: 145 (reprinted, 1862: 6); 1852: 321 m, 433 a-b (in subgen. *Onithochiton*); 1862: 242.—Orcutt, 1885: 544 (in subgen. *Trachydermon*)

Ischnochiton dentiens (Gould). Carpenter, 1864: 649 (in subgen. *Trachydermon*) (reprinted, 1872: 135)—Packard, 1918: 292-293

Trachydermon dentiens (Gould). Cooper, 1867: 22—Dall, 1879: 323—Pilsbry, 1894a: 65; plt. 15, fig. 26; [?] 1898b: 51 (Socorro Island)

Lepidochitona dentiens (Gould). Dall, 1918: 3; 1921: 188—Smith, 1947a: 8-9; 1947b: 18—Abbott, 1974: 397—Roth, 1979: 420

Cyanoplax dentiens (Gould). Berry, 1948: 13-15 (with *Cyanoplax raymondi* as syn.)—Gómez, 1975: 28-29

Cyanoplax dentiens cryptica Kues, 1974: 297-300; figs. 1-9

Not *Ischnochiton (Trachydermon) dentiens* (Gould), Pilsbry, 1892: 73-74; plt. 8, figs. 61-65 [= *Lepidochitona keepiana* Berry, 1948]

Not *Lepidochitona dentiens* (Gould), Berry, 1922: 410, 415, 438, 439; tbl. 1; plt. 1, figs. 7-9 (fossil) [= *Lepidochitona keepiana* Berry, 1948]

Ischnochiton pseudodentiens Carpenter, 1864: 606 (reprinted, 1872: 92)

Trachydermon raymondi Pilsbry, 1894b: 46-47 (in subgen. *Cyanoplax*); 1894c: 57—[?] Heath, 1905: 390-393; 1907: 10-12—Berry, 1948: 13-14 (as syn. of *C. dentiens*)

Nuttallina thomasi Pilsbry, 1898a: 288-290—Heath, 1905: 390-393—Higley & Heath, 1912: 95-97—Dall, 1921: 190—Oldroyd, 1927: 867—Smith, 1947a: 16; 1947b: 18—Smith & Gordon, 1948: 206—Thorpe *in* Smith, 1966: 438—Burghardt & Burghardt, 1969b: 32-33; plt. 4, fig. 67—Abbott, 1974: 400—A. G. Smith *in* R. I. Smith & Carlton, 1975: 464

[For additional synonymy, see Smith, 1977: 224-225]

Type Material:

Chiton dentiens Gould, 1846: Holotype (USNM 5824)

Trachydermon (Cyanoplax) raymondi Pilsbry, 1894b: Syntypes (ANSP 65027); "San Francisco" [California]

Nuttallina thomasi Pilsbry, 1898a: Syntypes (ANSP 7190). **Lectotype and paralectotype designated herein**: "Pacific Grove," [Monterey County, California]

Cyanoplax dentiens cryptica Kues, 1974: Holotype (SDNH 51310), and paratypes (CASG 53589; USNM 735015); "Bird Rock, La Jolla, California"

Type Locality: Puget Sound, Washington [47°50′ N, 122° 30′ W].

Description: Pilsbry's (1894a) description of *Trachydermon raymondi* is adequate to identify the species. Specimens of *Lepidochitona dentiens* (Figures *3*, *4*) rarely exceed 2 cm in length; largest examined, 22.4 mm long (CASG 3970, Golden Gate, San Francisco, California, *leg.* H. Hemphill). Color greenish gray to brown, often with white flecks or blue-green dots; valves subcarinate, moderately beaked; tegmentum with minute, evenly round granules throughout; lateral areas poorly defined, not raised; articulamentum blue. Girdle's (Figure 5) upper surface uniformly covered with spiculoid scales, about 10-12 µm wide, to

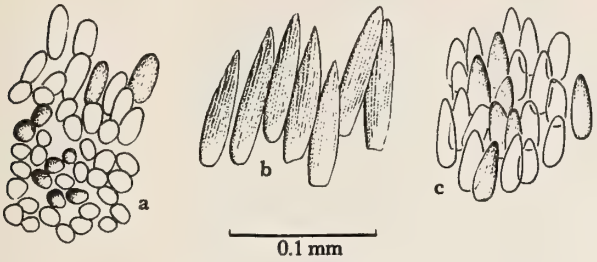


Figure 5

Lepidochitona dentiens (Gould, 1846): specimen, 12.4 mm long; Moss Beach, San Mateo Co., California (AJF 143). Girdle elements: a) upper surface scales, b) outer margin spicules, c) undersurface scales

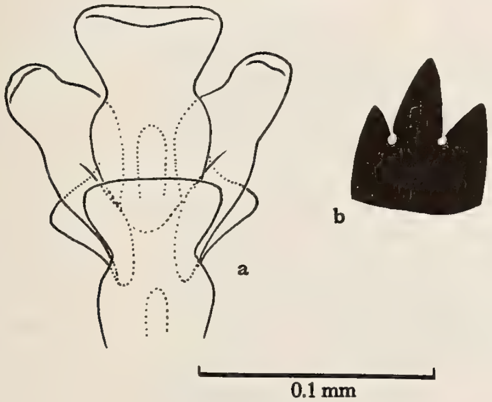


Figure 6

Lepidochitona dentiens (Gould, 1846): specimen 12.0 mm long; Moss Beach, San Mateo Co., California (AJF 144). Radula: a) median and first lateral teeth, b) head of second lateral tooth

50 μm long; undersurface covered with imbricated, translucent, lanceolate scales, about 50 × 12 μm, outer margin with fringe of translucent spicules, about 80 × 12 μm. Specimen 12 mm long (AJF 144, Moss Beach, San Mateo County, California) with radula (Figure 6) 3.3 mm long (27% of specimen's length) comprising 35 rows of mature teeth; median tooth, 88 μm long, 85 μm wide at anterior blade; first lateral teeth with small blade anteriorly; head of major lateral teeth, tricuspid, about 60 μm wide, 75 μm long (Figure 6b); outer marginal teeth, 62 × 38 μm (length/width ratio 1.65).

Other meristic characteristics are summarized in Table 2.

Distribution: Apparently continuous between latitudes 60° and 31° N, from Alaska to Baja California. Northernmost verified record, Boswell Bay, Hinchinbrook Island, near Prince William Id., Alaska (60°24′ N; 146°08′ W) (CASG 39424, *leg.* R. R. Talmadge, June 1965); southernmost verified record, Puerto Santo Tomas, Baja California, Mexico (31°34′ N; 116°40′ W) (LACM 67-2, *leg.* J. H. McLean, January 8-10, 1967). The presence of *Lepidochitona dentiens* at Socorro Island, Mexico, reported by PILSBRY (1898b), could not be corroborated (Ferreira, collecting trip to Socorro and San Benedicto Islands, 3-8 November 1979).

Lepidochitona dentiens seems to be confined to the intertidal and subtidal zone, from 0 to 6 m, usually on top of boulders covered with brown algae. KUES (1974) discovered a population of *L. dentiens*, which he regarded as a subspecies, *L. d. cryptica*, that lives and feeds upon the stipes and holdfasts of a common southern California kelp, *Eisenia arborea*.

Fossil record: *Lepidochitona dentiens* has been identified in the Pleistocene deposits of Santa Monica (CHACE, 1917b) and Humboldt County, California (ROTH, 1979).

Remarks: *Trachydermon (Cyanoplax) raymondi*, Pilsbry, 1894b, was placed in the synonymy of *Lepidochitona dentiens* by BERRY (1948), and SMITH (1977) upon examination of the type material. Smith's color slides of the holotype of *L. dentiens* (CASIZ nos. 2241, 2242) leave no doubt about the proper name for the species.

Cyanoplax dentiens cryptica Kues, 1974, is here regarded as a synonym of *Lepidochitona dentiens* on the basis of the description and the examination of a paratype (CASG 53589). Although KUES (*op. cit.*, p. 299) gave 6 points of contrast between *C. d. cryptica* and *C. d. dentiens* (coloration, width of girdle, slope, arch and contour of valves, and intensity of tegmental granules), the distinctions are well within the intraspecific range of variation of *L. dentiens.* KUES' *(op. cit.)* finding of *L. dentiens* on a kelp substrate is noteworthy since only one other chiton, *Lepidochitona lowei* (Pilsbry, 1918), is known to have such a habitat. In Monterey Bay, SMITH & GORDON (1948) reported collecting *L. dentiens* [as *"Nuttallina thomasi"*] on the holdfasts of the sea-palm *Postelsia.*

The type lot of *Nuttallina thomasi* Pilsbry, 1898a (ANSP 7190) consists of 2 dry specimens. One, partly disarticulated (with loose valves i, vi, vii, and viii), is here designated **lectotype**; the other, here designated **paralectotype**, comprises only 3 loose valves. Both specimens are very eroded and hardly show tegmental features. The **lectotype** (Figure 7) is 10.3 mm long; slit formula 10-1-11; width of valve i/width of valve viii, ratio 0.92. **Paralectotype**, slit formula 9-1-10; width of valve i/width of valve viii, ratio 0.93. The conspecificity of *thomasi* and *dentiens* was overlooked by former workers on account of a number of interesting intraspecific variations of *L. dentiens:* 1) the tegmental surface (due to erosion ?) from evenly granular to agranular and dull, 2) the girdle scales (usually uniform in size)

Table 2

Comparison of some meristic characteristics of *Lepidochitona dentiens* (Gould, 1846), *L. hartwegii* (Carpenter, 1855), and *L. keepiana* Berry, 1948, based on same size (ca. 10 mm long) specimens.

		L. dentiens n = 10	*L. hartwegii* n = 7	*L. keepiana* n = 5
Slit-formula	range	9/11-1-10/12	9/11-1-9/13	9/12-1-12/14
	mode	9-1-11	11-1-11	10-1-13
Slits on valves i + viii, mean		20.2	21.6	23.2
Valve i, length/width,	range	0.40 - 0.50	0.30 - 0.41	0.37 - 0.40
	mean	0.45	0.38	0.39
Valve i width/valve viii width,	range	1.01 - 1.14	1.03 - 1.28	1.12 - 1.20
	mean	1.09	1.11	1.15
Sinus width/sutural lamina width on valve viii	range	0.44 - 0.55	0.32 - 0.49	0.39 - 0.49
	mean	0.50	0.39	0.44
Girdle scales, mean diameter		10 μm	18 μm	35 μm

which in some specimens become unevenly larger (up to 150 × 40 μm) and spiculoid in a manner reminiscent of the spinules of *Nuttallina* (close examination shows that these spiculoid processes are not calcareous as in *Nuttallina*, but are simply overgrown scales), 3) the insertion teeth of the posterior valve varying in shape and thickness, quite robust in some specimens, misshapen in others, projecting radially in most, somewhat forward in a few.

Lepidochitona dentiens has been reported to brood the young (HEATH, 1905, as *"raymondi"* and *"thomasi;"* THORPE *in* SMITH, 1966, as *"thomasi"*). This observation has been corroborated in studies of *"thomasi"* currently underway at the Center for Coastal Marine Studies, University of California, Santa Cruz (D. J. Eernisse, personal communication). The species was also reported (HEATH, 1907) as an instance of hermaphroditism in chitons; however, the specimens of *"raymondi"* used by Heath have not been found (D. Lindberg, personal communication), and there remains some uncertainty about their true identity. The assumed confirmation of Heath's observations by PEARSE & LINDBERG (*in* PEARSE, 1979) was in error; examination of some of the material used in their study [10 May 1980] revealed its misidentification for *Lepidochitona hartwegii.*

An association between *Lepidochitona dentiens* and *Nuttallina californica* has been observed in the field, and tested in the laboratory (GÓMEZ, 1975). Apparently on a chemical clue and as an expression of negative phototaxis, *L. dentiens* is capable of detecting, seeking, and placing itself underneath specimens of *N. californica,* along the pallial groove, thus achieving protection against desiccation, sunlight, and predators.

Lepidochitona hartwegii (Carpenter, 1855)
(Figures *8, 9,* 10, 11)

Chiton hartwegii CARPENTER, 1855: 231-232; 1857b: 287, 318, 349; 1864: 554 [reprinted, 1872: 40]

Trachydermon hartwegii (Carpenter). CARPENTER, 1864: 649 [reprinted, 1872: 135]—COOPER, 1867: 22; 1870: 59—BERRY, 1907: 47—CHACE, 1917a: 44—PACKARD, 1918: 295

Explanation of Figures *2, 3,* and *4*

Figure *2: Trachydermon sharpii* Pilsbry, 1896: Lectotype (ANSP 69140). Close-up of intermediate valves and girdle

Figure *3: Lepidochitona dentiens* (Gould, 1846): specimen, 10 mm long; San Pedro, San Mateo Co., California, intertidal (AJF colln.)

Figure *4: Lepidochitona dentiens* (Gould, 1846): same specimen as in Figure *3.* Detail of tegmental surface

2

3

4

Chaetopleura hartwegii (Carpenter). Dall, 1879: 329-330—Wood & Raymond, 1891: 58—Wood, 1893: 72

"? Chaetopleura hartwegii" (Carpenter). Palmer, 1945: 100

Tonicella (Cyanoplax) hartwegii (Carpenter). Pilsbry, 1892: 45; plts. 14, figs. 81-85 (with *C. nuttalli* as possible syn.)

Trachydermon (Cyanoplax) hartwegii (Carpenter). Pilsbry, 1894b: 45-46; 1898: 287

Cyanoplax hartwegii (Carpenter).
Chace & Chace, 1919: 2 (fossil)—Berry, 1922: 435-436; plt. 2, figs. 6-8 (fossil); 1926b: 456 (fossil)—Smith, 1947a: 14; 1947b: 18—Smith & Gordon, 1948: 205—Palmer, 1958: 264; plt. 27, figs. 8-10, plt. 28, figs. 8-15—Burghardt & Burghardt, 1969b: 14; plt. 1, fig. 13—Abbott, 1974: 398; fig. 4676—A. G. Smith *in* R. I. Smith & Carlton, 1975: 462, 465—Robb, 1975: 34-37—DeBevoise, 1975: 47-50—Lyman, 1975: 63-69—McGill, 1975: 109-112—Pearse, 1979: 41-43; fig. 7A

Lepidochitona hartwegii (Carpenter). Dall, 1921: 189 (in section *Cyanoplax*)—Oldroyd, 1924: 187-188; 1927: 862-863—Fraser, 1932: 65

Lepidochiton hartwegii (Carpenter). Leloup, 1940: 19-23; figs. 43-46 (with *L. nuttalli* as a var.)—La Rocque, 1953: 9

Chiton nuttalli Carpenter, 1855: 231-232; 1857a: 221; 1857b: 198, 318, 349; 1864: 527 [reprinted, 1872: 13]

Ischnochiton (Trachydermon) nuttalli (Carpenter). Carpenter, 1864: 627 [reprinted, 1872: 113]

Trachydermon nuttalli (Carpenter). Carpenter, 1864: 649 [reprinted, 1872: 135]—Cooper, 1867: 23; 1870: 59

Chaetopleura nuttalli (Carpenter). Dall, 1879: 330 (? var. of *C. hartwegii*)

Lepidochitona hartwegii nuttalli (Carpenter). Dall, 1921: 189 (in section *Cyanoplax*)—Oldroyd, 1924: 188; 1927: 863

Lepidochiton hartwegii nuttalli (Carpenter). La Rocque, 1953: 9

Cyanoplax hartwegii nuttalli (Carpenter). Palmer, 1958: 264; plt. 27, fig. 11

Type Material:

Chiton hartwegii Carpenter, 1855: Syntypes (Redpath Museum No. 68) [*fide* Palmer, 1958: 264]; **lectotype and paralectotypes** designated herein

Chiton nuttalli Carpenter, 1855: Holotype (BMNH 65.5.20.102) [*fide* Palmer, 1958: 265]; "Monterey" [California]

Type Locality: Monterey, California [36°37′ N; 121°55′ W].

Description: Pilsbry (1892) described and illustrated the species both as *Tonicella hartwegii* (*l. c.,*: 45; plt. 14, figs. 81-85) and *T. h.* var. *nuttalli* (*l. c.,*: 46). Specimens of *Lepidochitona hartwegii* (Figures *8, 9*) rarely exceed 3 cm in length; largest examined, 32 mm long (LACM 67-67, Isla Asunción, Baja California, Mexico). Color grayish green tones, most often drab; tegmentum with coarse, irregular, warty granules. Girdle's (Figure 10) upper surface covered with juxtaposed (*i. e.,* not imbricated), spiculoid scales, about 12-20 μm wide, 50 μm long; undersurface covered with imbricated, translucent, lanceolate scales, about 60 × 20 μm. Specimen 17 mm long (AJF 147, White's Point, California) with radula (Figure 11) 7.5 mm long (44% of specimen's length) comprising 55 rows of mature teeth; median tooth 180 μm long, 140 μm wide at anterior blade; first lateral teeth about 180 μm long, with small blade at anterior end; head of second lateral teeth, tricuspid, 150 μm long, 150 μm wide; outer marginal teeth, 120 × 80 μm (length/width ratio, 1.50).

Other meristic characteristics are summarized in Table 2.

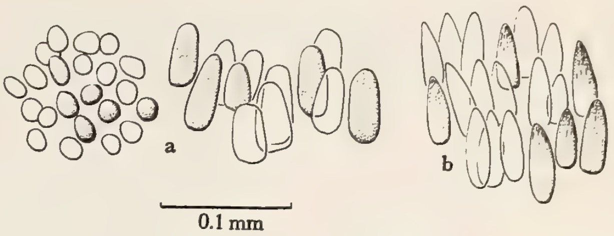


Figure 10

Lepidochitona hartwegii (Carpenter, 1855): specimen, 21.5 mm long; White's Point, Los Angeles Co., California (AJF 147). Girdle elements: a) upper surface scales, b) undersurface scales

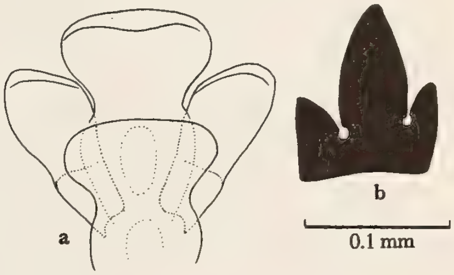


Figure 11

Lepidochitona hartwegii (Carpenter, 1855): specimen, 17 mm long; White's Point, Los Angeles Co., California (AJF 147). Radula: a) median and first lateral teeth, b) head of second lateral tooth

Fossil Record: *Lepidochitona hartwegii* has been reported from the Pleistocene in the San Pedro Formation of southern California (Chace & Chace, 1919; Berry, 1922), and San Quintín, Baja California, Mexico (Berry, 1926b).

Distribution: Seemingly continuous between latitudes 38° N and 27° N. Northernmost verified record, Sausalito, California (37°51′ N; 122°29′ W) (CASG 3971, *ex* H. Hemphill colln.); southernmost verified record, Punta Abreojos, Baja California, Mexico (26°45′ N; 113°40′ W) (CASG 3977, *ex* H. Hemphill colln.). *Lepidochitona hartwegii* has been collected also in the offshore islands of Asunción (LACM 67-67), Cedros (LACM 71-151), San Benito (CASIZ 006179; AJF 484), San Gerónimo (LACM 67-62), Guadalupe (CASG 32746; AJF 211, AJF 240), San Martin (CASG 24041; LACM 68-31; AJF 95), Todos Santos (AJF 487), San Nicolas (*leg.* D. Lindberg), and Santa Cruz (CASG-SU 988).

Bathymetrically, *Lepidochitona hartwegii* is found between 0 and 17 m (LACM 67-62, Isla San Gerónimo, Baja California, Mexico). The species is most often found in the intertidal zone, on top of rocks exposed to moderate surf, amidst brown algae.

Remarks: *Chiton nuttalli* Carpenter, 1855, has long been known to be a synonym of *Chiton hartwegii*, "the young stage" of the species (SMITH & GORDON, 1948: 205). The holotype (BMNH 61.5.20.102), figured by PALMER (1958: plt. 17, fig. 11), leaves no doubt about the identity of the two nominal species.

The syntype series of *Chiton hartwegii* Carpenter, 1855 (Redpath Museum no. 68) [not examined] consists of three units of specimens (PALMER, 1958: 264); the specimen figured by PALMER *(op. cit.)* on plt. 27, as figs. 8-10, measuring 15.4+ mm (attached plates) in length, and 10.3 mm in width, is here designated **lectotype**; the other two units of specimens, one also figured by PALMER (*op. cit.*, plt. 28, figs. 8-15) are designated **paralectotypes.**

In an investigation still in progress, Dr. J. Pearse and D. R. Lindberg (personal communication) have observed that in a central California population of *Lepidochitona hartwegii*, individuals seasonally change their sexual phase. Small specimens (up to 13 mm in length) were noted to be mostly "males" in early fall when sperms accumulate in the gonad, simultaneous hermaphrodites in late fall to early spring when eggs also accumulate, and "females" in late spring and early summer, after spawning, when only eggs are retained in the gonads. In the laboratory, animals held in isolation were found to be self-fertile, producing viable eggs in January and February.

The diet of *Lepidochitona hartwegii* in three intertidal habitats of central California has been shown to consist of algae *Pelvetia, Hildenbrandia, Gigartina, Petrocelis,* and *Endocladia*, among others (ROBB, 1975). The sea star *Pisaster ochraceus* appears to be an important predator on *L. hartwegii*, at least in the laboratory (DEBEVOISE, 1975). In experiments on osmotic stress, *L. hartwegii* has been found to be an osmoconformer over the range of 75% to 125% of normal sea water concentration, an ability considered to be an important factor in adaptation to fluctuating conditions in the upper mid-tide zone (MCGILL, 1975). Specimens of *L. hartwegii* have been observed to be negatively phototactic, and more active at night than in the day time (LYMAN, 1975).

Lepidochitona beanii (Carpenter, 1857c)
(Figures *12*, 13, 14, *15*, *16*, *17*)

Lepidopleurus beanii CARPENTER, 1857b: 252, 317 *(nomen nudum)*; 1857c: 197—PALMER, 1951: 33—BRANN, 1966: 45; plt. 20, fig. 256—KEEN, 1968: 434; plt. 59, fig. 94

Ischnochiton beanii (Carpenter). CARPENTER, 1864: 622 (reprinted, 1872: 108)

Chaetopleura beanii (Carpenter). PILSBRY, 1892, 14: 32-33—OLDROYD, 1927: 888-889—SMITH, 1947b: 18—PALMER, 1958: 266—KEEN, 1958: 524, Amphineura sp. 32—ABBOTT, 1974: 401

Mopaliella beanii (Carpenter). THORPE *in* KEEN, 1971: 879, Polyplacophora, sp. & fig. 44 (with *Chiton flavescens* Carpenter, 1857, and *Basiliochiton lobium* Berry, 1925, as syn.)

Chiton bipunctatus Sowerby (1st.) *in* BRODERIP & SOWERBY, 1832: 104—SOWERBY (2nd.), 1840, sp. no. 66, figs. 27, 155 [not FISCHER, 1807]

Tonicella (Cyanoplax) bipunctata (Sowerby). PILSBRY, 1892: 46; plt. 14, fig. 90

Mopaliella bipunctata (Sowerby). THIELE, 1909: 16; 1910: 123; 1929: 9

Chiton flavescens CARPENTER, 1857c: 198—PALMER, 1951: 33—BRANN, 1966; plt. 21, fig. 257—KEEN, 1968: 434; plt. 59, fig. 103—THORPE *in* KEEN, 1971: 870 (as syn. of *Mopaliella beanii*)

Chaetopleura flavescens (Carpenter). PILSBRY, 1892: 33—KEEN, 1958: 524, Amphineura sp. 43

Tonicella (Mopaliella) stigmata DALL, 1909: 244 (new name for *C. bipunctatus* Sowerby, 1832, not FISCHER, 1807: 111-112)

Basiliochiton lobium BERRY, 1925: 27-28; plt. 2, figs. 1-2 (in subgen. *Lophochiton*)—SMITH, 1947b: 19—THORPE *in* KEEN, 1971: 897 (as syn. of *Mopaliella beanii*)

Mopalia lobium (Berry). ABBOTT, 1974: 403

Type Material:

Lepidopleurus beanii Carpenter, 1857c: Lectotype (designated by KEEN, 1968), and 2 loose valves, Carpenter's Mazatlan Collection, Tablet 905 (BMNH) (*fide* KEEN, 1968)

Chiton bipunctatus Sowerby (1st.), 1832: **Lectotype** (herein designated), and 5 **paralectotypes** (BMNH 1978147); *"ad oras Peruviae* (Inner Lobos Island)"

Chiton flavescens Carpenter, 1857c: **Lectotype** and **paralectotypes** (herein designated), Carpenter's Mazatlan collection, tablet 906 (BMNH 1857.6.4.906); "Mazatlan," Sinaloa, Mexico

Basiliochiton (Lophochiton) lobium Berry, 1925: Holotype, "Shell preserved dry (S.S.B. 1353) entered as Cat. No. 4908" in S. S. Berry's private collection: "Tide pool in the 'Devil's Slide,' La Jolla, California"

Type Locality: Mazatlan, Sinaloa, Mexico (23° 13′ N; 106° 25′ W).

Description: CARPENTER's original description (1857c: 197) and illustration (BRANN, 1966, plt. 20, fig. 256) of *Chiton beanii*, supplemented by KEEN's (1968, plt. 59, fig. 94) photograph of the lectotype provide a good account of the species. Specimens of *Lepidochitona beanii* (Figure *12*) rarely exceed 1 cm in length; longest examined, 14.2 mm long (LACM 74-11, Isla Lobos de Afuera, Peru, at 1-10 m). Color variable, most often brownish-red hues. Valves subcarinate, mucronate; tegmentum smooth but not shiny, often showing the aesthetes conspicuously lined longitudinally in central areas, radially in lateral areas; lateral areas weakly defined; mucro anterior; postmucro moderately concave; articulamentum white; slit formula, 7/9-1-8/9; gills along 80% of foot. Girdle's (Figure 13) upper surface with juxtaposed, spiculoid scales, 10 µm wide, 20 µm long, and variable number of curved, hyaline spicules (up to 500 µm in length), interspersed or bunched at the sutures in groups of 3-4; underside covered with imbricated, translucent, lanceolate scales, about 80 × 15 µm. Specimen 4.5 mm long (LACM 67-66, Isla Asunción, Baja California), with radula (Figure 14) 1.5 mm long (33% of specimen's length), comprising 35 rows of mature teeth; median tooth 40 µm long, 20 µm at anterior blade; first lateral teeth, rectangular; head of major lateral teeth, tricuspid, 30 µm long, 34 µm wide; outer marginal teeth, 35 × 25 µm (length/width ratio, 1.80).

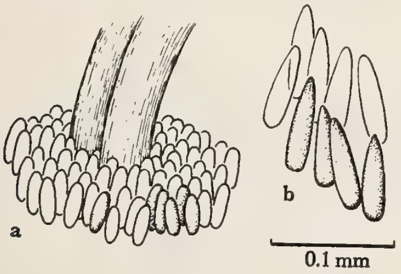


Figure 13

Lepidochitona beanii (Carpenter, 1857): specimen, 8.2 mm long; Bahía de San Francisquito, Baja California, Mexico (AJF 36). Girdle elements: a) upper surface scales and hyaline spicules, b) undersurface scales

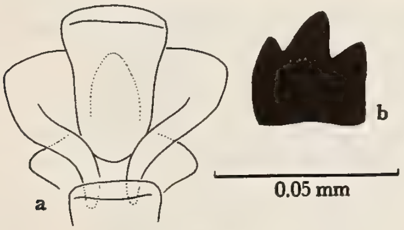


Figure 14

Lepidochitona beanii (Carpenter, 1857): specimen, 4.5 mm long; Isla Asunción, Baja California, Mexico (LACM 67-66). Radula: a) median and first lateral teeth, b) head of second lateral tooth

Distribution: *Lepidochitona beanii* ranges between latitudes 33° N and 7° S, from southern California to Peru and throughout the Gulf of California. Northernmost verified record, Gulf of Santa Catalina, California (33°27′ N; 118° 29′ W) (CASG 44106, at 27-82 m); southernmost verified record, Isla Lobos de Afuera, Peru (6°57.1′ S; 80°42.3′ W) (LACM 74-6, *leg.* J. H. McLean *et al.*, 19 & 20 January, 1974, at 2-10 m). Specimens have been collected at many localities in between.

Lepidochitona beanii is one of the only three lepidochitonids (along with *Dendrochiton lirulatus* Berry, 1963, and *Nuttallina crossota* Berry, 1956) present in the Gulf of California, and the only one south of 26° N, through Central America into Peru (Figure 1).

The depth range of *Lepidochitona beanii* extends from 0 to 230-165 m (CASG 41601, Gulf of Santa Catalina, California).

Remarks: The type material of *Chiton bipunctatus* Sowerby, 1832, consists of 6 specimens (BMNH 1978147). They are accompanied by a museum label which reads, in part, "*Chiton bipunctatus* Sowerby / Probable Syntypes / Loc. ? (should be: Inner Lobos Id, Peru) / H. Cuming colln. / 6 specs. Acc. No: 1829 / Proc. Zoo. Soc. Lond. 1832: 104 / *Possible Fig. Spec.* Sow: Conch. Illust. fig. 155 (largest spec.)" Three of the specimens are glued to a small wooden tablet which bears the marks of the 3 other specimens now loose. On the tablet is written in ink, "Chiton bipunctatus *Sow.*," and in pencil, by a different writer, "Peru." The specimens are mostly green, except for the postmucro area of valve viii which is mottled with cream in one specimen, solid white-cream in two others. In size, the specimens, dried and perfectly flat, range from 8.5 mm to 13.3 mm in length. Tegmentum sculptureless, smooth, with a streaky texture arranged longitudinally in central areas, radially in lateral areas; lateral areas faintly outlined, otherwise; mucro at anterior ⅓ point. Girdle brownish, leathery, paved with small (10-15 µm wide), spiculoid scales and (in one specimen only) a few glassy-looking, curved spicules, about 400 µm long, 40 µm wide. The specimen 12.3 mm long is here designated **lectotype** (Figures *15, 16*), the other 5 specimens, **paralectotypes.**

Side-by-side comparisons between the type specimens of *Chiton bipunctatus* and specimens of *Lepidochitona beanii* from the Gulf of California and west side of Baja California demonstrated their conspecificity. However, the provenance of Sowerby's specimens of *C. bipunctatus* remains in doubt. Recognizing that the name *punctatus* had been preoccupied by Fischer (1807), Dall (1909) renamed the species *stigmata;* but Dall's name is unnecessary since Carpenter's (1857c) *beanii* is the oldest name for the species.

The syntypes of *Chiton flavescens* Carpenter, 1857c, kept in two separate containers bearing the same museum number (BMNH 1857.6.4.906), are accompanied by a pink label which reads, in part, "Syntypes... Mazatlan Mollusca p. 198 / Loc. Mazatlan, on shells very rare / Coll. Reign." One container has a single specimen in a glass vial; it is well preserved, dry, flat, 3.7 mm long, uniformly cream colored, beaked, sculptureless tegmentum, anterior mucro, slightly concave postmucro. The other container encloses a glass slide to which two whole specimens and two isolated valves are glued; hand-written in white ink on the slide is "906, part / Mazatlan / flavescens *n. s.*" The larger specimen, strongly curled, is estimated to be 6mm long; the smaller specimen, less curled, ca. 1.7mm long. Isolated on the glass slide are an anterior valve (corresponding to the one illustrated in Brann, 1966: plt. 21, fig. 257), 1.2mm long, 2.2mm wide, with 10 slits, and an intermediate valve, 2.5mm wide, single-slitted. Girdle elements are not present in any of the specimens. The larger, curled specimen glued to the glass slide, photographed by Keen (1968: plt. 59, fig. 103), is here designated **lectotype**; the others, **paralectotypes**. As anticipated by Thorpe (*in* Keen, 1971), *C. flavescens* is here recognized as a junior synonym of *Lepidochitona beanii*.

Basiliochiton lobium Berry, 1925, from the original description and illustration, appears as a synonym of *Lepidochitona beanii*, as already recognized by Thorpe, (*in* Keen, 1971).

Lepidochitona beanii is quite variable in color and in the number of glassy spicules in the girdle. In a lot of 32 specimens from Isla Lobos de Afuera, Peru (6°57.1′ S; 80° 42.3′ W) (LACM 74-6, *leg.* J. H. McLean *et al.*, 19-20 January 1974, at 2-10m), 15 specimens are a uniform brick-red, 7 orange mottled with red and cream, and 10 pale rose to cream; 20 of these specimens have a differently colored (mostly grayish to brown) valve viii, at least in its post-mucro area; 15 specimens have a bilateral light colored "dot" in the girdle at the i-ii suture (as noted by Sowerby, 1832, for *bipunctatus*) while 17 do not; as to number of girdle spicules, 3 specimens have many, 8 a moderate number, 7 few, 11 very few, and 3 none. There is no apparent relationship between the size of the specimen and the color of the tegmentum or the abundance (or absence) of girdle spicules. Although specimens as small as 4.5mm long are found to have spicules in the girdle, it seems that the appearance of girdle spicules is a relatively late development in the life of the animal. At least, that was the impression derived from the examination of 24 small specimens (from 15 localities between northern Baja California and Peru, at a depth of 0 to 27m) with the characteristics of *L. beanii* except for the total absence of girdle spicules. The specimens—1.8 to 11.7mm long, pale-rose to light salmon color (often with faint clouds of cream and pink), sculptureless and, often, streaky-textured tegmentum, poorly defined lateral areas, anterior mucro, girdle with spiculoid scales, round in cross section (about 14mm in diameter), slit formula 9-1-11, tricuspid radula—could not be recognized with certainty; but their conchological characteristics and geographic distribution strongly suggest their being juveniles of *L. beanii* which had not yet developed the diagnostic glassy spicules in the girdle.

These presumed juveniles of *Lepidochitona beanii* (Figure *17*) are morphologically indistinguishable from juveniles of *Tonicella lineata*. Thus, attempts to identify such small specimens from the area of overlap of the two species (33° N) were repeatedly frustrated, and resulted in some of the most baffling moments in the course of this study. This similarity suggests a much closer phylogenetic relationship between the two species than heretofore realized; in fact, it could raise questions even about the generic assignment of *beanii* were it not for its glassy spicules in the girdle (present in about 90% of adult specimens), and the radular features that belie *Tonicella* and favor *Lepidochitona*.

Lepidochitona flectens (Carpenter, 1864)
(Figures *18*, 19, *20*, 21)

Ischnochiton (Trachydermon) flectens Carpenter, 1864: 603 *(nomen nudum)* (reprinted, 1872: 89); 1865: 60

Ischnochiton flectens Carpenter, 1864: 606 *(nomen nudum)* (reprinted, 1872: 92)—Pilsbry, 1892: 75 (in section *Trachydermon*)

Trachydermon flectens (Carpenter). Carpenter, 1864: 649 (reprinted, 1872: 135)—Cooper, 1867: 23; 1870: 59—Pilsbry, 1893: 15: 64; plt. 15, figs. 34-37—Berry, 1907: 51; 1917: 230, 232, 239, 245-248; 1918: 12—Willett, 1919: 27

Lepidochitona flectens (Carpenter). Dall, 1921: 189 (in section *Basiliochiton*)—Oldroyd, 1924: 187—Oldroyd, 1927: 260—Willet, 1935: 42-43 (with *Dendrochiton semiliratus* Berry, and *Lepidochitona heathii* (Pilsbry), as syn.)

Basiliochiton flectens (Carpenter). Berry, 1918: 12; 1925: 23-28; 1927: 160—Burch, 1942: 7—Burch & Burch, 1943: 5—Smith & Gordon, 1948: 206—Palmer, 1958: 285—Burghardt & Burghardt, 1969b: 10; plt. 1, fig. 2

Explanation of Figures *7*, *8*, *9*, *12*, *15*, and *17*

Figure *7*: *Lepidochitona dentiens* (Gould, 1846): *Nuttallina thomasi* Pilsbry, 1898, Lectotype (ANSP 7190)

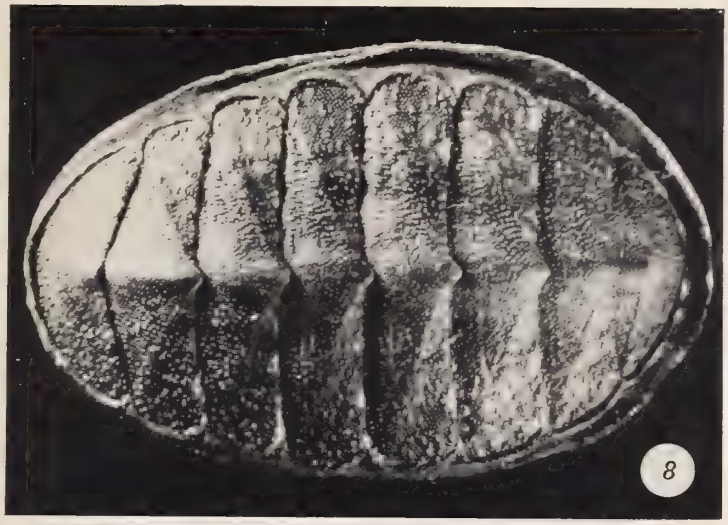
Figure *8*: *Lepidochitona hartwegii* (Carpenter, 1855): specimen, 11.0 mm long; White's Point, Los Angeles Co., California (AJF 147)

Figure *9*: *Lepidochitona hartwegii* (Carpenter, 1855): same specimen as in Figure *8*. Detail of tegmental surface

Figure *12*: *Lepidochitona beanii* (Carpenter, 1857): specimen, 11.5 mm long; Isla Lobos de Afuera, Peru (LACM 74-6)

Figure *15*: *Lepidochitona beanii* (Carpenter, 1857): *Chiton bipunctatus* Sowerby, 1832, Lectotype (BMNH 1978147)

Figure *17*: *Lepidochitona beanii* (Carpenter, 1857): specimen, 7.8mm long; Pt. Fermin, Los Angeles Co., California (LACM 69-43) [or juvenile specimen of *Tonicella lineata* ?]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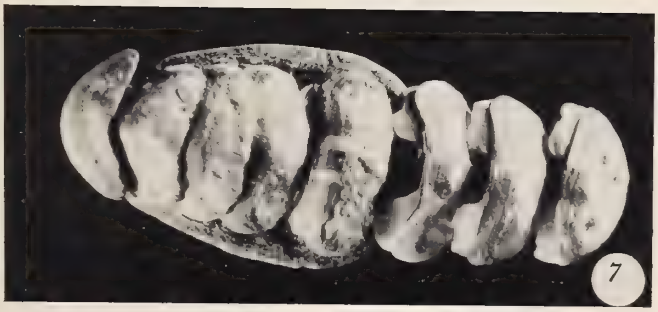
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12


15


17

Lepidochiton flectens (Carpenter). La Rocque, 1953: 9

Mopalia (Dendrochiton) flectens (Carpenter). Leloup, 1942: 59-61 (with *Mopalia heathii* as syn.)—Abbott, 1974: 403 (with *Mopalia heathii* Pilsbry, and *Dendrochiton semiliratus* Berry, as syn.)

Mopalia heathii Pilsbry, 1898a: 288-289—Keep, 1904: 350—Thiele, 1909: 108-109—Berry, 1911: 490-492; plt. 40, figs. 1-3, 7, text figs. 4-7 (in subgen. *Dendrochiton*)—Oldroyd, 1927: 913—Leloup, 1940: 29-31, figs. 62-63, 70-73, 78—Abbott, 1974: 403 (in subgen. *Dendrochiton*, as syn. of *Mopalia flectens)*

Trachydermon heathii (Pilsbry). Berry, 1917a: 245-248

Basiliochiton heathii (Pilsbry). Berry, 1918: 12; 1925: 24-26, figs. 1-2—Chace & Chace, 1933: 124—Smith & Gordon, 1948: 206—Berry, 1951: 219—Burghardt & Burghardt, 1969b: 10-11; plt. 1, fig. 3—A. G. Smith *in* R. I. Smith & Carlton, 1975: 461, 464

Lepidochitona flectens heathii (Pilsbry). Dall, 1921: 189 (in section *Basiliochiton*)

Type Material:

Trachydermon flectens Carpenter, 1864: "The type...has not been found" (Palmer, 1958: 285)

Mopalia heathii Pilsbry, 1898a: Lectotype (ANSP 71902), designated by Berry (1925: 26; text figs. 1-2, plt. 2, figs. 3-5); Paralectotypes, "one alcohol lot and one dry lot (ANSP A4653e and ANSP 344934, respectively)" (M. Miller, *in litt.*, August 8, 1978); "Pacific Grove, near Monterey" [California]

Type Locality: Carpenter's original specimens were from "the Vancouver and California Provinces," having been collected at four different localities; Monterey, Puget Sound, Vancouver region, and "the region between San Diego and San Pedro" (Carpenter, 1864: 637, table). The type locality is here restricted to Pacific Grove, Monterey County, California (36°38′ N; 121°56′ W), which is also the type locality of *Mopalia heathii* Pilsbry, 1898a.

Description: *Lepidochitona flectens* is adequately described and illustrated in the combined works of Carpenter (1864), Pilsbry (1893, 1898a), and Berry (1925). Specimens of *L. flectens* (Figure *18*) do not usually exceed 1cm in length; however, the largest specimen examined in this study measures an astonishing 30.6mm (George A. Hanselman collection, Breakwater, Victoria, British Columbia, *leg.* G. H. Hanselman, July 21, 1966). Color variable with predominance of red and orange hues, often with blotches of cream to green; tegmentum sculptureless, microgranular with occasionally larger granules randomly arranged (a feature reminiscent of *Lepidochitona hartwegii*); mucro slightly anterior; articulamentum often intense red to violet, sometimes "toning lighter near the margin." (Berry, 1925: 24); slit formula 8-1-8; sutural laminae wide with small lamina bridging sinus, particularly noticeable on valve viii [a *Callochiton*-like feature]. Girdle's (Figure 19, *20*) upper surface with spiculoid, scales 10 µm wide, 30 µm long and, mostly at sutures, long (up to 1mm), fragile corneous "hairs," often dendritic, conspicuous in fresh specimens, but easily rubbed off in dry ones; undersurface with imbricating translucent, lanceolate scales, about 30 × 10 µm. Specimen 11.3mm long (CASG-SU 15085, Garden Bay, Vancouver Island, British Columbia, *leg.* I. Oldroyd, January 1945, at 55m) with radula (Figure 21) 2.8mm long (25% of specimen's length), comprising 45 rows of mature teeth; median tooth 75 µm long, 50 µm wide at anterior blade; first lateral teeth convex outwardly; head of second

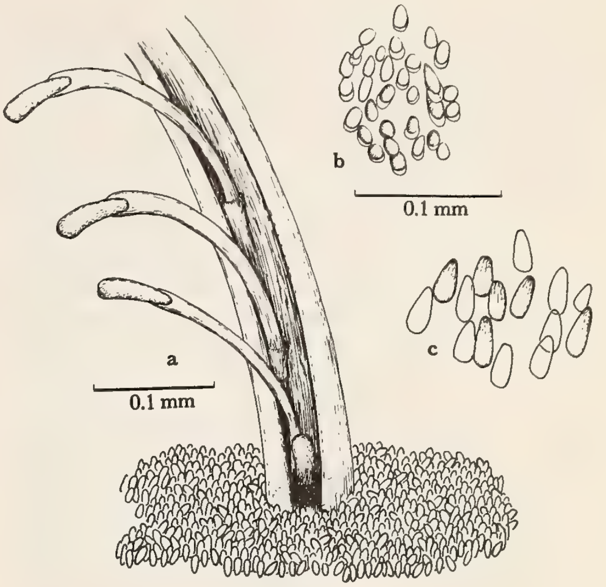

Figure 19

Lepidochitona flectens (Carpenter, 1864): specimen, 15.5 mm long; Monterey Bay, California (AJF 56). Girdle elements: a) upper surface scales and horny bristles, enlarged upper surface scales, b) undersurface scales

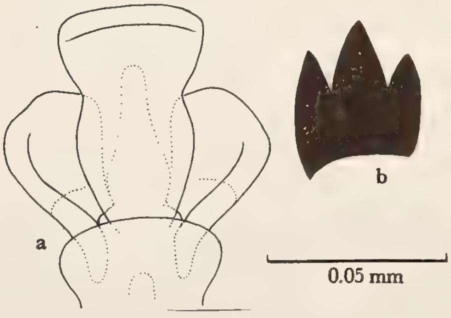

Figure 21

Lepidochitona flectens (Carpenter, 1864): specimen, 11.3 mm long; Garden Bay, Vancouver Id., British Columbia, Canada (CASG-SU 15085). Radula: A) median and first lateral teeth, B) head of second lateral tooth lateral teeth, tricuspid, 50 µm long, 50 µm wide; outer marginal teeth, 70 × 65 µm (length/width ratio, 1.08).

Distribution: *Lepidochitona flectens* appears to be continuously distributed from 53° N to 30° N. Northernmost verified record, Hot Springs Island, off Queen Charlotte Island, British Columbia (53°35′ N; 131°26′ W) (CASG 37545, *leg.* I. McT. Cowan, July 21, 1961, at 4 m); southernmost record, Isla San Gerónimo, off Baja California, Mexico (29°47′ N; 115°47′ W) (LACM 67-61, *leg.* J. H. McLean & P. Oringer, Dwyer Exped., December 10, 1967, at 6-8 m). Bathymetrically, specimens of *L. flectens* have been found from the intertidal zone to 27-38 m (LACM-AHF 1295-41, Santa Cruz Island, California).

Remarks: It has long been apparent that Carpenter's *Trachydermon flectens* and Pilsbry's *Mopalia heathii* represent the same biological entity. Berry (1925) suggested that *flectens* may be the immature stage of *heathii.* Willett (1935) regarded *heathii* as a shore form of *flectens.* A comparison of the original descriptions, and the examination of many lots of *"heathii"* and *"flectens"* from different localities and depths, comprising the whole range of sizes and color phases, permitted the unequivocal conclusion that the two nominal species are conspecific.

Pilsbry (1898a) assigned the species to Mopaliidae on account of the hairy bristles at the sutures, and the 8-slitted anterior valve; later authors (Berry, 1925; Smith, 1960) placed it, as *Basiliochiton,* in Ischnochitonidae, with no explicit justification. However, the body plan of *L. flectens*—the sculptureless tegmentum, poorly defined lateral areas, small posterior valve, anterior mucro, girdle processes, and radula—identifies it as a lepidochitonid as already proposed by Dall (1921).

Lepidochitona lowei (Pilsbry, 1918)
(Figures *22, 23,* 24, 25, *26, 27*)

Trachydermon lowei Pilsbry, 1918: 127

Lepidochitona lowei (Pilsbry). Dall, 1921: 189 (in section *Cyanoplax*)—Oldroyd, 1927: 683-864 (in section *Cyanoplax*)

Cyanoplax lowei (Pilsbry). Smith, 1947a: 14; 1947b: 18—Burghardt & Burghardt, 1969b: 14—Abbott, 1974: 398

Cyanoplax fackenthallae Berry, 1919a: 5; 1922: 437, plt. 2, figs. 9-10 (fossil)—Smith, 1947a: 14; 1947b; 18—Smith & Gordon, 1948: 205—Abbott, 1974: 398—A. G. Smith *in* R. I. Smith & Carlton, 1975: 464

Lepidochitona fackenthallae (Berry). Dall, 1921: 189 (in section *Cyanoplax*)—Oldroyd, 1927: 864 (in section *Cyanoplax*)

Type Material:

Trachydermon lowei Pilsbry, 1918: Holotype (ANSP 117955); Paratype (Lowe colln. no. 1545, *fide* Pilsbry, 1918)

Cyanoplax fackenthallae Berry, 1919: Type(s) presumed to be in S. S. Berry private collection (Oldroyd, 1927); "Pacific Grove, California"

Type Locality: Long Beach, San Pedro Bay, California (33°47′ N; 118°15′ W).

Description: Pilsbry's original description (1918) is quite adequate to identify the species despite the absence of a figure. Specimens of *Lepidochitona lowei* (Figures *22, 23*) rarely exceed 2 cm in length; largest examined, 24.5 mm long (LACM 1098, Anaheim Bay, California). Color rather constant, olive-green to tan; anterior valve with 8-12 weakly defined, radial ribs; lateral areas poorly defined; central areas often with transversal rugae; articulamentum white; slit formula 9-1-10. Girdle's (Figure 24) upper surface with spiculoid scales 12 µm wide, 30 µm long; (Figure 24A); undersurface with imbricated, transparent, lanceolate scales, 60 µm long, 12 µm wide. (Figure 24B). Specimen 18.2 mm long (LACM 63-2, Great Tidal Pool, Monterey, California, with radula (Figure 25) 4.5 mm long (28% of specimen's length) comprising 36 rows of mature teeth; median tooth

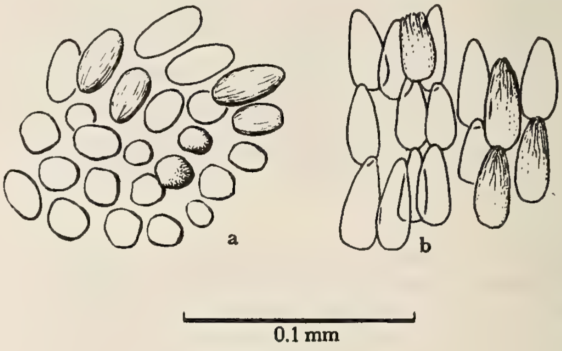

Figure 24

Lepidochitona lowei (Pilsbry, 1918): specimen, 16.2 mm long; "Great Tide Pool," Point Pinos, Monterey Co., California (LACM 63-2). Girdle elements: a) upper surface scales, b) undersurface scales

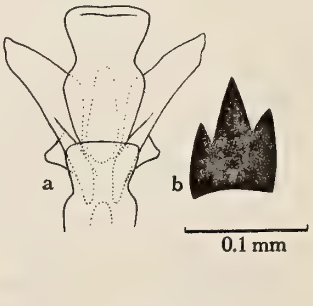

Figure 25

Lepidochitona lowei (Pilsbry, 1918): same specimen as in Figure 24. Radula: a) median and first lateral teeth, b) head of second lateral tooth

110 μm long, 75 μm wide at anterior blade; first lateral teeth aliform with small blade anteriorly (Figure 25A); head of second lateral teeth, tricuspid, 90 μm long, 75 μm wide (Figure 25B); outer marginal teeth, 100 × 90 μm (length/width ratio 1.10).

Fossil record: A single head valve of *Lepidochitona lowei* [identified as *Cyanoplax fackenthallae,* Berry, 1919] was found in the Pleistocene of Point Fermin, California (Berry, 1922).

Distribution: *Lepidochitona lowei* has been recorded from one each of two regions in California, Monterey Bay [36°37-38′ N] in the north and Anaheim to San Diego [33°51′ to 32°51′ N] in the south, but not from the area in between. *Lepidochitona lowei* is known only from the intertidal, or shallow subtidal zone, always attached to the holdfasts of the giant brown kelp *Macrocystis.* Whether only one or both species present in the eastern Pacific [*M. integrifolia* and *M. pyrifera* (see Abbott & Hollenberg, 1976)] provides habitat for *L. lowei* is not known.

Remarks: Side-by-side examination of Monterey and southern California specimens clearly demonstrated their conspecificity. The distinctions enumerated by Berry (1919) concerning *L. fackenthallae* are but aspects of intraspecific variation of *Lepidochitona lowei.*

Lepidochitona lowei is morphologically close to *L. hartwegii* from which it differs in 1) consistently lighter color, 2) evenly microgranular tegmental surface (instead of the irregularly granose surface of *L. hartwegii*), 3) frequent presence of 8-12 radial ribs in the anterior valve (not seen in *L. hartwegii*), 4) white articulamentum (usually dark blue in *L. hartwegii*), 5) median and first lateral teeth of the radula, and 6) unique habitat.

The holotype of *Trachydermon lowei* Pilsbry, 1918 (ANSP 117955) (Figures *26, 27*) agrees with the original description. The label, accompanying the single dry specimen, reads: "kelp roots, Long Beach, Los Angeles County / 33:47 N; 118:15 W / California / ex H. N. Lowe." Valves v, vi, and vii are in place; other valves are loose, and broken; about half of valve i is missing; valve viii is intact.

Lepidochitona keepiana Berry, 1948
(Figures *28, 29, 30,* 31, 32, *33*)

Lepidochitona keepiana Berry, 1948: 13-15—McLean, 1969: 61; fig. 34.3 (reprinted, 1978)—Burghardt & Burghardt, 1969b: 19, plt. 2, figs. 24-25—Abbott, 1974: 397

[?] *Lepidochitona* sp., Smith, 1963: 148

Lepidochitona dentiens (Gould). Berry, 1922: 410, 415, 438-439; tbl. 1, plt. 1, figs. 7-9 (fossil) [Not *Lepidochitona dentiens* (Gould, 1846), *fide* Berry, 1948: 15]

Ischnochiton (Trachydermon) dentiens (Gould). Pilsbry, 1892: 73-74; plt. 8, figs. 61-65; 1894: 65, plt. 15, fig. 26 [Not *Lepidochitona dentiens* (Gould, 1846), *fide* Berry, 1948: 15]

Type Material:

Lepidochitona keepiana Berry, 1948: Holotype (S. S. Berry colln., Cat. No. 11992); Paratypes (S. S. Berry colln., Cat. No. 3978; SDNH T.S. 18; USNM; BMNH; A. G. Smith colln. [now at CASG]; and E. P. Chace colln., *fide* Berry, 1948)

Type Locality: Newport Bay, Orange County, California [33°37′ N; 117°56′ W].

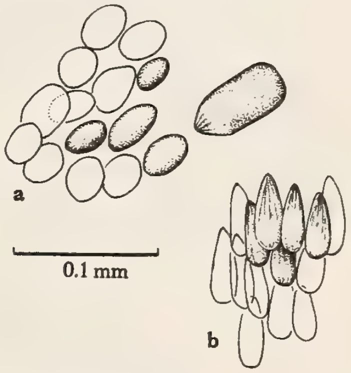

Figure 31

Lepidochitona keepiana Berry, 1948: specimen, 10.0 mm long; Monterey Bay, California (AJF 154). Girdle elements: a) upper surface scales, b) undersurface scales

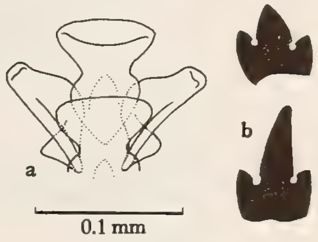

Figure 32

Lepidochitona keepiana Berry, 1948: specimen, 9.8 mm long; Camalu-by-the-Sea, Baja California, Mexico (LACM 66-2). Radula: a) median and first lateral teeth, b) heads of second lateral teeth [demonstrating intra-specimen variation]

Description: The original description (Berry, 1948) is quite adequate to define the species. Specimens of *Lepidochitona keepiana* (Figures *28, 29, 30*) do not usually exceed 1 cm in length; largest specimen examined, 16.0 mm long (CASG 43705, San Diego, California). Color variable, creamy white to orange, brown, rose, often mottled. Girdle's (Figure 31) upper surface covered with translucent, spiculoid scales, about 35 μm wide, 65 μm long; undersurface with imbricated, transparent scales, about 60 × 10 μm at outer margin, much shorter (20 × 10 μm) at inner margin. Specimen 9.8mm long (LACM 66-2, Camalu-by-the-Sea, Baja California, Mexico),with radula (Figure 32) 3.0mm (38% of specimen's length) comprising 46 rows of mature teeth; median tooth 65 μm wide at anterior blade; first lateral teeth somewhat quadrangular with small blade anteriorly; head of second lateral teeth, tricuspid 60 μm wide, 75 μm long; outer marginal teeth, 75 $\times$ 63 μm (length/width ratio 1.20).

Distribution: *Lepidochitona keepiana* appears to have a continuous distribution between 36° and 26° N, being particularly abundant in the southern part of the range. The northernmost verified record is Otters' Point, Monterey Bay, California (36°38′ N; 121°54′ W) (AJF 154, leg. A. J. Ferreira, June 1, 1974, at 1m) southernmost verified record, Rancho Socorro, Baja California, Mexico,(30°20′ N; 115°45′ W) (LACM 66-3, leg. J. H. McLean & P. Oringer, January 7, 1966, intertidal zone). Berry's (1948) report from San Ignacio Lagoon, Baja California, Mexico [26° 42′ N] was not corroborated.

Bathymetrically, specimens of *L. keepiana* range from the intertidal zone to 8-10m (LACM 62-12, Pacific Grove, Monterey County, California).

Fossil Record: Obtained "abundantly" in the Nob Hill Cut, San Pedro, California, Lower San Pedro Series, Pleistocene, first identified by Berry (1922) as *Lepidochitona dentiens* (Gould, 1846), later corrected (Berry, 1948) to *L. keepiana* Berry, 1948.

Remarks: Until Berry's (1948) discussion, specimens of *Lepidochitona keepiana* were identified as *L. dentiens* (Gould, 1846). But differential diagnosis between the two species has remained difficult. To obviate confusion, meristic features of *L. keepiana* and *L. dentiens* are contrasted in Table 2, based on specimens of about the same size (ca. 10mm long). Specimens of *L. keepiana* differ from those of *L. dentiens* (and from juveniles of *L. hartwegii* in the 1) much lighter color, often with orange-browns and creams, 2) white articulamentum, 3) straight side slopes (convex in *L. dentiens*), 4) jugum carinate (more rounded in *L. dentiens*), 5) tegmental surface shagreened (granulose in *L. dentiens,* and in juveniles of *L. hartwegii*), 6) mucro slightly anterior, 7) narrower sinus, 8) more numerous, smaller and often less well defined insertion teeth, and 9) much larger girdle scales. In addition, specimens of *L. dentiens* 1) often display bright blue dots or lines, or both, throughout the valves, (blue dots are never seen in *L. keepiana*), 2) have a clearly oval outline with sides almost parallel (in *L. keepiana* the outline is rather curved so that the anterior and posterior ends seem pointed), 3) have ray-slits well defined by lines of minute orifices (absent in *L. keepiana*) (Figure *33*), and 4) possess very spongy eaves (not so in *L. keepiana*).

Dendrochiton Berry, 1911

Definition: Small in size, bright in color. Strongly carinate. Tegmental surface smooth to microgranular. Lateral areas raised, well defined. Central areas with longitudinal riblets defining sulci, not latticed. Anterior and posterior valves with about 8 slits; intermediate valves 1-slitted. Girdle with small, spiculoid scales, and, in some species, with chitinous bristles, mostly at the sutures.

Type Species: *Mopalia (Dendrochiton) thamnopora* Berry, 1911 by OD.

Remarks: *Dendrochiton* Berry, 1911, was erected as a subgenus of *Mopalia* Gray, 1847, to accommodate two species of chitons common to the fauna of Monterey Bay, California; *Mopalia (Dendrochiton) thamnopora* Berry, 1911, and *Mopalia heathii* Pilsbry, 1898a [= *Lepidochitona flectens* (Carpenter, 1864)]. In 1917, Berry proposed full generic rank for *Dendrochiton* and in 1919 concluded that the then poorly known *Trachydermon gothicus* Carpenter, 1864, also belonged in *Dendrochiton.* In 1927, Berry described *Dendrochiton semiliratus* from Vancouver, British Columbia, and in 1963 added three other nominal species to the genus, *D. psaltes* from San Diego, California, *D. laurae* and *D. lirulatus* from the Gulf of California, Mexico.

The presence of bristles in the girdle, and the 8-slitted anterior valve have induced authors to allocate *Dendrochiton* erroneously to the Mopaliidae (Berry 1911, 1917a; Smith, 1960; Thorpe *in* Keen, 1971; Abbott, 1974). For, contrary to what Berry (1919) believed, the presence of

Explanation of Figures *16, 18, 20, 22, 23, 26,* and *27*

Figure *16: Lepidochitona beanii* (Carpenter, 1857: *Chiton bipunctatus* Sowerby, 1832, **Lectotype** (BMNH 1978147). Close-up of intermediate valves

Figure *18: Lepidochitona flectens* (Carpenter, 1864): specimen, 14.5 mm long; Whalers' Cove, Monterey Co., California (AJF colln.)

Figure *20: Lepidochitona flectens* (Carpenter, 1864): specimen, 13mm long; Monterey Bay, California (AJF 56). Close-up of front valves to show girdle's horny bristles

Figure *22: Lepidochitona lowei* (Pilsbry, 1918): specimen, 14mm long; "Great Tidal Pool," Point Pinos, Monterey Co., California (LACM 63-2)

Figure *23: Lepidochitona lowei* (Pilsbry, 1918): same specimen as in Figure *22.* Close-up of posterior valves

Figure *26: Lepidochitona lowei* (Pilsbry, 1918): *Trachydermon lowei* Pilsbry, 1918, Holotype (ANSP 117955)

Figure *27:: Lepidochitona lowei* (Pilsbry, 1918): *Trachydermon lowei* Pilsbry, 1918, Holotype (ANSP 117955). Posterior valve

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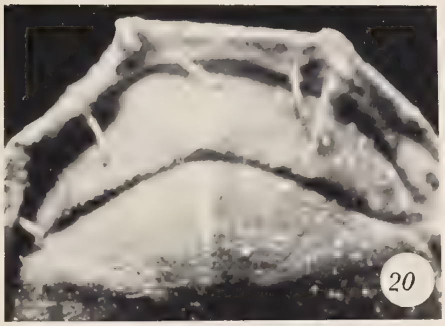
18



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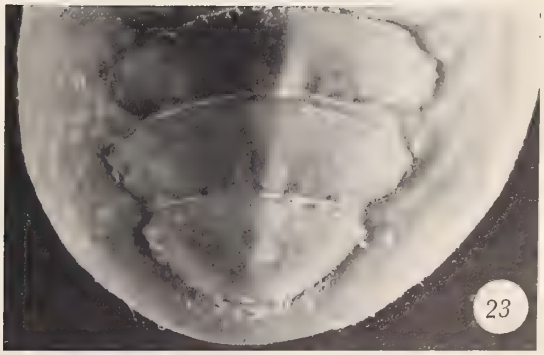

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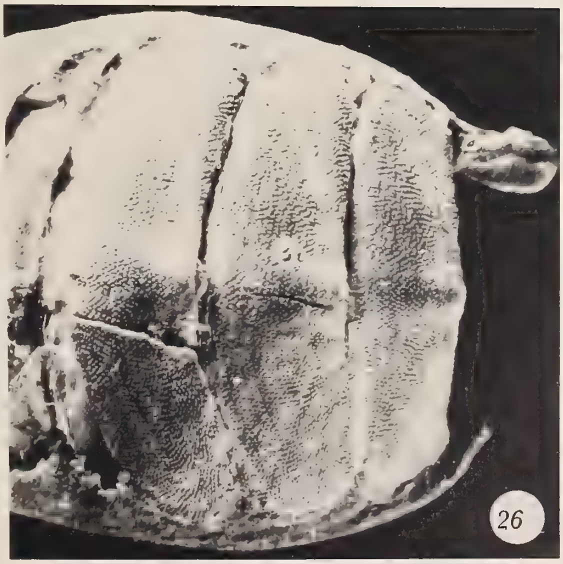

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27

bristles or "hairs" in the girdle of *Dendrochiton* is not genus-specific: *Dendrochiton gothicus* (Carpenter, 1864) does not have such appendages. Further, the characteristics of the different species of *Dendrochiton,* such as smooth tegmentum, posterior valve without a posterior sinus, girdle scales elements, and radula reveal the general body plan of the lepidochitonids, and separate them from the mopaliids. Recently, VAN BELLE (1977) arrived at the same conclusion, treating *Dendrochiton* (considered as a junior synonym of *Mopaliella* Thiele, 1909) as a subgenus of *Lepidochitona.*

The genus *Dendrochiton,* confined to the north-eastern Pacific, is represented by 4 species:

- *Dendrochiton gothicus* (Carpenter, 1864)
- *Dendrochiton thamnoporus* (Berry, 1911)
- *Dendrochiton semiliratus* Berry, 1927
- *Dendrochiton lirulatus* Berry, 1963

In the combined geographical range of these species (Figure 1) *Dendrochiton* is seen to extend from Vancouver Island, British Columbia to Punta Abreojos, Baja California, between latitudes 49° and 26° N, reappearing in the upper part of the Gulf of California, between latitudes 31° and 27° N.

Dendrochiton thamnoporus (Berry, 1911)
(Figures *34,* 35, 36, *37*)

Mopalia (Dendrochiton) thamnopora BERRY, 1911: 487-492; 3 text figs.; plt. 40, figs. 4-6, 8—SMITH, 1947b: 19—ABBOTT, 1974: 403

Dendrochiton thamnoporus (Berry). BERRY, 1917a: 247 footnote (as syn. of *Chaetopleura rosetta* Berry, 1907, a *nomen nudum*); 1919: 3-5; figs. 1-2—SMITH & GORDON, 1948: 206—BURGHARDT & BURGHARDT, 1969b: 14-15; plt. 1, fig. 16—BURGHARDT, 1971: 65-66; text fig.—A. G. SMITH *in* R. I. SMITH & CARLTON, 1975: 465—SMITH, 1977: 217, 252 (as syn. of *Chaetopleura rosetta* Berry, 1907, a *nomen nudum*)

Chaetopleura thamnopora (Berry). DALL, 1921: 193 (in section *Dendrochiton*)—OLDROYD, 1927: 891-892 (in section *Dendrochiton*)—BURCH, 1942: 7—BURCH & BURCH, 1943: 5—LA ROCQUE, 1953: 12 (in section *Dendrochiton*)

Mopalia thamnopora Berry. LELOUP,1940: 37; figs. 68-69, 77, 85-88

Chaetopleura rosetta Berry, 1907, *(nomen nudum)* [attributed to "Bartsch MS"]; 1917a: 247 footnote (as syn. of *Dendrochiton thamnoporus*)—SMITH, 1977: 217, 252 (as syn. of *D. thamnoporus*)

Dendrochiton psaltes BERRY, 1963: 15

Mopalia (Dendrochiton) psaltes (Berry). ABBOTT, 1974: 403

Type Material:

Mopalia (Dendrochiton) thamnopora Berry, 1911: Syntypes (presumably in S. S. Berry private colln.).

Dendrochiton psaltes Berry, 1963: Holotype (S. S. Berry colln., No. 29877), Paratypes (S. S. Berry colln. No. 8776; CASG 12619; LACM 1448; SDNH 43471); "Near entrance to Mission Bay, San Diego Co., California."

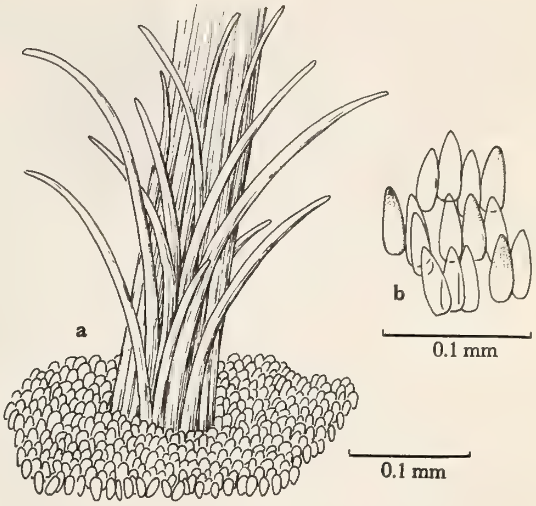


Figure 35

Dendrochiton thamnoporus (Berry, 1911): specimen 8.8 mm long; Monterey Bay, California (AJF 56). Girdle elements: a) upper surface scales and horny bristles, b) undersurface scales

Type Locality: "Off Monterey, California [36°40′ N; 121° 38′ W] in about 15 fathoms [27 m]" (BERRY, 1911: 489).

Description: BERRY (1911; 1919) gave an excellent account of the species. Specimens of *Dendrochiton thamnoporus* (Figure *34*) do not usually exceed 1 cm in length; largest specimen examined 15.5 mm in length (SDNH 43471, False Bay, San Diego County, California, *leg.* E. Wilson, January 8, 1944, a paratype of *Dendrochiton psaltes*). Color variable from reds to greens; tegmentum smooth; lateral areas raised, well defined, smooth; central areas with 7 to 10 strong longitudinal riblets, defining deep furrows, not latticed, absent at jugum; mucro anterior; gills extend 75% of foot; slit formula 7/9-1-7/8. Girdle's (Figure 35) upper surface paved with translucent, spiculoid scales, 15 μm wide, 30 μm long and tufts of fragile, short (up to 0.5 mm) dendritic bristle-like hairs at sutures, also, less regularly, at outer margin; undersurface with imbricated, transparent, lanceolate, vaguely striated scales, $15 \times 60\,\mu$m (Figure 35 B). Specimen 8.8 mm long (AJF 56, Monterey Bay, California) with radula (Figure 36) 2.9 mm long (33% of specimen's length), comprising 36 rows of mature teeth; median tooth, rectangular, 65 μm long, 45 μm wide at anterior blade; head of second lateral teeth tricuspid (Figure 36 b) 50 μm wide, 60 μm long; outer marginal teeth $65 \times 45\,\mu$m (length/width ratio, 1.45).

Distribution: The verified range of *Dendrochiton thamnoporus* extends from Bodega Bay, Sonoma County, California (38°20′ N; 123°05′ W) (CASIZ 014114) to Punta Abreojos,

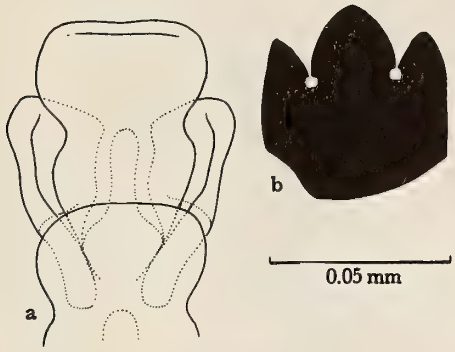


Figure 36

Dendrochiton thamnoporus (Berry, 1911): same specimen as in Figure 35. Radula: a) median and first lateral teeth, b) head of second lateral tooth

Baja California, Mexico (26°42′N; 113°34.5′W) (LACM 71-3, *leg.* J. H. McLean on R/V *Searcher,* January 27, 1971, at 6-10m). The report from Resurrection Bay, Alaska (Oldroyd, 1927: 892) could not be corroborated. The species has been collected at the offshore islands of Anacapa (CASG 39609), San Gerónimo (LACM 67-61; LACM 67-62; LACM 71-91), Cedros (LACM 71-159), Natividad (LACM 71-165), and Asunción (LACM 67-66).

Bathymetrically, *D. thamnoporus* ranges from the intertidal zone to 29m (LACM 65-2, off Point Fermin, Los Angeles County, California, *leg.* J. H. McLean, January 11, 1965).

Remarks: In comparing *D. psaltes* with other members of *Dendrochiton,* Berry (1963: 135) stated only that "The low arching, heavy flattened pleural costae, smooth jugal tracts, and smooth flattish lateral areas are noteworthy. The species attains a much larger size than either of the two [actually three, *D. gothicus, D. thamnoporus,* and *D. semiliratus*] previously described in the genus, and is of much less lively coloring." None of these distinctions can be regarded as species-specific. The necessity of placing *Dendrochiton psaltes* Berry, 1963, in the synonymy of *D. thamnoporus* became evident upon examination of paratypes of the former (LACM 1448; SDNH 43471) (Figure *37*), and color slides of the type specimens in the S. S. Berry private collection, kindly provided by Leroy and Forrest Poorman, Westminster, California.

Dendrochiton gothicus (Carpenter, 1864)
(Figures *38, 39, 40,* 41, 42)

Ischnochiton (Trachydermon) gothicus Carpenter, 1864: 612 *(nomen nudum)* (reprinted, 1872: 98); 1866: 212—Pilsbry, 1892: 74-75 (in section *Trachydermon*)

Trachydermon gothicus (Carpenter). Carpenter, 1864: 649 (reprinted, 1872: 135)—Cooper, 1867: 22—Pilsbry, 1894a: 65; plt. 15, figs. 28-29—Keep, 1904: 348—Palmer, 1945: 100

Dendrochiton gothicus (Carpenter). Berry, 1919: 3-5; figs. 3, 4—Smith & Gordon, 1948: 206—Palmer, 1958: 284; plt. 32, fig. 3—Smith, 1963: 148-149—Burghardt & Burghardt, 1969b: 14; plt. 1, fig. 15—Burghardt, 1971: 65—Smith, 1977: 217, 248

Chaetopleura gothica (Carpenter). Dall, 1921: 193 (in section *Dendrochiton*)—Oldroyd, 1927: 892 (in section *Dendrochiton*)—Burch, 1942:7

Mopalia (Dendrochiton) gothica (Carpenter). Leloup, 1942: 61—Smith 1947b: 19—Abbott, 1974: 403

Type Material:

Ischnochiton (Trachydermon) gothicus, Carpenter, 1864: Syntypes, one specimen consisting only of 4 valves (USNM 16271) [Dr. J. Rosewater, *in litt.,* October 3, 1978], and a set of 5 specimens (Redpath Museum No. 13, *fide* Palmer, 1958). From the latter, the figured specimen (Palmer, *l. c.,* plt. 32, fig. 3) is herein designated as **Lectotype.**

Type Locality: Santa Catalina Island, California [33°23′N; 118° 24′W].

Description: Carpenter's description (*in* Pilsbry, 1892: 74-75), supplemented by illustrations in Pilsbry (1894: plt. 15, figs. 28-29) and Berry (1919: figs. 3-4) are adequate to identify the species. Specimens of *Dendrochiton gothicus* (Figures *38, 39, 40*) are very small; largest examined 9.1mm long (LACM 67-62, San Gerónimo Island, Baja California, Mexico). Color variable, mostly brilliant reds or greens; lateral areas raised, smooth surface; central areas with 12-16 longitudinal riblets per side, defining shallow narrow furrows, not latticed, extending onto jugal area; slit formula 8/9-1-7/8. Girdle's (Figure 41) upper surface with no hairs, only translucent, spiculoid scales, 10 μm wide, 25 μm long (Figure 41 A); undersurface with transparent, lanceolate scales, 40 × 12 μm; marginal fringe of striated spicules, 60 × 10 μm. Specimen 7.2mm long (LACM 63-41, Middle Coronado Island, Baja California, Mexico) with radula (Figure 42) 2.1mm long (30% of the length of the specimen) comprising 40 rows of mature teeth; median tooth 35 μm wide at anterior blade; first lateral teeth aliform; head of second lateral teeth tricuspid, 35 μm wide, 60 μm in length; outer marginal teeth, 45 × 35 μm (length/width ratio, 1.28).

Distribution: The geographical range of *Dendrochiton gothicus* extends between 34° and 27° N. Northernmost verified record, Santa Cruz Island, Los Angeles County, California (34°00′N; 119°31′W) (LACM-AHF 295-41, at 27-38m); southernmost record, Isla Asunción, Baja California, Mexico (27°06′N; 114°17′W) (LACM 67-66, *leg.* J. H. McLean & P. Oringer, Dwyer Expedition, December 12, 1967, at 8-21m). *Dendrochiton gothicus* seems to be more abundant in the offshore islands, having been collected at Santa Catalina (CASG 41601; LACM 62-5), Coronados (CASG 45214; LACM 63-41), San Gerónimo (LACM 67-62), Guadalupe (CASG 32819), and Cedros (LACM 67-65).

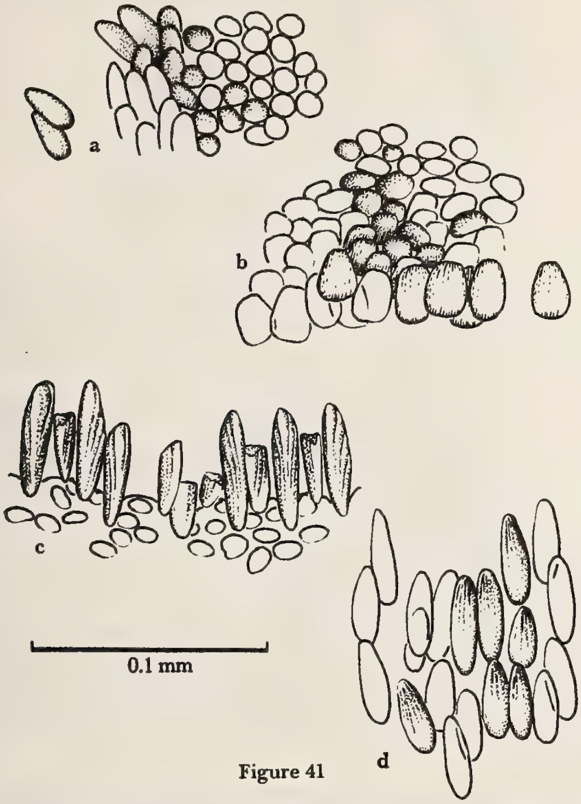


Figure 41

Dendrochiton gothicus (Carpenter, 1864): specimen, 7.2 mm long; Middle Coronado Id., Baja California, Mexico (LACM 63-41). Girdle elements: a) upper surface scales at the middle of the girdle, b) upper surface scales at the inner margin of the girdle, c) spiculoid processes at the outer margin, d) undersurface scales

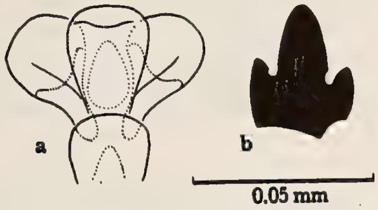


Figure 42

Dendrochiton gothicus (Carpenter, 1864): same specimen as in Figure 41. Radula: a) median and first lateral teeth, b) head of second lateral tooth

From the collections examined, it seems that *D. gothicus* is mostly a subtidal species, having been found down to a depth of 165-230 m (CASG 41601, off Santa Catalina Island, California), and only rarely in the intertidal zone (CASG 32819, Guadalupe Id., Baja California, Mexico, *leg.* M. W. Williams, 7 December 1946).

Remarks: The type material of *Ischnochiton (Trachydermon) gothicus* Carpenter, 1864 (USNM 16271) was examined by the late Allyn G. Smith who left the following unpublished observation [in "Chiton Notes" on file at CASG]: "The type [material] consists of 3 incomplete intermediate valves... along with a tail valve that is complete. All valves evidently had been glued to a glass slide... at one time. No vestiges of a girdle remain. The valves agree with S. S. Berry's (1919: 2-5; figs. 3, 4) interpretation and illustrations of *Dendrochiton gothicus.*" Color photograph of the valves, here designated paralectotypic, is in CASIZ Color Slides Series, No. 2472.

Dendrochiton was erected "largely because of its girdle characters" (Berry, 1919b: 3) as exhibited in the type species, *D. thamnoporus.* Realizing that *Ischnochiton gothicus,* with "evidently... the same general plan," belonged to the same genus, Berry interpreted the absence of setae [hairs, bristles] in the dried specimens of *D. gothicus* before him as having fallen off, being "complex and fragile." Confronted with a fresh specimen where no setae could be seen, either, Berry surmised that a few "pore-like dots" at the sutures corresponded to "the position of the major setae in *D. thamnoporus,"* adding "No doubt the receipt of good alcoholic material of *gothicus* will reveal additional important features of taxonomic value in the girdle" (Berry, *loc. cit.*). But, in this study, the examination of a few hundred specimens of *D. gothicus,* many of them perfectly preserved in alcohol, failed to substantiate Berry's hypothesis: neither "setae" nor "pore-like dots" were observed in the girdle of any of the specimens. Among the known species of *Dendrochiton, D. gothicus* is the only one with a bristleless girdle. This observation, however, has more than heuristic value, for it underlines the notion that the presence or absence of girdle ornaments, such as bristles or spicules, in the lepidochitonids cannot be made the basis for generic subdivisions.

Dendrochiton semiliratus Berry, 1927
(Figures *43, 44,* 45, 46)

Dendrochiton semiliratus Berry, 1927: 159-163; plt. 13; 4 text figs.—Burghardt, 1971: 65

Mopalia (Dendrochiton) semiliratus (Berry). Willett, 1935: 42-43 (as syn. of *Lepidochitona flectens*)—Abbott, 1974: 403 (as syn. of *Mopalia flectens*)

Type Material:

Dendrochiton semiliratus Berry, 1927: Holotype (CASG-SU 6238); Paratypes (S. S. Berry colln. No. 5129 and 5130; CASG-SU 6273).

Type Locality: Departure Bay, Vancouver Island, British Columbia, Canada [49° 12′ N; 123° 58′ W].

Description: Berry (1927) described *Dendrochiton semiliratus* with precision. Specimens (Figures *43, 44*) do not usually exceed 1cm in length; largest examined, 15mm long (LACM-AHF 1624-48, Santa Catalina Island, California, at 66m). Color uniformly solid reddish-brown; valves (Figures *43*, *44*), strongly carinate, beaked; lateral areas weakly defined, sculptureless; central areas with 6-11 longitudinal lirae per side, mostly short (*i.e.*, not reaching anterior part of valve); mucro anterior; articulamentum rose-pink; posterior valve much smaller than anterior valve; sutural laminae short, almost confluent in midline hardly defining shallow sinus; insertion teeth short, rough-edged; slit formula 8-1-7. Girdle's (Figure 45) upper surface with juxtaposed, translucent, spiculoid scales, 10 µm wide, 25 µm long, and sutural tufts of 3-6 fragile, long (up to 1mm), moderately dendritic bristles (Figure 45 A); undersurface with imbricated, transparent, lanceolate scales, 15 µm wide, 50 µm long (Figure 45 B).

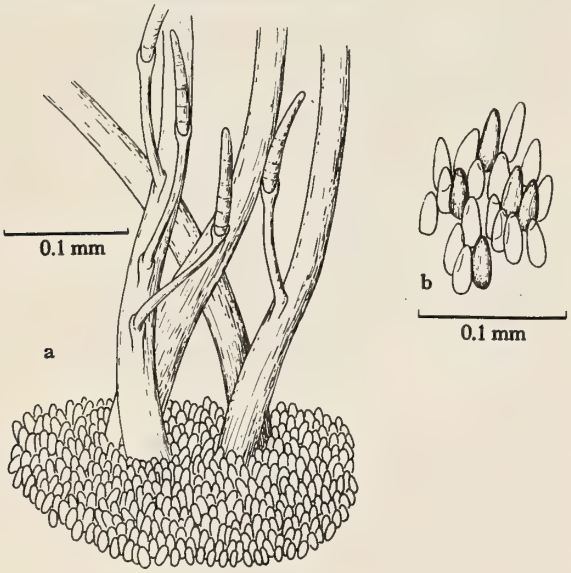


Figure 45

Dendrochiton semiliratus Berry, 1927: same specimen as in Figure *43*. Girdle elements: a) upper surface scales and horny bristle, b) undersurface scales

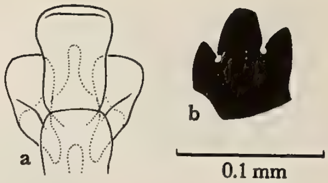


Figure 46

Dendrochiton semiliratus Berry, 1927: same specimen as in Figure *43*. Radula: a) median and first lateral teeth, b) head of second lateral tooth

Specimen 15mm long (LACM-AHF 1624-48, Santa Catalina Island, California) with radula (Figure 46) 3.5mm long (23% of specimen's length) comprising 35 rows of mature teeth; median tooth 80 µm long, 55 µm wide at anterior blade; first lateral teeth about 85 µm long; head of second lateral teeth tricuspid, about 80 µm wide, 80 µm long; outer marginal teeth 100 × 60 µm (length/width ratio, 1.67).

Distribution: Northernmost record of *Dendrochiton semiliratus* is also the type locality, Departure Bay, Vancouver Island, British Columbia (49° 12′ N; 123°58′ W) (CASG-SU 6238; CASG-SU 6273; CASG 44124). Apparently it has not been collected between 49° N and 34° N. In southern California waters it has been found in San Pedro Bay (CASG 32536), Santa Catalina Island (SDNH 23463; LACM-AHF 1381-41; LACM-AHF 1426-41; LACM-AHF 1624-48), and south of Pyramid Cove, San Clemente Island (LACM-AHF 1012-39), its southernmost record (32°45′55″ N; 118°26′10″ W). Based on meager data (only 6 of the 9 lots examined had information of the collecting depth), the bathymetric range extends from 38-75m (LACM-AHF 1426-41, Santa Catalina Island) to 141m (CASG 32536, San Pedro Bay).

Remarks: Besides a color slide of a paratype in S. S. Berry private collection, graciously provided by Leroy and Forrest Poorman, only 21 specimens of *Dendrochiton semiliratus* were examined in this study. Thus, *D. semiliratus* must be considered rare.

Explanation of Figures *28, 29, 30, 33, 34, 37,* and *38*

Figure *28*: ***Lepidochitona keepiana*** Berry, 1948: specimen, 10.0mm long; White's Point, Los Angeles Co., California (AJF 147)

Figure *29*: ***Lepidochitona keepiana*** Berry, 1948: specimen, 10.2mm long; El Socorro, Baja California, Mexico (LACM 66-2)

Figure *30*: ***Lepidochitona keepiana*** Berry, 1948: same specimen as in Figure *28*. Close-up of tegmental surface

Figure *33*: ***Lepidochitona dentiens*** [on the left] vs. ***Lepidochitona keepiana*** [on the right]: articulamental surfaces of valves ii

Figure *34*: ***Dendrochiton thamnoporus*** (Berry, 1911): specimen, 13.0 mm long; Point Conception, California (LACM 63-39)

Figure *37*: ***Dendrochiton thamnoporus*** (Berry, 1911): ***Dendrochiton psaltes*** Berry, 1963, paratype (LACM 1448)

Figure *38*: ***Dendrochiton gothicus*** (Carpenter, 1864): specimen, 13.0 mm long; Middle Coronado Id., Baja California, Mexico (LACM 63-41)


28


29


30


33


34


37


38

Dendrochiton lirulatus Berry, 1963
(Figures *47, 48, 49,* 50, 51, *52, 53*)

Dendrochiton lirulatus Berry, 1963: 136-137—Thorpe *in* Keen, 1971: 880, Polyplacophora sp. & fig. 48—Burghardt, 1971: 65
Mopalia (Dendrochiton) lirulata (Berry). Abbott, 1974: 403
Dendrochiton laurae Berry, 1963: 136—Thorpe *in* Keen, 1971: 880, Polyplacophora sp. 47
Mopalia (Dendrochiton) laurae (Berry). Abbott, 1974: 403

Type Material:

Dendrochiton lirulatus Berry, 1963: Holotype (S. S. Berry Colln. No. 29879); paratypes (S. S. Berry Colln.)
Dendrochiton laurae Berry, 1963: Holotype (S. S. Berry Colln., No. 29878); "Bahía de los Angeles, Baja California," Mexico

Type Locality: North shore of Punta San Felipe, Baja California, Mexico [31°03′ N; 114°50′ W].

Description: Berry's (1963) original description is quite adequate to characterize the species. Specimens of *Dendrochiton lirulatus* (Figures *47, 48, 49*) do not usually exceed 1cm in length; largest 13.1mm long (AJF 27, San Felipe, Baja California, Mexico). Color variable, mostly in light greenish hues; lateral areas rugose surface, often with chevron-like vermiculations and random pitting; central areas with 10-18 longitudinal riblets, defining smooth, not latticed furrows; mucro central inconspicuous; slit formula 8-1-8. Girdle's (Figure 50) upper surface with juxtaposed, translucent, spiculoid scales, about 15 × 10 µm, and sutural tufts of 3-4 short (up to 0.5mm long), not branching, horny bristles, together with hyaline, curved spicules, up to 300 µm long, 40 µm thick, often in groups of 2-4 at basis of bristles [not previously described]; underside with imbricated, transparent, rectangular scales, about 12 µm wide, 75 µm long; marginal fringe of spicules up to 100 µm long, 10 µm wide. Specimen 11.2mm long (AJF 27, San Felipe, Baja California) with radula (Figure 51) 3.8mm long (34% of specimen's length), comprising 42 rows of mature teeth; median tooth, 90 µm long, 60 µm wide at anterior blade; first lateral teeth about 80 µm in length; head of second lateral teeth tricuspid 80 µm wide, 100 µm long; outer marginal teeth 75 × 45 µm (length/width ratio, 1.67).

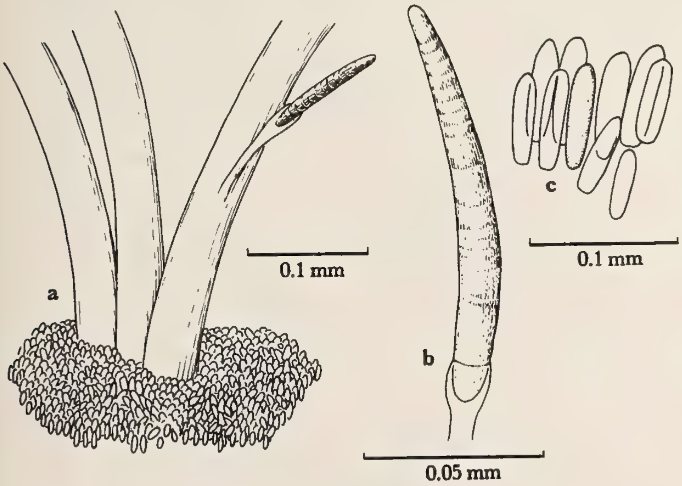


Figure 50

Dendrochiton lirulatus Berry, 1963: specimen, 11.2mm long; San Felipe, Baja California, Mexico (AJF Colln.). Girdle elements: a) upper surface scales and tuft of horny bristles with hyaline spicule growing out of a bristle, b) close view of hyaline spicule, c) undersurface scales

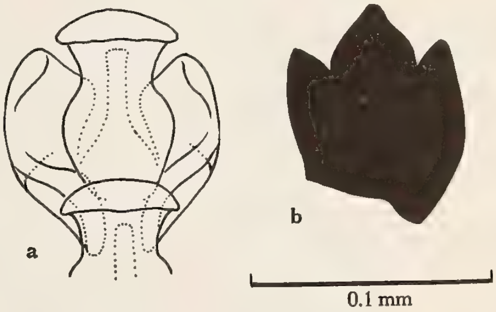


Figure 51

Dendrochiton lirulatus Berry, 1963: same specimen as in Figure 50. Radula: a) median and first lateral teeth, b) head of second lateral tooth

Distribution: *Dendrochiton lirulatus* is confined to the northern part of the Gulf of California, Mexico, from San Felipe to Bahía de los Angeles (type locality of *"laurae"*) on the Baja California side, and from Cholla Bay, Puerto Peñasco (LACM 63-56) to Saladita Bay, Guaymas, Sonora (LACM 68-27) on the mainland side. This represents a range of about 2° on the western side, and less than 4° on the eastern side of the Gulf of California. All specimens examined were collected in the intertidal zone.

Remarks: *Dendrochiton lirulatus* was left unfigured by Berry (1963). A photograph of a type specimen in the Berry collection (*via* L. and F. Poorman) is published here for the first time (Figure *52*). *Dendrochiton lirulatus* is similar to *D. thamnoporus* of the California coast from which it differs in 1) rugose lateral areas, with chevron-like vermiculations, 2) finer and more numerous longitudinal riblets in the central areas, 3) jugal area with riblets (smooth in *D. thamnoporus*), and 4) hyaline spicules [in addition to hairs] in the girdle.

Berry (1963: 136) distinguished *Dendrochiton laurae* for its "...nearly smooth lateral areas; central areas with 5 to 8 wide, flat, spreading costae...jugal tracts smooth and rather wide...(girdle) minutely scaled, bearing the usual spinulose setae...remarkable coloring..." The species, left unfigured, is known only from the type specimen collected at Bahía de los Angeles, Baja California, Mexico [29°00′ N; 113°30′ W] by C. L. Hubbs *et al.*, April, 1962 (depth unstated). A color slide of the holotype (*via* L. and F. Poorman) here reproduced (Figure *53*), reveals a specimen that, as Berry (1963: 136) observed, is remarkable for the paucity of riblets in the central areas, and the smooth lateral areas. In the course of this study a single specimen was found that fits Berry's description of *laurae;* collected at Puerto Peñasco, Sonora, Mexico, in the intertidal zone (*leg.* Hans Bertsch, December 1975); the specimen is 10 mm long, with valves i, ii, vii, and viii bright green, contrasting sharply with the black valves iii-vi, smooth jugum, central areas with only 6-8 riblets, and smooth lateral areas. The smooth or almost smooth lateral areas and/or small number of riblets in the central areas of a few other specimens of *Dendrochiton* from the northern part of the Gulf did bring to mind Berry's description of *D. laurae,* but on closer examination all appeared to fall well within the expected intraspecies variation of *D. lirulatus.* Thorpe (*in* Keen, 1971: 880) claimed to know of three specimens of *D. laurae* "from depths of 10 to 90 m in the southern part of the Gulf of California," but made no reference to museum material or illustrations. Thus, unless further collecting in the Gulf of California should reveal evidence to the contrary, it is here recommended that the two nominal species, *lirulatus* and *laurae,* be regarded as conspecific. Although *laurae* has page priority, the name *lirulatus,* better recognized and accepted, is chosen herewith for the taxon.

The *"laurae"* form is intermediate between the Gulf of California *Dendrochiton lirulatus* and the southern California, outer Baja California, *D. thamnoporus,* emphasizing the similarity between the two species.

Tonicella Carpenter, 1873

Definition: Chitons of medium size, colored in bright reds and oranges. Tegmental surface smooth to microgranular, sculptureless otherwise. Lateral areas weakly defined. Mucro often anterior. Eaves spongy. Anterior and posterior valves with about 8 slits each; intermediate valves 1-slitted. Merobranchial. Girdle with small, spiculoid scales, often leathery looking as if scale-less.

Type Species: *Chiton marmoreus* Fabricius, 1780, by M.

Synonyms: *Clathropleura* Tiberi, 1877 (in part)
Type: *Chiton laevis* Pennant 1777 [= *Chiton ruber* Linnaeus, 1767 *fide* Pilsbry, 1892, Smith *in* Beu *et al.*, 1969] by SD, Iredale, 1914.
Boreochiton Sars, 1878
Type: *Chiton ruber* Linnaeus, 1767, by SD, Pilsbry, 1893.
Toniciella Fischer, 1885 *(nomen nullum)*
Toniciella Thiele, 1893 *(nomen nullum)*
Tornicella Step, 1945 *(nomen nullum)*

Remarks: Pilsbry (1892: 40) recognized *Tonicella* as differing from other genera, such as *"Trachydermon, Callochiton, Ischnochiton, Chaetopleura,* etc." by its "naked, scale-less girdle." This proved to be an erroneous distinction, inasmuch as all species of *Tonicella* have girdle scales albeit small, sparse, and inconspicuous.

Species of *Tonicella* are confined to the boreal and circumboreal regions. In the eastern Pacific the following species are here recognized:

Tonicella rubra (Linnaeus, 1767)
Tonicella marmorea (Fabricius, 1780)
Tonicella lineata (Wood, 1815)
Tonicella insignis (Reeve, 1847)

The combined geographical range of these 4 species of *Tonicella* in the eastern Pacific (Figure 1) extends between 75° N and 33° N, from the Arctic Ocean to southern California. The nominal species, *Tonicella granulata* Jakovleva, 1952, *T. zotini* Jakovleva, 1952, *T. beringensis* Jakovleva, 1952, and *T. beringensis lucida* Sirenko, 1974, are here regarded as synonyms of *T. rubra* (Linnaeus, 1767). In Japanese waters, *T. squamigera* Thiele 1909, appears to be a valid species (Sirenko, 1974b).

Chiton sitchensis Middendorff, 1847a (not Reeve, 1847), referred to *Tonicella* by most authors since Dall (1879), is here regarded a *nomen dubium.* The species is based on a single specimen "in very bad condition" (Sirenko, 1974b: 990) comprising radula and 4 eroded valves at the Zoological Museum of USSR, Leningrad (B. Sirenko, *in litt.*, 20 July 1979). Since Middendorff's (1847a: 122; 1847b: 112-114; plt. 13, figs. 1, 2) "figures and descriptions do not agree upon several points" (Pilsbry, 1892: 44), and fail to differentiate between *C. sitchensis* and other species of *Tonicella* now known to share the type locality (Sitka, Alaska), it is quite apparent that the species-name *C. sitchensis* is not applicable with certainty to any known taxon (Sirenko, 1974b).

Tonicella saccharina Dall, 1879, described from Alaska, is retained here as a *nomen inquirendum.* The type material consists of four lots preserved dry: One specimen, partly disarticulated, 7 mm long, with a label reading, in part, "...Small Pass / Kyska Harbor, Aleutians, W. H. Dall" (USNM 30911); one specimen, 8 mm long, with label, "...Pass, 10 fms., rky. / Kyska Harbor, Aleutians, W. H. Dall" (USNM 30912); one specimen, 9 mm long, with label "...Iliuliuk Harb. / Captain's Bay, Unalaska, W. H. Dall" (USNM 30913); two specimens, 5 and 7 mm long, with label

"...(Type) / Yukon Harb., 13 fms., Sd. Gr. / Shumagin Ids., Dall" (USNM 30914). The specimens, curled, rather eroded and decayed, have subdued red-orange color with paler lateral areas; none exhibits the "candy" appearance mentioned by Dall (1878a: 2). In the absence of evidence to the contrary, all 5 specimens are here regarded as syntypes. The larger specimen in lot labeled "Type" (USNM 30914), is here designated **lectotype** (Figures *54, 55*), with type locality Yukon Harbor, Shumagin Islands [55°07′ N; 159°45′ W]: orange color with paler lateral areas; valves moderately beaked, subcarinate, sculptureless; lateral areas vaguely defined; mucro somewhat anterior; valves i and viii, disarticulated, 3.2 and 3.0 mm wide, respectively; articulamentum white; slit formula 13-1-10; on valve viii, sutural laminae [broken ?] 1.2 mm wide, sinus 0.9 mm wide (sinus width/sutural lamina width, ratio 0.75); girdle's upper surface scaleless and leathery to the naked eye. A fragment of the girdle of a **paralectotype** (here designated) (USNM 30911) examined under microscope (× 100) with transmitted light, reveals the presence of spiculoid scales [not unlike those of *T. marmorea*] scattered throughout the upper surface (Figure 56). Thus, notwithstanding discrepancies in the number of slits in the end valves and the possibly much wider sinus on valve viii, the type specimens of *T. saccharina* could not be segregated with certainty from juveniles of *T. marmorea*. Under the circumstances, it seems prudent to leave the taxonomic position of *T. saccharina* under inquiry until the Aleutian chiton fauna and the particular features of juvenile specimens of *T. marmorea* are better known.

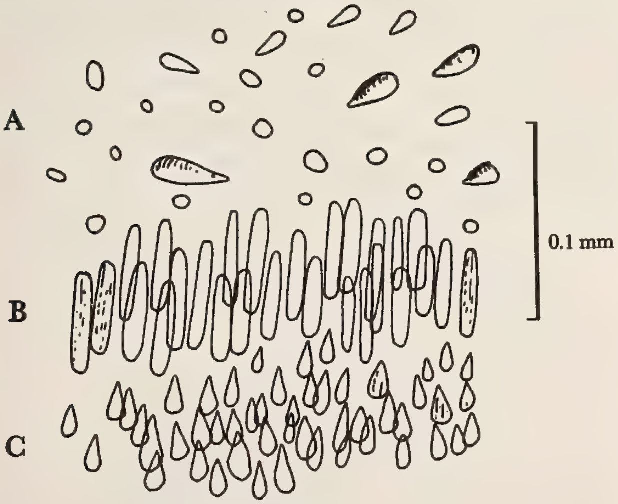


Figure 56

Tonicella saccharina Dall, 1878: **Paralectotype** (USNM 30911). Girdle elements: A) upper surface scales, B) outer margin spiculoid processes, C) undersurface scales

In the northern Atlantic, *Tonicella* is represented by *T. marmorea* and *T. rubra*. Both species range from the Arctic to about 50° N.

Tonicella blaneyi Dall, 1905, known only from the holotype (USNM 185504) collected in 20 fathoms [37 m] of water at Frenchman's Bay, Maine, is here retained as a *nomen inquirendum*. The specimen (Figures *57, 58*), dry, partly disarticulated, is about 13 mm long; valves carinate, beaked; tegmentum red marbled with white; tegmental surface micrgranular, sculptureless except for inconsistently defined, irregularly spaced radial ribs, about 20 in the anterior valve, 2 to 5 in the lateral areas of the intermediate valves; mucro central; articulamentum white, rose tinted; slit formula 10-1-4(+); on valve viii, sinus relative size (sinus width/sutural lamina width), 0.50 mm/1.72 mm = 0.29; soft parts in place; gills extend 75% length of foot; girdle leathery looking with scattered, small spiculoid scales (Figure 59) [similar to those of *T. marmorea*]. The characteristics of the specimen strongly suggest its identity with *T. marmorea*, despite the presence of unusual (? pathologic) ill-formed, ill-spaced radial ribs.

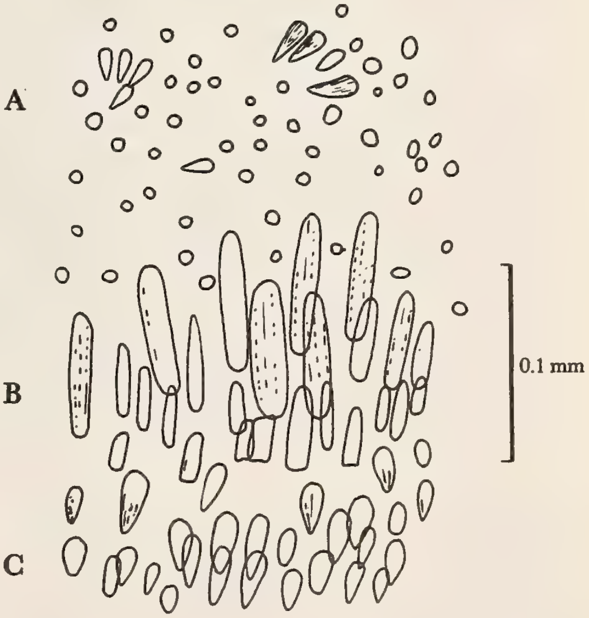


Figure 59

Tonicella blaneyi Dall, 1905: Holotype (USNM 185504). Girdle elements: A) upper surface scales, B) outer margin spiculoid processes, C) undersurface scales

No species of *Tonicella* are known in the southern hemisphere. *Tonicella (Mopaliella) stigmata* Dall, 1910, [nom.

nov. pro *Chiton bipunctatus* Sowerby, 1832 (not Fischer, 1808)] from Peru, is here shown to be a junior synonym of *Lepidochitona beanii* (Carpenter, 1857). *Tonicia horniana* Rochebrune, 1889, from Orange Bay, Patagonia, was assigned to *Tonicella* by Leloup (1956) on insufficient evidence; Rochebrune's type material could not be found at the Muséum National d'Histoire Naturelle, Paris (A. Tillier, *in litt.*, 14 June 1979). Leloup's (1956: 19-22) single specimen, referred to *"Tonicella horniana* (Rochebrune, 1889)," from Cape Horn remains without a name awaiting further study.

In the fossil record, *Tonicella* appears first as *T. tenuissima* (Sandberger, 1859) in the Oligocene of Europe (Janssen, 1978); in the Pacific, its earliest recorded presence is in the Pleistocene deposits of Oregon, Baja California, and Japan, as *T. lineata* (Wood, 1815).

Tonicella marmorea (Fabricius, 1780)

(Figures *60, 61*, 62, 63, *64, 65, 66, 67, 68*)

Chiton marmoreus Fabricius, 1780: 420-422—Middendorff, 1847b: 103-109 (in subsection *Stenosemus*); 1851: 178-183 (in subsect. *Stenosemus*)—Forbes & Hanley, 1853: 414-417; plt. 58, fig. 2; plt. 59, fig. 4—Clark, 1855: 251—Jeffreys, 1865: 227-229; 1869: 199 (with *Chiton submarmoreus* Midd. as probable syn.)—Winkley, 1894: 78

Tonicia marmorea (Fabricius). Adams & Adams, 1854: 474

Tonicella marmorea (Fabricius). Carpenter, 1873: 154—Dall, 1874: 1; 1879: 324-326; 1885: 343—Pilsbry, 1892: 41; plt. 10, figs. 8-15—Sykes, 1893: 36-37; plt. 3, fig. 9—Pilsbry, 1894a: 66; 1895: 113—Plate, 1899: 127-133; plt. 7, fig. 242; plt. 8, figs. 243-247—Thiele, 1902: 284—Schweikart, 1905: 394-397—Lermond, 1908: 16—Johnson, 1915: 8—Bergenhayn, 1930: 4—Løyning, 1932: 5-6; figs. 1-4—Leloup, 1945: 8-12; figs. 5, 8, 10—Smith, 1947a: 10;1947b: 18—Jakovleva, 1952: 57-59; text figs. 5, 7-10, 11-4, 21; plt. 2, fig. 3—Taki, 1962: 39—Taki, 1964: 409—Burghardt & Burghardt, 1969b: 37; plt. 4, fig. 78—Macpherson, 1971: 5-6; plt. 1, fig. 1, map 2—Abbott, 1974: 398; fig. 4670—Sirenko, 1974b: 993-994; figs. 1-4, 3-C

Boreochiton marmoreus (Fabricius). Sars, 1878: 116-117; plt. 8, fig. 3, a-1—Pelseneer, 1899: 7-35; plt. 1, fig. 4; plt. 6, fig. 61

Toniciella marmorea Thiele, 1893: 389; plt. 32, fig. 1

Lepidochitona marmorea (Fabricius). Dall, 1921: 188 (in section *Tonicella*)—Oldroyd, 1927: 856-857 (in section *Tonicella*)

Lepidochiton (Tonicella) marmorea (Fabricius). La Rocque, 1953: 10

Chiton marmoreus caeruleus Winkley, 1894: 78

Tonicella marmorea caerulea (Winkley). Johnson, 1915: 8

"Chiton ruber. Linnéi" Spengler, 1797: 92-94 [not Linnaeus, 1767]—Pilsbry, 1892: 41 (as syn. of *T. marmorea*)

Chiton laevigatus Fleming, 1815, 6(2): 725—Reeve, 1847, sp. 179—Pilsbry, 1892: 41 (as syn. of *T. marmorea*)—Lermond, 1908: 16 (as syn. of *T. marmorea*)

Chiton latus Lowe, 1825: 103-105; plt. 5, figs. 6-7—Sowerby, 1839: 6—Pilsbry, 1892: 41 (as syn. of *T. marmorea*)

Chiton fulminatus Couthouy, 1838: 217—Pilsbry, 1892: 41 (as syn. of *T. marmorea*)—Lermond, 1908: 16 (syn. of *T. marmorea*)

Chiton pictus Bean *in* Thorpe, 1844: 264—Pilsbry, 1892: 41 (as syn. of *T. marmorea*)

Chiton submarmoreus Middendorff, 1847b: 98 (in section *Hamachiton,* subsection *Platysemus*); 1851: 178-183; plt. 14, figs. 7-10; plt. 15, figs. 7-8 (in subsect. *Stenosemus*)—Carpenter, 1857b: 214; [?] 1864: 598 (reprinted, 1872: 84) [? = *lineata*]

Tonicia submarmorea (Middendorff). [?] Carpenter, 1864: 648 (reprinted 1872: 134) ["perhaps = *lineata* var. without lines"]—[?] Cooper, 1867: 21

Tonicella submarmorea (Middendorff). Dall, 1886: 210—[?] Berry, 1917a: 234; [?] 1917b: 3—[?] Willett, 1919: 27—Taki, 1938: 340-344; plt. 16, fig. 16; plt. 18, figs. 6-8; plt. 19, figs. 1, 3-8 (with *C. insignis* and *C. sitchensis* as syn.)—[?] Smith, 1947a: 12; [?] 1947b: 18—[?] Smith & Gordon, 1948: 205—Jakovleva, 1952: 62-63; text fig. 25; plt. 3, fig. 1 (with *C. insignis* as syn.)—Taki, 1962: 39 (with *Tonicella sitchensis* and *T. insignis* as syn.)—Taki, 1964: 410—Sirenko, 1974a: 792; 1974b: 994; figs. 1-1, 3-B

Lepidochitona submarmorea (Middendorff). [?] Dall, 1921: 188 (in sect. *Tonicella*)—Oldroyd, 1924: 185; [?] 1927: 857 (in sect. *Tonicella*)

Tonicella submarmorea (Middendorff). Thiele, 1893: 389; plt. 32, fig. 2

Boreochiton submarmoreus (Middendorff). Pelseneer, 1899: 7-35

Lepidochiton (Tonicella) submarmorea (Middendorff). [?] La Rocque, 1953: 11

Chiton flemingius Leach, 1852: 230—Pilsbry, 1892: 41 (as syn. of *T. marmorea*)

Explanation of Figures *39, 40, 43, 44, 47, 48, 49, 52,* and *53*

Figure *39: Dendrochiton gothicus* (Carpenter, 1864): same specimen as in Figure *38.* Close-up of lateral and central areas

Figure *40: Dendrochiton gothicus* (Carpenter, 1864): specimen, 6.5 mm long, same locality as specimen in Figures *38* & *39.* Close-up of lateral and central areas

Figure *43: Dendrochiton semiliratus* Berry, 1927: specimen, 15 mm long; Santa Catalina Id., Los Angeles Co., California (LACM-AHF 1624-48)

Figure *44: Dendrochiton semiliratus* Berry, 1927: same specimen as in Figure *43.* Close-up of lateral and central areas

Figure *47: Dendrochiton lirulatus* Berry, 1963: specimen, 11.5 mm long; San Felipe, Baja California, Mexico (AJF 27)

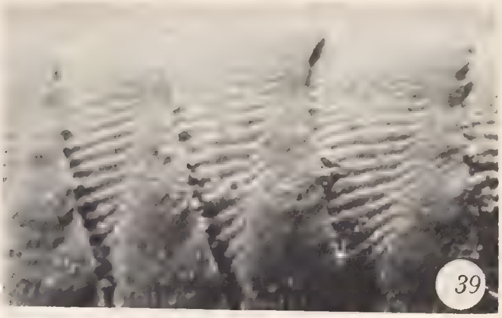
Figure *48: Dendrochiton lirulatus* Berry 1963: same specimen as in Figure *47.* Close-up view of central and lateral areas

Figure *49: Dendrochiton lirulatus* Berry, 1963: specimen 10 mm long: Puerto Peñasco, Sonora, Mexico (*ex* H. Bertsch) [*"laurae"* form]

Figure *52: Dendrochiton lirulatus* Berry, 1963: *Dendrochiton lirulatus* Berry, 1963: Type specimen in the S. S. Berry colln. (*ex* color slide by L. & F. Poorman)

Figure *53: Dendrochiton lirulatus* Berry, 1963: *Dendrochiton laurae* Berry, 1963, Holotype in the S. S. Berry colln. (*ex* color slide by L. & F. Poorman)


43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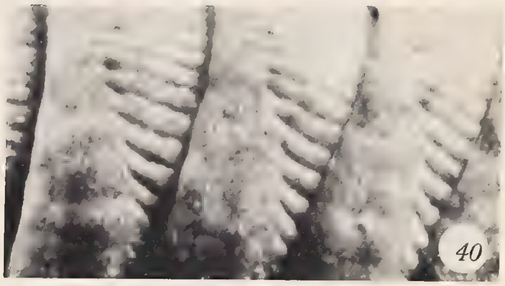
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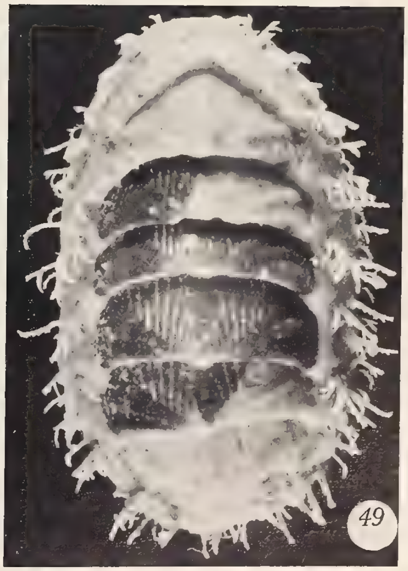
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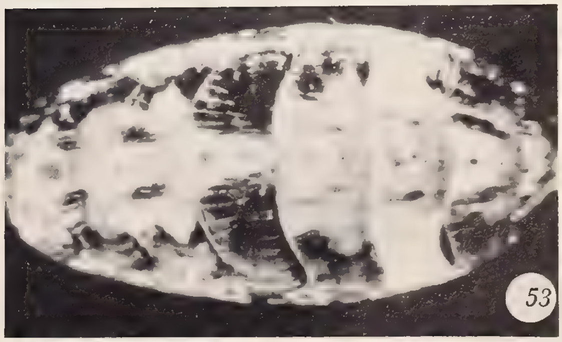
53

Type Material:

Chiton marmoreus Fabricius, 1780: **Lectotype** (herein designated) and 4 **paralectotypes** (Zoologisk Museum, Copenhagen).

Chiton marmoreus caeruleus Winkley, 1894: Holotype (Museum of Comparative Zoology, MCZ 32856), and 9 paratypes MCZ 32857): "Eastport," Maine.

Chiton laevigatus Fleming, 1815: No type material found at USNM (Dr. J. Rosewater, *in litt.*, 1 May 1979), BMNH (A. Blake, *in litt.* 2 July 1979), or the Royal Scottish Museum (Dr. D. Heppell, *in litt.*, 20 August 1979); "Zetland," Shetland Islands.

Chiton latus Lowe, 1825: No type material found at USNM (Dr. J. Rosewater, *in litt.*, 1 May 1979), BMNH (A. Blake, *in litt.*, 2 July 1979), or the Royal Albert Memorial Museum, Exeter (R. Brind, *in litt.*, 19 September 1979); "Oban," Scotland.

Chiton fulminatus Couthouy, 1838: "Cotypes" (MCZ 154830); **Lectotype** and **paralectotypes** (herein designated); "Massachusetts Bay."

Chiton pictus Bean *in* Thorpe, 1844: **Lectotype** (herein designated), and 2 **paralectotypes** (Wood End, Museum of Natural History, Scarborough Borough Council); "British."

Chiton submarmoreus Middendorff, 1847b: "11 syntypes from Shantar Is. collected in 1844 by Middendorff," in the Zoological Museum of the U.S.S.R., Leningrad (B. Sirenko, *in litt.*, 20 July 1979); "Tugurbusen und die Schantarischen Inseln, im Süden des Ochotzlischen Meeres." [55°N; 137°E] Middendorff, 1847b: 98).

Chiton flemingius Leach, 1852: No type material found at USNM, BMNH, or the Royal Scottish Museum; "Dr. J. Fleming discovered it in the Shetland seas." (Leach, 1852: 230).

Type Locality: Greenland [71°N; 40W], and Kragere, Norway [58°52′N; 9°25′W] as per the Copenhagen Zoologisk Museum label.

Description: Fabricius' (1780) original description of *Tonicella marmorea*, partially reprinted in Oldroyd (1927), is remarkably detailed, and quite sufficient to identify the species. Specimens (Figures *60, 61*) may reach 4 cm in length; color red, from light to dark tones, often marbled; tegmental surface microgranulose to smooth, sculptureless except for concentric growth rugae; valves carinate, moderately beaked; lateral areas hardly distinct; mucro central, not well defined; articulamentum white, rose tinted; slit formula, range 7/9-1-5/11, mode 9-1-8; sutural plates, broad, semi-oval; sinus narrow, relatively deep; on valve viii, relative width of sinus (width of sinus/width of sutural lamina) mean = 0.32 (range 0.24-0.58); eaves moderately spongy; gills extending 70-90% of foot; width of valve i/valve viii, mean ratio = 1.23 (range, 1.09-1.30). Girdle (Figure 62) as if nude or sparsely pubescent, leathery in dry specimens; upper surface with spiculoid, often pediculated scales, about 30 μm long, 10 μm wide (larger at inner margin), regularly distributed some 30-40 μm apart (density, 30 scales/0.06 μm^2 of girdle), and occasional to abundant hair-like spinelets, up to 100 × 5 μm interspersed (Figure 62 d); in young specimens, marginal fringe of spicules, up to 100 μm long, 15 μm wide; undersurface with imbricated, transparent, rectangular to triangular, scales, 40 × 15 μm (Figure 62 e). Specimen 35 mm long (CASIZ 005386, Amchitka Island, Aleutian Islands, Alaska) with radula (Figure 63) 11.5 mm long (35% of specimen's length), comprising 72 rows of mature teeth; median tooth 125 μm wide at anterior blade; first lateral teeth long, spatular head of second lateral teeth oval 225 μm long, 165 μm wide, with short denticle on inner side; outer marginal teeth, 135 × 212 μm (length/width ratio, 0.64).

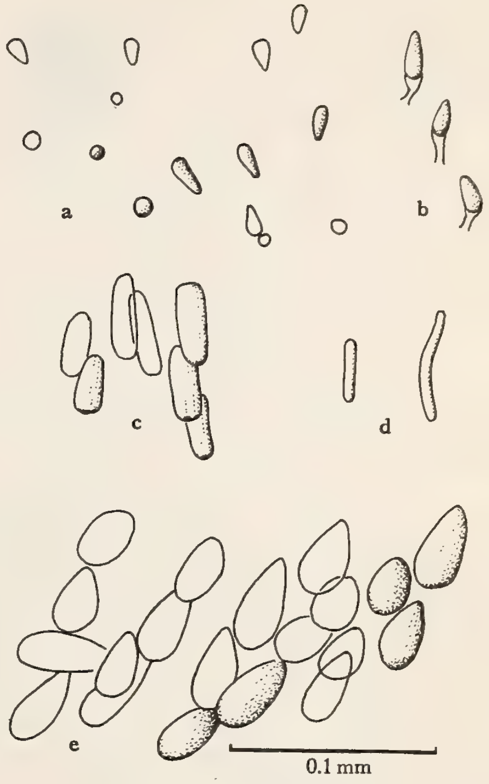

Figure 62

Tonicella marmorea (Fabricius, 1780): same specimen as in Figure *60*. Girdle elements: a) upper surface scales at the middle of the girdle, b) upper surface scales at the inner margin of the girdle, c) upper surface scales at the outer margin of the girdle, d) hair-like processes interspersed throughout upper surface of the girdle, e) undersurface scales

Specimens from Aleutian Islands when compared with those from eastern Atlantic and White Sea show no essential differences in valves, girdle, or radula. The only noticeable distinction is in the insertion plate of the posterior valve which projects beyond the tegmentum (when the valve is seen from above) in the Aleutian specimens but not in the Atlantic specimens examined. This single difference is here regarded as an expression of geographic variation with no taxonomic significance.

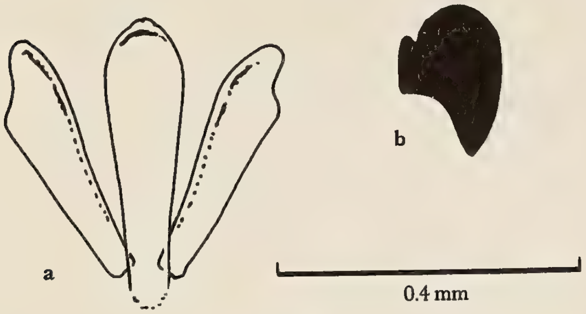

Figure 63

Tonicella marmorea (Fabricius, 1780): same specimen as in Figure *60*. Radula: a) median and first lateral teeth, b) head of second lateral tooth

Distribution: *Tonicella marmorea* has long been known to have a circumboreal to Arctic distribution. It has been reported in northern Japan Sea, Sachalin Islands, Sea of Okhotsk, Kurile Islands, Commander Islands, Aleutian Islands, Bering Sea, and northern Alaska (Sirenko, 1974b). In North Canada, *T. marmorea* has been collected from the Belcher Islands, in Hudson Bay, to as far north as Penny Strait [76°30′ N; 97°00′ W] (Macpherson, 1971). It has been reported also in the White Sea, Kara Sea, Spitzbergen, and Franz Josef Land [81° N], and along the coast of Norway to the southwest coast of Sweden, Kattegat, Denmark, Shetland Islands, east coast of England and Ireland (Jakovleva, 1952). On the east coast of North America it has been found as far south as Massachusetts Bay (CASIZ 005400), the southernmost record for the species [42°20′ N; 70°50′ W]. Reports of *Tonicella marmorea* in the Gulf of Alaska (Dall, 1921; Oldroyd, 1927; A. G. Smith, 1947a, 1947b; Jakovleva, 1952; Burghardt & Burghardt, 1969; Sirenko, 1974; Abbott, 1974), southward to Forrester Island [54°48′ N; 133°32′ W] were not confirmed. The very few lots of *T. marmorea* examined from the eastern half of the Pacific were all from Amchitka Island, Aleutian Islands, Alaska [51°30′ N; 179°00′ W] (USNM, alc. 1506, ? *leg.* W. H. Dall; CASIZ 005386 & CASIZ 005390, *leg.* L. Barr *et al.,* 12 June, 1973, at 15-25 m). However, in a lot of well characterized specimens of *Tonicella lineata* from Ketchikan, Alaska [55°21′ N; 131°35′ W] (UCLA 22286), a specimen (now recatalogued as UCLA 58429) dried, 38 mm long, reddish orange but with no lines, back more rounded and mucro more anterior than in most specimens of *T. lineata,* was determined tentatively as *Tonicella cf. T. marmorea.*

The bathymetric range of *Tonicella marmorea* has been recorded from 0 to 230 m (Sirenko, 1974b).

Remarks: The type material of *Chiton marmoreus* Fabricius, 1780, in the repository of the Zoologisk Museum, Copenhagen, Denmark, consists of 5 well preserved specimens, dry, strongly curled, reddish brown marbled with white. The accompanying museum label, hand-written, says "Chiton marmoreus O. Fabr. / Heri tilligen Ch. ruber Var. A sp. / No. 20 / Loc. Grønland og Kragerød / Type / Legit: O. Fb.;" other labels, also handwritten, state "Chiton marmoreus Fab. / *Orig. specimina* / (Heri tilligen eu Ch. ruber) / Gronland & Kragerod," and "*Ch. marmoreus* O. Fab. / Fn. Gs. 420 - Ch. viii f.812 / Ch. ruber var. 1. Sp. no. 20 / var. ? / Groenlandia et Kragerod. O.F." "Fn. Gs. 420" is a reference to Fauna Groenlandica; "Ch. viii f. 812" to Chemnitz' work; and "Sp. no. 20" to Spengler's (1797). The specimens agree with Fabricius' (1780) description. The largest specimen has an estimated length of 4 cm; the soft parts had been removed from 3 of the specimens. The specimen here selected as **lectotype** (Figure *64*) is about 2 cm long and partly disarticulated; tegmentum microgranular; girdle leathery, scaleless to the naked eye; mucro central, inconspicuous; postmucro convex; on valve viii, sinus 1.0 mm wide and sutural laminae 3.0 mm wide (sinus width/sutural laminae width 0.33), slit formula 9-1-11.

Chiton marmoreus caeruleus Winkley, 1894, was considered to be, from its inception, simply a variety of *C. marmoreus* Fabricius. The types (MCZ 32856; MCZ 32857) were not examined, but the alleged differences in size ("1¼ inches") and color ("rose...to a delicate light blue") do not warrant independent taxonomic status.

Chiton submarmoreus Middendorff, 1847b, has been regarded by most authors as a valid species. However, Middendorff's distinctions from *Chiton marmoreus* Fabricius, 1780—the color and size of the specimens, the height of the shell, the width of the girdle, and the slit formula—are of less than specific or even subspecific importance. In this study there was no opportunity to examine the type material of *Chiton submarmoreus* Middendorff [at the Zoological Museum of USSR, Leningrad, *fide* B. Sirenko, *in litt.,* 20 July 1979], or large number of specimens identified, or identifiable as either *marmoreus* or *submarmoreus,* but careful investigation of the specimens at hand from many different localities in the Pacific, Arctic, and Atlantic, failed to support the notion of two species. The distinctions between *marmoreus* and *submarmoreus* in color, size, height, width of girdle, tegmental surface, and radula enunciated by Middendorff (1847b), and elaborated upon by Jakovleva (1952), and Sirenko (1974) appear to be well within the intraspecific variation expected of a species with such wide geographical distribution. Reports of *Tonicella submarmorea* in the eastern Pacific (Berry, 1917a, 1917b; Willett, 1919; Dall, 1921; Oldroyd, 1924, 1927; Smith, 1947a, 1947b; Smith & Gordon, 1948; La Rocque, 1953) have been made in error, reflecting the confused status of the taxonomy, with *T. submarmorea* variously interpreted as a synonym of *T. insignis* (Dall, 1879, 1886; Pilsbry, 1892, 1895; Jakovleva, 1952; Is. Taki, 1938, 1962), *T. lineata* (Thiele, 1910), or *T. rubra* (Leloup, 1945; Abbott, 1974).

Chiton laevigatus Fleming, 1815, *Chiton latus* Lowe, 1825, and *Chiton flemingius* Leach, 1852 are placed in the synonymy of *Tonicella marmorea* (Fabricius, 1780) on the basis of the original descriptions and the authority of Pilsbry (1892) and Jakovleva (1952); their type material, if ever designated, could not be located. *"Chiton ruber* Linnei" Spengler, 1797 (not Linnaeus, 1767) is also placed in the synonymy of *T. marmorea, teste* Pilsbry (1892) and Dodge (1952: 22).

Chiton fulminatus Couthouy, 1838, was placed in the synonymy of *Tonicella marmorea* first by Pilsbry (1892), more recently by Jakovleva (1952). The type material, (MCZ 154830) consists of "cotypes," 5 dry specimens, relatively intact, and 18 loose valves accompanied by a museum label, dotted red, which reads in part, "fish stomachs, nr. Cohasset Rocks, Mass. / Couthouy;" other, older labels add the following information: "Cat. 8979...Orig. 972," *Tonicella marmorea* Fabr. sp. [with, superimposed] Orig. Spec. Gould '41, p.," and *"Chiton cinereus* Lowe / *fulminatus* Couthouy." The largest specimen in the lot, about 14.5 mm long, is here designated **lectotype** (Figures *65, 66*).

Chiton pictus Bean *in* Thorpe, 1844, has been regarded as a synonym of *Tonicella marmorea* since Pilsbry (1892) and Jakovleva (1952). Three specimens of *C. pictus* are part of the Bean shell collection at Wood End, Museum of Natural History, housed at Scarborough Council; they are on a blue card bearing the notation "3461.4.5.6," in a circular glass-top box (labeled "*Callochiton achatinus* (Brown), in cabinet "G"; the middle specimen fits Bean's (*in* Thorpe, 1844: 246) description (D. J. Waterman, *in litt.*, 27 September, 1979). The specimens were studied through photographs graciously provided by The Crescent Museums of the Scarborough Borough Council, Yorkshire, Great Britain. The middle (largest) specimen, 15 mm long, 10 mm wide, is here designated **lectotype** (Figures *67, 68*).

The questions related to the taxonomic positions of *Tonicella saccharina* Dall, 1878, and *T. blaneyi* Dall, 1905, and their possible entrance into the synonymy of *T. marmorea* were treated above in the general discussion of the genus.

Tonicella rubra (Linnaeus, 1767)
(Figures *69, 70,* 71, 72, 73)

Chiton ruber Linnaeus, 1767: 1107, no. 7—Schröter, 1786: 499-500—Gmelin, 1791: 3203-3204 (with *C. marmoreus* Fabricius as syn.)—Wood, 1815: 14—Lowe, 1825: 101; plt. 5, fig. 2—Sowerby, 1839: 6, sp. no. 8—Gould, 1841: 149-150; fig. 24—Brown, 1844: 66; plt. 21, figs. 6, 9—Middendorff, 1847b: 117-120—Reeve, 1847, sp. 176; plt. 26, fig. 176—Leach, 1852: 230—Shuttleworth, 1853: 67 (in section *Acanthopleura* Gray)—Forbes & Hanley, 1853: 399-402; plt. 59, fig. 6; plt. AA, fig. 6—Clark, 1855: 251—Hanley, 1855: 17—Jeffreys, 1865: 224-226 (with *C. minimus* Spengler, and *C. latus* Leach, as syn.)—Hidalgo, 1867: 417 (reprinted, 1890: 150)—Jeffreys, 1869: 63—Gould, 1870: 260-261; fig. 523—Marshall, 1898: 63—Dodge, 1952: 22

Tonicia rubra (Linnaeus). Gray, 1847a: 67; 1857: 185

Leptochiton ruber (Linnaeus). Adams & Adams, 1858: 473

Trachydermon ruber (Linnaeus). Carpenter, 1873: 153—Dall, 1874: 1-2; 1879: 295, 321-322; fig. 3 (radula); 1886: 210; 1889: 172—Pilsbry, 1894b: 15: 65; plt. 15, fig. 25 (girdle scales)—Blainey, 1904: 110—Nierstrasz, 1905a: 142—[?] Berry, 1907: 47 ("Monterey Bay, California")—Odhner, 1915: 50-51—Johnson, 1915: 9

Boreochiton ruber ("Lowe" [= Linnaeus]). Sars, 1878: 116; plt. 8, fig. 4—Aurivillius, 1885: 317

Ischnochiton ruber (Linnaeus). Pilsbry, 1892, 14: 80; plt. 7, figs. 50-56 (in section *Trachydermon*)—Plate, 1899: 122-127; plt. 7, figs. 239-241

Toniciella rubra (Linnaeus). Thiele, 1893: 390; plt. 32, fig. 4 (radula)

Tonicella rubra (Linnaeus). Sykes, 1893: 36; plt. 3, fig. 12—Thiele, 1902: 283; 1909: 18; plt. 2, fig. 51; 1910: 107—Berry, 1917a: 233—Willett, 1919: 27—Thiele, 1929: 8—Taki, 1938: 335-340; plt. 14, fig. 3; plt. 17, figs. 1-4; plt. 18, figs. 1-5 (with *Tonicella squamigera* Thiele, as syn.)—Leloup, 1945: 1-6, figs. 1, 2, 4 (with *T. submarmorea* as syn.)—Smith, 1947a: 10; 1947b: 18—Smith & Gordon, 1948: 205—Jakovleva, 1952: 59-60; text figs. 6-B, 22; plt. 2, fig. 4—Taki, 1962: 39-40 (with *T. squamigera* as syn.)—Taki, 1964: 410—Burghardt & Burghardt, 1969b: 37; plts. 4, fig. 79—Sirenko, 1974b: 990-991; text figs. 2-A, 2-C—Abbott, 1974: 398 (with *T. submarmorea* as syn.)

Tonicella ruber index Balch, 1906: 62-68

Lepidochitona ruber (Linnaeus). Dall, 1921: 188 (in section *Tonicella*)—Oldroyd, 1924: 185-186; 1927: 858-859 (in section *Tonicella*)

Lepidochiton ruber (Linnaeus). La Rocque, 1953: 10 (in subgen. *Tonicella*)

Chiton laevis Pennant, 1777: 72; plt. 36, fig. 3—Pilsbry, 1892: (as syn. of *C. ruber*)—Smith *in* Beu *et al.*, 1969: 184

Chiton cinereus Fabricius, 1780: 423 [not *C. cinereus* Linnaeus, 1767]—Middendorff, 1847b: 117 (as syn. of *C. ruber*)—Pilsbry, 1892, 14: 81 (as syn. of *C. ruber*)—Taki, 1938: 335 (as syn. of *C. ruber*)—Jakovleva, 1952: 59 (as syn. of *C. ruber*)

Tonicella beringensis Jakovleva, 1952: 60-61; text fig. 23; plt. 2, fig. 5—Sirenko, 1974a: 792; 1974b: 988-989, 992; text figs. 2-B, D; plt. 1, fig. 11

Tonicella granulata Jakovleva, 1952: 63-64; text fig. 26; plt. 3, fig. 2—Taki, 1962: 40—Taki, 1964: 410—Sirenko, 1974b: 996; text fig. 5-A; plt. 1, fig. 5; 1976: 89—Klimova & Sirenko, 1976: 78-79

Tonicella zotini Jakovleva, 1952: 64-65; text fig. 27; plt. 3, fig. 3—Taki, 1964: 410—Sirenko, 1974b: 995-996; text fig. 5-B; plt. 1, fig. 6; 1976: 89

Tonicella beringensis lucida Sirenko, 1974a: 792-794; plt. 1; 1976: 90

Type Material:

Chiton ruber Linnaeus, 1767: Type (Linnaean Collection, in custody of the Linnean Society of London, *fide* Dodge, 1952).

Chiton laevis Pennant, 1777: types not found at BMNH (A. Blake, *in litt.* 28 Feb. 1980); "Loch Broom in West Ross-shire," British Islands.

Chiton cinereus Fabricius, 1780 (not Linnaeus, 1767); types or equivalent material not found at Zoologisk Museum, Copenhagen, or British Museum (Natural History); locality not stated except for inclusion in "Fauna Groenlandica."

Tonicella beringensis Jakovleva, 1952: Type (Zoological Institute of USSR, Leningrad, *fide* Sirenko, 1974); "Bering Sea, Sea of Okhotsk" (Jakovleva, 1952: 61).

Tonicella granulata Jakovleva, 1952: Type (Zoological Institute of USSR, Leningrad, *fide* Sirenko, 1974); "the seas of Japan and Okhotsk and Bering Sea" (Jakovleva, 1952: 64).

Tonicella zotini Jakovleva, 1952: Type (Zoological Institute of USSR, Leningrad, *fide* Sirenko, 1974); "Sea of Japan and Okhotsk" (Jakovleva, 1952: 65).

Tonicella beringensis lucida Sirenko, 1974a: Type (Zoological Institute of USR, Leningrad, *fide* Sirenko, 1974a); "Posjet, Japan Sea."

Type Locality: *"Oceano septentrionali"* (Linnaeus, 1767: 1107).

Description: Linnaeus' original description (1767: 1107) was rather inadequate to identify the species with precision:

> *"C. testa octovalvi arcuati-substriata, corpore rubro... Habitat in Oceano septentrionali instar Patella affixa... Testa ovalis, oblongiuscula dorso carinata, valvulis oblique subarcuato-striatis."*

Fortunately, the recognition of *Chiton ruber* in the Linnean Collection was "very easy" (Hanley, 1855: 17), for "this was one of the few chitons owned by Linnaeus, and since the specimen found in the collection agrees, and uniquely agrees, with the description, its identification has been universally admitted" (Dodge, 1952: 22).

Specimens of *Tonicella rubra* (Figures *69, 70*) reach 3 cm in length; largest reported (as *"beringensis beringensis,"* Sirenko, 1974b: 992), 35 mm long; largest examined, 28 mm long (LACM A.2777, Seattle, Washington). Color bright to dull red, often marbled or mottled; valves elevated, subcarinate, beaked; tegmentum micrograqnular to smooth, even shiny, often with concentric growth rugae; lateral areas poorly defined; posterior valve inflated; mucro prominent, central to slightly anterior; postmucro sloping sharply, often at 90° angle; articulamentum light rose to pink; sutural laminae broad; sinus well defined, but not "deep, narrow, and angular" as stated by Pilsbry (1892: 80); on valve viii, relative width of sinus (sinus width/sutural laminae width), mean = 0.51 (range 0.37-0.64) (Table 3); slit formula range 8/10-1-7/12, mode 8-1-8; width of valve i/width of valve viii, mean ratio = 1.09 (range 0.97-1.21). Girdle's (Figure 71) upper surface with juxtaposed, translucent, spiculoid scales about 25 µm wide, 50 µm long (density, 40-120 scales/0.06 μm^2 of girdle); undersurface with imbricated, transparent, rectangular scales, 40 µm long, 15 µm wide, larger towards outer margin; marginal fringe of spicules (80 × 30 µm) with vague longitudinal striations. Specimen 10.0 mm long (LACM 73-31, Kodiak Island, Alaska) with radula (Figure 72) 3.2 mm long (32% of the specimen's length), comprising 42 rows of mature teeth; median tooth 50 µm long, 20 µm wide at anterior blade); first lateral teeth aliform, head of second lateral teeth round, 25 µm long, 30 µm wide, with two very small notches in inner edge defining three denticles or cusps; outer marginal teeth 60 × 55 µm (length/width ratio, 1.09).

Distribution: *Tonicella rubra* is an Arctic-circumboreal species (Forbes & Hanley, 1853; Pilsbry, 1892; Odhner, 1915; Dall, 1921). However, Jakovleva (1952) and Sirenko (1974b) expressed the opinion that most records of *T. rubra* in the Pacific were in error inasmuch as several other species (*Tonicella beringensis* Jakovleva, 1952, *T. beringensis lucida* Sirenko, 1974a, *T. granulata* Jakovleva, 1952, and *T. zotini* Jakovleva, 1952) had been confused with *T. rubra.* The results of this study refute Jakovleva and Sirenko's

Explanation of Figures *54, 55, 57, 58, 60, 61,* and *64*

Figure *54: Tonicella saccharina* Dall, 1878: **Lectotype** (USNM 30914)

Figure *55: Tonicella saccharina* Dall, 1878: **Lectotype** (USNM 30914). Close-up view of central and lateral areas

Figure *57: Tonicella blaneyi* Dall, 1905: Holotype (USNM 185504)

Figure *58: Tonicella blaneyi* Dall, 1905: Holotype (USNM 185504). Close-up view of central and lateral areas

Figure *60: Tonicella marmorea* (Fabricius, 1780): specimen 35 mm long; Amchitka Id., Aleutian Islands, Alaska (CASIZ 005386)

Figure *61: Tonicella marmorea* (Fabricius, 1780): same specimen as in Figure *60.* Posterior valve

Figure *64: Tonicella marmorea* (Fabricius, 1780): *Chiton marmoreus* Fabricius, 1780, **lectotype** (Zoologisk Museum, Copenhagen, Denmark)


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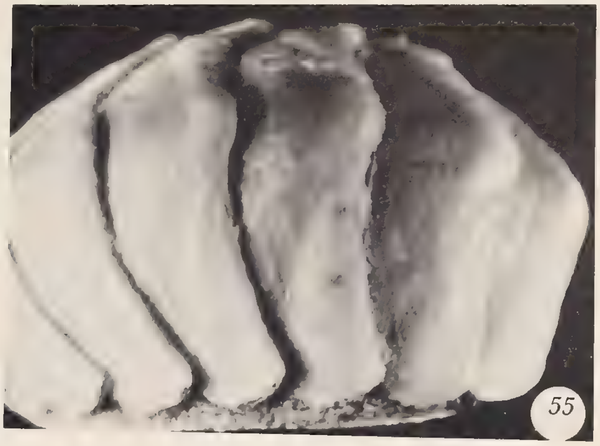
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Table 3

Some meristic characteristics of specimens of *Tonicella rubra* (Linnaeus, 1767) from different localities.

Locality	specimen length mm	width of valves			valve viii			slit
					width		width sinus/ sutural lamina ratio	
		i mm	viii mm	i/viii ratio	sinus mm	sutural lamina mm		
Barents Sea (*ex* Sirenko, *"rubra"*)	8.0	3.1	2.8	1.11	0.66	1.18	0.56	8-1-9
Alaska (LACM 73-31)	10.0	3.3	3.0	1.10	0.63	1.75	0.50	8-1-10
Kurile Is. (*ex* Sirenko, *"beringensis lucida"*)	11.3	3.5	2.9	1.21	?	1.42	?	8-1-?
Massachusetts (CASIZ 005393)	13.0	3.9	3.5	1.11	0.76	1.55	0.49	8-1-8
Kurile Is. (*ex* Sirenko, *"beringensis lucida"*)	14.0	4.0	3.9	1.03	0.92	1.91	0.48	8-1-11
Alaska (LACM 73-22)	15.0	4.5	3.9	1.15	1.06	1.82	0.58	8-1-9
Japan Sea (*ex* Sirenko, *"granulata"*)	15.8	5.3	4.6	1.15	1.06	1.98	0.53	9-1-8
Alaska (LACM 73-8)	17.8	5.3	5.0	1.06	0.96	2.47	0.39	8-1-10
Norway (*ex* P. Kaas Colln.)	19.2	6.4	5.5	1.16	0.99	2.71	0.37	8-1-8
Alaska (LACM 73-20)	19.6	5.8	5.4	1.07	1.48	2.31	0.64	9-1-10
Bering Sea (*ex* Sirenko, *"beringensis beringensis"*)	20.0	6.0	5.8	1.03	1.48	2.64	0.56	9-1-8
Kurile Is. (*ex* Sirenko, *"beringensis lucida"*)	20.2	5.5	5.4	1.02	1.25	2.41	0.52	8-1-9
Bering Sea (*ex* Sirenko, *"beringensis beringensis"*)	24.0	6.8	6.6	1.03	1.65	3.04	0.49	10-1-7
Kurile Is. (*ex* Sirenko, *"beringensis lucida"*)	24.7	6.7	6.9	0.97	1.65	2.81	0.59	8-1-12

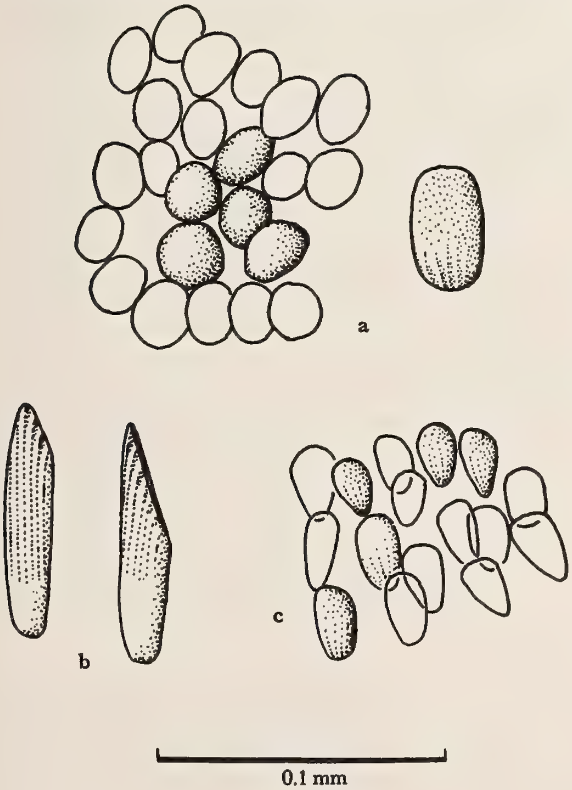

Figure 71

Tonicella rubra (Linnaeus, 1767): specimen 10.0 mm long; Kodiak Id., Alaska (LACM 73-31). Girdle elements: a) upper surface scales, b) outer margin spiculoid processes, c) undersurface scales

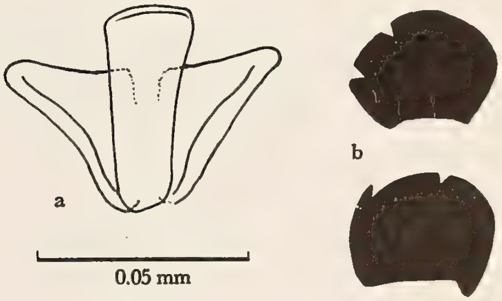

Figure 72

Tonicella rubra (Linnaeus, 1767): same specimen as in Figure 71. Radula: a) median and first lateral teeth, b) heads of second lateral teeth

conclusions, and reestablish the view of early authors. Thus, the distribution of *T. rubra* extends from the Arctic to both north Atlantic and Pacific oceans. In the Arctic, it is recorded in the White and Barents Seas (SIRENKO, 1874b); northernmost reported record, Devon Island, Canada [75° N] (MACPHERSON, 1971). In the Atlantic, it is present along the coast of Norway (? to Bergen), Kattegat, North Sea, England, Shetland, Faroes Islands, and Iceland (JAKOVLEVA, 1952); along the eastern coast of North America, it has been collected as far south as New London, Connecticut [41°21′ N; 72°07′ W] (JOHNSON, 1915). In the Pacific, it is known (albeit as *"beringensis," "granulata," "zotini,"* or *"lucida")* from the northern part of the Sea of

Japan, Sea of Okhotsk, Sachalin and Kurile Islands, Bering Sea, Aleutian Islands (CASG-SU 33749), and along the coast of North America from Alaska to Seattle, Washington [47°36′ N; 122°20′ W] (LACM A.2777).

The bathymetric range of *Tonicella rubra* is recorded from 0 to 300 m (Jakovleva, 1952).

Remarks: The study of *Tonicella rubra* was made particularly difficult by the differing opinions of Jakovleva (1952) and Sirenko (1974a, 1974b, 1976). Jakovleva (1952: 60) stated that "*T. rubra* does not occur in the Pacific" having been misidentified as *T. granulata*, *T. beringensis*, or *T. zotini*. These species were segregated from *T. rubra* on the basis of 1) tegmental surface (smooth, without costae [growth rugae] in *T. rubra;* smooth, with costae, in *T. beringensis;* slightly granular, with costae, in *T. zotini;* coarsely granular, without costae, in *T. granulata*), 2) mucro (poorly developed, in *T. rubra*, and *T. granulata;* well developed, in *T. zotini*, and *T. beringensis*), 3) head of second lateral teeth of radula (as long as wide, in *T. rubra* and *T. zotini;* wider than long in *T. beringensis;* longer than wide in *T. granulata*), and 4) girdle scales (very large, in *T. rubra* and *T. zotini;* short, in *T. granulata;* minute, in *T. beringensis*). However, these distinctions are of less than specific or even subspecific significance. A comparison of specimens of *Tonicella rubra* (and *rubra*-like) from the Atlantic, Arctic, and Pacific, showed no appreciable quantitative or qualitative discrepancies (Table 3), and demonstrated that the different geographic populations represent a single species properly referred to *Tonicella rubra* (Linnaeus, 1767). As should be expected from a species with such wide geographic distribution, specimens of *T. rubra* do exhibit considerable variation. In 4 specimens from Kurile Islands identified as *"lucida"* by Sirenko, the girdle has smaller (25 × 10 μm), and fewer scales (40/0.06 μm²) with a few filamentous processes (about 35 × 5 μm) interspersed. In one specimen of *"granulata"* and 2 specimens of *"beringensis beringensis"* as determined by Sirenko, the girdle has average size scales (about 60 × 30 μm) and density (50 scales/0.06 μm²); and in the latter, it shows some long filamentous processes (about 300 × 20 μm) interspersed. Noteworthy variations of the radula were observed in its relative length (average 35% of specimen's length, range 30-50%, longer in the young), the number of rows of mature teeth (average 50 per specimen, range 42-60), and in the size and shape of the denticles of the head of the second lateral teeth (varying appreciably even within the same specimen; more deeply cut and wider apart in smaller specimens than in larger ones) (Figure 73). Considerable intra-species variation was also noted in color (different shades of red, uniform to marbled), carination (moderate to absent), tegmental surface (microgranular to smooth, with or without growth rugae, or "costae"), mucro from slightly anterior to slightly posterior (mostly central), postmucro slope (from 139° to 80°), posterior margin of valve viii (slightly notched in some large specimens), gills (extending 60-80% of the foot).

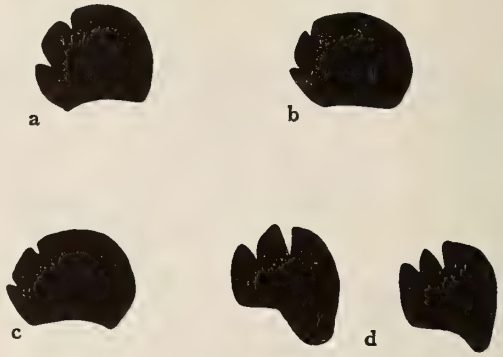

Figure 73

Tonicella rubra (Linnaeus, 1767): Variations in the shape of heads of second lateral teeth: a) specimen 15.8 mm long, Vostok Bay, Japan Sea [*"granulata" ex* Sirenko colln.], b) specimen 20.2 mm long, Kurile Islands [*"beringensis lucida" ex* Sirenko colln.], c) specimen ca. 20 mm long, Cohen Id., Kenai Peninsula, Alaska (LACM 73-20), d) specimen 5 mm long, Kodiak Id., Alaska (LACM 73-31)

The geographic and bathymetric range of *Tonicella rubra* virtually duplicates that of *T. marmorea*, which may explain some of the confusion in sorting out the two species.

Chiton minimus Gmelin, 1791, *Chiton laevis* Gmelin, 1791, and *Chiton latus* Leach, 1852, have long been considered in the synonymy of *C. ruber* Linnaeus, 1767. However, from the original accounts it is impossible to say with reasonable assurance what these species are; the descriptions conform well to *C. ruber*, but they also conform to other species known in the area, particularly to *Tonicella marmorea*. It is here suggested, therefore, that the names be dropped from contention, not as synonyms of *C. ruber* but as *nomina dubia*. Similar action is proposed for *Chiton incarnatus* Reeve, 1847, for which no locality was given.

Chiton puniceus Gould, 1846, regarded as a synonym of *C. ruber* by early authors (Pilsbry, 1892), has been placed by Thiele (1908) in the genus *Callochiton* Gray, 1847b. *Chiton cinereus* Fabricius, 1780, is not the Linnean (1767) species of that name, but *Chiton ruber* Linnaeus, 1767, *fide* Pilsbry (1892, 14: 81).

A search for the type material of *Chiton laevis* Pennant, 1777, proved futile: "the types do not seem to have been part of the Pennant collection when it came to this museum [BMNH] and I cannot suggest where they might now be found" (A. Blake, *in litt.*, 29 February 1980).

Tonicella insignis (Reeve, 1847)
(Figures *74, 75,* 76, 77)

Chiton insignis Reeve, 1847, sp. no. 149; plt. 22, fig. 148—Middendorff, 1847b: 109 (as possible syn. of *Chiton lineatus* Wood)—Pilsbry, 1892, 14: 42 (as syn. of *Tonicella submarmorea* (Middendorff)—Jakovleva, 1952: 62 (as syn. of *T. submarmorea*)

Tonicia insignis (Reeve). Adams & Adams, 1858: 474—Carpenter, 1857b: 317

Tonicella insignis (Reeve). Leloup, 1945: 6-7; figs. 3, 6, 9—Berry, 1951: 218-219—Taki, 1962: 39 (as syn. of *T. submarmorea*)—Burghardt & Burghardt, 1969b: 36; plt. 4, fig. 75—Rice, 1971: 16; plt. 1, fig. 2—Sirenko, 1974b: 994; text fig. 3-A; plt. 1, fig. 2—Abbott, 1974: 398—Himmelman, 1979: 215-225

Type Material:

Chiton insignis Reeve, 1847: 2 syntypes (BMNH 1842.1.22.482-483); "Sitka, Pres. R. B. Hinds" (A. Blake, *in litt.*, 2 May 1979). **Lectotype**, herein designated as the larger, figured specimen (in Reeve, 1847, fig. 148).

Type Locality: Sitka, Alaska [57°03′ N; 135°14′ W].

Description: Based upon specimens collected by Hinds during the expedition of the *Sulphur*, Reeve's (1847) original description and illustration are quite adequate to identify the species. Specimens of *Tonicella insignis* (Figures *74, 75*) often reach 3 cm in length; largest examined 52.5 mm long (CASIZ 008946, Victoria Harbour, British Columbia, Canada). Color pattern strikingly unique, uniform red-wine to orange in anterior valve, lateral areas and postmucro area, with undulating transverse white lines on dark maroon background in central areas; in 22% of specimens examined, lateral areas of valves v and vi, white instead. Tegmentum microgranulose to smooth, even shiny; lateral areas hardly raised; mucro anterior, often marked by change in color; postmucro straight to mildly concave, sloping at 30°-40°; gills along 75% of foot; articulamentum white to rose-tinted; sutural laminae short, semioval; sinus narrow, angulated; on valve viii, relative width of sinus (sinus width/sutural lamina width) mean = 0.25, (range, 0.22-0.29); slit formula range 8/10-1-8/11, mode 8-1-8; widths of valve i/valve viii, mean ratio = 1.19 (range, 1.17-1.21).

Girdle as if nude to the naked eye, leathery in dry specimens; upper surface shows spiculoid, often pediculated scales (Figure 76), about 5 μm wide (larger at inner margin) 20-25 μm long, close together (density, 100 scales/ 0.06 μm^2), with occasional spinelets, up to 100 × 10 μm, interspersed; undersurface with loosely imbricated, transparent, oval to lanceolate scales, 35 × 15 μm, longer (to 60 μm) at outer margin. Specimen 37.8 mm long (LACM 73-13, Sitka Sound, Baranof Island, Alaska) with radula (Figure 77) 12.4 mm long (32% of specimen's length) comprising 94 rows of mature teeth; median tooth rectangular, 350 μm long, 70 μm wide at anterior blade; first lateral teeth rectangular, about 350 μm long, 120 μm wide; head of second lateral teeth about 190 μm long, 150 μm wide with single, well defined denticle on inner side; outer marginal teeth squarish, about 150 × 150 μm.

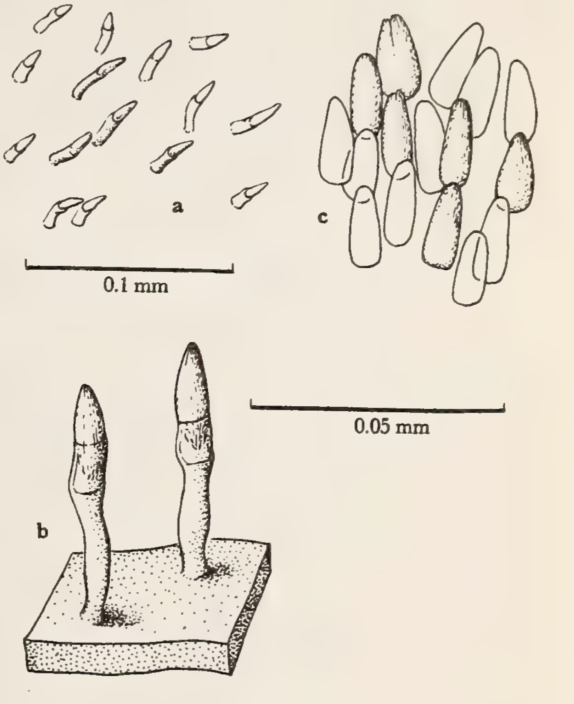

Figure 76

Tonicella insignis (Reeve, 1847): same specimen as in Figure *74*. Girdle elements: a) upper surface scales, b) much enlarged upper surface scales, c) undersurface scales

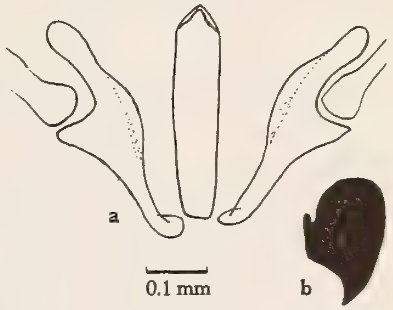

Figure 77

Tonicella insignis (Reeve, 1847): specimen, 37.8 mm long. Radula: a) median and first lateral teeth, b) head of second lateral tooth

Distribution: *Tonicella insignis* is confined to the northeastern Pacific between latitudes 60° N and 47° N. Northernmost verified record, Montague Island, Prince William Sound, Alaska [60°10′ N; 147°15′ W] (CASG 39423, *leg.* R. R. Talmadge, 26 June, 1965; CASG 41790, *leg.* G D. Hanna);

southernmost record, Tacoma Narrows, Puget Sound, Washington [47°17′N; 122°36′W] (CASIZ 008943 *leg.* A. R. Wingard, May 1961; CASIZ 008944, *leg.* E. C. Starks; USNM 752826, *leg.* C. C. Engberg, 1921-22). The species has not been recorded in the Aleutians.

Tonicella insignis has a narrow depth range, extending from the intertidal zone to 6-12m (LACM 73-33, Kodiak Island, Alaska, *leg.* J. H. McLean & G. Powell, 15 Aug. 1973).

Remarks: The similarities between *Tonicella insignis* and *T. marmorea* are impressive and explain why the two species have often been confused. Yet they differ in: 1) color pattern, 2) mucro (anterior in *T. insignis,* central in *T. marmorea*), 3) density of girdle's scales (about 100/0.06 μm^2 in *T. insignis,* 40/0.06 μm^2 in *T. marmorea*), 4) radula (more rows of mature teeth in *T. insignis* than in *T. marmorea;* head of major lateral teeth with one deep notch in *T. insignis,* one or often two small notches in *T. marmorea*). Contrary to Sirenko's (1974b: 988) findings, the relative size of the sinus on valve viii (width of sinus/width of sutural laminae) did not distinguish *T. insignis* from *T. marmorea* in the specimens examined.

The syntypes of *Chiton insignis* (BMNH 1842.1.22.482-483) were not examined. Reeve's (1847, fig. 148 [numbered in error for sp. no. 149]) figured specimen is here designated **lectotype**, a figure which corresponds to the larger of the two type specimens (A. Blake, *in litt.,* 2 May 1979).

Tonicella insignis appears to have an annual reproductive cycle with spawning cued by the spring phytoplankton (Himmelman, 1979).

Tonicella lineata (Wood, 1815)

(Figures *78,* 79, 80, 81)

Chiton lineatus Wood, 1815: 15-16; plt. 2, figs. 4-5; 1828: 2—Sowerby, 1840: 5, 10, sp. no. 71; fig. 77—Reeve, 1847, sp. no. 33; plt. 7, fig. 33—Middendorff, 1847b: 109-112; plt. 12, figs. 8-9 (with *C. insignis* as syn.)—Carpenter, 1857b: 208, 214, 223, 229—Chenu, 1859: 381 (in subgen. *Tonicia*)—Carpenter, 1864: 523 (reprinted, 1872: 9)

Tonicia lineata (Wood). Gray, 1847a: 67—Carpenter, 1857b: 317—Gray, 1857: 185—Adams & Adams, 1858: 474—Carpenter, 1864: 648, 684 (reprinted, 1872: 134, 170)—Cooper, 1867: 21; 1870: 58

Tonicella lineata (Wood). Dall, 1879: 296, 326-327—Wood & Raymond, 1891: 58—Pilsbry, 1892, 14: 42-43; plt. 11, figs. 25-28; 1895: 112, 1898: 287—Berry, 1907: 47—Thiele, 1909; (with *C. submarmorea* as syn.)—Berry, 1917: 234—Packard, 1918: 292; plt. 34, fig. 3—Chace & Chace, 1919: 3 (fossil)—Willett, 1919: 27—Berry, 1922: 433-435; plt. 2, figs. 1-5 (fossil)—Taki, 1938: 331-335; plt. 14, fig. 12; plt. 18, figs. 9-15; plt. 19, fig. 2—Leloup, 1945: 12-15; figs. 7, 11, 12—Smith, 1947a: 9-10; 1947b: 18—Jakovleva, 1952: 61-62; text fig. 24; plt. 2, fig. 6—Thompson & Chow, 1955: 31—Taki, 1962: 39—Thorpe, 1962: 203, 205—Taki, 1964: 410—Addicott, 1964: 658, tbl. 2 (fossil)—Roth, 1966: 249—Burghardt & Burghardt, 1969a: 228-229; 1969b: 37; plt. 4, figs. 76-77—Johnson, 1969: 273-274—Zullo, 1969: 350; tbl. 1 (fossil)—Rice, 1971: 16; plt. 1, fig. 1—Barnes, 1972—Barnes & Gonor, 1973: 259-264—Kohl, 1974: 214; tbl. 1 (fossil)—Sirenko, 1974b: 995; text figs. 4-A, C; plt. 1, fig. 3—Abbott, 1974: 398; fig. 4671—A. G. Smith *in* R. I. Smith & Carlton, 1975: 461, 465—Andrus & Legard, 1975: 7-8; tbl. 1—Demopulos, 1975: 42-46—Seiff, 1975: 54-56—Kincannon, 1975: 87-93—Robbins, 1975: 98-102—Kennedy, 1978: 696 (fossil)—Itoigawa *et al.,* 1978: 149-153; figs. 3-4; tbl. 1-2; plt. 16, figs. 2-7 (fossil)—Roth, 1979: 418 (fossil)—Himmelman, 1979: 215-225

Toniciella lineata (Wood). Thiele, 1893: 390; plt. 32, fig. 3 (radula)

Lepidochitona lineata (Wood). Dall, 1921: 188 (in section *Tonicella*)—Oldroyd, 1924: 185; 1927: 857-858—Johnson & Snook, 1927: 561; fig. 657 (in subgen. *Tonicella*)—Fraser, 1932: 65—Chace & Chace, 1933: 123—Burch & Burch, 1943: 5—Andrews, 1945: 26, 28, 32

Lepidochitona lineata (Wood). La Rocque, 1953: 10 (in subgen. *Tonicella*)

Tonicella undocaerulea Sirenko, 1973: 663-666; 1974b: 995; text figs. 4-B, D; plt. 1, fig. 7; 1976: 89-90

Type Material:

Chiton lineatus Wood, 1815: Original material presumed lost. No type material found at BMNH (A. Blake, *in litt.,* 21 September 1979).

Tonicella undocaerulea Sirenko, 1973: Holotype and paratypes in the Zoological Museum of USSR, Leningrad; "Bay of Minonosok, Posjet Strait, Sea of Japan."

Explanation of Figures *65* to *70, 74,* and *75*

Figure *65: Tonicella marmorea* (Fabricius, 1780): *Chiton fulminatus* Couthouy, 1838, **lectotype** (MCZ 154830)

Figure *66: Tonicella marmorea* (Fabricius, 1780): *Chiton fulminatus* Couthouy, 1838, **lectotype** (MCZ 154830). Close-up of central and lateral areas

Figure *67: Tonicella marmorea* (Fabricius, 1780): *Chiton pictus* Bean, 1844, **lectotype** (Museum of Natural History of Scarborough Borough Council, Yorkshire, United Kingdom) [Photograph by The Crescent Museums of Scarborough]

Figure *68: Tonicella marmorea* (Fabricius, 1780): *Chiton pictus* Bean, 1844, **lectotype** (Museum of Natural History of Scarborough Borough Council, Yorkshire, United Kingdom) [Photograph by The Crescent Museums of Scarborough]. Lateral view

Figure *69: Tonicella rubra* (Linnaeus, 1767): specimen 25mm long; Seldovia Bay, Alaska (LACM 73-18)

Figure *70: Tonicella rubra* (Linnaeus, 1767): same specimen as in Figure *69.* Lateral view

Figure *74: Tonicella insignis* (Reeve, 1847): specimen, 36mm long; Negei Id., British Columbia, Canada (LACM 63-32)

Figure *75: Tonicella insignis* (Reeve, 1847): same specimen as in Figure *74:* Lateral view


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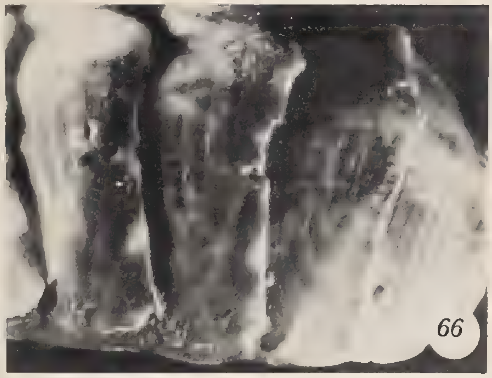
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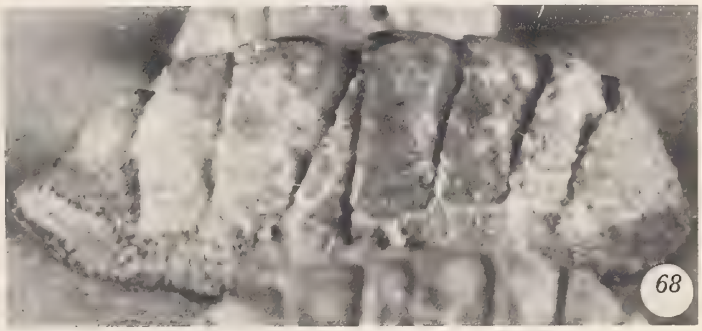
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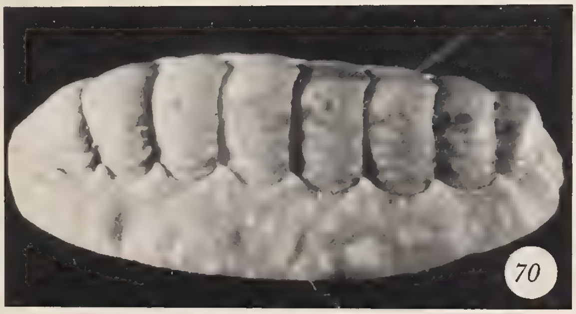
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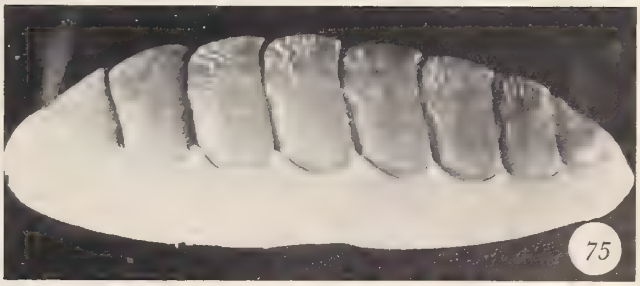
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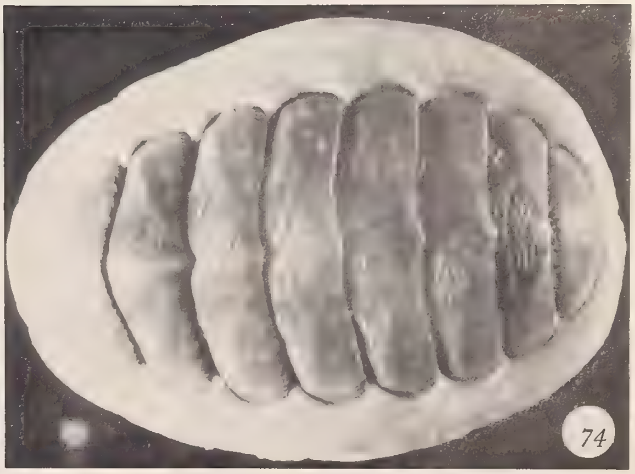

74

Type Locality: "Their country is unknown" (WOOD, 1815: 16). Here designated as Monterey Bay, Monterey County, California (36°45′ N; 121°55′ W).

Description: WOOD's (1815) original description is very short: "18. Chiton lineatus. *Ch. testa octavi laevi, valvis lineatis, limbo lato coriaceo,*" but together with illustrations in plt. 2, figs. 4-5 *(op. cit.)* quite adequate to identify the species. Specimens of *Tonicella lineata* (Figure 78) often reach 4 cm in length; largest specimen examined, 50.3 mm long (LACM 66-37, Puget Sound, Washington, *leg.* J. H. McLean, 19 June 1966, intertidally). Color pattern very characteristic, bold white and dark-maroon zigzag lines on salmon to orange background, quite variable in number, extending from lateral areas into pleural areas but sharply discontinuous at jugum (where background color, often in darker hues, forms well delineated triangles); one or more valves of solid (brown, red, or white) color; in adults, zigzag lines practically always present on valve i and (less constantly) on valve viii; in very small specimens, zig-zag lines absent or vaguely indicated. Valves subcarinate, beaked (particularly in the young); tegmentum sculptureless, smooth to shiny; lateral areas weakly defined; mucro anterior; postmucro straight to mildly convex (slightly concave in the young); articulamentum white with midline pink to brown discoloration; eaves spongy; sutural laminae wide, semioval; on valve viii, sinus relative width (sinus width/sutural laminae width), mean = 0.41 (range, 0.26-0.60), larger in smaller (young) specimens (correlation between length of specimen and relative width of sinus on valve viii, $r = -0.57$; $p < 0.01$); slit formula range, 8/10-1-8/12, mode 8-1-9. Girdle in living specimens, blotched or banded with blue, maroon and white, but colors vanish when animal dies; in dry specimens, leathery as if nude. Upper surface with scales (Figure 79) varying in shape, size, and number as function of specimen's size (age). Large specimens, practically scaleless (density down to 27 scales/0.06 μm^2); scales small (7-9 μm wide), spiculoid, except for 1-4 rows of much larger (up to 12 μm wide, 25 μm long), globulose, mammillated, jaggedly striated scales at inner margin (Figure 79 B). In small specimens, scales abundant, crowded (density up to 225 scales/0.06 μm^2), round, large (12-14 μm wide). A growth series of 11 specimens (Table 4) reveals statistically significant ($p < 0.02$) correlations between the length (age) of the specimens and the average width of the girdle scales ($r = -0.90$), the number of scales per unit of girdle's surface ($r = -0.66$), and the percentage of scaleless, "naked" girdle area ($r = 0.75$). Undersurface with loosely imbricated, lanceolate scales, 35 × 10 μm, smaller, almost round, scarcer towards inner margin. Specimen 25 mm long (AJF 143, Moss Beach, San Mateo County, California) with radula (Figure 80) 7.6 mm long (30% of specimen's length) comprising 65 rows of mature teeth; median tooth 80 μm wide at anterior blade; first lateral teeth aliform; head of second lateral teeth round, about 80 μm long, 130 μm wide, usually with two notches at inner edge, innermost deeper, defining a denticle; outer marginal teeth squarish, 110 × 110 μm. The head of the second lateral teeth displays considerable

Table 4

A "growth series" of *Tonicella lineata* (Wood, 1815) showing the relationship between the specimen's length vs. number of girdle scales per unit of surface ($r = -0.66$), average diameter of scales ($r = -0.90$), and percentage of "naked" girdle ($r = 0.75$).

Locality	Specimen length (mm)	Mean number of scales in 0.06 mm² of girdle (no.)	Diameter of scales (mode) (µm)	Area covered by scales in 0.06 mm² of girdle (µm²)	Girdle area covered by scales (%)	"Naked" area of girdle (%)
LACM 72-91, San Pedro, Calif.	6.5	225	14	34 650	55	45
CASIZ 009296, Edna Bay, Alaska	8.4	161	12	18 193	29	71
CASIZ 009296, Edna Bay, Alaska	9.7	159	12	17 967	29	71
CASIZ 009296, Edna Bay, Alaska	11.5	119	11	11 305	18	82
CASIZ 009296, Edna Bay, Alaska	13.9	85	10	6 630	11	89
LACM 73-35, Vancouver Id., B.C.	15.0	161	9	10 304	16	84
AJF 152, Bolinas, Calif.	20.0	100	10	7 800	12	88
CASIZ 009296, Edna Bay, Alaska	20.5	112	10	8 736	14	86
LACM 73-35, Vancouver Id., B.C.	25.1	27	8	1 350	2	98
CASIZ 009296, Edna Bay, Alaska	26.1	123	9	7 872	13	87
CASG-SU, Vancouver Id., B.C.	35.0	94	7	3 572	6	94

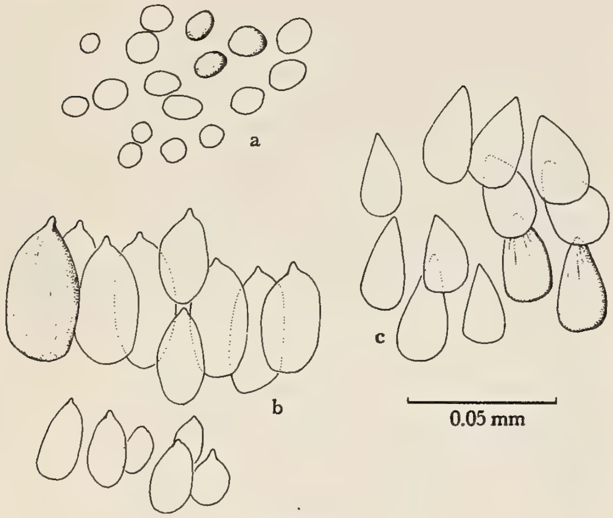


Figure 79

Tonicella lineata (Wood, 1815): specimen, 20.5 mm long; Edna Bay, Alaska (CASIZ 009296). Girdle elements: a) upper surface scales at the middle of the girdle, b) upper surface scales at the inner margin of the girdle, c) undersurface scales

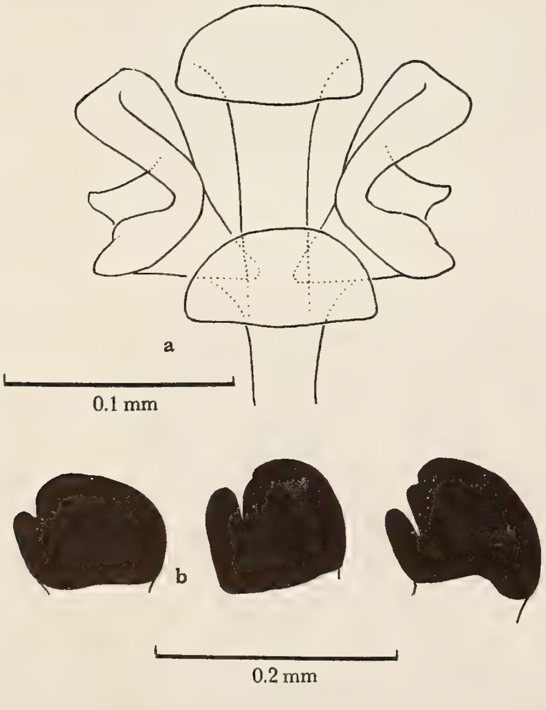


Figure 80

Tonicella lineata (Wood, 1815): specimen, 25 mm long; Moss Beach, San Mateo Co., California (AJF 143). Radula: a) median and first lateral teeth, b) heads of second lateral teeth [illustrating intra-specimen variation]

variation in outline and degree of separation of the denticle(s); in young specimens (smaller than 10 mm long) the notches are deeper and the denticles are much more clearly defined and separated (Figure 81) than in adults, resulting in a definitely tricuspid appearance, a character trait of Lepidochitonidae.

Figure 81

Tonicella lineata (Wood, 1815): specimen, 8.4 mm long; Edna Bay, Alaska (CASIZ 009296). Radula: heads of second lateral teeth [illustrating intra-specimen variation]

Distribution: *Tonicella lineata* is found from the Sea of Okhotsk and Sea of Japan through the Bering Sea and Aleutians to the coast of North America. In the eastern Pacific, northernmost verified record, Montague Island, Prince William Sound, Alaska [60° 10′ N; 147° 15′ W] (CASG 41449); southernmost verified record, off Point Fermin, Los Angeles County, California [35°35′ N; 118°20′ W] (LACM 65-2). The species is very abundant in the intertidal zone from Alaska to Monterey Bay [36°45′ N] but noticeably scarcer south of Monterey.

The reported bathymetric range of *Tonicella lineata* is 0-130 m (Sirenko, 1973); the verified range for eastern Pacific specimens extends from the intertidal zone to 55 mm (CASG 29304).

Fossil Record: *Tonicella lineata* has been recorded from Pleistocene deposits in southern Oregon (Addicott, 1964; Zullo, 1969; Kennedy, 1978), Humboldt County, northern California (Kohl, 1974; Kennedy, 1978; Roth, 1979), Point Fermin, southern California (Chace & Chace, 1919; Berry, 1922), Turtle Bay, Baja California, Mexico [27°40′ N; 114° 53′ W] (Loc. No. B-3024, University of California Department of Paleontology, *ex* Dr. Edwin C. Allison, identified by Allyn G. Smith, unpublished), and at Boso Peninsula, Japan (Itoigawa *et al.*, 1978).

Remarks: Sirenko (1973) stated that his *Tonicella undocaerulea* differs from *T. lineata* in 1) inhabiting depths of 1-27 m, 2) length rarely exceeding 14 mm, and 3) width of the outer portion of the head of the second lateral tooth of the radula. These distinctions are of less than specific, or even subspecific importance. The type material of *T. undocaerulea* was not examined; but the description of the species (Sirenko, 1973, 1974b) and the study of a few specimens generously donated by Dr. B. I. Sirenko leave no doubt about its conspecificity with *T. lineata.*

The profound similarity between juvenile specimens of *Tonicella lineata* and of *Lepidochiton beanii* posed considerable difficulties in this study, and frustrated attempts to determine the boundaries (or overlap) between the two species at about 33° N latitude. The problem was compounded by the (later) finding that juveniles of *T. lineata* differ from adults in some important aspects (color pattern, girdle elements, sinus width, and radula). A measure of the difficulties involved may be appreciated from the fact that for several years such juveniles remained unrecognized and were regarded as members of a "new" species.

Reports of *Tonicella lineata* from Peru and Chile by early workers (Deshayes & Edwards, 1836; Paetel, 1869, and 1873) must be judged in error, probably misidentifications for *Tonicia fremblyana* Kaas, or *Chiton cumingsii* Frembley, 1827, common species in the southeastern Pacific with similarly lined tegmental color patterns.

The biology of *Tonicella lineata* has received considerable attention (Thorpe, 1962; Barnes & Gonor, 1973; Andrus & Legard, 1975; Robbins, 1975; Himmelman, 1979). The association between *T. lineata* and a coralline algal substratum has been well documented; coralline algae have been found to be essential to the settling of *T. lineata's* trochophore larvae (Barnes, 1972), and comprise about 50% of the adult's diet (Demopulos, 1975). Asteroid predation on *T. lineata,* particularly by *Pisaster ochraceus* and *Leptasterias hexactis,* does not seem to be as important as previously assumed (Seiff, 1975). Fish predation may well be more significant as suggested by the frequent finding of valves of *T. lineata* in the gut of Rainbow Seaperch, *Hypsurus caryi,* at Monterey Bay, California (Dustin D. Chivers, personal communication). A clearly annual reproductive cycle has been shown for *T. lineata* with natural spawning possibly cued by the spring phytoplankton (Himmelman, 1979).

Nuttallina Dall, 1871

Definition: Elongate, medium sized chitons with granulose tegmentum. Head valve with low radiating ribs; intermediate valves with 2 low ribs on lateral areas; mucro definitely posterior. Sutural laminae well developed, elongate; sinus deep. Insertion teeth of posterior valve directed forward. Intermediate valves with 1 or 2 slits, the posterior one often obsolete. Eaves spongy. Girdle covered with small spiculoid scales and pointed spines.

Type Species: *Chiton scaber* Reeve, 1947 (not Blainville, 1825) [= *Chiton californicus* Reeve, 1847], by OD.

Synonyms:

Nuttalina Fischer, 1885 *(nomen nullum)*
Nutallina Pallary, 1900 *(nomen nullum)*

Remarks: Pilsbry (1893), Fischer-Piette & Franc (1960), and Smith (1960) placed *Nuttallina* in the Callistoplacidae probably impressed by the two-ribbed lateral areas, and the correspondence of the articulamental slits with the tegmental ribs. But Thiele (1929), Keen (1958), Thorpe (*in* Keen, 1971), and Van Belle (1977) regarded *Nuttallina* as part of the Lepidochitonidae. *Nuttallina* shares several features with other members of the Lepidochitonidae, 1) granulose, weakly sculptured tegmentum, 2) posterior valve smaller than the anterior valve, 3) tricuspid radula, and 4) small and simple girdle scales.

The genus *Nuttallina* is confined to the north Pacific. *Chiton alternatus* Sowerby, 1840, described from Japan, was referred to *Nuttallina* by Pilsbry (1893). Although listed by Is. Taki (1962) and Iw. Taki (1964) as part of Japanese and Formosan fauna, the species has not been recognized by other authors.

In the eastern Pacific, *Nuttallina* is confined between latitudes 49° N and 24° N (Figure 1). As is recognized here, it is represented by two allopatric species.

Nuttallina californica (Reeve, 1847)
Nuttallina crossota Berry, 1956

Nuttallina thomasi Pilsbry, 1898a, is placed herein, in synonymy with *Lepidochitona dentiens* (Gould, 1846).

The two *"Nuttallina"* species by Dall (1919) in the eastern Pacific were assigned to the wrong genus, as shown by Smith (1977) upon examination of the type material. *Nuttallina magdalena* Dall, 1919, belongs in the synonymy of *Chaetopleura lanuginosa* (Dall, 1879); and *Nuttallina allantophora* Dall, 1919, appears to be conspecific with *Liolophura japonica* (Lischke, 1874), the locality label no doubt being in error.

Nuttallina californica (Reeve, 1847)
(Figures *82, 83, 84,* 85, 86)

Chiton californicus Reeve, 1847, sp. no. 89; plt. 16, fig. 89; detail plt. fig. 89—Shuttleworth, 1853: 67 (in section *Acanthopleura*)—Carpenter, 1857b: 229 (as syn. of *C. scaber* Reeve)

Nuttallina californica (Reeve). Pilsbry, 1893; 14: 279-280; plt. 54, figs. 23-24; plt. 56, figs. 12-18—Raymond, 1894: 133-134—Pilsbry, 1898a: 288—Berry, 1907: 51—Dall, 1921: 189—Berry, 1922: 439-441; plt. 3, figs. 1-12 (fossil)—Oldroyd, 1924: 189; 1927: 865-866—Johnson & Snook, 1927: 562; fig. 662—Thiele, 1929: 9—Leloup, 1940: 23-27; figs. 50-53, 60-61 (with *N. scabra* and *N. fluxa* as "varieties")—Smith, 1947a: 16; 1947b: 18—Smith & Gordon, 1948: 206—Smith; 1952: 385—La Rocque, 1953: 11—Thompson & Chow, 1955:31—Chace, 1958: 330—MacGinitie & MacGinitie, 1968: 386—Burghardt & Burghardt, 1969a: 228; 1969b: 32; plts. 4, figs. 65—Abbott, 1974: 400—Gómez, 1975: 28-29—Nishi, 1975: 30-33—Moore, 1975: 51-53—Robbins, 1975: 98-102—Piper, 1975: 103-108—Simonsen, 1975: 113-116—Tenold, 1975: 128—A. G. Smith *in* R. I. Smith & Carlton, 1975: 462, 464—Smith, 1977: 242

Chiton scaber Reeve, 1847, sp. no. 106, plt. 17, fig. 106 [not *Chiton scaber* Blainville, 1825]—Jay, 1850: 99—Carpenter, 1857b: 229, 290, 317—Tryon, 1883: 344; plt. 86, fig. 85 (in subgen. *Nuttallina*)—Orcutt, 1885: 544 (in subgen. *Nuttallina*)

Acanthopleura scabra (Reeve). Carpenter, 1864: 603, 649 (as syn. of "*californicus* Nutt.") [reprinted, 1872: 89, 135]—Cooper, 1867: 22, 1870: 59

Nuttallina scabra (Reeve). Dall, 1871: 134; 1879: 298, fig. 31 (radula)—Wood & Raymond, 1891: 58—Pilsbry, 1893, 14: 280-281; plt. 54, figs. 21-22; plt. 56, figs. 19-20 (with *Acanthopleura fluxa* as syn.)—Thiele, 1893: 394; plt. 32, fig. 16 (radula)—Wood, 1893: 72—Raymond, 1894: 133-134—Nierstrasz, 1905a: 149—Smith, 1907: 67—Iredale, 1914: 130—Packard, 1918: 294-295—Berry, 1935: 89-90—Leloup, 1940: 25-27 (as syn. of *N. fluxa*, and var. of *N. californica*); 1956: 26—Abbott, 1974: 400; fig. 4694a (as syn. of *N. fluxa*)

Acanthopleura fluxa Carpenter, 1864: 612 *(nomen nudum)*, 649 [reprinted, 1872: 98, 135]; 1866: 211—Cooper, 1867: 22

Nuttallina fluxa (Carpenter). Pilsbry, 1898a: 290 (with *C. scaber* Reeve as syn.)—Dall, 1921: 190—Oldroyd, 1927: 866-867—Berry, 1935: 89-90—Leloup, 1940: 25, 27 (as syn. of *N. scabra*, and var. of *N. californica*)—Smith, 1947a: 16; 1947b: 18—McLean, 1969: 61-62; fig. 34-4—Burghardt & Burghardt, 1969a: 228; 1969b: 32; 44, plt. 4, fig. 66—Abbott, 1974: 400; fig. 4694a (with syn. *C. scaber*)—McLean, 1978: 61-62; fig. 34-4

Nuttallina cf. *N. fluxa* (Carpenter). Berry, 1918: 63—Chace & Chace, 1919: 42 (fossil)—Berry, 1922: 441 (fossil)

Type Material:

Chiton californicus Reeve, 1847: **Lectotype** (herein designated) and 7 "possible syntypes" (BMNH 19798), here designated **paralectotypes**; "California, H. Cuming Colln." (A. Blake, *in litt.* 2 May 1979).

Chiton scaber Reeve, 1847: 2 syntypes (BMNH 19799), "California, H. Cuming Colln." (A. Blake, *in. litt.*, 2 May 1979).

Acanthopleura fluxa Carpenter, 1864: Holotype (USNM 15690b); "Santa Barbara Island." California.

Type Locality: "California" (Reeve, 1847), here restricted to Pacific Grove, Monterey Peninsula, California (36°37′ N; 121°55′ W).

Description: Reeve's (1847, sp. & fig. 89) account, attributed to Nuttall's manuscript, is quite adequate to identify the species. Specimens of *Nuttallina californica* (Figures *82*, *83*, *84*) often reach 3.5 cm; largest examined, 53 mm long (CASG-SU, Farallon Island, California). Color orange to brown, often striped; soft parts reddish orange; valves beaked; tegmentum coarsely granulose, recurved at posterior edge: jugum often smooth; anterior valve elongate, with 8-11 weakly defined, radial ribs; posterior valve depressed; mucro posterior, to terminal, often pointed; lateral areas gently raised, with 1-2 low ribs or undulations; eaves very spongy; articulamentum intense blue, often with brown discoloration in midline; sutural laminae long, quadrate; sinus deep; on valve viii, sinus relative width (width of sinus/width of sutural laminae) mean = 0.65 (range 0.40-0.84); valve i wider than valve viii in adults (mean ratio = 1.10), equal or slightly smaller in juveniles (mean ratio = 0.94); insertion teeth extend considerably beyond tegmentum in valve i, strongly recurved forward in valve viii; slit formula, range 8/11-1-6/11, mode 11-1-9; intermediate valves often with second, incipient or obsolete slit; total number of slits (valves i + viii) range 17-22, mode 20, not correlated to locality or size of specimens; gills along 100% of specimen's foot. Girdle's (Figure 85) upper surface with small 15-20 μm) translucent, round to oval spiculoid scales, reddish brown to white (often in bands), and abundant, calcareous spines, reddish brown to white, up to 500 μm long, 150 μm wide; undersurface with transparent, round to oval scales, separated to juxtaposed, about 10 × 15 μm at inner margin, progressively elongated to spiculoid, 100 × 25 μm, at outer margin. Specimen 29 mm long (LACM 62-18, Baja California, Mexico) with radula (Figure 86) 12 mm long (41% of specimen's length) comprising 50 rows of mature teeth; median tooth rectangular, about 180 μm long, 100 μm wide at anterior blade; first lateral teeth 150 μm long; head of second lateral teeth, tricuspid, 170 μm long, 170 μm wide; outer marginal teeth, 200 × 130 μm (length/width ratio, 1.54).

Distribution: *Nuttallina californica* seems to have a continuous distribution between latitudes 38° N and 24° N. Reports of the species at Vancouver Island [49°45′ N] (Pilsbry, 1893; Oldroyd, 1924), and Strait of Juan de Fuca, Washington [48° 18′ N] (Dall, 1921; Oldroyd, 1927; La Rocque, 1953; Burghardt & Burghardt, 1969b) could not be corroborated; no authenticated record of *N. californica* is known

Explanation of Figures *78*, *82* to *84*, *87*, *88*, *91*, *94*, and *95*

Figure *78: Tonicella lineata* (Wood, 1815): specimen, 40 mm long; Seldovia Bay, Alaska (LACM 73-18)

Figure *82: Nuttallina californica* (Reeve, 1847): specimen, 13 mm long; Guadalupe Id., Baja California, Mexico (AJF 241)

Figure *83: Nuttallina californica* (Reeve, 1847): specimen, 20 mm; Point Lobos, Monterey Co., California (AJF colln.). Anterior valves

Figure *84: Nuttallina californica* (Reeve, 1847): same specimen as in Figure *82*. Posterior valves

Figure *87: Nuttallina crossota* Berry, 1956: specimen 10.3 mm long; Puerto Peñasco, Sonora, Mexico (LACM 63-56)

Figure *88: Nuttallina crossota* Berry, 1956: same specimen as in Figure *87*. Close-up of central and lateral area

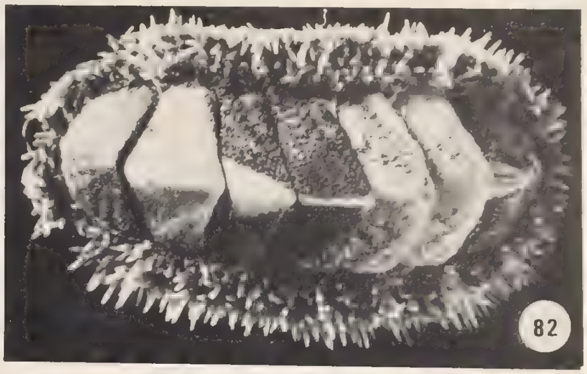
Figure *91: Schizoplax brandtii* (Middendorff, 1847): specimen 15 mm long; Wrangel, Alaska (CASG-SU). Anterior, intermediate, and posterior valves [intermediate valve broken at the longitudinal slit to show both articulamentum and tegmentum]

Figure *94: Spongioradsia aleutica* (Dall, 1878): specimen, 5.3 mm long; Amchitka Id., Aleutians, Alaska (LACM 69-43)

Figure *95: Spongioradsia aleutica* (Dall, 1878): same specimen as in Figure *94*. Lateral view

[FERREIRA] Figures *78, 82* to *84, 87, 88, 91, 94,95*


78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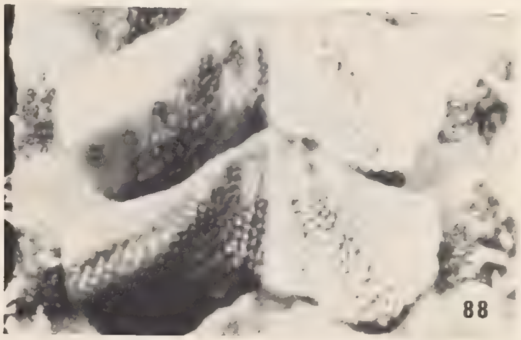
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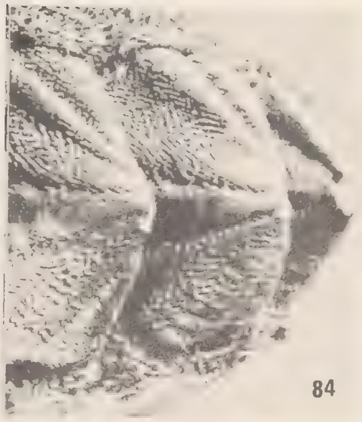
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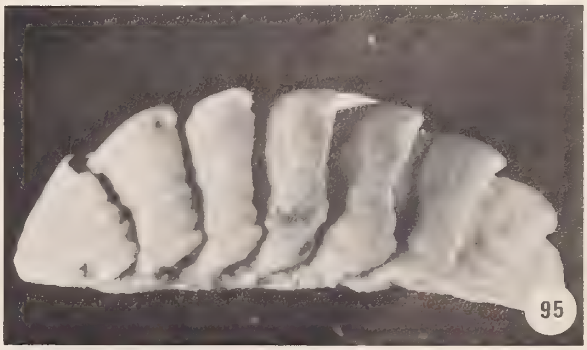
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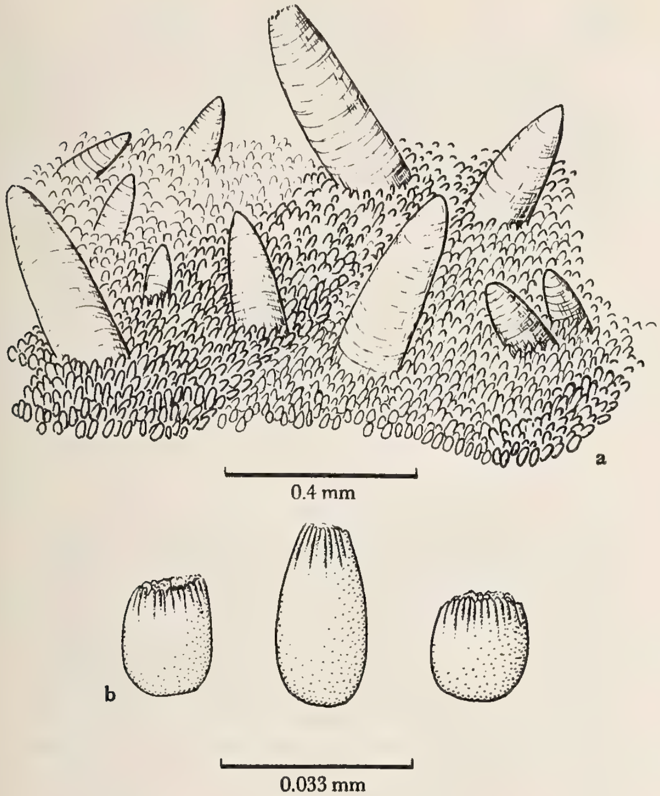

Figure 85

Nuttallina californica (Reeve, 1847): specimen, 15 mm long; San Pedro, Los Angeles Co., California (AJF 147). Girdle elements: a) upper surface scales and spinelets, b) much enlarged upper surface scales

from Canadian shores (Dr. I. McT. Cowan, *in litt.*, 18 February, 1979). Northernmost verified record, Doran Beach, Sonoma County, California [38°29′ N; 123° 10′ W] (CASIZ 009416); southernmost verified record, Magdalena Island, Magdalena Bay, Baja California, Mexico [24°36′ N; 112° 06′ W] (LACM 63-72). The species has been collected at the offshore islands of Farallon (SDNH 23422; CASIZ 009413; CASG-SU), Anacapa (CASG 39609), Santa Cruz (CASG 4086), San Miguel (CASG 13773; CASG 23749), San Nicolas (SDNH 23424), Coronados (SDNH 57705), Guadalupe (CASIZ 001015; CASIZ 001064; CASIZ 002794; CASIZ 002993; CASIZ 009418; AJF 211), San Roque (CASG 24064), Asunción (LACM 67-67) and San Benitos (CASIZ 002812; CASIZ 002990).

Specimens of *Nuttallina californica* are found only in the middle and upper intertidal zone, in crevices in the rock, usually eroded and encrusted; it has been shown that the western gull, *Larus occidentalis*, is one of its major predators (Moore, 1975).

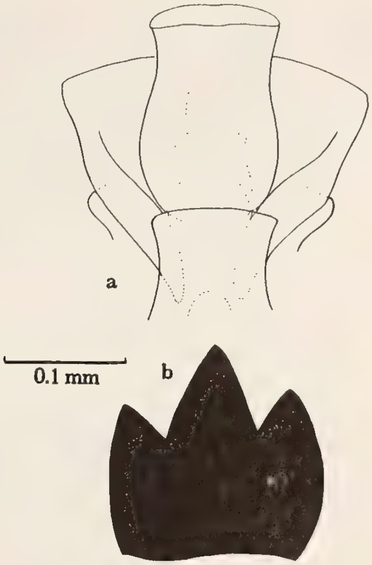

Figure 86

Nuttallina californica (Reeve, 1847): specimen, 29 mm long; Las Gaviotas, Baja California, Mexico (LACM 62-18). Radula: a) median and first lateral teeth, b) head of second lateral tooth

Fossil Record: *Nuttallina californica* has been found in the Pleistocene deposits at San Pedro, California (Chace & Chace, 1919; Berry, 1922) and in the Pleistocene formations of Guadalupe Island, Baja California, Mexico (Lindberg *et al.*, 1980).

Remarks: It has been a persistent view among chiton workers that there were two species of *Nuttallina* on the California coast, *N. californica* north of Point Conception, California (34°27′ N) and *N. fluxa* south. The supposed distinctions between these two nominal species were never clearly spelled out. Pilsbry's differential diagnosis rested on the observation that *N. fluxa* has "the individual valves very much shorter in proportion to their width" (Pilsbry, 1893: 280), and that specimens of *N. californica* tend to be larger in size and have a girdle "generally wider at the sides, especially in old specimens" (Pilsbry, *op. cit.*, 281). The examination of a large number of specimens of *Nuttallina* from many localities along the California and Baja California coast did not reveal consistent differences such as described by Pilsbry. Intraspecific variations are particularly striking in *N. californica*. Specimens vary considerably in size, proportions of the individual valves, tegmental sculpture (usually obliterated by erosion and encrustations), and in the density, size, and color of the girdle spines. But such variations do not correlate with latitude in general, or locality in particular.

The type specimens of *Chiton californicus* Reeve and *Chiton scaber* Reeve were not examined. An inquiry and search carried out most generously by Aileen Blake, Mollusca Section, British Museum (Natural History), revealed that "In the case of *scaber* the largest of the three syntypes was found to be missing... It was probably the figured specimen [in Reeve, 1847; fig. 106]. In the case of *californicus* none of the seven specimens appear to have the correct proportions to be the figured specimen [in Reeve, 1847: fig. 89] and that is why [they are] labelled... 'possible' syntypes" (A. Blake, *in litt.*, 2 May 1979). The figured specimen (Reeve, 1847: fig. 106), although missing, is here designated **lectotype.**

For its abundance and accessibility along the California coast, *Nuttallina californica* has been a favorite subject in investigations on chiton biology. An association between *N. californica* and *Lepidochitona dentiens* has been demonstrated both in the field and in the laboratory (Gómez, 1975). The diet of *N. californica,* investigated for two contrasting habitats in central California, was found to consist mostly of macro-algae (*Corallina* spp., *Cladophora trichotoma, Endocladia muricata,* and *Gelidium* spp., among others). The diet indicates that "feeding activity must occur when animals emerge from their shelters at high tide" (Nishi, 1975: 31). In the laboratory, it was shown that high intertidal specimens of *N. californica* can better cope with osmotic stress than specimens from the low intertidal zone (Simonsen, 1975). The effects of air exposure upon respiration and metabolism have been investigated (Robbins, 1975; Piper, 1975).

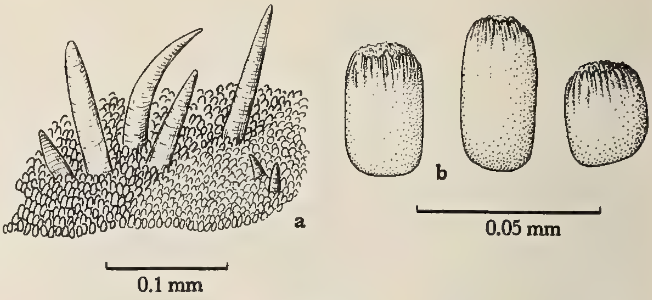

Figure 89

Nuttallina crossota Berry, 1956: specimen, 11.5 mm long; Puerto Peñasco, Sonora, Mexico (LACM 63-56). Girdle elements: a) upper surface scales and spinelets, b) much enlarged upper surface scales

Nuttallina crossota Berry, 1956
(Figures *87, 88,* 89, 90)

Nuttallina crossota Berry, 1956: 71-72—Keen, 1958: 528, Amphineura sp. & fig. 49—Smith, 1961, 30(4): 82-83 (with *N. mexicana* Pilsbry, 1932, as syn.)—Thorpe *in* Keen, 1971: 880, Polyplacophora sp. & fig. 45

Nuttallina mexicana Pilsbry *in* Pilsbry & Lowe, 1932, 84: 129 (*nomen nudum*)—Steinbeck & Ricketts, 1941: 549—Smith, 1961, 30 (4): 82-83 (as syn. of *N. crossota* Berry, 1956)

Type Material:

Nuttallina crossota Berry, 1956: Holotype (S. S. Berry Collection No. 15133), paratypes (S. S. Berry Collection No. 14966; USNM 612207; SDNH Type Series 17; CASG TC-10268; CASG-SUPTC 8646).

Type Locality: Puerto Peñasco, Sonora, Mexico [31°20′ N; 113°33′ W].

Description: Berry's (1956) original description is quite adequate. Specimens of *Nuttallina crossota* (Figures *87, 88*) rarely exceed 15 mm in length; largest examined, 23 mm long (LACM HH-1047). Color brown to light brown to tan, often mottled or streaked; valves subcarinate, beaked; tegmentum granulose, granules often linearly arranged; radial ribs, usually well defined, 2 in lateral areas, 10-12 in anterior valve; mucro posterior, often pointed, upswept; postmucro sloping sharply; articulamentum white; slit formula 10/11-1-8/9, intermediate valves often with second, incipient or obsolete slit; insertion teeth extend beyond tegmentum on valve i, recurved forward on valve viii; sutural laminae elongated; sinus deep; on valve viii, sinus relative width, 0.80; gills extend 90% of foot's length. Girdle's (Figure 89) upper surface with small (8-15 μm wide), translucent, round to oval scales, and calcareous spine, white to tan, up to 400 μm long, 80 μm wide; undersurface with transparent scales, round to oval, about 10 × 10 μm, separated to juxtaposed at inner margin, progressively elongated to spiculoid, up to 80 × 20 μm at outer margin. Specimen 11.5 mm long (LACM 63-56), Puerto Peñasco, Sonora, Mexico), with radula (Figure 90) 3.8 mm long (33% of specimen's length) comprising 40 rows of mature teeth; median tooth rectangular, 75 μm long, 50 μm wide at anterior blade; first lateral teeth about 70

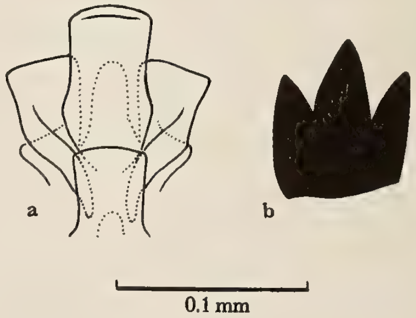

Figure 90

Nuttallina crossota Berry, 1956: same as in Figure 89. Radula: a) median and first lateral teeth, b) head of second lateral tooth µm long; head of second lateral teeth, tricuspid, 70 µm long, 70 µm wide; outer marginal teeth, 100 × 50 µm (length/width ratio, 2.0).

Distribution: *Nuttallina crossota* is endemic to the Gulf of California. It has been collected on the Sonora side, at Puerto Peñasco (LACM 63-56; AJF, Dec. 1971), Libertad (LACM 67-17), Guaymas (CASIZ 009414; LACM 63-12; LACM 63-13; LACM 64-3; LACM 64-5); and on the Baja California side, at San Felipe (CASIZ 009415; LACM 61-6; AJF, Feb. 1971), Puertecitos (LACM 62-19), Bahía de los Angeles (AJF 158), and Puerto Ballandra, north of La Paz CASIZ 009419, *leg.* A. G. Smith, 3 Nov. 1959), its southernmost record [24°20′ N; 100° 18′ W]. It has also been found at Isla San Jose (AJF Colln., *leg.* Lois Lippincott, R/V *Marisla,* 7 Aug. 1973), and Isla Partida (CASIZ 009417). The species seems to be confined to the intertidal zone.

Remarks: *Nuttallina crossota* differs from *N. californica* in 1) much smaller size, 2) much lighter color, 3) girdle spines white to tan and 4) bolder radial ribs in anterior valve and lateral areas of intermediate valves (a variable character, some specimen's ribs very subdued), 5) tegmentum more coarsely granose, 6) white articulamentum, and 7) habitat, favoring the underside (not the top) of rocks in quiet water. Each one of these differences by itself has little taxonomic value, but together they constitute a convincing argument to regard the species as distinct.

Schizoplax Dall, 1878

Definition: Small chitons. Intermediate valves divided by longitudinal, cartilage-filled slit at the jugum. Girdle's upper surface covered with juxtaposed, simple, small, round to oval scales. Eaves spongy. End valves with about 11 slits.

Type Species: *Chiton brandtii* Middendorff, 1847a, by OD.

Remarks: As currently known, *Schizoplax* is a monotypic genus. The recognized taxonomic importance of changes in the articulamentum of chitons (Ashby, 1929) led Bergenhayn (1955) to erect the family Schizoplacidae [emended by Smith, 1960] to accommodate the genus. This arrangement was followed by Smith (1960) and Van Belle (1977). However, it seems appropriate that when grouping species and genera, the whole body plan, not just the articulamentum, be considered. In the case of *S. brandtii,* it is apparent that were it not for the presence of a slitted articulamentum—a unique feature—the species would have been accepted unhesitatingly in *Lepidochitona.* In fact, specimens of *S. brandtii* so resemble those of *L. dentiens* in size, color, shape, tegmental surface, girdle elements, radula, even habitat, that the two species are often confused and misidentified in museum collections. The slitted articulamentum of *S. brandtii* appears, then, as a modification of the *Lepidochitona* body plan important enough to warrant distinct generic but not family (or even subfamily) placement. With only one major character distinguishing *S. brandtii* from *L. dentiens,* the placing of both genera in one family seems to be amply justified.

The uniqueness of the slitting suggests that *Schizoplax* is phylogenetically younger than *Lepidochitona,* and *S. brandtii* an evolutionary offspring of *L. dentiens.*

Schizoplax brandtii (Middendorff, 1847a)
(Figures *91,* 92, 93)

Chiton brandtii Middendorff, 1847a: 117-118; 1847b: 128; 1851: 174-177; plt. 15, figs. 1-6 (in section *Stenosemus*)—Carpenter, 1857b: 215, 219, 223; 1864: 533 (reprinted, 1872: 19)

Tonicia brandtii (Middendorff). Adams & Adams, 1858: 474

Schizoplax brandtii (Middendorff). Dall, 1878: 2-3; 1879: 328-329; 1884: 344—Pilsbry, 1892: 47-48; plt. 11, figs. 32-37—Berry, 1917a: 235; 1917b: 3—Dall, 1921: 189—Oldroyd, 1927: 868-869—Smith, 1947a: 12; 1947b: 18—Jakovleva, 1952: 68-69; text fig. 30, plt. 4, fig. 1—La Rocque, 1953: 11—Kussakin, 1960: 1145-1150; figs. 1-2—Taki, 1962: 38-39—Taki, 1964: 410—Smith, 1966: 437—Burghardt & Burghardt, 1969b: 36 (with *S. multicolor* as syn.)—Abbott, 1974: 399

Schizoplax multicolor Dall, 1920: 22-23; 1921: 189—Oldroyd, 1927: 867-868—Smith, 1947a: 13; 1947b: 18—La Rocque, 1953: 11—Burghardt & Burghardt, 1969b: 36 (syn. of *S. brandtii*)—Abbott, 1974: 399—Smith, 1977: 238-239

Type Material:

Chiton brandtii Middendorff, 1847a: "Type in Academy, St. Petersburg [Leningrad, USSR]" (Oldroyd, 1927: 869).

Schizoplax multicolor Dall, 1920: Holotype (USNM 383018); "St. Paul Island, Bering Sea," Pribilof Islands.

Type Locality: "Insulae Schantar et Sinus Tuguricus maris Ochotici—Ins. Sitcha" (Middendorff, 1847a: 118), here restricted to Sitka, Alaska [57°03′ N; 135° 14′ W].

Description: *Schizoplax brandtii* was clearly described by Middendorff (1847a; 1847b). Except for a wider sinus, and the presence of a central longitudinal slit dividing the intermediate valves into symmetrical halves, the species is extraordinarily similar to *Lepidochitona dentiens.* Specimens of *S. brandtii* (Figure *91*) rarely reach 2 cm in length; largest examined, 23 mm long (CASG 18520, Unalaska Island, Alaska; eaves very spongy; slit formula 11-1-14; width of valve i/width of valve viii, mean ratio = 1.16; sinus relative width on valve viii, 0.83. Girdle's (Figure 92) upper surface with translucent brown to orange, round to oval scales, about 30-40 µm long, 15-20 µm wide; undersurface with imbricated, transparent, triangular scales, about 40 × 15 µm. Specimen 15 mm long (CASGSU, Wrangell, Alaska) with radula (Figure 93) 4.4 mm long (29% of specimen's length), comprising 60 rows of mature teeth; median tooth 110 µm long, 52 µm wide at anterior blade; first lateral teeth quadrangular; head of second lat-

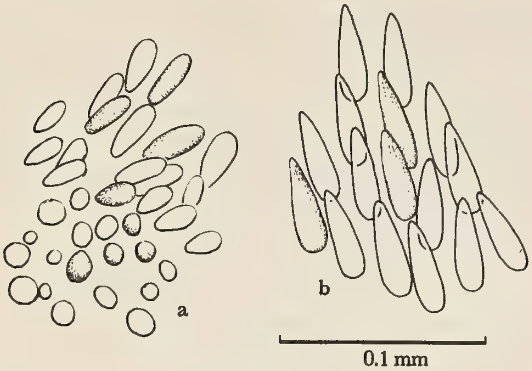

Figure 92

Schizoplax brandtii (Middendorff, 1847): same specimen as in Figure *91*. Girdle elements: a) upper surface scales, b) undersurface scales

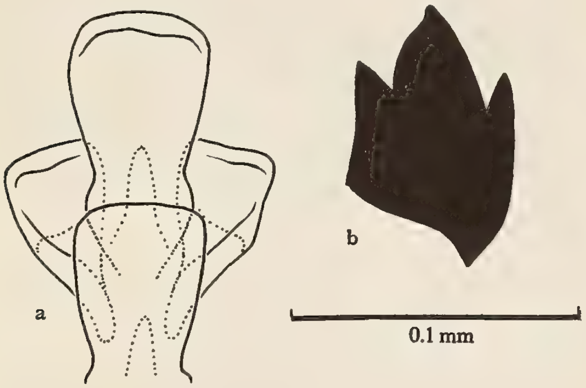

Figure 93

Schizoplax brandtii (Middendorff, 1847): same specimen as in Figure *91*. Radula: a) median and first lateral teeth, b) head of second lateral tooth

eral teeth, tricuspid, about 60 μm long, 55 μm wide; outer marginal teeth, about 70 × 70 μm (length/width ratio, 1.0).

Distribution: *Schizoplax brandtii* has been reported in the sea of Japan, Sea of Okhotsk, Bering Sea, Aleutian Islands, and the Pacific coast of North America (Jakovleva, 1952; Taki, 1962). Northernmost verified record, Auk Bay, Alaska [60°01′ N; 148°24′ W] (CASG 44002); southernmost record, at "the southern extension of Queen Charlotte Strait…at Dead Point Bay, Harbledown Id [British Columbia, Canada]…50°35′40″ N; 126°35′09″ W…" (Dr. I. McT. Cowan, *in litt.*, 18 April 1979).

The bathymetric range of *S. brandtii* is reported as 0-40 m (Jakovleva, 1952); however, all specimens here examined were collected in the intertidal zone.

Remarks: *Schizoplax multicolor* was first placed in the synonymy of *S. brandtii* by Burghardt & Burghardt (1969). The synonymy was confirmed by Smith (1977) upon examination of the holotype of *S. multicolor.* Color slide of the holotype at CASIZ Color Slide Series no. 2247.

Schizoplax brandtii is one of the several chiton species reported to brood its young (Kussakin, 1960; Smith, 1966).

Spongioradsia Pilsbry, 1894a

Definition: Very small chitons, colored purplish-red. Tegmental surface smooth, sculptureless. Lateral areas almost indistinct. Eaves extremely spongy. Intermediate valves with two (or more) slits. Sutural laminae long and narrow; sinus very wide. Girdle with imbricated, elongated scales.

Type species: *Trachydermon (Trachyradsia) aleutica* Dall, 1878, by OD.

Synonyms:

Trachyradsia Dall, 1878 (in part)
Type: *Chiton fulgetrum* Reeve, 1847, by OD.

Remarks: Pilsbry (1892) had accepted *Trachyradsia* (attributed to Carpenter MS) as a subgenus of *Trachydermon* Carpenter, 1864. But on recognizing that *Chiton fulgetrum* Reeve, 1847, type species of *Trachyradsia,* was in fact a *Callochiton,* Pilsbry (1894a, 15: 65-66) replaced it with *Spongioradsia* to cover two species, *S. aleutica* (Dall, 1878) and *S. multidentata* (Carpenter *in* Pilsbry, 1892). Elevated to full generic rank (Smith, 1947), *Spongioradsia* was suppressed later (Smith, 1960) as a synonym of *Lepidochitona* Gray; but it seems that Smith [unpublished manuscript on file at CASG] intended to reinstate it as a distinct genus in a revision of the classification of chitons.

Isao Taki (1938) suggested the placement of *Spongioradsia* with the callochitonids (based upon his own observations on *Spongioradsia foveolata* Taki, 1938 which, from the description, may indeed belong in the *Callochiton* group). However, characteristics of *S. aleutica* do not conform to those of the callochitonids, for there are no eyes on the shell, the sinus is deep, and the sutural laminae are not bridged by a sinusal lamina. Probably on such realizations, Iwao Taki (1962) placed *Spongioradsia* in the Ischnochitonidae, instead.

The genus *Spongioradsia* is known only in the cold waters of the north Pacific. In addition to *S. aleutica* (Dall, 1878) in the eastern Pacific, three other nominal species have been considered: *S. multidentata* (Carpenter *in* Pilsbry, 1892) in the Bonin Islands, *S. foveolata* Taki, 1938, in Mutsu Bay, Japan, and *S. subaleutica* Sirenko, 1976, from Kurile and Sachalin Islands.

Without explanation, Van Belle (1977) placed *Oligochiton* Berry, 1922 (type species: *O. lioplax* Berry, 1922, by M) in the synonymy of *Spongioradsia. Oligochiton lioplax* is based upon 4 valves from the Sooke Formation, Oligocene of Vancouver Island, British Columbia. Berry (1922: 433) acknowledged that *Oligochiton* resembled *Spongioradsia* but regarded the differences in the sponginess of the valves and the shape of the insertion teeth significant enough to warrant separation at the generic level. Smith (1960) accepted *Oligochiton* as a distinct genus in the family Ischnochitonidae. Examination of the holotype and a paratype of *O. lioplax* (Stanford University Paleontology Type Collection No. 280, and 281, respectively, now at CASG) reveals that, although the numerous slits, short teeth, and sculptureless tegmental surface of *O. lioplax* suggest affinities to *Spongioradsia,* some significant features militate against joining them: 1) length of animals (less than 1cm in specimens of *Spongioradsia aleutica;* over 4cm, judging from the size of the valves, in *Oligochiton lioplax*), 2) shape of valves (beaked in *Spongioradsia;* not beaked in *Oligochiton*), 3) jugal angle (narrow in the high-arched, carinate *Spongioradsia;* wide in the relatively low-arched, not carinate *Oligochiton*), 4) posterior valve (inflated with posterior mucro in *Spongioradsia;* flattish with central mucro in *Oligochiton*), 5) sponginess of valves (conspicuous in *Spongioradsia;* discrete in *Oligochiton*) 6) insertion teeth (smaller and more poorly developed in *Spongioradsia* than in *Oligochiton*), and 7) sutural laminae (narrow and long in *Spongioradsia;* broad and short in *Oligochiton*).

Spongioradsia aleutica (Dall, 1878)

(Figures *94, 95,* 96, 97)

Trachydermon (Trachyradsia) aleutica Dall, 1878: 1-2; 1879: 323-324

Trachyradsia aleutica (Dall). Dall, 1884: 343

Ischnochiton aleuticus (Dall). Pilsbry, 1892: 84-85 (in section *Trachyradsia*)

Trachydermon (Spongioradsia) aleutica (Dall). Pilsbry, 1894a: 65-66; plt. 15, figs. 30-33

Lepidochitona aleutica (Dall). Dall, 1921: 189 (in subgenus *Spongioradsia*)—Oldroyd, 1927: 865 (in subgen. *Spongioradsia*)—Abbott, 1974: 397

Spongioradsia aleutica (Dall). Smith, 1947a: 13; 1947b: 18—Burghardt & Burghardt, 1969b: 35—Sirenko, 1976: 51-52, fig. 1

Lepidochiton aleuticus (Dall). Jakovleva, 1952: 66-67; text fig. 28; plt. 3, fig. 4—La Rocque, 1953: 10—Taki, 1964: 409

Type Material:

Trachydermon (Trachyradsia) aleutica Dall, 1878: Syntype series (USNM 30915), comprising 4 specimens (Dr. J. Rosewater, *in litt.,* 3 October 1978).

Type Locality: "Western Aleutians" (Dall, 1878: 2), here restricted to Amchitka Island [51°30′ N; 179°00′ W].

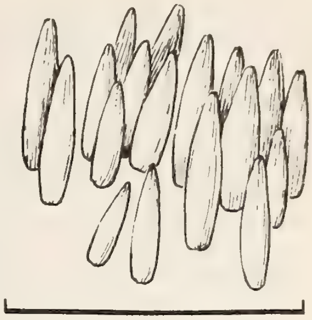

Figure 96

Spongioradsia aleutica (Dall, 1878): same specimen as in Figure *94.* Girdle elements: spiculoid scales of upper surface

Description: Adequately described by Dall (1878; 1979), the identification of specimens of *Spongioradsia aleutica* poses no problems. Specimens (Figures *94, 95*) do not usually exceed 5mm; largest examined, 6.0mm long. Color solid brownish red; valves thick, high arched, carinate; jugal angle 85°; tegmentum microgranulose, sculptureless; lateral areas barely defined; posterior valve inflated; mucro central; postmucro strongly convex; eaves very spongy; articulamentum rosy-white; insertion teeth very small,particularly in valve viii; slit formula 13-2-11, some intermediate valves with only 1 slit on one side; slit-rays conspicuous; sutural laminae narrow; sinus wide; sinus relative width on valve viii, 1.67; gills extend along 80% of foot. Girdle's (Figure 96) upper surface pilose looking, covered with imbricated, closely packed, translucent, spiculoid scales, 75 μm long, 25 μm wide; undersurface covered with imbricated, transparent, spiculoid scales, about 50 × 20 μm. Specimen 5.4mm long (LACM 69-43, St. Makarius Bay, Amchitka Island, Aleutian Islands, Alaska) with radula (Figure 97) 2.0mm long (37% of specimen's length) comprising 40 rows of mature teeth; median tooth, rectangular, 50 μm long, 28 μm wide at anterior blade; first

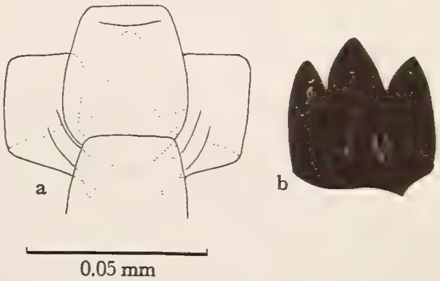

Figure 97

Spongioradsia aleutica (Dall, 1878): same specimen as in Figure *94.* Radula: a) median and first lateral teeth, b) head of second lateral tooth lateral teeth squarish; head of second lateral teeth, tricuspid, 45 µm long, 45 µm wide; outer marginal teeth about 50 × 45 µm (length/width ratio, 1.11).

Distribution: *Spongioradsia aleutica* has been reported in the Aleutian Islands, Bering Sea, and the Sea of Japan. (Jakovleva, 1952; Sirenko, 1976). In the eastern Pacific, the species is poorly represented in the museum collections; all specimens examined are from Amchitka Island, Aleutian Islands, Alaska (LACM 69-43; CASIZ) and Boswell Bay, Hinchinbrook Island, Prince William Sound, Alaska [60°40′ N; 147°00′ W] (CASG 39424). The species seems to be confined to the intertidal zone.

Remarks: The possible similarities between *S. aleutica* and other nominal species of *Spongioradsia—S. multidentata, S. foveolata,* and *S. subaleutica*—were not closely investigated for lack of sufficient material.

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Lucina s. s.

(Mollusca : Bivalvia)

in the Western Atlantic: A Reappraisal

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(2 Plates; 3 Text figures)

THE BIVALVE SUBGENUS *Lucina s. s.* lives throughout the Caribbean and along the coast of the southeastern United States; it occurs also in the fossil record of the region. It is not known, however, in the Eastern Pacific province. Despite its present wide distribution only a single Recent species has been recognised: *Lucina (L.) pensylvanica* (Linnaeus, 1758). It lives in shallow water and prefers a carbonate environment.

In the collections of the Linnean Society of London there are five specimens of *Venus pensylvanicus* Linnaeus, 1758, one of which bears the number 139 (Figures *4*, *5*). An accompanying explanatory note by S. P. Dance (1963) reads as follows:

> "*V. pensylvanica* L.
> Syst. Nat., Ed. 10, p. 688 No. 114; Syst. Nat., Ed. 12, p. 1134 No. 138.
> Hanley 1855, Ipsa Linn. Conch., p. 75.
> Dodge 1952. Hist. Rev. Moll. Linn., Pt. 1, p. 110.
> Remarks.—Hanley has isolated five valves one of which is marked 139. As Dodge and Hanley state this is the Ed. 12 number for *Venus incrustata* [Indian Ocean] and that the number was, therefore, an error for 138. On the other hand no specimens have been found in the collection which can be assigned to *V. incrustata.* Hanley says that Linnaeus did not possess *incrustata.*"

Also appended is the comment of Hanley (1855: 75) which ends:

> "The violet edged shell subsequently distinguished as *V. pensylvanica* in the "Museum Ulricae" is, of course, distinct (a *Cyrena*?)."

These statements illustrate some of the problems concerning the identity of the species *pensylvanica* whose locality is given as "America septentrionali." Even the geographical trivial name is cause for suspicion, having little to do with the known distribution which is, according to ABBOTT (1974: 458), "North Carolina to south Florida and the West Indies." It has been reported also, however, from Panamá (Caribbean coast) by OLSSON & MCGINTY (1958: 20) and by RADWIN (1969: 233); from Curaçao by DE JONG & KRISTENSEN (1968: 20) and from the Bahamas by BRETSKY (1976: 322).

Venus is a venerid genus and *pensylvanica,* a lucinid, has been assigned variously to *Lucina, Phacoides* Gray, 1847 (after Blainville, 1825) and *Linga* de Gregorio, 1884. Over the years there has been much discussion and little agreement as to the author of *Lucina:* Bruguière, 1797; Lamarck, 1799, or Lamarck, 1801. The same applies to the related problem of the type-species: *pensylvanica* Linnaeus, 1758; *edentula* Linnaeus, 1758, or *jamaicensis* Lamarck, 1801 (= *pectinata* Gmelin, 1791).

KEEN & ABBOTT (1972: 158) once again review the evidence and conclude that *Lucina* Bruguière can be accepted. They also conclude that, while usage and legal considerations would favour *pensylvanica,* acceptance of *pectinata* as a matter of expediency, would lead to less confusion simply because this was the choice of CHAVAN (in Moore, 1969) in the "Treatise on Invertebrate Paleontology," a work which will be used as a standard reference for a long time to come. In this work, incidentally, *pensylvanica* receives no mention. Accordingly *(loc. cit),* they presented a petition to the International Commission on Zoological Nomenclature (ICZN).

The latest review to be published is that of BRETSKY (1976: 247) which, however, is based on an earlier unpublished thesis (1969) and does not refer to KEEN & ABBOTT (1972). She also reviews the evidence at length and concludes, likewise, that *Lucina* Bruguière and *pensylvanica* are the validly established genus and type-species, although with some reservations in the case of the latter. Furthermore, she considers the subgenera assigned by CHAVAN (in Moore, 1969) to *Lucina* and *Linga* to constitute a single lineage, the former having priority.

In the interim, REHDER *et al.* (1973: 70) had entered a counter-petition to the ICZN proposing that *Venus pensylvanica* Linnaeus, 1758, should be designated the type-species of *Lucina* Bruguière, 1797. The Commission voted in favour of this counter-petition, a decision which was promulgated in November 1977 (Bull. zool. Nomencl. vol. 34, part 3, p. 150). This placed *Lucina* Bruguière, 1797, on the Official List of Generic Names in Zoology with *Venus pensylvanica* Linnaeus, 1758, as type-species (Opinion 1095).

Had the present study been undertaken earlier, calling in question, as it does, the identity of *pensylvanica*, would the voting have been affected?

Other Recent species of *Lucina s. s.* have been named from the region and BRETSKY (1976: 251) has this to say about them: "Deshayes's *Lucina aurantia* apparently differs from *L. pensylvanica* (Linnaeus) only in possessing internal and external coloration. Since in several other lucinid species, individuals may have or lack color on the shell, *L. aurantia* is here synonymized with *L. pensylvanica*. The name *Lucina virgo* Reeve applies to shells which have been smoothed by post-mortem abrasion (Abbott, 1954). Reeve also proposed that the name *L. grandinata* replace *L. pensylvanica* because he "doubted whether the *Lucina pensylvanica* really inhabits the shores from whence it derives its name"; however, emendations for such reasons have no status in nomenclature." This, then, leaves *pensylvanica* as the only Recent representative of *Lucina s. s.* in the region. Nor does this subgenus occur in the Eastern Pacific where the nearest relative belongs to the subgenus *Here* Gabb, 1866.

In her review of the fossil record of *Lucina s. s.*, BRETSKY (1976: 150) traces its origins back to the Eocene of the southeastern United States and Colombia. She notes that *L. carinifera* Conrad from the Eocene Gosport Sand is essentially identical with *L. pensylvanica*, an indication of the conservative nature of the genus as found in many other bivalve genera. Of particular interest to us, however, are the more immediate ancestors of the Pliocene and Pleistocene. *Lucina pensylvanica* is reported from the Caloosahatchee formation of Florida (DUBAR, 1958: 166; OLSSON & HARBISON, 1953: 80) which is recognised now as early Pleistocene in age (BLACKWELDER, 1981: 24). This species has also been reported from the Pleistocene of Grand Cayman Island by REHDER (1962: 585) and Barbados by DALL (1903: 1368). *Lucina podagrina* (Dall, 1903) comes from the Pliocene Bowden Formation of Jamaica and was said to occur in beds of equivalent age on Curaçao (DALL, 1903: 1365). Later, WOODRING (1925: 119, 120) split the Bowden material into two subspecies, *L. podagrina podagrina* and *L. podagrina alaranta*, and a second species, *L. browni*. From the Miocene Pirabas limestone of Brazil, MAURY (1924: 295) described *L. glomeramen*, a very globose form (D/L > 100%), which she compared to *podagrina*. The only other record from the southern Caribbean is that from Colombia of *L. woodringi* Clark, 1946, from the Eocene of the El Carmen area. Although HUNTER (*in* MacGillvary & Beets 1978: 195) places part, at least, of the El Carmen beds in the Oligocene, it has been pointed out to us by Dr. J. Wyatt Durham *(in litt.)* that Clark's locality is in beds that unquestionably underlie the Oligocene as the associated fauna indicates (CLARK, *in* Clark & Durham, 1946: 6). In our collecting of the Venezuelan Neogene, we have not come across *Lucina s. s.*, so far.

In 1970 we collected in Islas Los Roques, Venezuela, a coralline archipelago, a large number of dead specimens of what we supposed were *Lucina pensylvanica;* they occurred at a depth of 2 m on carbonate sand and many retained some periostracum. In 1980 one of us (W.G.S.) had the opportunity to collect at Key Biscayne our first comparative material from Florida; it included 44 worn valves and a live specimen of *L. pensylvanica*. It was found, however, that the periostraca of the two suites, whilst basically similar, differed in detail. In the collections of the British Museum (Natural History) a specimen from Belize labelled *pensylvanica* had a periostracum which differed yet again, and markedly so. Finally, a specimen in the wet collections of the Museum from Grand Cayman Island, also labelled *pensylvanica*, had a periostracum similar to that of the Islas Roques specimens, but of a different colour, confirmation of which was forthcoming in 1981 when we collected a large suite on Grand Cayman Island.

The wide geographical separation of the localities will have been noted. Also to be noted is that the differences in the periostraca are not reflected by immediately obvious differences in the shells themselves. This raises the question of the identity of *pensylvanica* which cannot be related directly to any of these forms because the five "type" specimens are very worn and only one, the smallest, retains an inadequate vestige of periostracum. As a corollary, of course, the tracing of lineages in the absence of morphological differences between the shells proper, presents an insoluble problem. Should these forms indeed be distinguishable only by the periostraca, it may represent a unique case amongst the bivalves. A somewhat analogous case is that of *Modiolus squamosus* Beauperthuy, 1967, for long confused with *Modiolus americanus* (Leach, 1815), although the periostraca are quite distinct; in this case, however, there are minor morphological differences between the shells.

In view of the stated provenance of *Lucina pensylvanica*, the only practical solution seems to be to recognise the form from Florida as representative of the species. This solution is here formally proposed.

Lucina s.s. has a remarkable periostracum, but it has received scant attention, generally being described as, "thin, yellowish." A more detailed account is that of BRETSKY (1976: 250) who describes it as, "yellow-brown, thin, covering entire surface of valves; elevated ridges of periostracum, which are superimposed on concentric ribs and sometimes broken up to form dorsally reflected spines, give an impression of coarse surface sculpture." ABBOTT (1958: 119) is the first to mention that, "The fimbriations on the outside of the valves are calcareous in nature." In their work on periostracal structures BOTTJER & CARTER (1980: 213) make the following comments: "Within the Veneroida, projecting periostracal structures such as thorns and hairlets are largely or entirely restricted to the Carditacea, Arcticacea, and Glossacea. Among the fossil groups possibly allied with the Carditacea, the Upper Paleozoic Permophoridae may have shown periostracal calcification, based on descriptions of radiating spikes and pustules by Girty (1904), Licharew (1925) and Elias (1957).... Other than the Permophoridae, spike or granule-like periostracal calcification is rare but not entirely absent in the Veneroids. Among the Lucinacea, the modern *Lucina pensylvanica* (Linnaeus) shows aragonitic granules within a moderately thick, laminar periostracum (Carter, pers. obs.), but similar structures have yet to be reported in fossil lucinaceans."

In *Lucina s.s.* the periostracum is composed of two elements; the normal covering of conchiolin, concentrically flanged in this case, and a great number of minute, calcareous plates or spines adhering to the ventral surface or partially embedded in the edges of the flanges. The plates and spines are concave dorsally and the ventral surface is granular. It is the morphology of the flanges, the plates and spines and their mode of attachment which differ in the various forms of *Lucina s.s.*

STANLEY (1970: 152) discusses the life habits of *Lucina pensylvanica* which in Florida he found living in shallow, subtidal environments in poorly sorted, carbonate sand beneath *Thalassia* beds. In laboratory experiments he found it to be a slow burrower, penetrating directly downwards and adopting a life orientation unique among the lucinids. He states that, "The animal rotates posteriorily from its burrowing orientation to adopt a position with its anterior region uppermost and its lunule surface approximately horizontal." In the lucinids he found the burrowing action to consist of a rotation of up to 45° about an axis normal to the disc. In the case of *Divaricella quadrisulcata* (Orbigny, 1842) he believes that the divaricate sculpture is an aid to burrowing. He does not discuss the role of the complex periostracum in *L. pensylvanica* which, presumably, provides a stabilizing mechanism by trapping sand. It may also assist in the burrowing action when, in the rotational or rocking movement, which he says does not exceed 15° to 20°, the flexible flanges would collapse on the downward-moving half of the shell and would spread on the upward-moving half to provide anchorage, thus tending to drive the animal down. The periostracum must also prove awkward for predators who, nevertheless, had managed to kill 31 (44%) out of 71 paired specimens from Islas Los Roques, most entries being effected near the ventral margin. However, in the suite of 72 paired specimens from Grand Cayman Island, only 7 (10%) had been perforated successfully, with two failures.

How significant are the differences in the periostraca? All forms live in a coralline environment but not all are confined to subtidal depths beneath *Thalassia* beds, as is said to be the case in *Lucina pensylvanica*. Whatever their respective niches, the fact remains that each has evolved a morphologically different mechanism for burrowing and stabilisation, if these are the main purposes of the periostracum. They thus represent different lineages, herein being given formal recognition as: ***Lucina (Lucina) podagrina caymanana*** subspec. nov.; ***L. (L.) belizana*** spec. nov.

The periostracum disintegrates rapidly with wave action and abrasion and, once dried out, is easily damaged by handling. Therefore, all our specimens retaining some periostracum have been treated with a varnish (lacquer solvent/styrofoam).

SYSTEMATIC TREATMENT

Superfamily LUCINACEA Fleming, 1828

Family LUCINIDAE Fleming, 1828

Genus *Lucina* Bruguière, 1797

Subgenus *Lucina s.s.*

Type-species (by S.D., ICZN Opinion 1095, 1977, Bull. zool. Nomencl. vol. 34, part 3, p. 150), *Venus pensylvanica* Linnaeus, 1758.

Lucina (Lucina) pensylvanica (Linnaeus, 1758)

(Figures 1, *4, 5, 6, 7, 13*)

Venus pensylvanicus Linnaeus, 1758, Syst. Nat., Ed. 10, p. 688, No. 114.

Description: Based on a suite from Key Biscayne, Florida. Shell white, thick, strong, almost circular and of medium size. Largest specimen: height 39.0mm, length 40.0mm. Equivalve with variation in the convexity of the shell. Ligament external, sunken, long, opisthodetic. Umbones strongly prosogyrate, curling around the small, pit-like lunule. Pseudo-lunule large, cordate, deeply impressed. Posterior area marked off by a deep umbonal groove which indents the ventral margin. Sculpture of regularly spaced, shallow, concentric grooves separated by low, fine ridges; grooves crowded over the upper disc, wide over the central disc and narrowing towards the ventral margin. Earliest sculpture marks off a prodissoconch-like area where the concentric ridges are abruptly lower and the grooves between show microscopic, crowded, concentric threads. In the grooves over the disc the radial element in the sculpture sometimes feebly indicated, terminating in the minute denticles crenulating the inner margin. Careful removal of the periostracum reveals that the ridges are narrowly laminate, the laminae projecting ventrally at a low angle to the disc and fractionally overhanging the subsequent groove; thus, viewed across the disc from anterior or posterior margin the sculpture can be said to be broadly imbricate. These laminae no doubt assist in anchoring the periostracum; they are very weak and immediately lost, in nature, upon removal of the periostracum. Several strongly marked growth stages. Posterior adductor scar elliptical, anterior long, narrow and almost parallel to the pallial sinus which is whole. Area from sinus to ventral margin with irregular radial wrinkles. Hinge-plate wide, strong; anterior, and more distant posterior, laterals are single in the right valve and double in the left. Both valves have two cardinals, the anterior bifid in the left valve and the posterior bifid in the right valve. Periostracum produced into high lamellae coincident with the concentric, fine laminae of the shell; colour a very light grey-brown. Adhering ventrally along the lamellae are numerous, flattened, blunt-ended, tapering calcareous spines having a weak convexity towards the ventral margin and having a granular ventral surface. The tips of the spines are level with the edge of the lamellae which is often broken back between spines in a dry specimen to give a pseudo-scalloped effect. The base of the spines is bi-lobed and some rows are bipartite (Figure 1). Towards the umbo the spines are crowded but towards the ventral margin the interspaces are as wide as, or wider than, the spines. The spines are radially aligned and large ones measure approximately: width 0.75 mm, length 1.75 mm. In a dry state the lamellae maintain an erect position, i.e.,normal to the disc.

Figure 1

Periostracal lamella of *Lucina pensylvanica* (Linnaeus)

Discussion: It has already been said that *Lucina pensylvanica* can be distinguished from *L. caymanana*, *L. roquesana* and *L. belizana* by its different periostracum (Figures 1, 2, 3). It may also be smaller than *L. caymanana* and *L. roquesana* (40mm versus 50mm), but the suite is small; it is usually said to measure from 25mm to 50mm, but it is not known whether the larger measurement refers to true *L. pensylvanica* from the east coast of the United States. In the case of H/L the range in all the taxa lies mainly between 95% and 105% with most being almost circular. For D/L (Tables 1, 2) the convexity is 45% to 74% (average 56%) for *L. pensylvanica;* 46% to 83% (average 59%) for *L. caymanana* and 46% to 79% (average 65%) for *L. roquesana.* Therefore, *L. pensylvanica* may have the least average inflation.

Lucina (Lucina) podagrina podagrina (Dall, 1903)

Lucina pennsylvanica Guppy, 1866, (non Linnaeus), Quart. Journ. Geol. Soc. London, 22: 292. Guppy, 1874, (part, non Linnaeus), Geol. Mag., decade 2, 1: 442, (list).
Phacoides (Here) podagrinus Dall, 1903, Trans. Wagner Free Inst. Sci. Philadelphia, 3(6): 1365, 1366; plt. 50, figs. 12, 13.
Phacoides (Linga) podagrinus podagrinus Dall, 1903. Woodring, 1925, Carnegie Inst. Washington, publ. No. 366: 119, plt. 15, figs. 8 to 11.
Phacoides (Linga) podagrinus alarantus Woodring, 1925, *ibid.*, p. 119, plt. 15, fig. 12.
Phacoides (Linga) browni Woodring, 1925, *ibid.*, p. 120, plt. 16, fig. 1.

Discussion: In placing *Lucina podagrina alaranta* Woodring and *L. browni* Woodring in synonymy, the authors simply accept a greater degree of variation in the shell morphology of *L. podagrina podagrina* (see under Shell Morphology). Considering the similarity in shell morphology between *L. pensylvanica* and *L. podagrina podagrina*, the latter might have been made a subspecies of the former. However, as we see now, this would have been wrong, the differing periostraca indicating that the lineages are distinct.

Explanation of Figures *4* to *12*

Figures *4, 5: Lucina (Lucina) pensylvanica* (Linnaeus, 1758), type numbered "139," a left valve, height 24mm, length 25mm (both approximately). The Linnean Society of London

Figures *6, 7: Lucina (Lucina) pensylvanica* (Linnaeus, 1758), live-taken specimen from Key Biscayne, Florida; external and internal views of left valves; height 35.3mm, length 37.7mm, diameter 9.6mm

Figures *8, 9, 10: Lucina (Lucina) **roquesana*** spec. nov.; Figures *8, 9,* external and internal views of left valve of holotype, BM(NH) Reg. No. 1980105/1; height 38.4mm, length 40.2mm, diameter 13.3mm; Figure *10,* dorsal view of paratype, BM(NH) Reg. No. 1980105/2. Both specimens from Islas Los Roques, Venezuela

Figures *11, 12: Lucina (Lucina) podagrina **caymanana*** subspec. nov., internal and external views of left valve of holotype, BM(NH) Reg. No. 1980104, from Grand Cayman Island, Caribbean; height 27.5mm, length 28.0mm, diameter 9.6mm

Figure *4*

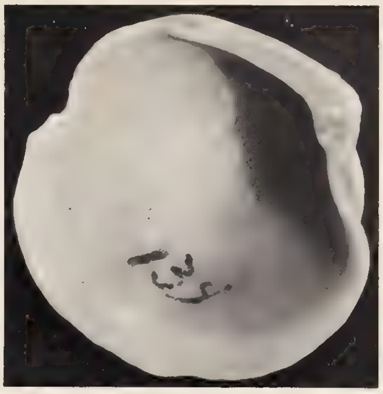

Figure *5*

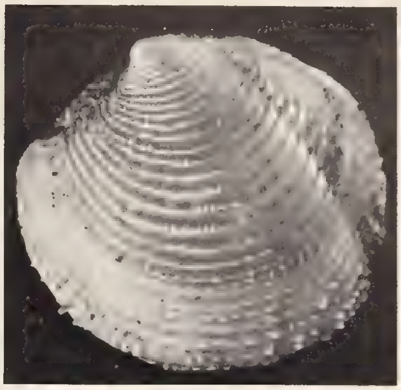

Figure *6*

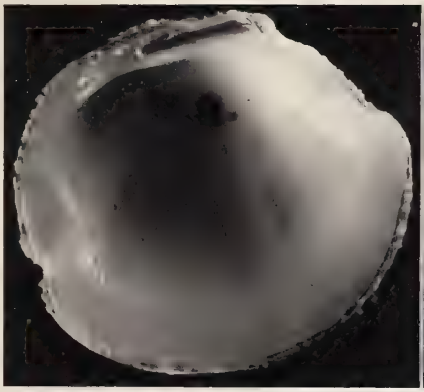

Figure *7*

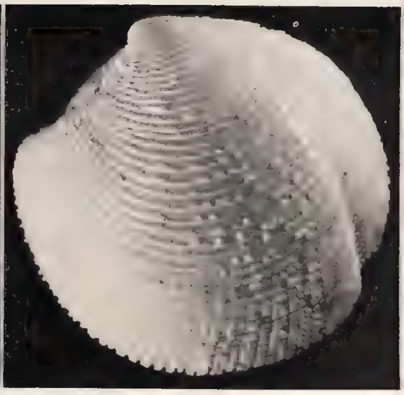

Figure *8*

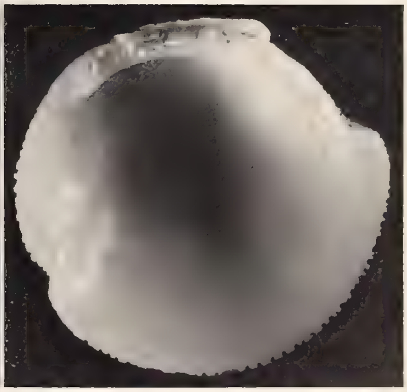

Figure *9*

Figure *10*

Figure *11*

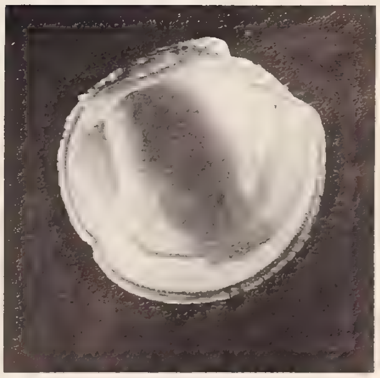

Figure *12*

Lucina (Lucina) podagrina caymanana Gibson & Gibson, subspec. nov.

(Figures 2, *11, 12, 15*)

Description: One valve faintly pink over the umbo and upper disc, remainder pure white. Shell morphology as for *Lucina pensylvanica* with large specimens reaching 49.0 mm. The concentric lamellae of the pale brown periostracum are neatly scalloped between the attached plates to a level below the base of the plates themselves (Figure 2). The rectangular, white, calcareous plates are embedded to about one-quarter of their height in the outer edge of the scalloped lamellae; they are broader than high, are rather strongly curved, being convex ventrally with a granular ventral surface and measure approximately: width 1.75 mm, height 0.75 mm. The plates are closely packed with only narrow interspaces which hardly widen from umbo to ventral margin; there is a strong radial alineation. Towards the anterior margin the plates become narrower. In a dry state the plates fold flat towards the umbo, trapping sand in the interspaces between successive lamellae.

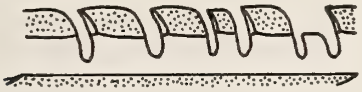

Figure 2

Periostracal lamella of *Lucina podagrina caymanana* subspec. nov. and *Lucina roquesana* spec. nov.

Holotype: British Museum (Natural History), Reg. No. 1980104/1, a paired specimen; height 27.5 mm; length 28.0 mm; diameter 18.2 mm.

Type locality: North Sound, Grand Cayman Island.

Paratypes: British Museum (Natural History), Reg. No. 1980104/2; USNM 784690; Paleontological Research Institution, Ithaca, No. 29846; Natural History Museum Basel; Universidad Central de Venezuela, Escuela de Geología, UCVG 7060; remainder in the collections of the authors.

Remarks: The holotype, a lone specimen from the wet collections in the British Museum (Natural History), bore the label: "*Lucina pensylvanica* (L.), 2.8 m, *Thalassia* marl, N. Sound 620400, Grand Cayman Island, Leg. L. Hull, 12/9/74, Acc. No. 2270." Paratype material consists of 72 paired specimens, 54 right valves and 51 left valves; it is from the north edge of North Sound behind coral reefs on open sand at 3 m. It was not associated with *Thalassia* beds. A few worn valves were collected on the west coast at 7-Mile Beach. No live specimen was found. Abbott (1958: 119) reports that, "Large live specimens were dredged commonly at 15 stations in the north half of North Sound, in Frank Sound, West Bay, and the east end of Grand Cayman in 6 to 40 feet of water over clear sand and sparse algae.... Some specimens were stained with a rose blush." All these he assigned to *L. pensylvanica*. Other records of *"pensylvanica"* from the greater Antilles are those of McLean (1951: 63: 12: 10) and Warmke & Abbott (1961: 176) from Puerto Rico; of Nowell-Usticke (1959: 10) from St. Croix and Humfrey (1975: 236) from Jamaica. In McLean's figure the periostracum is that of *L. caymanana*, which it presumably is; it is a larger specimen than any other to hand with a length of 54 mm. Bretsky (1976: plt. 25, fig. 1) illustrates a right valve of *"pensylvanica"* from the Bahamas; again the periostracum is like that of *L. caymanana*.

Comparisons: The structure of the periostracum distinguishes *Lucina caymanana* from *L. pensylvanica* and *L. belizana*. From *L. roquesana* it differs in having a pale brown, rather than pale yellow, periostracum, and it is a less globose form (average convexity 59% versus 65%). The colour of the periostracum might be regarded as of little consequence were it not for the other associated morphological differences in *L. pensylvanica* and *L. belizana*, and the fact that in *L. belizana* it is colourless; it is believed that the colour is significant. *L. p. podagrina* Dall is smaller than *L. podagrina caymanana* (42 mm versus 54 mm) and achieves a greater convexity (D/L 94% and 107% versus 83%). Nevertheless, because of the great variability, there is, presumably, a large degree of overlap between the two taxa. As regards *L. podagrina alaranta* Woodring and *L. browni* Woodring, such forms can be matched in the large suite of *L. caymanana* where they call for no special recognition, being integral components of the suite. The shell colour in *L. caymanana*, when present, is pink whereas in *L. aurantia* Deshayes it is orange; it would be interesting to know the provenance of the latter because the colour difference may be diagnostic.

Lucina (Lucina) roquesana Gibson & Gibson, spec. nov.

(Figures 2, *8, 9, 10, 14*)

Description: Shell morphology as for *Lucina pensylvanica* with large specimens reaching 50 mm. Morphology of periostracum as in *L. podagrina caymanana* (Figure 2).

Holotype: British Museum (Natural History), Reg. No. 1980105/1, a paired specimen; height 38.4 mm, length 40.2 mm, diameter 26.6 mm.

Paratypes: USNM 784691; Paleontological Research Institution, Ithaca, No. 8222; Natural History Museum Basel; British Museum (Natural History), Reg. No. 1980105/2; Universidad Central de Venezuela, Escuela de Geología, UCVG 7061; remainder in the collections of the authors.

Distribution: Venezuela: Islas Los Roques, type locality (71 pairs, 10 singles), where it occurs on white carbonate sand, without *Thalassia,* at a depth of 3m; Isla Tortuga (22 singles); Islas Los Testigos (4 singles); Tucacas, Falcón State (1 single) and Borburata, Carabobo State (4 singles).

Remarks: The few examples from the Venezuelan mainland at Tucacas and Borburata, both coralline environments, are sub-Recent and no fresh specimens have been found.

Comparisons: ***Lucina roquesana*** is distinguished from *L. pensylvanica* and *L. belizana* by the structure of its periostracum, and from *L. caymanana* by its greater average inflation (D/L 65% versus 59%; see under Shell Morphology) and its pale yellow, instead of pale brown, periostracum.

Lucina (Lucina) ***belizana*** Gibson & Gibson, spec. nov.

(Figures 3, *16, 17, 18*)

Description: Shell morphology as for *L. pensylvanica* but with closer and finer concentric ribs. The conchiolin element of the periostracum consists of delicate, closely packed concentric lamellae, colourless to translucent white, the outer edge deeply serrated to give a fringe of fine, sharp, flexible spines of differing heights, the edges of the spines (in a dry specimen) somewhat inrolled to become hollow dorsally (Figure 3). The calcareous element consists of minute, sub-rectangular, almost transparent plates attached along the ventral surface of the lamellae below the level of the fringe; they abut closely one against the other, their ventral surface is granular and there is essentially one plate for each spine; the width of the plates varies. There is no obvious radial alineation and, in the dry state, the concentric lamellae stand normal to the disc. The shell itself is white.

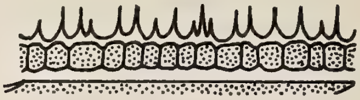

Figure 3

Periostracal lamella of *Lucina* ***belizana*** spec. nov.

Holotype: British Museum (Natural History), Reg. No. 1980103; a paired specimen; height 29.6mm, length 31.0 mm, diameter 19.2mm.

Type locality: Lighthouse Reef, Belize.

Remarks: Known from the holotype only. The specimen, in the collections of the British Museum (Natural History), bears the label: "Collected between 21st November and 14th December 1977; 2nd Squadron, 13th Signal Regiment; in weed on sand, depth 4 feet."

Comparisons: ***Lucina belizana,*** with its delicate, fringed periostracum, cannot be mistaken for any of the other taxa heretofore described. The calcareous plates are invisible to the naked eye and, indeed, are hardly noticeable even under the microscope.

OTHER MATERIAL

A single, worn specimen comes from Isla de Aves lying 500km to the north of Isla Margarita, Venezuela. From Barbados there are 24 specimens, a few of which retain vestiges of periostracum; it has the pale yellow colour and plates of *Lucina roquesana,* but the neat scallops to be seen in the latter are not evident. From the Bahamas 3 specimens lack any periostracum and, lastly, there is a single example from a Pleistocene reef on Cancun Island, Yucatan (H. Krause *leg.*).

Explanation of Figures *13* to *18*

Figure *13: Lucina (Lucina) pensylvanica* (Linnaeus, 1758), close-up of left valve from Key Biscayne, Florida (Figure *6*)

Figure *14: Lucina (Lucina)* ***roquesana*** spec. nov., holotype, BM(NH) Reg. No. 1980105/1; close-up of right valve (see figures *8, 9, 10*)

Figure *15: Lucina (Lucina) podagrina* ***caymanana*** subspec. nov., holotype, BM(NH) Reg. No. 1980104; close-up of left valve (Figure *11*)

Figures *16, 17, 18: Lucina (Lucina)* ***belizana*** spec. nov., holotype, BM-(NH) Reg. No. 1980103, paired specimen from Belize; internal and external views of left-valve and close-up of Figure *17;* height 29.6mm, length 31.0mm, diameter 9.6mm


13


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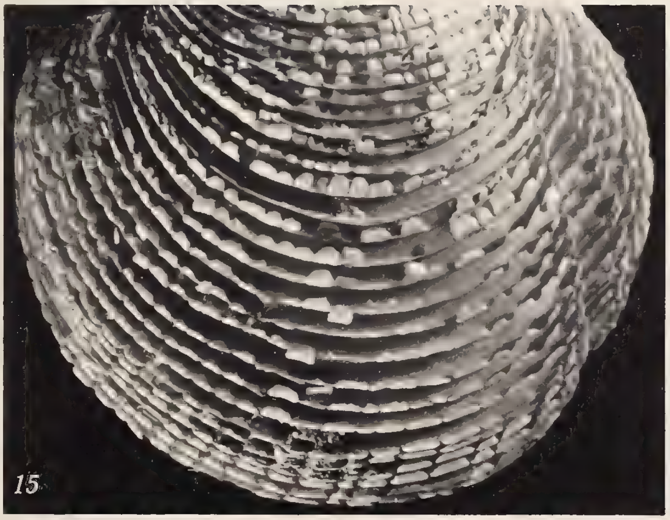
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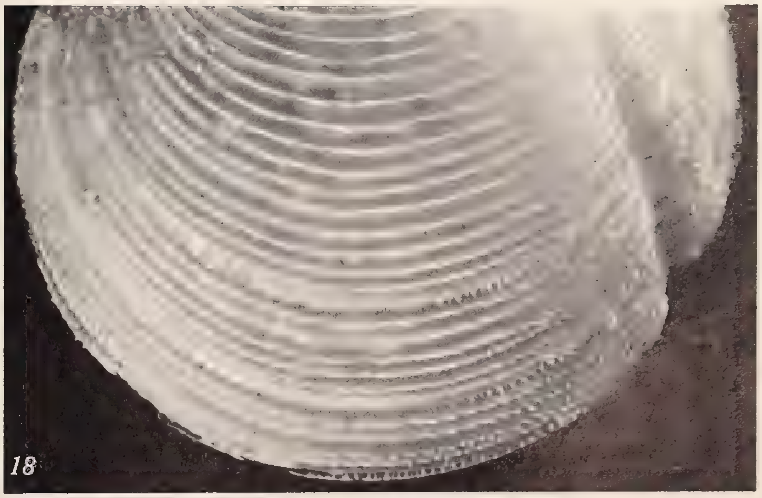
18

SHELL MORPHOLOGY

It is important, of course, to be able to differentiate, if possible, between the shells themselves in the four described taxa. As noted earlier, no significant trends are apparent in the case of H/L. However, a comparison of shell convexities (D/L) seems to have a limited significance and average convexities have already been discussed. At the outset it should be stated that for *Lucina belizana*, with only a single specimen, no comparison, obviously, is possible; that for *L. pensylvanica* the suite is not large and that the *L. roquesana* suite is somewhat deficient in smaller examples. It should also be said that only a few published measurements for fossil shells are available.

The condensed results of the convexity determinations are presented in Tables 1 and 2.

Table 1

Number (percentage) of specimens within given convexity (D/L%) range for *Lucina pensylvanica*, *L. caymanana* and *L. roquesana*.

D/L%	*L. pensylvanica*	*L. caymanana*	*L. roquesana*
40-50	8(22)	10(6)	1(1)
50-60	19(53)	47(29)	15(21)
60-70	7(19)	85(53)	31(42)
70-80	2(6)	18(11)	26(36)
>80	–	1(0.5)	–
Totals	36(100)	161(99.5)	73(100)

Immediately obvious is the great range in convexity at virtually all shell sizes. This is demonstrated again in Table 3 where the extreme convexities for shells of similar size are shown; between these extremes, however, there is a complete gradation in convexity.

Tables 1 and 2 lend support to the contention that there are certain differences between the shells of the three taxa, as was suggested by the different average convexities. For example, in Table 1, a convexity in the 70 to 80% range is achieved by 26% of *Lucina roquesana* specimens, by 11% in *L. caymana* and by only 2% in *L. pensylvanica*. In Table 2, for shells of length greater than 30mm, 39% of *L. caymanana* specimens and 43% of *L. roquesana* specimens fall within the 60 to 70% convexity range, whereas in the 70 to 80% convexity range there are 26 (35%) specimens of *L. roquesana* and only 9 (5%) specimens of *L. caymanana*, notwithstanding the much larger suite of the latter. It seems that *L. caymanana* peaks in the 60 to 70% convexity range, whereas in *L. roquesana* inflation continues strongly into the 70 to 80% range.

Quoted dimensions for the Bowden fossils are given in Table 4.

With regard to *L. p. podagrina* the statement was made by Dall *(loc. cit.)* that, "Shell when young moderately convex, when senile having an exaggerated thickness and spherical convexity." Woodring *(loc. cit.)* commented that, "Although this species is represented by a large number of shells, there is a sharp break between the few excessively inflated largest shells and the smaller less inflated shells." This break he found at about 30mm with a convexity below of 71% and 94% above. The Bowden form *L. podagrina s. s.*,

Table 2

Number (percentage) of specimens within given convexity (D/L%) range as related to length of shell for *Lucina pensylvanica*, *L. caymanana* and *L. roquesana*.

		Convexity (D/L%)				
Taxon	Length (mm)	40-50	50-60	60-70	70-80	80-90
Lucina pensylvanica	10-20	3(8)	3(8)	–	–	–
(36 examples)	20-30	3(8)	7(19)	3(8)	–	–
	30-40	2(8)	9(25)	4(11)	2(6)	–
	40-50	–	–	–	–	–
Lucina caymanana	10-20	3(2)	3(2)	1(0.5)	1(0.5)	–
(161 examples)	20-30	5(3)	13(8)	21(13)	8(5)	–
	30-40	2(1)	20(12)	48(30)	7(4)	1(0.5)
	40-50	–	11(7)	15(9)	2(1)	–
Lucina roquesana	10-20	1(1)	–	–	–	–
(73 examples)	20-30	–	3(4)	–	–	–
	30-40	–	10(14)	16(22)	12(16)	–
	40-50	–	2(3)	15(21)	14(19)	–

Table 3

Showing extreme convexities (D/L%) in shells of similar size, and number of associated growth stages (GS).

	Lucina pensylvanica				*Lucina caymanana*				*Lucina roquesana*			
	L	D	D/L%	GS	L	D	D/L%	GS	L	D	D/L%	GS
1a.	29.6	13.6	46	2	18.7	13.4	72	4	33.6	17.5	52	1
1b.	29.6	19.6	66	6	18.8	8.9	47	1	34.1	23.8	70	6
2a.	35.9	17.6	49	3	21.7	9.8	45	1	39.6	28.4	72	5
2b.	36.1	26.6	74	6	21.8	16.0	73	5	40.1	20.9	52	1
3a.					25.4	19.2	76	9				
3b.					26.2	12.8	49	1				
4a.					33.0	16.0	48	1				
4b.					34.0	26.7	79	3				
5a.					35.5	19.4	55	1				
5b.					35.6	29.4	83	8				
6a.					42.0	22.0	52	1				
6b.					43.3	31.4	73	6				

Table 4

Quoted dimensions of fossil *Lucina s. s.* from the Pliocene Bowden Formation, Jamaica.

	L	D	D/L%
Lucina podagrina podagrina (Dall)			
Dall (1903: 1365)	28.0	30.0	107
	42.0	35.0	83
Woodring (1925: 119)	28.0	20.0	71
	32.0	30.0	94
L. podagrina alaranta (Woodring)			
Woodring (1925: 119)	26.5	16.0	60
L. browni (Woodring)			
Woodring (1925: 120)	37.0	19.0	51

therefore, appears to represent an allometric progression, with convexity increasing with shell size. As we have seen, this is not the case in the Recent taxa.

Examination of the "twin" specimens of Table 3, and others, reveals that convexity is a function of the number of growth lines[1] present; the more growth lines there are, the more convex the shell; as many as 9 growth lines may be present (Table 3). It is also true that the "exaggerated thickness" is directly related to the number of growth lines. Theoretically, at least, the more globose shells should be more resistant to predator attack. In all shells, however, the thinnest part of the shell is towards the ventral margin which accounts, presumably, for the prevalence of predator attacks in that area; in two instances the commissure between the valves had been attacked directly and successfully, but resulting in an untidy, elongated boring.

Growth lines, when several occur, may be spread irregularly across the disc or are often concentrated towards the ventral margin. With each new growth stage the slope towards the ventral margin is increased, thus increasing the inflation. Good examples are to be seen in the figures of Woodring (1925: plt. 15, figs. *8*, *10*). The two shells are of similar size (about 35mm); in fig. *10* there is a single growth stage; in fig. *8*, on the other hand, the ventral margin drops off sharply and there are 5 or 6 growth stages in all, resulting in a much more inflated shell, as is very evident from the changed aspect of the posterior area.

Perhaps two questions remain to be answered. Why, in Recent assemblages and also probably in fossil assemblages, do some shells, small or large, grow intermittently, thus developing several growth stages, while others, equally small or large, continue their growth unchecked? The second question concerns burrowing proficiency as between shells with low convexity and those with high convexity. Stanley (1970: 152) described *L. pensylvanica* as, "a very slow burrower" amongst the lucinids. He omitted, however, to record the convexity of his trial specimen.

To sum up: in the absence of the periostracum, the variability of shell form in *Lucina s. s.* is such that comparison of a few specimens from different localities is meaningless; only by comparing very large suites is there any hope of achieving differentiation, a condition not always, or even often, satisfied in the fossil record.

PHYLOGENY

In view of the foregoing, the tracing of ancestral relationships presents a major problem. Discovery of the associated periostracal plates and spines may provide one line of

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[1] "Growth line." One of several lines on the surface of a shell marking the position of the margin of the shell at a previous stage of growth. Keen (1971: 913).

approach. Another might be through SEM micrographs of the shell surface. In some specimens of *Lucina caymanana* and *L. roquesana* sub-quadrate indentations within the broad, shallow concentric grooves of the shell surface seem to represent impressions of the periostracal plates. These impressions may explain the figure of Dall (1903: plt. 50, fig. 13) in which *L. podagrina* appears to have retained part of its periostracum.

The Recent forms of *Lucina s.s.* indicate that as many as four lineages occur throughout the region: Floridian *(L. pensylvanica)*, Greater Antillean *(L. podagrina)*, Central American *(L. belizana)* and southern Caribbean *(L. roquesana)*. The last three areas coincide with the Miocene faunal subprovinces established by Woodring (1974: 209) based on endemic genera and subgenera; that the southern Caribbean still displays today a degree of endemicity has only recently been recognised (Moore, 1974: 17; Petuch, 1976: 322; Gibson-Smith & Gibson-Smith, 1979: 20; Petuch, 1981: 307).

The ancestors of *Lucina pensylvanica*, as mentioned earlier, were discussed by Bretsky (1976: 250) and she notes that, "The oldest species of *Lucina s.s.* known to me are from the upper Middle Eocene of Alabama. One of these, *Lucina carinifera* Conrad, 1833, from the Gosport sand...except for its smaller size closely resembles other species of *Lucina s.s.;* it is essentially identical with *L. (L.) pensylvanica*... *L. (L.) hamata* (Dall, 1903) from the Lisbon Formation (middle Eocene) which underlies the Gosport sand, may be conspecific with *L. (L.) carinifera*." With regard to *L. pensylvanica*, Olsson & Harbison (1953: 80) comment that, "This well-known species is common in the Florida Pliocene [Pleistocene] but has not been shown to antedate the Pliocene [Pleistocene], although *Lucina glenni* Dall from the Chipola Miocene and *podagrinus* Dall from the Bowden are very closely related." Given only a modicum of the variability shown by the Recent forms of *Lucina s.s.*, one wonders how far back in time *L. pensylvanica* really goes.

The fore-runner of *Lucina p. podagrina* is unknown. Its author, Dall (1903: 1365), refers to a mention by Gabb of *Phacoides pensylvanicus* from the Miocene of the Dominican Republic and assumes it to be *L. podagrina*. Woodring (1925: 119) also refers to an undescribed species similar to *L. podagrina* from the late Miocene(?) Cercado Formation. The recent collecting of the Neogene in the Dominican Republic (by H. E. & E. H. Vokes and by P. Jung) will, it is to be hoped, have unearthed the ancestor of *L. podagrina*.

Lucina belizana has no known immediate ancestors.

The precursor(s) of *Lucina roquesana* may be either *L. woodringi* Clark from the Eocene of Colombia or *L. glomeramen* (Maury) from the Miocene Pirabas limestone of Brazil, or both. There is no successor to *glomeramen* in the Recent of Brazil and that line may have died out. No later reference to that of Dall (1903: 1365) to the presence on Curaçao of *L. p. podagrina* as a fossil, has been found; it was not reported by Buisonjé (1974). The absence, to date, of connecting links in the Neogene of Colombia, Venezuela and Trinidad, is puzzling; presumably it is because suitable coralline environments have yet to be discovered in this subprovince whose waters were turbid, and still are turbid, except in the carbonate environment of the offshore island arc from Aruba to Islas Los Testigos.

In conclusion, it is worth quoting the comment of Olsson & Harbison (1953: 80) that, "Recent specimens of *pensylvanica* vary much in size, in the convexity and solidity of their valves, and appear to form a complex of several species." They were correct in their supposition.

SUMMARY

In the Western Atlantic the sole representative, hitherto, of the genus *Lucina s.s.* was *L. (L.) pensylvanica* (Linnaeus, 1758), the type species of the genus. Three new Recent taxa from the Caribbean are now described, being named according to their type localities as: *L. (L.) podagrina* ***caymanana*** subspec. nov. (Grand Cayman Island); *L. (L.)* ***roquesana*** spec. nov. (Islas Los Roques, Venezuela) and *L. (L.)* ***belizana*** spec. nov. (Belize). The four taxa, representing four distinct lineages, are distinguished, primarily, by their differing periostraca, a possibly unique occurrence amongst the bivalves. The shells themselves are morphologically similar and not to be differentiated except, possibly, by the comparison of large suites. In the absence of the periostracum in the fossils, therefore, a major problem arises in inferring the phylogeny. The type specimen of *Lucina pensylvanica* lacks periostracum and cannot, therefore, be related directly to any of the four taxa; it was said to be from North America and it is proposed formally that the form from Florida be recognised as typical of the species.

ACKNOWLEDGMENTS

The authors would like to thank Dr. John Taylor and Ms. Solene Morris of the Mollusc Section, British Museum (Natural History), for the loan of specimens in their care. They are also grateful for the help given by Miss Elizabeth Young of the Linnean Society of London. For some of the illustrations we wish to thank Frances Gibson-Smith. Finally, a word of thanks is due to Dr. J. Wyatt Durham for his careful and constructive review of the manuscript.

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A Comparative Study of a New Variety of *Conus centurio* Born, 1780, from Barbados, West Indies and *Conus recurvus* Broderip, 1833, an East Pacific Cone

BY

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(1 Plate)

INTRODUCTION

Walls' (1978a) attempt to arrange the 309 *Conus* species recognized by Walls (1978b) as valid into supraspecific groupings emphasizes the close relationship of many of the species. Some of the forms, lumped in the same grouping, have overlapping geographic distributions or predictably belong to the same Province, but others are from widely separated areas. Two species, *Conus centurio* and *Conus cf. C. recurvus* (some workers now prefer *emarginatus* to *recurvus*), are placed in adjacent groupings which Walls admits are very close and perhaps should not be separated. The former is an uncommon cone from the Caribbean Province which has been collected from the northern coast of South America along the Central American coast and the Lesser Antilles to Florida. The latter, an uncommon Pacific cone, can be found from the Baja Peninsula south in the Panamic area to Ecuador (Walls, 1978b). Both species typically inhabit moderately deep water. In this connection, recent dredgings (approx. 175m) off the west coast of Barbados, West Indies, have produced two variant specimens of *C. centurio* (herein given the varietal name *antillensis*) which are uniform in shell morphology and colour pattern and are strikingly similar to an atypical specimen of *C. recurvus.* The three forms, *C. centurio* (typical), *C. c.* var. *antillensis* and *C. recurvus* intergrade broadly, with the variant *C. c.* var. *antillensis* serving as the link which suggests a common ancestral form. This possibility appears valid when the assumption is made that the ancestral form predated the Isthmus of Panama, the potential ecological obstacle instrumental in the formation of two daughter species. Further, since both *C. recurvus* and *C. c.* var. *antillensis* inhabit moderately deep water, environmental factors such as temperature, salinity and light are not only fairly stable, but predictably similar—encouraging minimal genetic divergence.

It is the dual purpose of this paper, therefore, to describe *Conus centurio* var. *antillensis* and demonstrate the apparent close relationship between two geographically isolated species, *C. centurio* and *C. recurvus,* specifically by comparing the new variant of the former with an atypical specimen of the latter which most closely resembles *C. c.* var. *antillensis.*

ACKNOWLEDGMENT

I wish to thank Mr. Ole Sørensen for bringing to my attention the similarity in appearance between *Conus centurio* var. *antillensis* and a specimen shell of *C. recurvus* (Panama) from his personal collection. This shell is used herein for comparative purposes. Also, I am indebted to Mr. Jerry Walls for examining the shells and commenting on their similarity for the purpose of this paper. Mr. David Hunt kindly lent some samples of *C. centurio,* which conformed to the traditional descriptions of this species.

DESCRIPTION AND COMPARATIVE DIAGNOSIS

Figures *1* and *2* depict the many anatomical features the shells of *Conus centurio* var. *antillensis* and *C. recurvus* have in common. All three specimens appear adult and the respective lengths of the larger and smaller *C. c.* var. *antillensis* and *C. recurvus* of 5.4cm, 4.9cm and 5.0cm are well within the range given by Walls (1978b) for the two species. Both *C. c.* var. *antillensis* and *C. recurvus* are light, whereas the shells examined for typical *C. centurio* are moderately heavy. In profile, both *C. c.* var. *antillensis* and *C. recurvus* have upper sides slightly convex, tapering to narrow base, and a moderately high spire. By contrast, typical *C. centurio* is usually low biconical, with straight or slightly concave sides and a low to moderate spire. Other *C. recurvus* examined by the author have sharply pointed spires with whorls slightly stepped. Protoconchs of *C. c.* var. *antillensis* specimens are eroded. Postnuclear whorls are concave for the three specimens as they are for the typical forms. However, the margins of the whorls of the three shells are not carinate as are those of the typical forms examined for both species. In typical *C. centurio*, *C. c.* var. *antillensis* and the *C. recurvus* specimen the earliest two whorls are weakly nodulose, contrasted to the 4-6 strongly nodulose whorls of typical *C. recurvus.* Spiral whorls of all forms of *C. centurio* and *C. recurvus* inspected have axial threads with traces of spiral threads. Regarding the body whorl, a uniformly moderately wide aperture and thin sloping lip also characterize all forms of the two species. Body sculpture is also similar. The anterior third is marked by a dozen or so spiral ridges, above which the surface is smooth except for weak spiral and axial threads. The colour patterns in the specimens shown in Figures *1* and *2* are very close. The body whorl is white, with zigzag variable shades of brown flammules that tend to concentrate in three spiral bands. The central band of *C. recurvus* appears more finely broken, rendering it the only visually apparent distinguishing feature in respect of the two *C. c.* var. *antillensis* specimens. The brown streaks are in continuation with markings of the same colour on the spire whorl. However, the typical form of *C. centurio* tends to have the condensed flammules as irregular blotches overlying distinct and continuous salmon bands, which are not evident in the *antillensis* variant. Also, unlike the specimen shell of *C. recurvus,* the more typical *C. recurvus* is decorated with axial flammules commonly fused vertically.

DISCUSSION

The above comparisons clearly exemplify the problems *Conus* taxonomists encounter in defining species, subspecies and varieties in closely related forms. Vink's (1977) paper on the *Conus cedonulli* complex is further testimony to this problem. A conservative approach has been adopted here in naming the new shells a variant of *Conus centurio.* Differences in shell anatomy between typical *C. centurio* and the two specimens herein described do not warrant naming of a subspecies. The varietal designation may be elevated to the subspecies or species level, but only if further collections enable inspection of the soft parts, radula and operculum. The striking resemblance of *C. c.* var. *antillensis* to an atypical specimen of *C. recurvus* also merits further investigation of the live animals, and it may be that *C. c.* var. *antillensis* deserves taxonomic attachment to the allopatric Pacific species, the Isthmus of Panama notwithstanding. In fact, after personally examining the shells depicted in Figures *1* and *2,* Mr. Jerry Walls communicated the following comment: "I see no obvious differences in shape, texture, sculpture, or pattern from a series of East Pacific *C. recurvus,* not even at what I would call subspecific level; same sloping lip, nodulose early whorls, and virtually absent spiral spire sculpture. I personally see nothing wrong with a species on both sides of Central America, as *Conus puncticulatus* or probably even *Conus cedonulli-archon.*" Two other possibilities are 1) that *C. c.* var. *antillensis* belongs to an existing population of a Caribbean fossil, although I am not sufficiently familiar with the literature on fossil species to comment further on this, or 2) that it is an extreme variant of *Conus villepini,* which I strongly doubt because of distinct differences in texture, length-to-width ratio, spire sculpture, and pattern of body whorl banding.

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Explanation of Figures *1* and *2*

Figure *1:* 1 and 3 denote *Conus centurio* var. *antillensis;* 2 denotes an atypical specimen of *Conus recurvus*

Figure *2:* 1 and 2 denote *Conus centurio* var. *antillensis;* 3 denotes *Conus recurvus*

Figure *1*

Figure *2*

Mucous Thread Attachment as a Position Maintenance Adaptation in *Ilyanassa obsoleta*[1]

BY

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(1 Plate; 1 Text figure)

THE MUD SNAIL, *Ilyanassa obsoleta*, is a common estuarine gastropod along the east coast of North America from the Gulf of St. Lawrence to northern Florida (MORRIS, 1973). SCHELTEMA (1964) described it as an omnivore and facultative scavenger, consuming micro- and macro-algae, detrital material, meiofauna, macrofauna and moribund megabenthic and nektonic organisms.

During the course of diver surveys of scallop *(Argopecten irradians)* beds in the Poquonock River estuary, Groton, Connecticut (Figure 1), observations on the mud snail were made opportunely. Surveys were conducted from July through October 1980. Distribution and densities of the mud snail were visually determined. On two occasions, densities and behaviors were documented photographically with a Nikonos II camera and electronic flash, 35 mm lens and 1:3 extension tube. Area of coverage is approximately 9 cm × 6 cm.

During field observations, it was noted that *Ilyanassa obsoleta* was the most abundant gastropod species in eel grass beds, *Zostera marina*, and adjacent *Agardhiella* sp. mats (macroalgae, Rhodophyta) in this estuary.

Age (size) classes were spacially segregated with 0-yr individuals (approximately 3-5 mm shell height) occurring on the upper halves of *Zostera* blades and on *Agardhiella* fronds (Figures *2* and *3*). Densities of 0-yr individuals on *Zostera* blades and *Agardhiella* mats were 50-75 individuals/0.25 m^2 and 50-100 individuals/0.25 m,^{2} respectively. Adults (approximately 12-16 mm shell height) were found in *Zostera* mulch on the bottom, in the mud/silt substrate in the *Zostera* bed proper, and on the sand/silt substrate adjacent to a saltmarsh shoreline (Figure *4*).

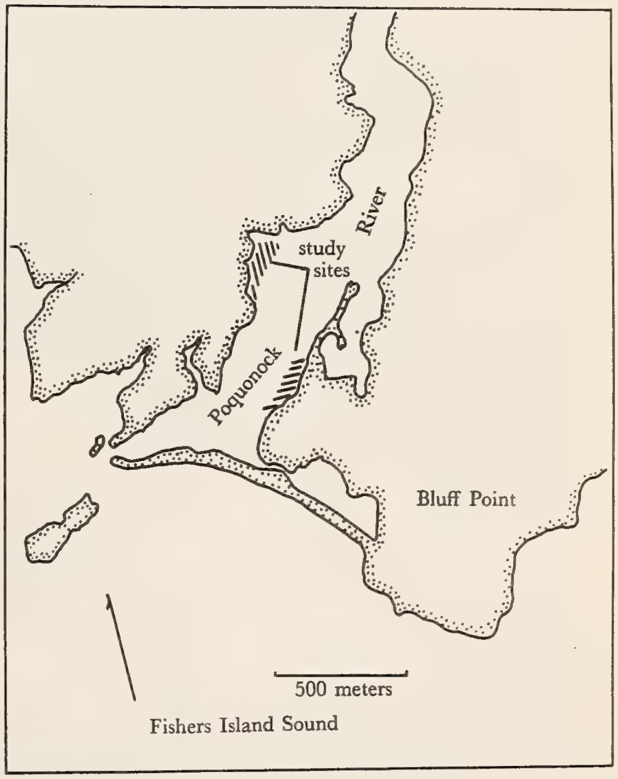

Figure 1

The study sites located in the Poquonock River, Groton, Connecticut

Mud snails commonly secrete a mucous trail which facilitates locomotion over the substrate (EDWARDS, 1979). Observations show that when the turbulence regime around a 0-yr class animal increases (due to natural disturbances, boat wake, diver disturbance, etc.) and it is dislodged from a "midwater substrate" (*i. e., Zostera* blade), a mucous thread is secreted which connects the animals by the foot to the substrate (Figure *5*). The individual then "climbs" back up

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[1] Contribution No. 145 from the University of Connecticut, Marine Research Laboratory, Noank, Connecticut 06340.

the thread to resume its position on the substrate. This behavior was observed during all surveys from July to October. Temperatures ranged from 21° C in August to 10° C at the end of October.

The use of a secreted mucous trail for ease in locomotion is the obvious predecessor to the mucous thread behavior described. The use of mucous thread attachment as an adaptive measure for position maintenance in a shallow river/estuary turbulent environment may be significant when one regards the food habits of the organism. Summer production of epiphytic fouling organisms is intense on the *Zostera* canopy of the bed. As *Zostera* and, secondarily, *Agardhiella* are the dominant canopy macrophytes, it may be energetically beneficial to take advantage of this seasonal peak production and maintain position in this region.

It must be noted that this behavior was only observed in 0-yr class individuals. Larger organisms were never observed on *Zostera* or *Agardhiella*. This is probably due to weight restrictions on the blades and fronds and food availability for these larger animals.

As fall-winter progresses with concurrent reduction in photoperiod, the *Zostera* and *Agardhiella* die back and the mud snails take up a benthic existence.

ACKNOWLEDGMENTS

I wish to thank Robert DeGoursey, Victoria L. Man, and Lance Stewart for reviewing the manuscript. I am also grateful to Joyce Lorensen for typing the drafts and final copy of this paper.

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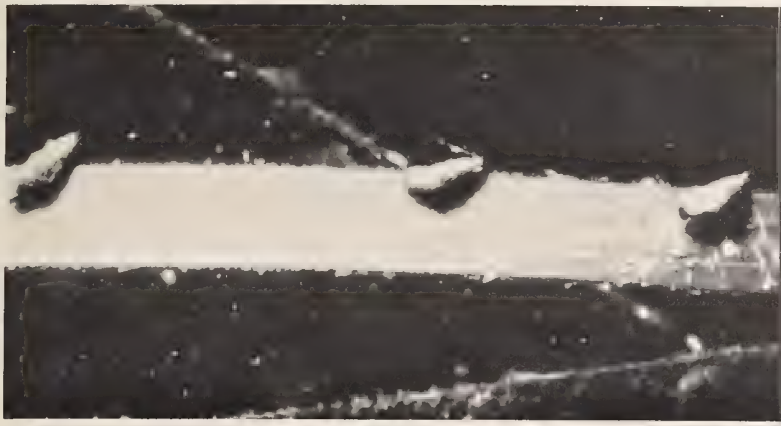
Explanation of Figures *2* to *5*

Figure *2:* The mud snail, *Ilyanassa obsoleta* in its normal position on a *Zostera* blade

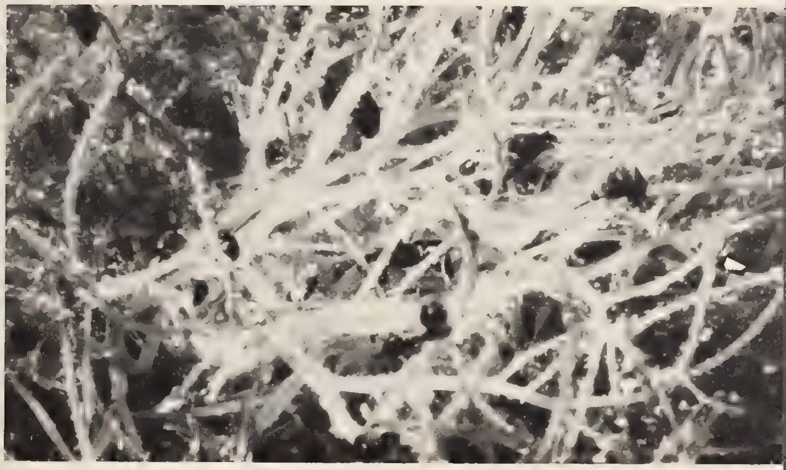
Figure *3:* Mud snails on an *Agardhiella* frond. Note the more spacially complex frond and its ability to accommodate a higher density of snails

Figure *4:* Adult mud snails on a sand flat at the edge of a salt marsh

Figure *5:* A 0-yr mud snail hanging from a *Zostera* blade by a mucous thread. The thread has attached flocculent material from the water column, making it more visible in this photograph



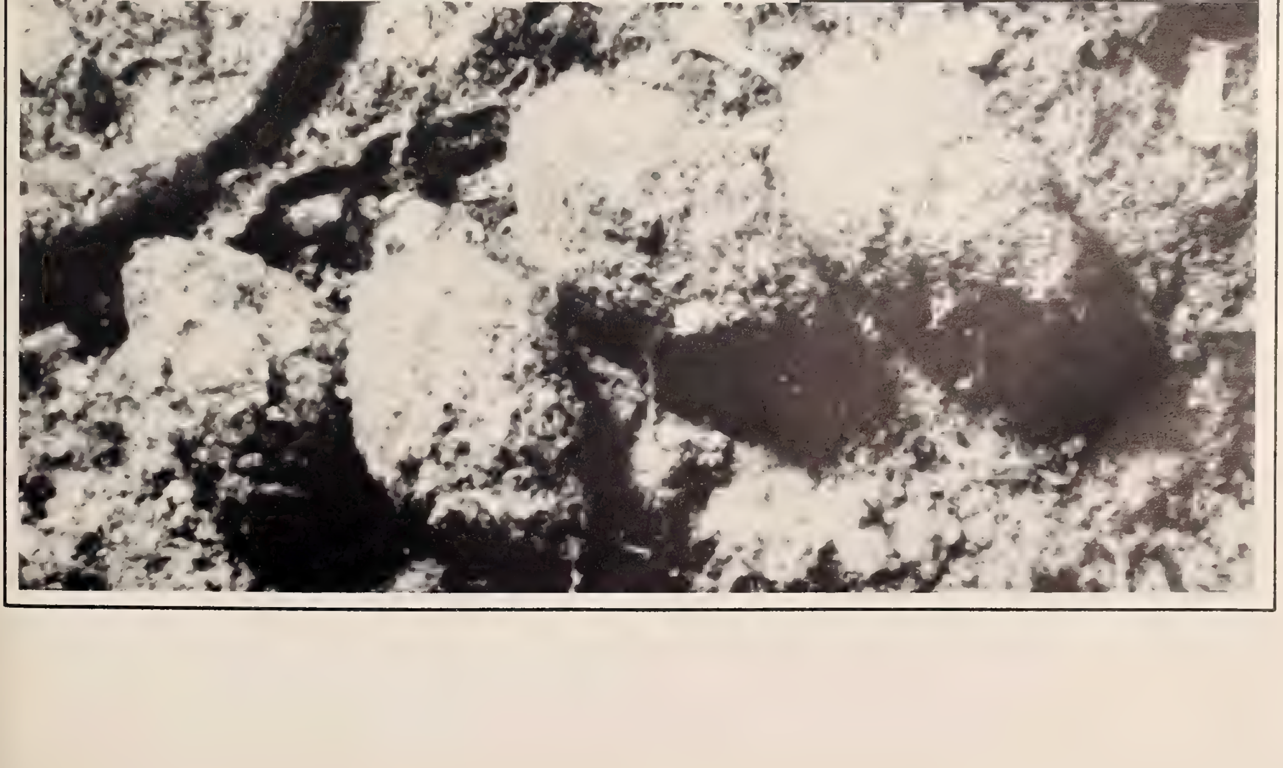
↑ Figure 2



↑ Figure 3

Figure 5 →

↓ Figure 4



Vestibular Response of *Tegula funebralis* to Shifts in Substrate Inclination

BY

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INTERTIDAL-DWELLING tegulid snails adhere very strongly to the rocky substrate on which they are found. This firm attachment enables them to resist wave action and predation.

During the spring of 1975, at the Scripps Institution of Oceanography, I maintained 10-12 specimens of *Tegula funebralis* (A. Adams, 1853) collected from a La Jolla, California beach. The snails were kept in a 30 × 45 × 30 cm glass aquarium furnished with fine beach sand and small (3-10 cm in diameter) rounded rocks. Snails weighed from 2 to 9 grams, the rocks from 20-150 g. Snails usually affixed themselves either to the aquarium glass or to the rocks, and were seldom seen on the sand.

When snails adhering to rocks were grasped by the shells and lifted out of the water, they continued to adhere, so that the rocks were also lifted free of the water. A 4 g snail, pulled out of water in this manner, could support the weight of a 40-60 g rock in air for several minutes (trials lasted 3-10 minutes). When a snail was attached to a rock more than 25-30 times its own weight, it usually could not maintain its adherence to the rock when lifted through the water. When adherence to a large rock was maintained during lifting, the snail always lost its grip when the rock broke free of the water's surface.

Table 1 shows relative weights of beach rocks in and out of seawater. Rocks were suspended by a wire loop from a Pesola balance, then lowered into a large beaker of seawater, to determine weights. Weighed rocks varied considerably in size, shape and apparent mineral composition, but the ratio of weight in seawater to weight out of water was fairly constant at 0.625. Snails lifted out of water while clinging to rocks therefore experienced approximately a 40% increase in the amount of force required to maintain their grip.

Table 1

Beach rock weights

Weight out of water	Weight in seawater	Ratio
65 g	40 g	0.61
100	60	0.60
136	83	0.61
61	44	0.72
405	250	0.61
74	46	0.62
56	35	0.63
49	31	0.63
6.1	3.7	0.61
8.4	5.1	0.61
	Average	0.625

In approximately 95% of trials, snails continued to cling when the rock surface they adhered to was tilted at angles of less than 90 degrees from the horizontal. If the surface of attachment was rotated 180 degrees, so that rock and adherent snail were turned upside down, the snails invariably released their hold voluntarily within a few seconds and dropped off into the water without being touched. Once in the water, snails immediately reattached themselves to the nearest firm surface (glass or rock). When the rock surface was tilted at angles between 90 and 180 degrees, some snails dropped off and some did not; the probability of a snail's dropping off increased with increased declination of the rock surface. Speed of tilting did not appear to significantly affect the probability of drop-offs, though some snails let go sooner if tilted faster.

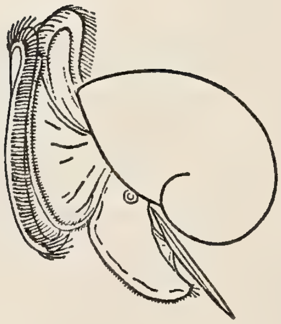
Tegulid snails in the field graze on small loose rocks during low tide, but are seldom seen resting on these. When the tide comes in, most *Tegula* attach to solid, massive rocky outcrops in the intertidal zone. In nature, therefore, it is likely that the only occasion on which a snail would find itself suddenly turned upside down would be if the rock to which it was attached were dislodged from its surroundings. In this case, the animal would run a high risk of being crushed as the rock rolled about in the surf. A vestibular response to sudden substrate shifts, of the sort described above, would seem to be of adaptive value.

Tegula funebralis individuals are sometimes found upside-down under rocky ledges on the beach, though they much more commonly occupy flat or vertical surfaces. It may therefore not be upside-downness *per se* to which the snails respond, but rather to (relatively) sudden shifts in substrate inclination. If this is the case, however, it is not clear why only shifts of more than 90 degrees should elicit voluntary drop-offs.

A final note: after several (5-10) trials per snail, some individuals began to drop off their rocks as soon as tilting began. Two snails, after repeated trials, released their hold as soon as their shells were grasped if attached to a rock, but still strenuously resisted detachment if resting on the aquarium glass. This may indicate that *Tegula funebralis* individuals can not only distinguish between substrates, but also adapt behavioral responses in the light of past experience.

ACKNOWLEDGMENT

I would like to thank M. C. Barnhart for technical assistance in obtaining and weighing beach rocks.



Microstructure of Shell Repair Materials in *Tegula funebralis* (A. Adams, 1855)

BY

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(2 Plates)

INTRODUCTION

There are numerous though scattered accounts of shell repair by gastropods in the literature (*e.g.* Currey & Kohn, 1976; Dudley, 1980; Vermeij, 1978, 1981), and examination of large samples of most species usually reveals individuals with healed fractures. Abrasion and shell erosion are additional shell injuries that can require repair. With the ubiquity of repaired shells, it is surprising that the microstructure of repair materials has not been addressed in the growing literature on molluscan shells. For example, in Bøggild's 1930 monograph, there is no mention of repair materials, nor in more recent reviews such as Gregoire (1972), Kobayashi (1969), or Carter (1980). The purpose of this paper is to describe repair materials used for apertural and apical repair in *Tegula funebralis* (A. Adams, 1855).

The spire of the shell of *Tegula funebralis,* a common trochid on the west coast of North America (see Morris *et al.,* 1980), is often heavily eroded. This erosion is the result of fungal or algal growth inside the shell or a combination of both (Figure *1*). The ascomycete fungus *Pharcidia balani* (Bauch, 1936), first described on *T. funebralis* and other west coast gastropods by Bonar (1936), is also sometimes associated with a green alga, in which case it is considered the lichen *Arthopyrenia halodytes* (Arnold, 1884). For further information on this fungus/lichen, see Peake & James (1965), Scinscow (1965), Kohlmeyer (1969), Kohlmeyer & Kohlmeyer (1974), and Tschermak-woess (1976).

Apparently to offset erosion of the shell, *Tegula funebralis* secretes a secondary layer of shell material on the inner surface of the shell. This material was briefly mentioned by Peppard (1964), who erroneously identified it as pigmented nacre. Also, *T. funebralis* is preyed upon by various predators, such as crabs, fish, and birds. Resultant nonlethal fractures are repaired, and are recognized as jagged vertical lines on the shell. The materials used in the repair of these injuries are described here, as well as, for comparison, the shell microstructure of *Tegula brunnea* (Philippi, 1848) and two other Trochids.

MATERIALS AND METHODS

Both species of *Tegula* were collected at Bodega Bay, California. Shells were cleaned by boiling in fresh water for five to ten minutes, followed by removal of soft parts by hand with forceps. *Astraea undosa* (Wood, 1828) was collected at La Jolla, California, and *Trochus niloticus* (Linnaeus, 1767) was collected at Gun Beach, Guam. These shells were cleaned similarly. All shells were prepared for scanning electron microscopy by either fracturing, or cutting, polishing, and acid etching. Specimens were coated with gold and viewed with an Hitachi S450 scanning electron microscope (SEM).

RESULTS

Normal Microstructure in *Tegula funebralis:* The normal shell structure of *Tegula funebralis,* that is, the structure of the shell deposited at the aperture in normal growth by the mantle margin, is as follows. There is an outer fibrous prismatic layer, resembling the irregular prisms and fibrous prisms defined by Carter (1980). This layer (Figure *2*) consists of thick, elongated crystals oriented perpendicularly to the shell surface and parallel to other overlapping prisms. The fibrous prismatic layer varies in thickness throughout the shell, typically comprising ten to twenty percent of the shell thickness. Beneath the fibrous prismatic layer is a thick nacreous layer (Figure *3*), which constitutes the remainder of the shell. The nacre does not differ in any noticeable way from that described in other molluscs: thin plate-like crystals deposited in a laminar configuration. In normal shells, the interior surface of the shell is the inner boundary of the nacreous layer.

Infected and eroded shell in *Tegula funebralis:* The fungus apparently consumes the organic matrix of both the inner and outer layers (Bonar, 1936), disrupting and pitting the crystalline structure. The pits are generally larger than the hyphae of the fungus, suggesting that other erosive agents are involved in the erosion of the shell. However, pitting of the exterior surface of the shell is likely facilitated by fungal growth. As the upper layer erodes away, the inner nacreous layer is exposed and is subsequently eroded (Figure *4*).

In the examination of infected shell material, previously undescribed objects were observed. Small spheres (0.5-1 μm) were seen in the fibrous prismatic layer (Figure *5*), sometimes in cavities in individual crystals (Figure *2*). These spheres, occurring in greatly varying densities, are neither the appropriate size nor morphologically similar to fungal spores. They were not always found in association with fungus, as they are in Figure *1*. If the objects are organic, the size range suggests either a cyanophyte or some other prokaryote organism.

Structure of secondary material in *Tegula funebralis*: Examination of *Tegula funebralis* shells reveals that a secondary layer is deposited on the interior of the shell underneath areas of fungal erosion on the exterior. The material is orange or yellow in color when observed in unprepared specimens. Peppard (1964) stated that the material is nacre; however, even cursory microscopic observation will show this is incorrect. Examination with SEM reveals that the secondary layer is composed of sheaths of crystals deposited in planes parallel to adjacent underlying sheaths. The longitudinal orientation of overlapping sheaths is dissimilar such that an angle is defined. This cross angle varies within the layer; the angle is small near the surface of the shell interior so that sheaths are nearly parallel in adjacent planes, and larger towards the outside of the shell, gradually reaching nearly ninety degrees (Figures *6*, *7*). The structure is termed complex cross laminar (Carter, 1980). In the terminology of cross laminar structures, the sheaths would be considered first order laths or lamels, and the individual crystals as second order laths or lamels.

Within the secondary layer, there are clearly visible sublayers (Figure *8*). At the contact between sublayers, the cross angle between first order lamels changes radically. The contact between sublayers forms a complete circle in a complete cross section of a shell. This suggests that sublayers are deposited in episodes. Figure 9 shows fungal erosion within the secondary material. If shell thickness is to be maintained, deposition must occur at least periodically. The contact line between sublayers apparently records periods of deposition.

Apertural repair material in *Tegula funebralis*: Shell material in repairs to apertural fractures are identical to those normally secreted by the mantle margin. In cross section of repaired fractures (Figure *10*), there are four layers visible: outer fibrous prismatic, nacreous, fibrous prismatic, and inner nacreous. Apparently after a fracture, the mantle retracts slightly inwards from the break before resuming shell deposition. The upper two layers are original pre-fracture shell materials, while the underlying two layers are newly deposited after the fracture has occurred. On the apertural side of the fracture, the lower two layers curve upwards to become the outer and only shell layers, as is the normal configuration.

Where a fracture has occurred on the shell where secondary material had been secreted, secondary material is also present in the repaired shell (Figure *11*). It is not clear whether secondary material in fracture repair is secreted by the mantle margin contemporaneously with fibrous prismatic and nacreous material, or whether it is secreted by the mantle surface later.

Tegula brunnea

The shell structure of *Tegula brunnea* consists of two layers, as in *T. funebralis*. Unlike *T. funebralis* however, the outer layer is a form of the cross lamellar structure. Foliated

Explanation of Figures *1* to *8*

Figure *1*: *Tegula funebralis*. Hyphae of the fungus *Pharcidia balani* in the outer fibrous prismatic shell material. Note the small spheres on the surface. These objects remain unidentified (see text) 5 μm scale bar

Figure *2*: *Tegula funebralis*. Outer fibrous prismatic layer. Pitting in individual crystals is associated with the unidentified spherical objects 10 μm scale bar

Figure *3*: *Tegula funebralis*. Transition from fibrous prismatic to nacreous shell layers 10 μm scale bar

Figure *4*: *Tegula funebralis*. Erosion and pitting on exposed surface of the nacreous layer 10 μm scale bar

Figure *5*: *Tegula funebralis*. Close-up of unidentified spheres in an area of high density in the fibrous prismatic layer 5 μm scale bar

Figure *6*: *Tegula funebralis*. Complex cross lamellar structure in secondary shell material secreted on the interior of the spire. The angle between overlying first order lamels is near ninety degrees 5 μm scale bar

Figure *7*: *Tegula funebralis*. Complex cross lamellar structure as in Figure *6*. Here the angle between first order lamels is more acute 5 μm scale bar

Figure *8*: *Tegula funebralis*. Contact line between sublayers within complex cross lamellar material. The cross angle between first order lamels changes radically across contact. This may represent two separate periods of shell deposition 5 μm scale bar

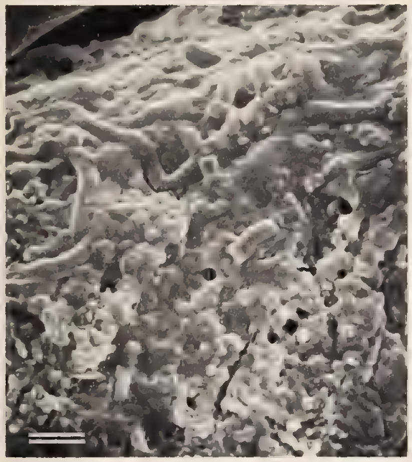

Figure *1*

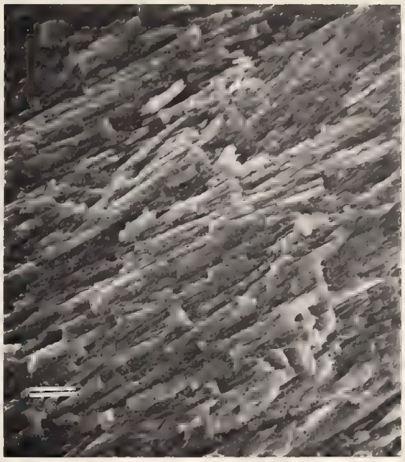

Figure *2*

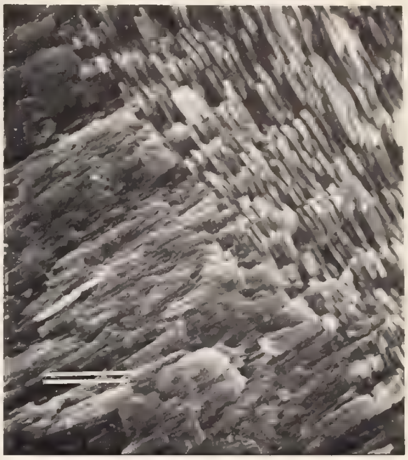

Figure *3*

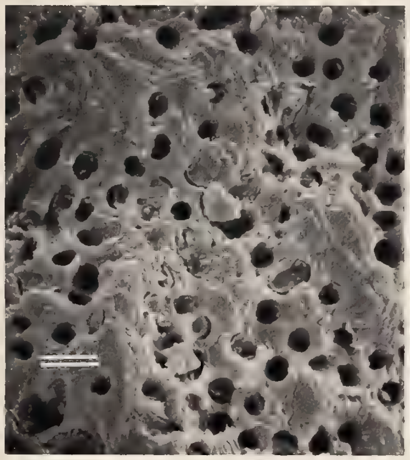

Figure *4*

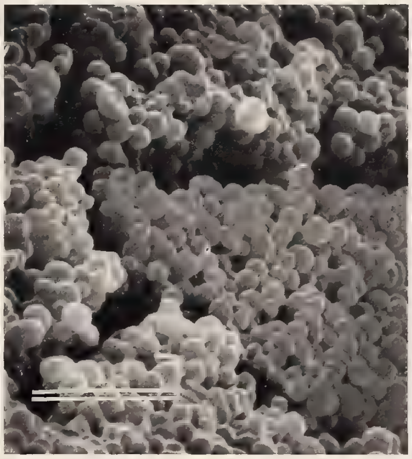

Figure *5*

Figure *6*

Figure *7*

Figure *8*

crystals form second order lamels, with stacks of these comprising first order lamels (Figure *12*). This structure resembles common cross lamellar with second order lamels expanded greatly in two dimensions. An appropriate name for this structure would be foliated cross lamellar. The inner layer is nacreous. No evidence of fungal erosion or secondary deposition was observed in *T. brunnea.*

Shell Structure in *Trochus niloticus* and *Astraea undosa*

The shells of both *Trochus niloticus* and *Astraea undosa* are quite similar to that of *Tegula funebralis.* In both there are two layers secreted by the mantle margin: upper fibrous prismatic and inner nacreous. No fungal growth or shell erosion was observed in either of these shells. The exterior of both shells has a thick periostracum and layer of epibionts, which may help inhibit boring organisms. Both snails deposited secondary material in the upper whorls of the shell. In *Astraea undosa,* the structure of this secondary material was homogeneous, showing no order at all (Figure *13*). In *Trochus niloticus,* the structure graded between unoriented irregular prisms and organized simple prisms. Layers of secondary material are deposited with a thick organic band between. In each layer, the outer portion is an unorganized jumble of crystals which gradually become organized towards the inner border of the layer, until the prisms are organized in a simple prismatic structure (Figure *14*).

DISCUSSION

Adaptiveness of Secondary Deposition in ***Tegula funebralis:*** As mechanical properties of shell materials are studied further, it is becoming apparent that the characteristics of structural types and combinations of types suit different functions that shells may serve (see Currey & Kohn, 1976; Currey, 1980; Carter, 1980). The secretion of secondary material in *Tegula funebralis* appears to be an adaptive response to shell erosion. It is not certain that the loss of the spire would result in the death of the snail; however, it is probable that uncovered soft parts would expose the animal to increased desiccation, predation, and parasitism. Secondary deposition ensures an intact shell and, in view of the risks of exposure, can be considered adaptive. It could be argued that secondary deposition in *T. funebralis* may be normal shell growth, as in the whorl infilling of *Trochus* and *Astraea.* One argument against this interpretation is that the congener *T. brunnea* does not deposit any secondary material. Another is that the secondary deposition in *T. funebralis* corresponds closely to eroded surfaces on the exterior of the shell. I could not find an uneroded *T. funebralis* at Bodega Bay among over 920 snails examined: it is not known whether uneroded *T. funebralis* would deposit secondary material.

The question arises, why is it the complex cross lamellar structure that is secondarily secreted by *Tegula funebralis?* A complete answer requires chemical and mechanical analysis of the shell materials involved, and a better understanding of the mechanisms of shell deposition. However, some inferences can be made on the basis of our current understanding of the physical characteristics of shell materials. Complex cross lamellar structure is relatively resistant to both abrasion and chemical attack (Currey, 1980). While not demonstrated in this study, it is likely that chemical attack by fungus or algae, or both, and subsequent mechanical abrasion are responsible for the shell erosion observed in *T. funebralis.* With our understanding of the mechanisms of shell deposition, it is not possible to predict what structures *T. funebralis* has the potential capacity to produce. Of the three structures observed, erosion would be slowed most by complex cross lamellar.

The function of spire infilling in general is not known; however, balance, weight, and shell strength may be involved. In any of these cases, the infilled material is not intended to interact with the outside environment. The homogeneous structure of the infilled material in *Astraea undosa* would be an energetically economical material if one assumes that order and structure in shell materials require more energy to produce than unordered materials. The same reasoning should apply to *Trochus niloticus,* yet the structure here shows, in places at least, a relatively high degree of order. The function of the structure of infilled material in *Trochus niloticus* remains unclear. Further studies of the mechanical behavior of shells and the process of shell deposition may clarify this problem.

MORPHOLOGICAL, ECOLOGICAL, AND EVOLUTIONARY IMPLICATIONS

A major effect of erosion and the subsequent pattern of secondary deposition is the loss of the nacreous layer from the apex of the shell (Figure *15*). Nacre is the strongest of shell materials in tension, compression, and bending (Currey, 1980). These are the stresses exerted on shells during attack by durophagous predators. The expected reduction in shell strength would likely increase susceptibility to predation. This latter prediction seems to be borne out. I observed the brachyuran crab *Cancer antennarius* (Stimpson, 1856) consistently to attack larger (and therefore older and more eroded) *Tegula funebralis* at the spire (Geller, ms.). This observation is opposite that of Bertness & Cunningham (1981), who observed crabs to attack larger snails at the aperture. This latter mode of attack intuitively seems to be a more general trait, as the dactylus or entire chelae of a crab will only fit into larger shells. The atypical crushing behavior of *Cancer* seems to be explained by the alteration of shell structure in larger *T. funebralis.* Unfortunately, I have no data on the ability of crabs to crush uneroded shells. This hypothesis remains to be tested with appropriate controls.

A second important ecological consequence of shell erosion and secondary deposition is the energy diverted from somatic growth and reproduction. As mentioned, the fungal erosion is ubiquitous. This being so, shell erosion does not necessarily reduce relative fitness. However, there should be strong selection for resistance to erosion, as uneroded snails would have more energy available for reproduction. It has been tentatively suggested that fungal inhabitation might be beneficial to gastropod hosts (Gerson & Seaward, 1977). For *Tegula funebralis,* this notion can be discarded on the basis of deleterious energetic and mechanical consequences.

Other than shell microstructure, there are three obvious morphological consequences of erosion and secondary deposition. First, as material is deposited on the inside of the shell, internal volume is progressively reduced. Second, erosion on the exterior causes the spire to become smaller, and produces a ledge on the border between eroded spire and uneroded body whorl. Lastly, the loss of the black outer layer results in the lightening of shell color. Each of these may have ecological consequences; for example, shell color may have thermal implications, and may be a factor in visibility to predators.

In conclusion, secondary shell materials, including those used for repair, are important components of the gastropod shell. As with most morphological traits, there is a range of functions associated with secondary materials. As the mechanism of shell deposition and the physical characteristics of shell materials become better understood, so will the functions that the shell serves. In addition, understanding of ecological and evolutionary significance of the shell will be enhanced.

SUMMARY

1. Shell erosion by a marine fungus, *Pharcidia balani,* apparently causes *Tegula funebralis* to secrete a secondary layer of complex cross lamellar material on the interior surface of the spire.
2. Shell materials used to repair apertural fractures are the same as those normally secreted by the mantle margin: fibrous prismatic and nacreous. Where secondary material had previously been deposited, the fracture repair includes a layer of secondary material.
3. Repair materials may be adaptive beyond the simple repair of shell injury: the complex cross lamellar material deposited by *Tegula funebralis* is relatively resistant to mechanical and chemical abrasive agents, thereby slowing further shell erosion.

ACKNOWLEDGMENTS

I would like to thank the following people for helpful discussion in the course of this study: K. Derstler, A. Kuris, N. Lang, P. Signor, and P. Ward. P. Signor kindly donated shells from Guam. This work was in part supported by a graduate research award from the University of California at Davis.

Explanation of Figures *9* to *15*

Figure *9: Tegula funebralis.* Fungal growth in apical secondary material 10 µm scale bar

Figure *10: Tegula funebralis.* Repaired fracture near the aperture. From the outside in, the first and third layers are fibrous prismatic, the second and fourth layers are nacre 500 µm scale bar

Figure *11: Tegula funebralis.* Repaired apertural fracture with secondary complex crossed lamellar material on the inner edge on both pre-fracture (left side) and post-fracture shell 500 µm scale bar

Figure *12: Tegula brunnea.* Outer shell layer. Foliated cross lamellar structure 10 µm scale bar

Figure *13: Astraea undosa.* Secondary material infilling the spire. Homogeneous structure 5 µm scale bar

Figure *14: Trochus niloticus.* Secondary material infilling the spire. Structure grading between errant irregular prisms (bottom) to simple prismatic (top), with band of organic material separating repeating bands 10 µm scale bar

Figure *15: Tegula funebralis.* Low magnification cross section showing the erosion of original material at the intersection of the spire and the body whorl. The spire is completely composed of secondary material. The secondary material is split at the contact between sublayers 500 µm scale bar

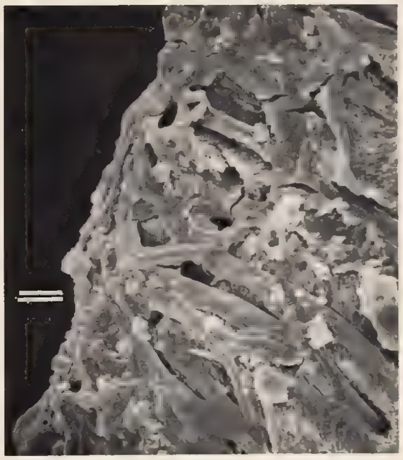

Figure *9*

Figure *10*

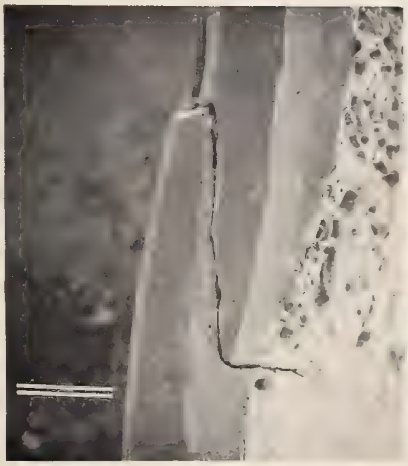

Figure *11*

Figure *12*

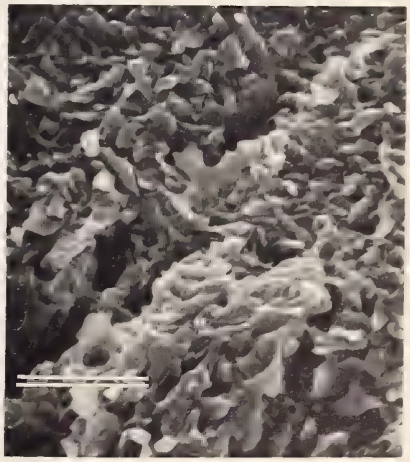

Figure *13*

Figure *14*

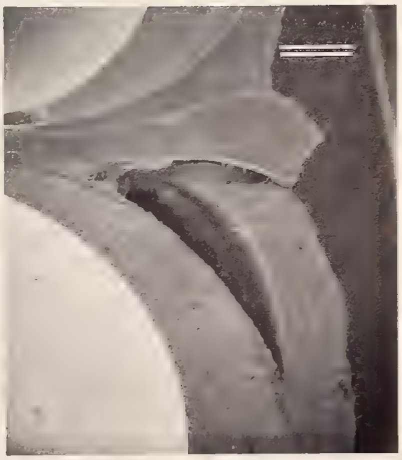

Figure *15*

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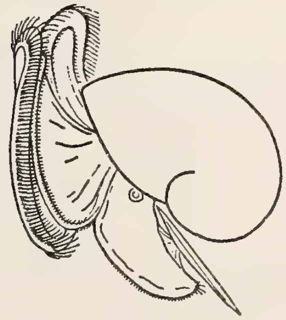

Reproductive Aspects of *Polystira barretti* (Guppy, 1866)

(Gastropoda, Turridae)

From Golfo Triste, Venezuela[1]

BY

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(1 Plate; 3 Text figures)

INTRODUCTION

Polystira barretti (Guppy, 1866) a Miocene fossil from Santo Domingo and Jamaica, was found to live in the Venezuelan Caribbean by Petuch (1980) in part revising some of our material; it is indeed one of the most abundant gastropods of the Golfo Triste shelf (30-80m deep) and is frequently associated with species of *Crucibulum.*

There are numerous references about oviposition of the family Turridae in other geographic areas where there appears to be a single type of egg-capsule in all species studied (Verrill, 1882; Lebour, 1934, 1938). No records seem to exist on the Caribbean species however, and as far as we know this is the first description of egg-capsules of a turrid of that area.

MATERIAL AND METHODS

Seventeen adult individuals of *Polystira barretti* were collected aboard vessels trawling between 42 and 50m depth in Golfo Triste, Venezuela, in October 1977. They were maintained in aquarium conditions for a period of three months. A sand layer 5-7cm thick was placed in each aquarium. A total number of 48 egg capsules were produced, which were fixed in 7% formaldehyde in different developmental stages until hatching.

RESULTS

The oviposition consists of isolated egg-capsules laid directly in the sandy substrate. The egg-capsules are circular or sub-circular in outline, flat-convex and are surrounded by sand grains attached to the surface by a mucilaginous secretion except for the upper, convex region, which is transparent and remains sand-free (Figure *1*). The egg-capsules have a marginal festoon that is totally covered by particles of sand and which extends downwards and along the side at about 40° angle (Figures 4 and 5). There is a preformed escape aperture, oval-fusiform in outline, covered by a transparent membrane, and situated in the upper subcentral part of the capsule. A ridge goes from one end of the exit aperture to the edge of the capsule, and two others originate from the opposite end of the aperture, a short one and a longer one that reaches the edge of the capsule (Figure *3*). The egg capsule measures between 5.0 and 10.7mm (mean value 7.4mm) along the longer axis and between 4.4 and 10.2mm (mean value 5.7mm) along the shorter axis.

The average number of eggs per egg-capsule was 73 (between 32 and 126). The mean egg diameter was 438μm

Explanation of Figures *1* to *3*

Figure *1:* Egg capsule of *Polystira barretti,* dorsal view.
Figure *2:* Larval shell of *Polystira barretti* at hatching.
Figure *3:* Opened escape aperture of an empty egg-capsule.

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[1] This work was supported by CONICIT Grant No. S1-0775.

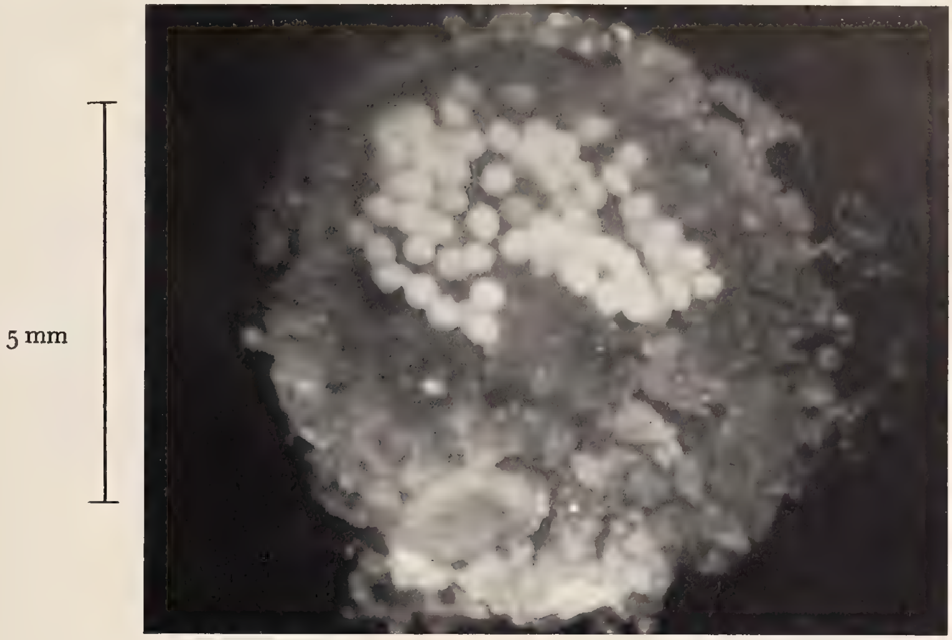

Figure *1*

Figure *2*

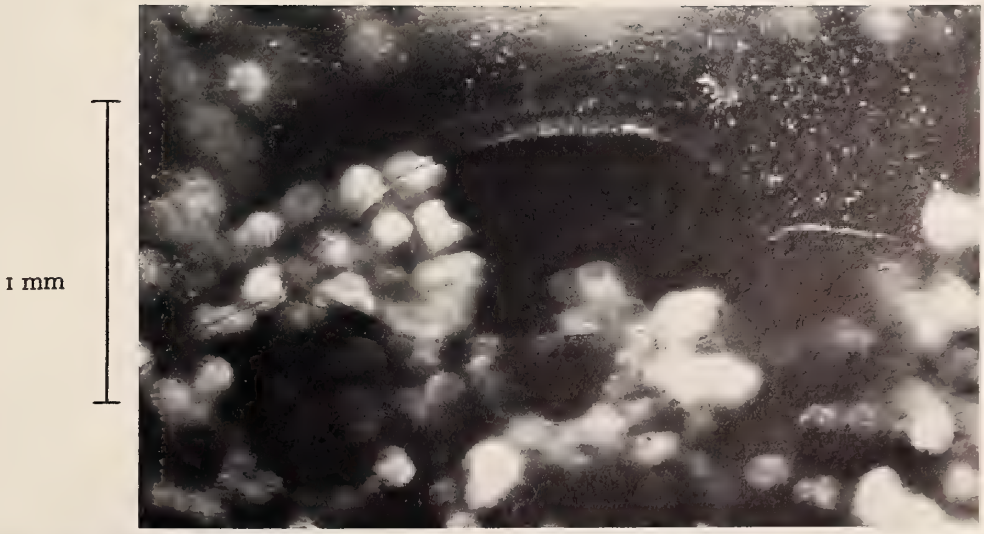

Figure *3*

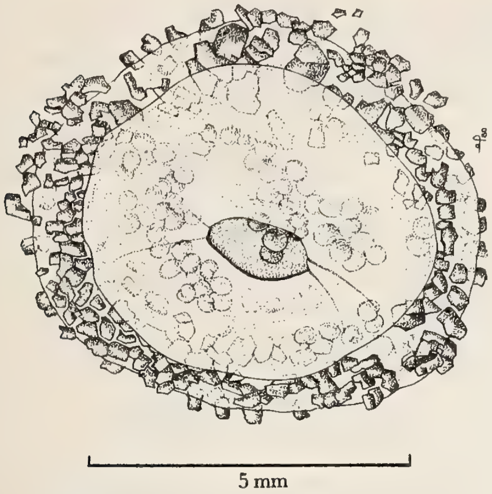

Figure 4

Diagram of the dorsal view of an egg-capsule.

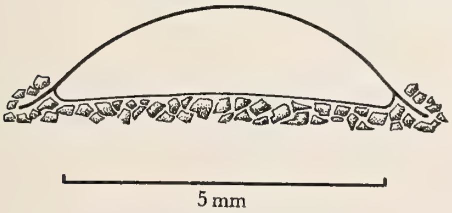

Figure 5

Cross-section diagram of an egg-capsule.

(320 eggs measured; 428-442μm). Each egg develops and eclosion takes place as free swimming veliger larvae with a shell size (across diameter) of 670μm (Figure *2*). No differences were observed on the size of the hatching larvae from capsules with different numbers of eggs.

DISCUSSION

The family Turridae is apparently characterized by a single type of oviposition consisting of isolated egg-capsules, which are lenticular and generally attached to the substrate by their flat side. On the convex side there is a preformed escape aperture which is covered by a membrane (Verrill, 1882; Lebour, 1934; 1938). The egg-capsules of *Polystira barretti* are typical of the family and closely resemble the descriptions of *Bela* and *Philbertia* (Lebour, 1938) among others. The more distinctive character of *P. barretti* is its condition of free egg-capsules, unattached to hard substrates but surrounded on most of their surface by grains of sand stuck to a mucosity. The sand grains are important in insuring that the egg-capsule stays buried in the bottom; at least,this is the situation observed in aquarium conditions; egg capsules were never found to adhere to the glass walls. Furthermore, in the considerable quantity of mollusc shells and other hard substrates collected during periodic sampling of the benthic material of the studied area of Golfo Triste, attached egg-capsules of *Polystira* were never found. Thorson (1935) indicates that in *Bela simplex* the capsules are attached to different kinds of hard substrata, but often they are laid directly in the sand, and if so, a small lump of sand adheres to the capsule.

All of the northern European species studied (Lebour, 1938; Vestergaard, 1935; Thorson, 1946) hatch as veliger larvae, while Thorson (1935) describes 5 species of the genus *Bela* from Greenland with direct development, hatching in the crawling stage. Amio (1963) also found direct development in *Clavus japonicus* from Japan. There is a defined difference of the egg diameter and the type of development of these species. The egg diameter of *Mangelia nebula, Philbertia gracilis* and *Ph. linearis* (species with free swimming larvae) is 140-160μm (Lebour, 1938) while in *Clavus japonicus* it is 650μm (Amio, *op. cit.*); *P. barretti* has an intermediate egg size (diameter 438μm); this and the size of the animal at hatching suggest that the larvae would only remain in the plankton for a short period of time.

Lebour (1938) states that two kinds of nepionic shells can be distinguished in adult Turridae, those with smooth

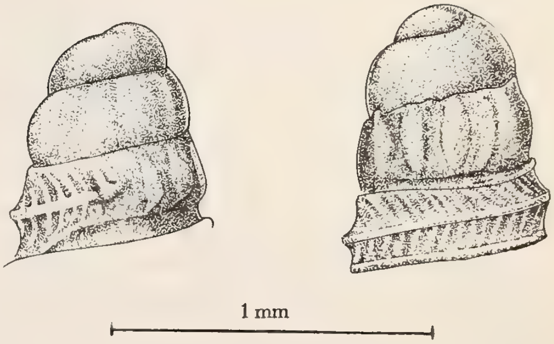

Figure 6

Apex region of an adult specimen of *Polystira barretti*.

apices *(Haedropleura, Lora, Mangelia)* and those with reticulate or sculptured apices *(Philbertia); Polystira barretti* presents a smooth protoconch and therefore corresponds to the first type (Figure 6).

SUMMARY

The oviposition of *Polystira barretti* is described as a single egg-capsule directly laid on the sand substrate. The egg-capsule is circular, flat-convex and surrounded by grains of sand attached to the external surface except the upper region. The average number of eggs per capsule was 73 (between 32 and 126); the egg diameter was 438 μm. Hatching occurred in a veliger stage, with a shell size of 670 μm.

ACKNOWLEDGMENTS

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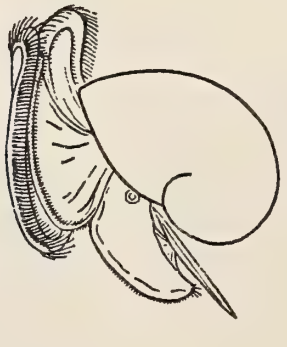

Escape Responses of *Turbo castanea* to the Predatory Gastropod *Fasciolaria tulipa*

BY

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(2 Text figures)

INTRODUCTION

Effective escape responses are important elements in the behavioral repertoire of many marine gastropods. The subject has been reviewed by Feder (1967) and Ansell (1969) and the similarity between gastropod righting movements and escape movements has been critically reviewed by Weldon & Hoffman (1979). Recent studies of gastropod escape behavior include those of Gore (1966); Kohn & Waters (1966); Snyder & Snyder (1971); Berg (1972, 1974); Phillips (1975, 1977); Field (1977); Hoffman *et al.* (1978); Hoffman & Weldon (1978); Parsons & MacMillan (1979); Hoffman (1980); Kent (1981) and Harrold (1982).

Turbo castanea Gmelin, 1791 is a common widely distributed shallow water Caribbean top shell (Family Turbinidae). It is often abundant in *Thalassia testudinum* seagrass meadows where it grazes on epiphytes. Near La Parguera, Puerto Rico, where this study was done, *Turbo castanea* is a frequent item in the diet of the tulip snail *Fasciolaria tulipa* Linnaeus, 1758. *Fasciolaria tulipa* is known to be a molluscivore that eats a variety of gastropods and bivalves (Paine, 1963) and also is cannibalistic (Snyder & Snyder, 1971).

Turbo castanea has a vigorous escape response to *Fasciolaria tulipa.* I investigated the effectiveness of three kinds of stimuli in inducing escape behavior; 1) contact with the predator, 2) waterborne chemicals from the predator, and 3) presence of escaping conspecifics. As *T. castanea* became fatigued from repeated stimulation by *F. tulipa,* characteristic changes in the escape response occurred. Ontogenic or size related differences in *T. castanea* escape behavior occurred also, and these are interpreted in the context of the relative likelihood for successful escape by snails of different sizes.

METHODS

Specimens used in this study were collected from seagrass beds, back reef habitats, and adjacent to mangroves on the SW coast of Puerto Rico near La Parguera, from June 1976 through June 1977. They were maintained in aquaria in the flow-through seawater system at the marine laboratory of the University of Puerto Rico, Department of Marine Sciences. The temperature and salinity paralleled those of ambient seawater and ranged from 25-30° C and 33-37%‰.

General observations were made of animals in glass aquaria, in water tables, or in the field, and experiments were performed in a smooth plastic pan approximately 30 × 40 cm. The pan was thoroughly rinsed, then wiped with a fresh towel between each trial.

Rates of locomotion by *Turbo castanea* were determined by measuring the distance (in mm) a specimen moved in 15 sec. *Turbo castanea* generally moved in fairly straight lines, thus facilitating accurate measurements. Rates of locomotion of *Fasciolaria tulipa* were similarly measured in a large cement holding tank as centimeters travelled over time intervals ranging from 10 to 90 seconds.

Turbo castanea size was measured as aperture diameter recorded to the nearest 1/10 mm using a dial caliper. This measurement is slightly larger than the longest dimension of the operculum and provides a very consistent measure of *T. castanea* size. *Fasciolaria tulipa* shell lengths were measured from the tip of the spire to the anterior tip of the siphonal canal to the nearest 1/10 mm.

RESULTS

A. Response to Contact by *Fasciolaria tulipa:*

Turbo castanea rotated the shell away from the place of contact when touched on the soft parts by *Fasciolaria tulipa,* and held the shell as far forward as possible. Simultaneously, locomotion directly away from the source of contact was initiated or increased dramatically. Occasionally the shell was rotated back and forth but generally it was simply held far anterior away from potential contact by the foot of the attacking *F. tulipa.* If the *T. castanea* was on a vertical surface, it sometimes would fall off during the twisting movements, and occasionally would tip over even on a horizontal surface and subsequently right itself. The caudal

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cirri and the tentacles were extended and waved as the *T. castanea* fled. Another reaction which was especially common in small individuals (<0.45 cm aperture diameter) was to turn directly toward the source of contact and raise the front half of the foot high off the substratum and wave it back and forth until touching a solid object which the snail then climbed. I called this the "turn and climb" response. The result of this behavior was that frequently the *T. castanea* climbed to the top of the shell of the attacking *F. tulipa*. Another frequent outcome of the "turn and climb" was that the *T. castanea* was captured and consumed by the *F. tulipa*. Therefore, this escape response is less effective than rapid flight.

The speed of *Turbo castanea* during escapes was more than three times faster than normal locomotion. The speeds of ten *T. castanea* were measured five times during normal locomotion and likewise five times during escapes and the mean speeds are plotted versus *T. castanea* size in Figure 1.

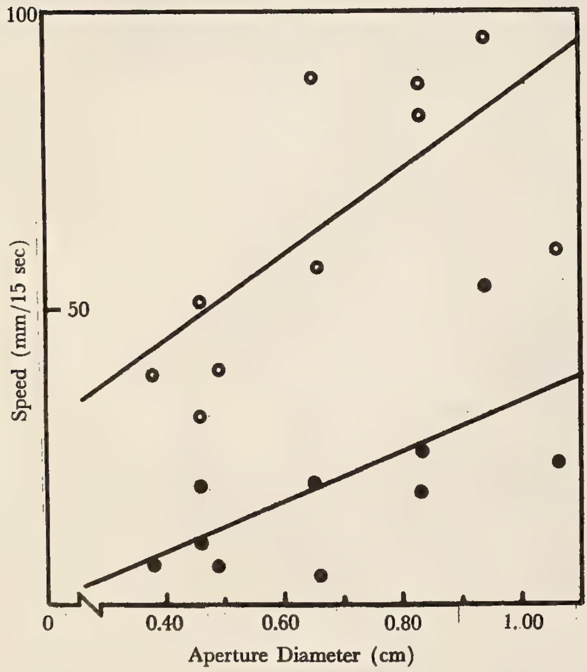

Figure 1

Turbo castanea crawling speed versus size. The speed of *T. castanea* during escape (open circles) is about three times that during normal locomotion (closed circles). In both cases the speed is highly correlated with size (escape, $r = 0.699$, $p < 0.05$; normal, $r = 0.671$, $p < 0.05$).

Both normal and escape speeds are positively correlated with size in *T. castanea* (normal, $r = 0.671$, $p < 0.05$: escape, $r = 0.699$, $p < 0.05$). The maximum speed attained by large *T. castanea* was nearly 100 mm/15 sec.

The maximum speed of the predator *Fasciolaria tulipa* was greater than that of *Turbo castanea*. The maximum speeds of 13 *F. tulipa* are plotted against size in Figure 2. *Fasciolaria tulipa* have a vigorous escape response to conspecifics (Snyder & Snyder, 1971), so maximum locomotion rates were obtained by clocking individuals stimulated to escape from other *F. tulipa*. The maximum speed was not significantly correlated with body size ($r = 0.147$, $p < 0.05$) over the fairly broad size range tested. Even relatively small *F. tulipa* attained speeds in excess of 150 mm/15 sec and all but one of the *F. tulipa* tested moved faster than the fastest *T. castanea* tested.

Two other gastropods, *Cerithium litteratum* (Born, 1778) and *Tegula fasciata* (Born, 1778), are common in the same habitats with *Turbo castanea* and are similar in size to *T. castanea*, but neither of them showed a pronounced escape reaction to *Fasciolaria tulipa*. Repeated contact by *F. tulipa* on the soft parts of those species failed to elicit shell twisting or obvious increases in locomotion rates.

B. Response to Waterborne Chemicals from *Fasciolaria tulipa*.

Water collected from the mantle cavity of *Fasciolaria tulipa* elicited quick reactions and escape behavior from many *Turbo castanea*. To test these reactions I assembled three groups of *T. castanea*, 10 "small" (aperture diameter 0.34 to 0.49 cm), 10 "medium" (aperture diameter 0.56 to 0.72 cm), and 10 "large" specimens (aperture diameter 0.78 to 0.87 cm). Each group was subjected to the following series of treatments in the plastic pan. A size group was placed in the pan in water about 3 cm deep, and allowed to adjust for five minutes. In treatment A (the control) a non-escaping *T. castanea* was introduced into the pan for two minutes. In treatment B an escaping *T. castanea* which had just been stimulated in another aquarium by contact with a *Fasciolaria tulipa* was introduced into the pan for two minutes. In treatment C approximately 2 ml of fluid from the mantle cavity of a *F. tulipa* was added to the water in the pan. The water was replaced after each trial and the pan wiped clean. Approximately five minutes were allowed between trials. The number of experimental animals which showed either the flight response or the "turn and climb" within the two-minute period was recorded (Table 1). The series was run twice with the "large" and "small" *T. castanea* and once with the "medium" group.

Flight or "turning and climbing" was observed in 5 of the 10 large *Turbo castanea* in one trial and 7 of 10 in the other trial (Table 1). In addition, most of the large, medium or small *T. castanea* that did not show escape responses did wave the caudal cirri and the antennae in apparent

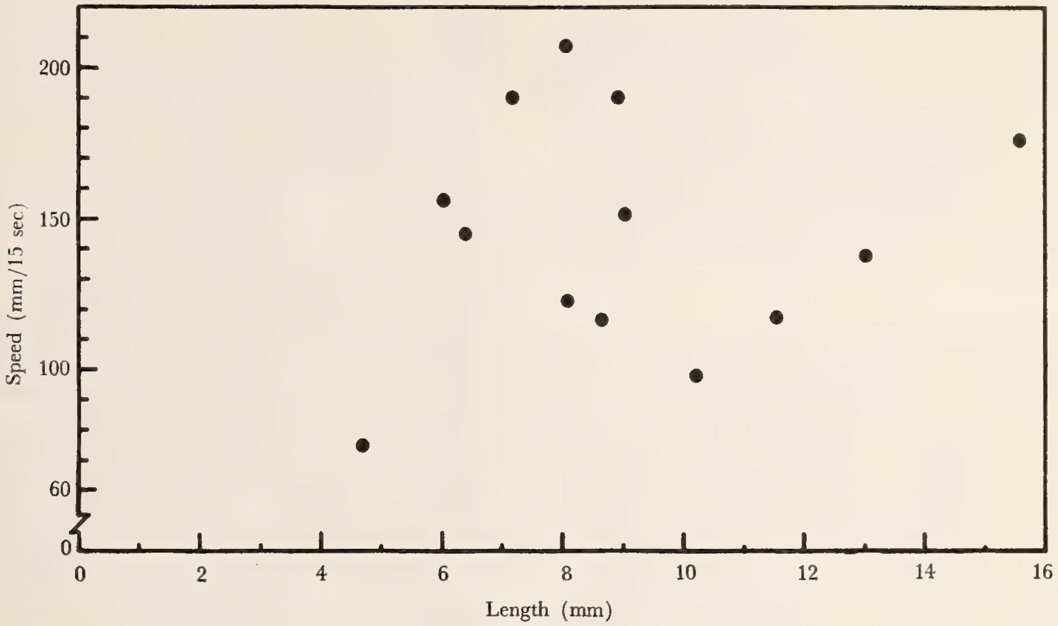

Figure 2

Fasciolaria tulipa crawling speed versus size. Over a large range of shell lengths *F. tulipa* maximum (escape) locomotion rates are not correlated with size (r = 0.147, not significant). Open dots are averages of five 10 second runs per animal, and closed dots are averages of two 30 second runs per animal.

Table 1

Incidence of escape responses of "small," "medium" and "large" *Turbo castanea* within two minutes of exposure to normal *T. castanea*, escaping *T. castanea* and mantle fluid from the predator *Fasciolaria tulipa*.

	Conspecific effects		Predator effects
	A normal *Turbo castanea*	B escaping *Turbo castanea*	C *Fasciolaria tulipa* mantle fluid
"Small"	0/20	0/20	1/20
"Medium"	0/10	1/10	3/10
"Large"	0/20	0/20	12/20
Total	0/50	1/50	16/50

recognition of some foreign chemical. The small *T. castanea* reacted much less vigorously to addition of *Fasciolaria tulipa* mantle fluid. Only one showed typical escape behavior and that was an almost immediate "turn and climb" response. None fled, though several waved their cirri. The kairomone induced a significantly greater proportion of large *T. castanea* than small to show escape behavior ($X^2 = 13.79$; $p < 0.01$). This series of tests suggests that a chemical, a kairomone, from *F. tulipa* can be recognized by *T. castanea* and can trigger escape behavior by the latter, and different sized individuals respond to the chemical differently.

C. Response to Fleeing Conspecifics:

Several *Turbo castanea* often fled simultaneously. This suggested that escaping *T. castanea* may have emitted a pheromone which warned others of the presence of a predator. Neither the addition of escaping nor non-escaping *T. castanea* induced any escape response by conspecifics of any size (Table 1). One medium sized *T. castanea* did increase its locomotion after the escaping *T. castanea* was introduced and this was recorded as an escape, though the movement was not very rapid and may not have been an escape response. In one of the trials with large *T. castanea* the escaping *T. castanea* bumped into and crawled over two experimental snails; nevertheless, they did not exhibit escape behavior. I conclude that no warning pheromone is emitted by escaping *T. castanea*.

D. Fatigue of the Response:

Repeated stimulation of medium sized *Turbo castanea* with *Fasciolaria tulipa* indicated that rapid locomotion was the primary component of their escape response and turning and climbing was a secondary component that was used only after they began to fatigue. Six *T. castanea* were tested for persistence of their escape responses (Table 2). Each *T. castanea* was touched with a *F. tulipa* and after the specimen came to rest following its rapid locomotion it was contacted again. Each *T. castanea* fled the first 14 to 24 times it was stimulated but after several repetitions the flights became briefer and the speed slower. Eventually each snail responded either by turning and climbing, then running, or only by turning and climbing. Ultimately, the subjects either did not react to contact by *F. tulipa* or responded only with very feeble turning and climbing. They were then prodded vigorously with a glass rod to determine if a novel stimulus would elicit the original level of response. (Dyal & Corning, 1973). Three of the 6 had no apparent response and the other 3 made weak turn and climb movements. Fresh *T. castanea* respond to prodding of a glass rod either by turning and crawling away at an increased speed or by withdrawing into the shell. The *T. castanea* did not habituate to contact with the predator. Instead the animals repeated the escape response until they were fatigued and could no longer flee.

Table 2

Fatigue of the flight response of "medium" *Turbo castanea* with repeated stimulation by *Fasciolaria tulipa.*

Aperture diameter (in cm)	Stimulation at which there was non-response	Stimulation at which first "turn & climb" occurred	Response to glass rod
0.52	27	19	None
0.55	17	16	Turn & climb
0.56	23	19	Turn & climb
0.56	26	25	None
0.57	23	15	Turn & climb
0.58	19	16	None
Mean	22.5	18.3	

E. Diet of *Fasciolaria tulipa:*

Casual observations of *Fasciolaria tulipa* fed *ad libidum* in the laboratory indicated that *Cerithium litteratum* and *Tegula fasciata* were not consumed until all the *Turbo castanea* in the aquarium were eaten, even though *Turbo castanea* resisted capture and the others did not. Meager data collected in the field on feeding paralleled these observations. Of 11 *F. tulipa* whose feeding was recorded, 6 were not feeding, one was eating a *Tegula fasciata* and 4 were eating *Turbo castanea.* One of the non-feeding individuals had a *Turbo castanea* on top of its shell.

DISCUSSION

Even fairly small *Fasciolaria tulipa* can crawl about twice as fast as medium sized *Turbo castanea* can, so it would seem that escape attempts by *T. castanea* would be futile, especially since *F. tulipa* can follow mucus trails and track down fleeing prey (Snyder & Snyder, 1971). In plain aquaria *F. tulipa* readily capture any available *T. castanea.* In the field it is not so simple. Most *T. castanea* are much smaller than *F. tulipa*, therefore they are lighter and can be supported on vegetation such as *Thalassia testudinum* blades from which they scrape epiphytes. In nature, *F. tulipa* must catch *T. castanea* that are moving from one grass blade to another or that fall off a blade, for example, during an escape. Occasionally *F. tulipa* may bend seagrass blades over and catch *T. castanea.* Topographic heterogeneity helps make the escape response of *T. castanea* effective by providing more vertical surfaces for *T. castanea* to climb and more interference for the larger predator to maneuver around or over.

The varied responses of different sized *Turbo castanea* can be interpreted in the context of their potential effectiveness in the field. Very small *T. castanea* are probably too slow-moving to escape any attack by *Fasciolaria tulipa.* Therefore, their most effective strategy when *F. tulipa* kairomones are present would be to remain stationary and possibly avoid detection by *F. tulipa.* Any movement by small *T. castanea* would leave fresh mucus trails and increase chances of contact with a foraging predator. Small *T. castanea* contacted by *F. tulipa* often were seen to turn and climb and this response might carry them to safety on a blade of seagrass or even onto the shell of the attacker. As *T. castanea* grow larger they become more likely to respond to the presence of *F. tulipa.* The experiments suggested that medium sized *T. castanea* would generally not flee prior to contact by *F. tulipa*, but once contacted they would run rather than turning and climbing. Larger (0.80 cm aperture diameter) *T. castanea* invariably ran from contact with *F. tulipa* and were very likely to run just in response to odors given off by *F. tulipa* (Table 1). *Turbo castanea* which ran from contact with *F. tulipa* responded that way repeatedly until nearly exhausted, then they would "turn and climb." Several times *F. tulipa* were seen in the field with *T. castanea* on their shells. This situation presumably resulted from an extended chase in which the exhausted prey finally turned and climbed and by good fortune succeeded in obtaining a grip on the attacker's shell and climbed up out of reach of the *F. tulipa* foot.

The following scenario suggests how the escape response by *Turbo castanea* may be modified adaptively during ontogeny. *Turbo castanea* too small and slow to mount an effective escape simply sit and wait until either they are caught or the predator passes. Larger individuals may resist attack by "turning and climbing" or by slow flight. Still larger *T. castanea* that are capable of attaining speeds of approximately 50 mm/15 sec (or roughly half the speed of *Fasciolaria tulipa*) flee when contacted by the predator, hold the shell away from the point of contact, and may climb to safety on seagrass blades or other vegetation. If pursued to the point of fatigue they may "turn and climb" as a last resort. Even larger individuals can flee faster and therefore probably have improved chances of escaping predation by *F. tulipa*. They flee in response to kairomones emitted by an approaching predator, in addition to contact with the predator. The speed of *F. tulipa* does not increase with size over a broad size range, so the *T. castanea* flight response is probably equally effective against any *F. tulipa*, large or small.

An interesting contrast to this development of progressively more elaborate escape behavior is provided by the study of Hoffman & Weldon (1978). They found that juveniles of the West Indian top shell *Cittarium pica* have vigorous escape responses to *Thais deltoidea*, but large *C. pica* show no response to the predator. *Thais deltoidea* is slow moving and small *C. pica* successfully flee from that predatory gastropod. The authors suggest that large *C. pica* may be less susceptible to predation by *T. deltoidea* due to the size disparity between large prey and small predator. In another case, the escape responses of *Strombus maculatus* do become more elaborate during ontogeny (Berg, 1972). It may be generally true that escape responses vary in their appropriateness and sequence of appearance during the development of gastropods, because the hazards to which gastropods are subject vary as the animals grow.

The lack of escape behaviors by *Cerithium litteratum* and *Tegula fasciata* may be related to feeding preferences of *Fasciolaria tulipa*. Though these species are similar in size and co-occur with *Turbo castanea*, they are seldom included in the diet of *F. tulipa*.

SUMMARY

Turbo castanea possesses an escape response elicited by contact with the predatory gastropod *Fasciolaria tulipa* or by water from the mantle cavity of *F. tulipa*. The response consists of rapid locomotion and holding the shell away from the source of contact.

No warning pheromone is emitted by fleeing *Turbo castanea*.

The escape response is altered during ontogeny from a weak response in small (young) *Turbo castanea* to very vigorous responses in large (older) specimens.

Heterogeneity in the habitat increases the effectiveness of the escape by interfering with the predator and providing refuges for the prey.

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On the Source of Cameral Liquid in the Chambered Nautilus

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INTRODUCTION

THE CHAMBERED NAUTILUS (*Nautilus* spp.) generally weighs between 1 and 5g in seawater, while weighing as much as 1600g in air. As is well-known, the source of the nautilus' buoyancy are the gas-filled chambers that make up the animal's shell (BIDDER, 1962; DENTON & GILPIN-BROWN, 1966). Before a new chamber is formed, the animal moves forward in its shell, leaving a volume of what will become the cameral liquid of the about-to-be-formed chamber. Then the posterior mantle of the animal secretes a calcified septum, and after sufficient calcification has occurred, the siphuncle begins the process of emptying the cameral liquid from the newly-formed chamber (WARD *et. al.,* 1981).

With regard to the source of this new cameral liquid, two alternatives exist, and both were suggested by DENTON & GILPIN-BROWN, 1966. These authors pointed out that cameral liquid may be formed by the animal itself "secreting a liquid behind its body and so making a liquid-filled space" or, alternatively, "the animal makes the liquid-filled space by allowing sea water to leak around its body and not by secreting some body fluid behind itself." This latter possibility (that new cameral liquid is seawater) was cast in doubt by the observation that the sulfate concentration of new cameral liquid is about one-tenth that of seawater (DENTON & GILPIN-BROWN, 1966). Also, BIDDER (1962) noted that "the animal is at all times found firmly fixed in its shell, and the possibility of either air or sea-water being included in a new formed chamber must be rejected."

In the present study, we present data and arguments that further support the aforementioned conclusion that new cameral liquid is not seawater and is, rather, either a secreted body fluid or an ultrafiltrate of the blood.

MATERIALS AND METHODS

Chambered nautilus *(Nautilus macromphalus)* were trapped outside of the barrier reef near Nouméa, New Caledonia. The animals were kept in running seawater aquaria (16° C) and were fed scraps of fish and lobster molts. Cameral liquid was obtained by drilling a hole through the shell. Blood was obtained (in terminal experiments) by heart puncture. Sodium and potassium analyses were done with a Coleman flame photometer with corrections for the Na intererence on K. Chloride analyses were done with a Buchler-Cotlove chloride titrator. Osmolality was measured with a Wescor vapor pressure osmometer using standards supplied by the manufacturer. Magnesium analyses were done using neutron activation and then comparing selected spectral activities (*e.g.,* the 0.844 Mev gamma ray of Mg-27) with similarly activated standards. The observed half-life of the Mg-27 activation product was identical to the predicted value of 9.5 min.

RESULTS AND DISCUSSION

The composition of seawater, nautilus blood, and cameral liquid from chambers that were so new that they had not yet been subject to any emptying by the siphuncle are shown in Table 1.

The first cameral liquid sample in Table 1 (Π = 1022) was taken from a chamber that was still in the process of being formed, and for which calcification was still incomplete. The other cameral liquid samples were from chambers that appeared to be completely calcified. Apparently, there is some pre-emptying reduction in concentration of cameral liquid, as can be seen in the second two samples which were taken from chambers that were well-calcified but still completely filled with liquid.

The results in Table 1 show that the osmolality of new cameral liquid as well as its Na, K, and Cl concentrations resemble those same parameters in both nautilus blood and seawater. The Mg concentration of new cameral liquid (as well as its SO_4 concentration—DENTON & GILPIN-BROWN, 1966) is significantly less than that of seawater, allowing the conclusion that newly-formed cameral liquid is not merely

Table 1

Sample	Osmolality mosm/kg H_2O	Na meq/L	Cl meq/L	K meq/L	Mg meq/L
seawater	1050	485	556	11.4	55
blood	1062±8[a]	486±2[b]	549±5[b]	11.5±1[b]	71[c]
cameral liquids	1022	470	490	12	<9
	894	450	503	10.5	<8
	724	370	401	10	—

[a] Range of 17 samples (animals).

[b] 95% confidence internal.

[c] Mean of 78, 69, and 65 meq/L.

seawater that the animal has allowed to leak in around its body.

The alternative possibilities for the source of cameral liquid are either that cameral liquid is a secretion of the posterior mantle (and perhaps the newly-forming siphuncle) or that cameral liquid is an ultra-filtrate of the blood. To investigate these possibilities, we attempted to determine whether the Mg of nautilus blood could be precipitated with trichloroacetic acid (TCA). In these experiments, we found that while the Mg of seawater was not precipitable with TCA, the Mg of nautilus blood was. Thus, the Mg appears to be bound to protein and our results cannot therefore rule out the possibility that cameral liquid is an ultrafiltrate of blood as opposed to a Mg-free secretion of the posterior mantle.

Previously published results (Ward & Greenwald, 1982) showing that nautilus is capable of partially refilling a chamber that we had previously emptied further supports the notion that cameral liquid is not seawater and that the siphuncle itself may be the source of cameral liquid. Our basis for this is that the refilled cameral liquid was identical (in terms of osmolality) to what we had removed from the chamber. In the unlikely event that the refilled liquid was seawater, then of course its osmolality would have been that of seawater (1050) and independent of the concentration of cameral liquid that was originally in the chamber. Thus, those observations, too, support the hypothesis that the siphuncle may be a source of cameral liquid.

Although there is little doubt that the siphuncle was the source of the refilled cameral liquid studied by Ward & Greenwald (1982), those results do not necessarily reflect on the question of the source of newly-secreted cameral liquid since the cellular structure of pre-emptying and emptying siphuncles are so different (Denton & Gilpin-Brown, 1966; Greenwald *et al.,* 1982).

In summary, our results and observations support the previous observations of Bidder, 1962, and Denton & Gilpin-Brown, 1966, that cameral liquid is not formed from seawater. Our results were not able to distinguish amongst the other potential sources of newly-formed cameral liquid, namely an ultrafiltrate of the blood or a secreted body fluid. The results of Mangum & Towle (1982) that show unbound Mg concentrations in *Nautilus pompilius* blood of 41mM suggest that newly formed cameral liquid is not an ultrafiltrate of blood and is, rather, a secreted Mg-free body fluid.

ACKNOWLEDGMENTS

This work was supported by NSF Grant PCM 7823624. For their kind cooperation and assistance, we thank Dr. Yves Magnier, Director of the Aquarium of Nouméa, New Caledonia, and Dr. Paul de Boissezon, Director of the Orstom Laboratory in Nouméa where this work was done. We also thank Mr. Joe Talnagi of The Ohio State University Nuclear Reactor Laboratory for his help with the neutron activation analyses.

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METHODS & TECHNIQUES

A New Method for Sampling the Nematocysts of Aeolid Nudibranchs

BY

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INTRODUCTION

THAT AEOLID NUDIBRANCHS retain the nematocysts which they receive from their cnidarian prey has long been known (KEPNER, 1943). The nematocyst content of a nudibranch's cnidosac can provide information about the type of prey eaten (KEPNER, *op. cit.;* THOMPSON & BENNETT, 1970; CONKLIN & MARISCAL, 1977; DAY & HARRIS, 1978), and the time since the nudibranch last fed upon that prey (CONKLIN & MARISCAL, *op. cit;).* The most common method of sampling the nematocysts in an aeolid is to remove a ceras and squash it between a slide and a coverslip (THOMPSON & BENNETT, *op. cit.;* CONKLIN & MARISCAL, *op. cit.;* DAY & HARRIS, *op. cit.*).

PANTIN (1942) found that saliva rubbed on a glass rod and then touched to a tentacle of a sea anemone would cause the nematocysts to fire and attach to the glass rod. This method of effecting the release of nematocysts can also be used with aeolid nudibranchs.

MATERIALS AND METHODS

Saliva is rubbed upon a glass slide and allowed to dry until tacky. The cerata of the nudibranch are made to bristle by gently poking the animal. The slide is then applied to the dorsum of the animal, using slight pressure. This causes the cnidosacs to release the nematocysts which fire and attach to the slide.

To test for any chemical stimulus that might be necessary to release the nematocysts, a simple experiment was performed. The above method was repeated, using five sterile slides and five different individuals of *Aeolidia papillosa.* Five trials were again performed on five more individuals, using chemically inert stopcock grease instead of saliva. Sterile surgical gloves were worn throughout the experiment to prevent the possibility that a chemical stimulus might enter the water from the experimenter's hand.

RESULTS AND OBSERVATIONS

In 100% of the attempts, fired nematocysts were found on all the slides when using either method. There was no apparent difference between the effectiveness of the saliva or of the stopcock grease, although bubbles and ridges in the stopcock grease made it more difficult to find the nematocysts. The nematocysts are often released in clumps and the individuals may be teased out of the clumps for closer examination.

DISCUSSION AND CONCLUSIONS

The benefits of using this method are that it maintains the health of the population by decreasing the stress placed upon an animal during cerata removal, thus decreasing the chance of disease and maintaining the health of the population. It also allows the same animal to be sampled repeatedly over a period of time, and reduces the likelihood that a change in the nematocyst complement may be due, in part, to physical injury. A greater number of cerata are sampled when using this method and it is faster to use when a large number of animals need to be sampled.

Since stopcock grease also caused the release of the nematocysts, one can see that a chemical stimulus is not needed to effect their release from the cnidosac. Thus, apparently, there is a complex mechanism within the nudibranch which maintains the chemical portion of the nematocyst firing mechanism at a threshold level, while allowing the mechanical portion to remain functional.

This method strongly supports the hypothesis that the primary function of nematocysts is for the defense of the aeolid (KEPNER, 1943; THOMPSON & BENNETT, 1970), since they can be extruded voluntarily by the nudibranch and do fire upon release. This experiment has shown that the release of nematocysts is not haphazard, or a by-product of lacerations caused by fish attempting to consume the aeolids, but that it is governed by a highly complex mechanism within the animal.

ACKNOWLEDGMENTS

I would like to thank Dr. Larry G. Harris for his advice and assistance, Dr. Charles W. Walker, Wayne Lord and Jon Whitman for their valuable comments. This study was conducted at the University of New Hampshire, in Durham, New Hampshire, under the guidance of Dr. Larry G. Harris.

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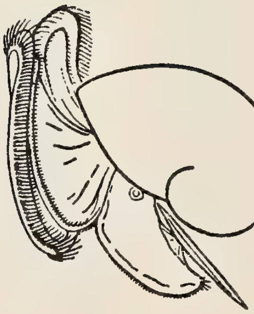

NOTES & NEWS

A Note on the Structure and Pigmentation of the Shell of *Notoacmea persona* (Rathke)

(Docoglossa : Acmaeidae)

BY

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(1 Text figure)

In an earlier paper, Lindberg *et al.* (1975: 384; fig. 2) described and illustrated the shell structure of *Notoacmea persona* (Rathke, 1833) and discussed its role in producing both translucent and opaque white markings on the dorsal surface of the shell. At that time we were unaware of MacClintock's (1967) comprehensive treatise on the shell structure of patellacean and bellerophontid gastropods. This oversight resulted in our use of terms, which if applied in the context of MacClintock (1967), results in an erroneous interpretation of the species shell structure. Because shell structure is an important character in patellacean systematics, and in order to correct our previous oversight, we present and illustrate the shell structure and pigmentation pattern of *N. persona* using the terminology of MacClintock.

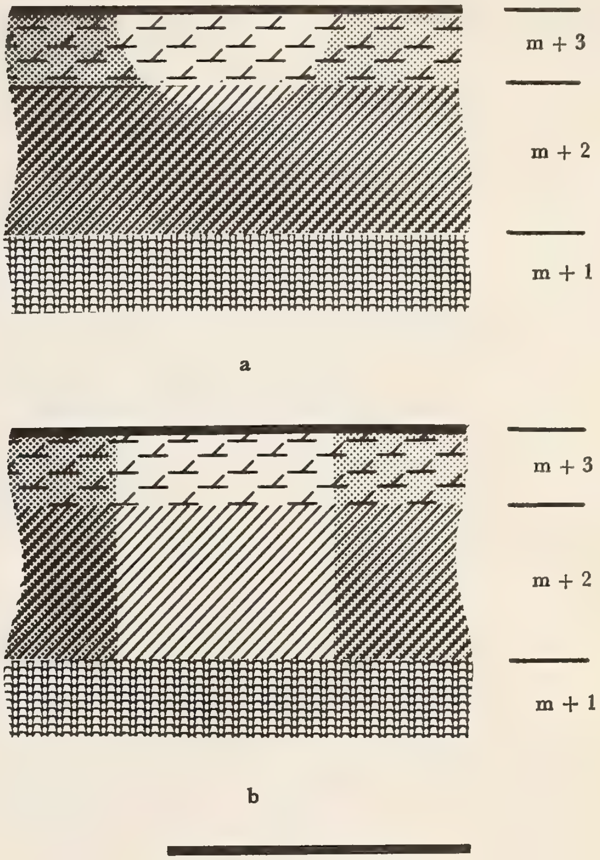

Figure 1

Schematic representation of sections through white markings on the dorsal shell surface of *Notoacmea persona*, showing shell layers and pigmentation. a. posterior marking; b. anterior marking. m + 1 = concentric crossed-lamellar layer, m + 2 = fibrillar layer, m + 3 = simple-prismatic layer (dorsal surface of shell). Distribution of dark shell pigmentation is shown by shading. Translucent m (myostracum) and m − 1 (radial crossed-lamellar) layers are present in the ventral portion of the shell and are not shown. Scale bar = 0.5 mm

Our use of the terms "opaque layer" and "translucent layer" to describe the darkly pigmented and white pigmented portions of the shell was unfortunate (Lindberg *et al.*, 1975: 384). Shell layers are defined by the type and arrangement of the calcium carbonate crystals, not the pigmentation of these layers. By our incorrect use of these terms we have indicated that the shell of *Notoacmea persona* is not composed of continuous shell layers and that the type of white marking on the dorsal surface of the shell depends on the presence or absence of shell layers; in neither case were we correct. Based on reexamination of the original material and newly prepared material, *N. persona* is a member of MacClintock's (1967) shell structure group no. 1. The outermost layer (m + 3) is a thin, simple-prismatic layer. Underlying this is a thick fibrillar layer (m + 2) followed by a concentric crossed-lamellar

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layer (m + 1), myostracum (m) and radial crossed-lamellar layer (m − 1). These layers maintain this sequence throughout the shell,and in no case does one layer protrude through another.

As described and illustrated earlier by Lindberg *et al.* (1975: 383; fig. 1), the white markings on the posterior surface of the shell are opaque and those on the anterior surface are translucent. The opaque, posterior white markings consist of white pigment in the m + 3 layer and the upper region of the m + 2 layer; the lower region of the m + 2 is darkly pigmented (Figure 1a). The translucent, anterior white markings are similar in cross section, but lack the underlying dark shell pigment in the lower region of the m + 2 layer (Figure 1b). The interior shell layers (m + 1, m, and m − 1) are always translucent. Thus, the type of white marking (opaque or translucent) on the dorsal surface of the shell is determined by the pigmentation of the shell layers and not by the placement of the shell layers as stated earlier (Lindberg *et al.*, 1975: 384).

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New Records of Living Marine Gastropoda of Venezuela

BY

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Among the specimens I had the opportunity to study from the shell collection of Mr. Fernando Fernández from Maracay, Venezuela, one new species was described (Princz, 1978b) and several resulted in new records for the Venezuelan waters. These species are listed below in addition to another one belonging to the collection of the Estación de Investigaciones Marinas de Margarita.

The abbreviations FF and EDIMAR stand for the mentioned collections, respectively.

Lucapinella limatula (Reeve, 1850). FF: Los Roques, 1973. Even though the distribution of this species is well known for the Caribbean Province, it has never been reported from the Venezuelan coasts. Only a non-specified *Lucapinella* was recorded from the Gulf of Cariaco by Ginés (1947).

Siliquaria squamata (Blainville, 1827). FF: Bahía de Cata, 1972.

Amaea mitchelli (Dall, 1896). FF: Punto Fijo, 1968. This is the same *Amaea sp.* from the Gulf of Venezuela in Princz (1978a). Bayer (1971) reported this species for the first time for the southwestern Caribbean based on one dead animal. Since the specimen found by Mr. Fernández was found alive, it becomes the first living record of this species for the whole southern Caribbean.

Tugurium longleyi (Bartsch, 1931). EDIMAR: Gulf of Paria, 1968. Three living specimens were dredged from 40 meters off the Orinoco River delta.

Cypraea surinamensis Perry, 1811. FF: Puerto Cabello, 1976. An uncommon species of wide longitudinal distribution reported for the Netherlands Antilles (Coomans, 1963), but as far as I know, it has never been reported from Venezuela.

Cyphoma intermedium (Sowerby, 1828). FF: Margarita Island, 1969; Puerto La Cruz, 1976.

Bursa corrugata (Perry, 1811). FF: Margarita Island, 1962. This species is not to be confused with *B. bufo* Bruguière, 1792 = *B. spadicea* Montfort, 1810 reported for the same locality by Princz (1973) and Princz & Gonzalez (1981). The latter is much more common than *B. corrugata.*

Calotrophon ostrearum (Conrad, 1846). FF: El Peñón, 1972. Two living collected specimens were studied. As far as I know this is the first southern Caribbean record of this species.

Agatrix cf. *A. smithii* (Dall, 1888). FF: Puerto La Cruz, 1976. Two specimens were collected alive. The morphology of the shells examined is extraordinarily close to that of *A. smithii.* Since the distribution of this species is only reported for off the Carolinas (Abbott, 1974), the identification of these specimens must be carefully reviewed.

Conus austini Rehder & Abbott, 1951. FF: Margarita Island, 1962; Gulf of Venezuela, 1969.

Conus dominicanus Hwass, 1792. FF: Puerto La Cruz, 1962; Margarita Island, 1976.

Terebra hastata (Gmelin, 1791). FF: El Peñón, 1972.

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The Occurrence of *Anodonta woodiana* Lea, 1837 in Indonesia

(Pelecypoda : Unionidae)

BY

MACHFUDZ DJAJASASMITA[1]

The freshwater mussel *Anodonta woodiana* Lea, 1837, is native to China and Taiwan. At present it may be found in some localities in Java and other islands in Indonesia. Its occurrence was first discovered in 1970 in the fishponds of the Inland Fisheries Research Institute at Bogor, West Java, after the introduction of two cultivated fish species from Taiwan, the silver carp (*Hypopthalmichthys molitrix* (Valenciennes)) and the Nile tilapia (*Tilapia niloticus* (Linnaeus)) in 1969.

Judging from the life cycle of the Unionidae, the only plausible explanation is that it has been carried in a larval stage. *Hypopthalmichthys molitrix* and *Tilapia niloticus* seem to be the host fishes and responsible for carrying the mussel. Apparently these fishes have been parasitized by the glochidia of *Anodonta woodiana*. While being bred in the Fishery ponds the glochidia have developed into young mussels, freed themselves from the fishes to live as ordinary mussels. The new habitat has proved to be suitable for the mussels; they thrive and multiply.

In 1972 a number of the mussels have been released in the ponds of the Bogor Botanical Garden, which are inhabited by several native fish species. The fishes seem to be suitable as host for the glochidia. The mussels propagate luxuriantly in the ponds. The broad oval shell is olivaceous green to dark green, ornamented with dark green rays; sculptured by irregular strong concentric folds. The umbo is inflated, reddish brown and sculptured by 3-4 undulating loops in the young shell. The nacreous inside is pinkish white to orange, especially below the umbo. Hinge teeth are absent; on some shells, however, the part below the umbo may be somewhat dilated as a pseudocardinal tooth. Many specimens attain over 150mm in length. A specimen collected in February 1979 measures: length 266mm, height 127mm and breadth 60.7mm. This is the largest freshwater bivalve ever recorded from Indonesia.

Conforming with the purpose of the importation of the two cultivated fish species, to increase the animal protein production, numbers of specimens have been introduced in several localities in Java, Sumatra, Sulawesi (Celebes), Nusa Tenggara Islands (the Lesser Sunda Islands) and the Moluccas. This may open the way to the mussel for a wider range of distribution, and this is proved by the fact that specimens of *Anodonta woodiana* have been collected from Manado in North Sulawesi, Kendari in Southeast Sulawesi and from Lombok Island in the Nusa Tenggara Islands, after the introduction of the fishes. This occurrence changes the known range of distribution of the family Unionidae in the Indonesian Archipelago. Unionid mussels were previously not present in Bali and the islands between the Wallace and Lydekker Lines (two faunal lines in the Indonesian Archipelago, the fauna between which has Asian and Australian affinities), Sulawesi, the Nusa Tenggara Islands and the Moluccas. Towards the east the unionid mussels are recorded again from Misool Island and New Guinea. If the introduction of the fishes proceeds to other islands of the archipelago, it is not impossible that in the long run *A. woodiana* will spread much further.

The occurrence of *Anodonta woodiana* in Indonesia, however, is economically considered to be profitable, since freshwater clams and mussels are traditionally consumed by local people as an additional source of animal protein or as a delicacy.

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BOOKS, PERIODICALS, PAMPHLETS

Editor's Note: The following book review was presented on page 91 of our July issue. However, several typographical errors and two misplaced corrected lines so distorted the tenor of the revue that we decided to re-print it, this time, however, correctly. We apologize to readers as well as the author of the review and the author of the book.

Acmaeidae: Gastropoda, Mollusca

by David R. Lindberg. xii + 122 pp. Boxwood Press, Pacific Grove, California. $12.50 1981

(The second volume in the series *Invertebrates of the San Francisco Bay Estuary System,* Welton Lee, Editor)

While still in graduate school, David Lindberg established himself as a world authority on acmaeid limpets and set new, uncompromising standards for the integration of detailed anatomical and ecological data into traditional taxonomy and systematics. His book on the acmaeid limpets of San Francisco Bay transcends the local geographic focus of the series and provides an excellent overview of the morphology, anatomy, systematics, distribution, and ecology of this taxonomically difficult group of common intertidal gastropods.

Techniques for study and identification of limpets are carefully described. A pictorial glossary provides an unusually fine clarification of terminology; and taxonomic keys to species are presented both for shell characters and radular characters. Each species is consistently illustrated by photographs of at least three views; and drawings of both the radular teeth and the configuration of the basal plates are presented in a style that facilitates comparison. One of the most helpful contributions of the book is the careful clarification of the range of ecological forms of a species that can develop on different substrata.

This is a thoroughly scholarly as well as eminently usable reference. Its value is augmented by a bibliography of Pacific Coast acmaeid literature by James T. Carlton.

Carole S. Hickman
Department of Paleontology
University of California

Pliocene Molluscs and Fishes from Northeastern California and Northwestern Nevada

by Dwight W. Taylor & Gerald R. Smith. Contributions from the Museum of Paleontology, the University of Michigan, vol. 25, no. 18, pp. 339-413; 19 plts.; 11 text figs. Available as a separate paper from the Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109. (31 December 1981)

Pliocene assemblages of freshwater mollusks and fishes from Honey Lake, Lassen County, California, and Mopung Hills, Churchill County, Nevada, are described. Dot maps indicate the distribution in time and space of pertinent species and genera. The two Honey Lake assemblages show the faunal imprint of the former course of the Snake River flowing from southern Idaho across Oregon into northeastern California. The environment was perennial water, either a lake or a river or creek not subject to flood scour. Assemblages from Mopung Hills indicate a large lake, subsequently eliminated by climatic and tectonic changes; the mollusks, restricted to lacustrine habitats, became extinct while the fishes, able to live also in streams, survived to populate the Pleistocene Lahontan basin. Evidently the Lahontan basin has enlarged by reduction of topographic divides from the late Pliocene onward. The paper is a harmonious wedding of vertebrate and invertebrate data.

Barry Roth

Malacological Review

Vol. 15 (1-2): 202 pp.; about 60 figs. in text (July 1982)

An important change has taken place: Subscription orders and payments should be sent to: Malacological Review, P. O. Box 637, Niwot, Colorado 80544, U. S. A. and manuscripts should be sent to Dr. Shi-Kuei Wu, University of Colorado Mueum, Campus Box 218, Boulder, Colorado 80309, U. S. A.

This latest issue of the Malacological Review contains, as its predecessors, several original articles as well as several brief communications and 13 abstracts of articles presented at the *Littorina* Minisymposium and Workshop held at Nahant, Massachusetts 28 to 30 August 1981. The title pages of malacological periodical publications are reproduced, thus allowing the reader in greatest comfort to scan the latest contributions in his field of specialisation.

The price of this paperbound volume is only US$19.00.

R. Stohler

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

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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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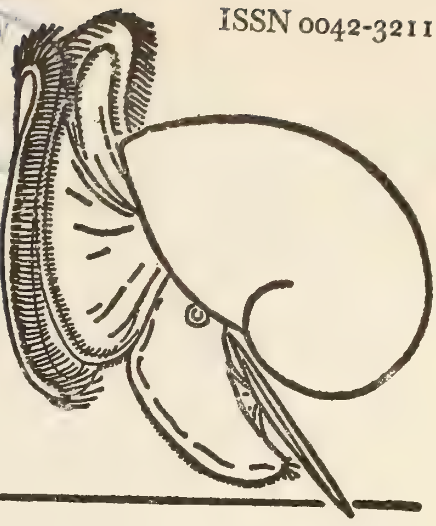

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, **Subdivision**, **SECTION**,
Superfamily, Family, Subfamily, ***Genus***, ***(Subgenus)***
New Taxa

New Recent Gastropod Species from Venezuela and a Bivalve Range Extension

BY

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(1 Plate)

I.

Thelecythara Woodring, 1928

(Mollusca : Gastropoda)

A Range Extension and a New Species

(Figures *1-5*)

The type species of the genus *Thelecythara* Woodring, 1928, is *Cythara mucronata* (Guppy, 1896), from the Pliocene Bowden Formation, Jamaica. A near relative is *Thelecythara floridana* Fargo, 1953, from the Caloosahatchee Formation of North St. Petersburg, Florida, of Pleistocene age. This is the only relative in the region, but *T. floridana* still lives in the Eastern Pacific from Mazatlán, Mexico, to Panamá Bay (Keen, 1971: 753, fig. 1808), the genus qualifying, therefore, as a "paciphile" (Woodring, 1966: 426).

However, *Thelecythara floridana* is now found to survive in the Caribbean, having been collected in shallow water, in carbonate environments, at three localities along the north coast of Venezuela between Puerto Cabello, Carabobo State, and Higuerote, Miranda State. None have been taken alive. By far the largest suite comes from Borburata, Carabobo State, where most of the 63 specimens were inhabited by hermit crabs.

Thus, *Thelecythara* loses its "paciphile" status, but *T. floridana*, at the same time, joins the select group of seven or eight taxa which occur on both sides of Central America and which are so similar that they can be regarded as disjunct populations of the same species (Vermeij, 1978: 213).

A second Recent species occurs in the carbonate province of the Venezuelan offshore islands: *Thelecythara dominguezi* Gibson-Smith & Gibson-Smith, spec. nov. It is the cognate of the only other known species, *T. dushanae* McLean & Poorman, 1971, from the Panamic province.

There is no representative of the genus in our collections of the Venezuelan Neogene faunas.

Thelecythara floridana Fargo, 1953

(Figures *1, 2*)

Description: Shell small, slender, reaching 7 mm in height. Protoconch almost cylindrical, of 2½ smooth whorls. Teleoconch of 3¼ whorls, the body whorl just over half the shell. Sculpture cancellate with, on the spire whorls, 4 spiral cords increasing to 6, crossing 20 to 25 axial ribs of about equal strength, the intersections finely noded; subsutural cord strong and the ribs sinuous where they cross the anal fasciole. On the bodywhorl the ribs increase to 30 or more and die out below mid-whorl. Aperture elongate, narrow; inner lip and interior of outer lip smooth. Outer lip thickened, varicose, carrying a stromboid notch. Anterior canal short, posterior canal deep, outlined by greatly thickened callus, opening restricted. Protoconch and first teleoconch whorl white, remainder dark brown, fading to orange-brown. The spire generally decollate.

Homeotypes: USNM 784696; PRI 8225; BM(NH) and NHMB.

Discussion: The Venezuelan form has more axial ribs than the Floridian fossil (30 versus 20) and probably more than the Panamic form, judging from the illustration of Keen (1971: fig. 1808), which reaches a greater height (10 mm versus 7 mm). *Thelecythara mucronata* is the smallest (5.8 mm) and has a protoconch of only 1½ mammiliform whorls.

Thelecythara dominguezi Gibson-Smith & Gibson-Smith, spec. nov.

(Figures *3, 4, 5*)

Description: Shell small, slender, reaching almost 10 mm in height. Protoconch of 1½ smooth whorls, blunt, with opisthocline axial riblets on the last quarter turn. Teleoconch of 5 whorls, the bodywhorl just over half the shell. Sculpture of fine, widely spaced, spiral cords, 4 increasing to 9 on the spire whorls and 20 on the bodywhorl. Subsutural cord very fine. Interspaces and anal fasciole with crowded, microscopic, spiral threads. Axial ribs rudimentary. Aperture elongate, narow; inner lip and interior of outer lip smooth. Outer lip thickened, varicose, carrying a stromboid notch. Anterior canal short, posterior canal deep, outlined by greatly thickened callus, opening restricted. Protoconch white, teleoconch mauve with white outer lip and aperture.

Holotype: USNM 256017, height 6.9 mm, diameter 2.7 mm.

Type locality: Recent, Isla La Orchila, Venezuela.

Paratypes: PRI 8226, BM(NH) and NHMB.

Remarks: The material consists of 11 specimens from Isla La Orchila which may be only partly flushed with mauve, or all white, and 2 white specimens from Islas Los Roques which reach a greater size: height 9.5 mm, diameter 3.3 mm.

Comparisons: *Thelecythara dominguezi* can be compared with its cognate, *T. dushanae* McLean & Poorman, from the Eastern Pacific (Keen, 1971: 753: fig. 1807). In both, the spiral sculpture is dominant, but in *T. dominguezi* the axial sculpture is even further reduced, the shell is mauve or white, not brown, the anterior canal is shorter and the outer lip is not recurved towards its base.

The shell is named in honor of geologist Dr. José Rafael Dominguez who donated the sample material from Isla La Orchila.

SUMMARY

In the genus *Thelecythara* Woodring, 1928, three species only are known: the type species *T. mucronata* (Guppy, 1896) from the Pliocene of Jamaica; *T. floridana* Fargo, 1953, from the Pleistocene of Florida and living in the Eastern Pacific, and *T. dushanae* McLean & Poorman, 1971, living also in the Eastern Pacific. The genus thus qualifies as a "paciphile." However, *T. floridana* is now found to survive along the north coast of Venezuela and becomes one of the few species known to occur on both sides of Central America; at the same time *Thelecythara* loses its "paciphile" status. A second species, *T. dominguezi* spec. nov. occurs on the Venezuelan offshore islands; it is the cognate of *T. dushanae.*

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Explanation of Figures *1* to *13*

Figures *1, 2: Thelecythara floridana* Fargo, 1953. Ventral views. Recent of Venezuela. Height 6.8 mm, diameter 2.7 mm. USNM 784696

Figures *3, 4, 5: Thelecythara dominguezi* Gibson-Smith & Gibson-Smith, spec. nov.; ventral and dorsal views of the holotype. Recent of Venezuela. Height 6.9 mm, diameter 2.7 mm. USNM 784697

Figures *6, 7: Pygmaepterys juanitae* Gibson-Smith & Gibson-Smith, spec. nov. Ventral and dorsal views of holotype, height 7.6 mm, diameter 3.7 mm. USNM 784694

Figures *8, 9: Pygmaepterys lourdesae* Gibson-Smith & Gibson Smith, spec. nov. Ventral and dorsal views of the holotype, height 6.0 mm, diameter 3.3 mm. USNM 784695

Figures *10, 11: Cyathodonta magnifica* (Jonas, 1850). Holotype, right and left valves, length 73.45 mm, height 47.22 mm, Honduras, BM-(NH) Reg. No. 1977177

Figures *12, 13: Cyathodonta magnifica* (Jonas, 1850). Recent, El Pico, Paraguaná Peninsula, Venezuela. Right valve, length 68.6 mm, height 45.7 mm, USNM 784692; left valve, length 72.1 mm, height 47.4 mm, USNM 784693


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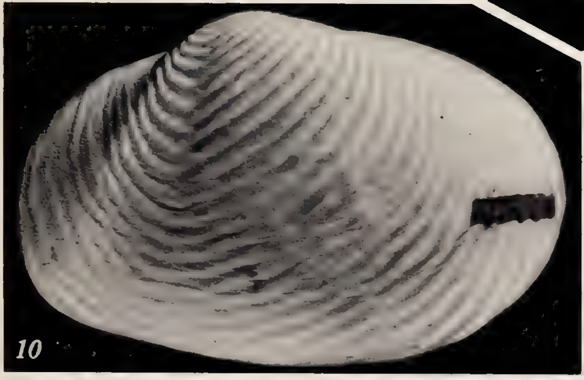
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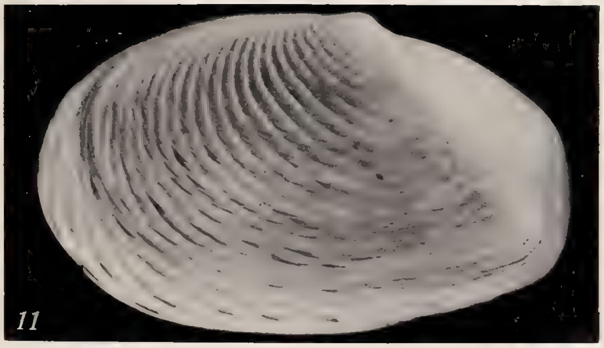
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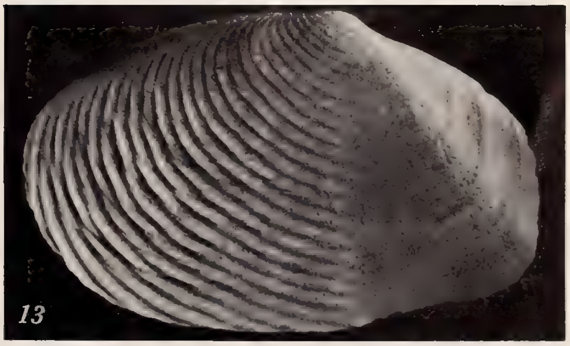
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II.

Two New Species of *Pygmaepterys* (Mollusca : Gastropoda) from the Recent of Venezuela

(Figures *6* to *10*)

INTRODUCTION

After we began collecting the Recent marine molluscs of Venezuela in 1967, there was a steady accumulation of two suites of apparently juvenile, but closely related, muricids; that from the mainland being brown-banded and the other, from the offshore islands, being white. The protoconch, buttressed by the varices of the first teleoconch whorl, resembled that in species of *Murexiella, Dermomurex* and *Favartia* in the collection, but later sculpture was distinct. Then came the gradual realisation that the specimens were limited to a height of about 8mm and thus were adult, not juvenile. The systematic placement, however, could not be resolved; there was nothing in the Recent or fossil record of the region with which to compare them. The problem was discussed with Dr. E. H. Vokes during a visit to Caracas in December 1977, but no conclusion was reached.

The solution to the problem came with the report of Vokes & D'Attilio (1980: 45) which showed, for the first time, the existence in the Neogene and Recent of the Western Atlantic of small muricids of the genus *Pygmaepterys.* This taxon had been established two years previously by Vokes (1978: 375) as a subgenus under *Pterynotus,* the type species being: *"Murex" alfredensis* Bartsch, 1915, from the Recent of South Africa; a second Recent species from the same area was named at the same time: *P. maraisi* Vokes, 1978.

Vokes & D'Attilio *(op. cit.)* assigned two forms to the genus *Pygmaepterys:* one without denticles on the inner lip (*P. alfredensis, P. maraisi* and *P. pratulum* Vokes & D'Attilio, 1980, from the early Miocene Chipola Formation, Florida) and one, tentatively assigned, having inner lip denticles (*?P. funafutiensis* (Hedley, 1899), from the Indo-Pacific; *?P. germainae* Vokes & D'Attilio, 1980, upper Miocene to Recent, Caribbean, and *?P. drezi* Vokes & D'Attilio, 1980, from Chipola). They found that the radula of *?P. germainae* places the second group in the Muricopsinae, but the radular affinities of the first group are unknown, so far; they believe that the two groups may represent an instance of parallelism, perhaps being shown eventually to represent two genus-groups. They comment also on the rarity of this small group of inconspicuous shells, suspecting that *?P. germainae* will be found in collections mis-labelled: *"Favartia cellulosa* (Conrad)."

The mainland and island forms from Venezuela, represented by 107 and 27 specimens, respectively, from several localities, belong with the group having a non-denticulate inner lip, their only relative in the Western Atlantic being *P. pratulum* from Chipola. They are identified as: ***Pygmaeoptery juanitae*** spec. nov. (mainland form) and ***Pygmaepterys lourdesae*** spec. nov. (island form).

The presence of *?Pygmaepterys germainae* off Colon, Panamá, and its apparent absence further east in Venezuela, is puzzling; it is known from beach-drift and to a depth of 90m. Both the Venezuelan forms occur in beach-drift and at depths down to 30m; they have not been found in sea-floor samples from eight offshore drilling locations in water depths from 55 to 150m. Obviously, they are one of the commoner elements in the shallow water fauna. We have found no representative of the genus, so far, in our collecting of the Venezuelan Neogene.

Pygmaepterys juanitae Gibson-Smith & Gibson-Smith spec. nov.

(Figures *6, 7*)

Diagnosis: Shell small with five and three-quarter whorls. Protoconch of one and one-quarter white, translucent, bulbous whorls; surface microscopically granular; terminating with a low, rounded, opisthocyrt varix, followed almost immediately by the first varix of the teleoconch, with nine, hook-like varices in all on the first turn, adhering to and projecting above the protoconch, thus hiding it. First sculpture of two spiral cords crenulating the simple varices. On the second turn a third spiral cord appears, the varices become compounded by axial growth lamellae which cover, also, the areas between varices. A fourth cord lies in the suture with a wider interspace between it and the earlier cords. Below, on the bodywhorl, are three more spiral cords decreasing in strength down to the base of the whorl, followed by five minor cords on the canal. The terminations of the varices accentuate the anterior fasciole. The nine varices, aligned along the spire, continue to the last whorl where one is missing, usually the penultimate. The top of each varix runs forward to meet the previous whorl at the subsequent varix. The spiral cords terminate on each varix in a minuscule open spine, except for the uppermost cord at the shoulder where there is a strong spine curved abaperturally. Aperture oval, the outer lip projecting well forward of the terminal varix. Inner lip smooth, outer lip with seven denticles corresponding to the interspaces between the major spiral cords. Anterior canal almost as long as the aperture, partially closed and slightly recurved. Shell cream-coloured with a narrow brown band just below the suture and another just above at mid-whorl, occupying the wider spiral interspace; the top of the aperture and the middle of the outer lip stained brown, accordingly.

Holotype: USNM 784694. Height 7.6mm, diameter 3.7 mm.

Type locality: Borburata, Carabobo State, Venezuela.

Occurrence: Recent, north coast of Venezuela from Tucacas, State of Falcón to Playa Colorada, State of Sucre.

Paratypes: Paleontological Research Institution, Ithaca, No. 8223; British Museum (Natural History); Natural History Museum Basel; Escuela de Geología, Universidad Central de Venezuela, UCVG 7062. Remainder in the collection of the authors.

Remarks: The largest suite (73 specimens) comes from Borburata, where most were garnered amongst congregations of hermit crabs at the edge of the beach; this is a carbonate environment and they may be washing out of a coralline dredge spoil-bank, but this is uncertain. None have been taken alive.

Comparisons: Apart from the absence of denticles on the inner lip, *Pygmaepterys juanitae* is otherwise very different from ?*P. germainae:* it has more varices, more spiral cords, is more elongate and the aperture is differently coloured. Furthermore, the varices in ?*P. germainae* are not said to extend above the protoconch, but this may be a matter of wear. From *P. pratulum* from Chipola, its closest Western Atlantic relative, *P. juanitae* differs in being smaller (7.6 versus 10.9mm), in having a larger, more bulbous protoconch of fewer turns. A more obvious difference concerns the scabrous, frilled varices: in *P. pratulum* the outer edge of the varix runs in a straight line to the tip of the anterior canal; in *P. juanitae* there is a marked re-entrant, the meeting of the portions bordering the canal and the outer lip subtending an obtuse angle. This same feature also distinguishes *P. juanitae* from its South African relative, *P. maraisi.*

The name of the shell recognises the valuable contributions made to our collections by SCUBA-diver Juanita Tyszka, including specimens from Tucacas and Chichiriviche de la Costa, Federal District.

Pygmaepterys lourdesae
Gibson-Smith & Gibson-Smith, spec. nov.

(Figures *8, 9*)

Diagnosis: Shell small, pure white. The protoconch and spire sculpture as in *Pygmaepterys juanitae.* On the body-whorl there are five primary spiral cords: the three of the spire whorls, followed below by the wider interspace, then by two more primary cords to the base of the shell; along the canal are two to five (usually four) minor cords. On the last whorl the varices reduce from nine to eight, sometimes seven. The outer edge of the scabrous varices is indented at the junction between outer lip and anterior canal. Inner lip smooth, denticles in outer lip rudimentary, numbering about five.

Holotype: USNM 784695. Height 6.0mm, diameter 3.3 mm.

Type locality: Isla La Orchila, Venezuela.

Occurrence: Recent, offshore islands along the north coast of Venezuela, a carbonate environment.

Paratypes: Paleontological Research Institution, Ithaca, No. 8224; British Museum (Natural History); Natural History Museum Basel; Escuela de Geología, Universidad Central de Venezuela, UCVG 7063. Remainder in the collection of the authors.

Remarks: Of the 27 specimens available, 19 come from Isla La Orchila and the remainder from Islas Roques and Isla Tortuga.

Comparisons: *Pygmaepterys lourdesae* differs from *P. juanitae* in being smaller, in being white, not coloured, but principally in the reduction of the number of primary spiral cords on the lower half of the whorl, from four to two; there are also fewer minor cords along the canal and fewer denticles in the outer lip, reflecting the reduction in the number of primary cords. It has fewer spiral cords from shoulder to whorl-base than does *P. pratulum* from Chipola, and the outline of the varix also differs, that in *P. pratulum* having no re-entrant. This last distinction is to be noted again in the case of *P. maraisi* from South Africa.

The shell is named after micropaleontologist Dr. Maria Lourdes Diaz de Gamero, a colleague in UCV who has also helped in our collecting.

SUMMARY

The taxon *Pygmaepterys* Vokes, 1978, was established for a small *Pterynotus*-like muricid from the Recent of South

Africa. Its presence in the Western Atlantic was reported, for the first time, with the publication of two species: *P. pratulum* Vokes & D'Attilio, 1980, from the early Miocene of Florida, and ?*P. germainae* Vokes & D'Attilio, 1980, from the late Miocene of the Dominican Republic, the Pleistocene of Costa Rica and still living from Puerto Rico to Panamá. The tentively assigned form has inner lip denticles which the other lacks. From Venezuela two, new, Recent species from shallow water are now reported; both have a smooth inner lip and are the first known successors to the early Miocene form, *P. pratulum*. They are identified as ***Pygmaepterys juanitae*** Gibson-Smith & Gibson-Smith, spec. nov. from the north coast and ***Pygmaepterys lourdesae*** Gibson-Smith & Gibson-Smith, spec. nov. from the offshore islands.

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III.

Cyathodonta magnifica (Jonas, 1850)

(Mollusca : Bivalvia)

in Venezuela

(Figures *11* to *13*)

The presence of *Cyathodonta magnifica* (Jonas, 1850) in Venezuela was reported by Gibson-Smith & Gibson-Smith (1979: 29) as follows: "The only recent mention of this species is that of Keen (1971: 297) who regards it as the homologue of *C. undulata* Conrad, 1949, of the Panamic province. The type of *C. magnifica* is in the BM(NH), Reg. No. 1977177; it is a perfect paired specimen (length 73.45 mm, height 47.22 mm). In the year of publication it was communicated also by Cuming (1850: 170: 6, 7), habitat unknown, and later by Reeve (1859, plt. 2, species 11), the habitat then being given as Honduras. Beach specimens are to hand from the west coast of the Paraguaná Peninsula."

The above statement is not strictly correct because Macsotay (1968: 87: 4: 1: 2) published a new species as: *Cyathodonta rectangulata;* it is synonymous with *C. magnifica.* His specimens came from sandy beaches on the north coast of the Paria Peninsula and from Boca de Uchire, Anzoategui State. He also records it as a fossil in the Cerro Gato Formation, Isla Tortuga, and in the Castillo de Araya beds, Araya Peninsula, both Pleistocene in age. An umbo with massive chondrophore from the late Pliocene Mare Formation, Cabo Blanco, was thought by Gibson-Smith & Gibson-Smith *(loc. cit)* to represent the species. *Cyathodonta magnifica* is larger and more produced anteriorly than *C. undulata.*

The opportunity is taken to publish photographs, courtesy of the British Museum (Natural History), of the holotype of this little known species (Figures *10, 11*) and of a Recent specimen from El Pico, Paraguaná Peninsula (Figures *12, 13*).

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Long-Term Natural Resistance of Some Central American Hardwoods to Attacks by the Shipworm *Bankia setacea* (Tryon) and the Gribble *Limnoria quadripunctata* Holthuis in Monterey Harbor

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(4 Plates)

INTRODUCTION

Boat builders and harbor engineers still use wood as structural material due to its availability, versatility, and relatively low cost. In fresh water and in many brackish water situations in temperate regions, submerged wood deteriorates very slowly and has a useful lifetime of many years. In the marine environment, however, where a variety of boring organisms are often present, submerged wood may become severely damaged and fail after a few months or years. In tropical and temperate coastal regions the major wood borers are bivalve molluscs (Teredinidae and Pholadidae) and isopods (Limnoriidae).

The replacement of hull planking on boats and wooden pilings and sea walls which have been damaged by marine borers is very expensive, so a number of techniques have been used in attempts to protect the wood. The most common practice is to impregnate the wood with creosote or with chromated copper arsenate. This treatment, although expensive and often environmentally damaging, usually increases the effective lifetime of the wood significantly, but rarely gives permanent protection against marine borers. In some coastal areas in tropical and temperate regions where the gribble *Limnoria tripunctata* Menzies, 1951, is present, even creosote treatment gives little protection.

For many years it has been known that certain woods, such as pine and fir, are highly susceptible to damage by marine borers, while other woods, such as greenheart, teak, and angélique, are relatively resistant. Starting in the 1950s, C. R. Southwell and J. D. Bultman of the Naval Research Laboratory began a systematic survey of Central American tropical woods to determine which, if any, of these possessed natural resistance to attack by fungi, termites and marine borers. As part of this study they collected wood from 115 species of trees, mainly from the forests of Panama, and exposed these woods in three different tropical waters for periods up to 90 months (Southwell & Bultman, 1971). At their test sites in Panama, Southwell and Bultman identified over 30 species of marine borers, and several kinds of wood tested were resistant for long periods of time to one or more of these. Of the woods tested, four species gave the best long-term resistance. These were cedro espino (*Bombacopsis quinata* (N. J. Jacq.) Dugand), laurel negro (*Cordia alliodora* (Ruiz & Pavon)), cocobolo (*Dalbergia retusa* Hemsl.), and guayacán (*Tabebuia guayacan* (B. C. Seem.) Hemsl.). The species most resistant to all marine borers in Panamanian waters was cocobolo.

Earlier test exposures had shown that woods naturally resistant to borers in one geographic locality showed little or no resistance in other localities. It was therefore decided to initiate an international exposure program to test borer resistant woods at a few widely separated sites. The program was established by the Wood Group of the Permanent International Committee for Research on the Preservation of Materials in the Marine Environment (COIPM). A limited amount of exposure work has been carried out and the results through 1977 have been summarized (Bultman, Haderlie & DePalma, 1980). Starting in 1973 samples of all four of the resistant woods mentioned above were exposed at Burrard Inlet, British Columbia, Penobscot Bay, Maine, and Follonica, Italy, and were continued for four years. In 1974 a similar exposure program was

Figure *1*

Figure *1*: Monel metal rack with 6 wooden panels before exposure in the water of Monterey Harbor

Figure 2: One set of wooden panels photographed prior to exposure in Monterey Harbor, September 1974. Each panel 23 cm long

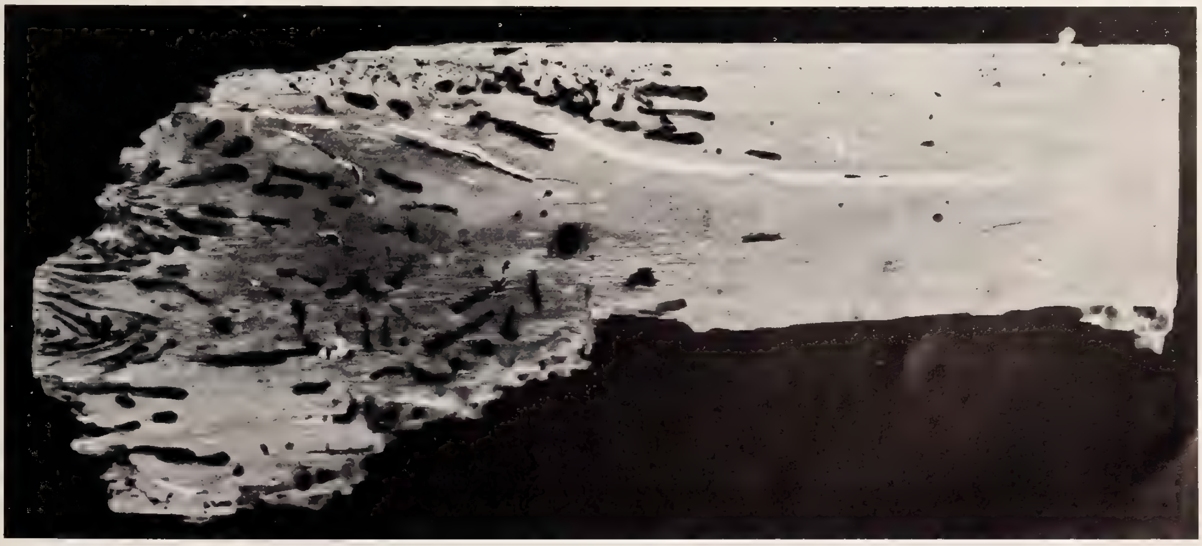

Figure 3: Typical Douglas Fir panel after 1 year exposure in water of Monterey Harbor, showing damage caused by *Bankia setacea*. Panel 23 cm long

started in Monterey Bay, California which has now continued for 7½ years or the same period of time of exposure as the original studies in Panama.

Results of the first four years of exposure at the four sites illustrate the variability referred to earlier. After four years there was a complete absence of borer attack on any of the tropical woods exposed in Penobscot Bay and in Monterey Bay. Yet several species of marine borers were present in the water at the exposure sites, for control panels of pine and oak were repeatedly destroyed during the first four years of exposure. At Penobscot Bay control panels were destroyed exclusively by gribbles *(Limnoria),* but in Monterey Bay both *Limnoria quadripunctata* Holthuis, 1949, and the shipworm *Bankia setacea* (Tryon, 1863) contributed to the destruction of the controls. At Burrard Inlet, however, three of the tropical woods (guayacán, cedro espino, and cocobolo) were heavily damaged by *Bankia setacea* after two years exposure. At Follonica, cocobolo and guayacán were badly damaged or destroyed after three years by teredinids and limnorians.

This present short report will give the results of the exposure tests in Monterey Bay over the entire 7½ year period from September 1974 until February 1982.

The author wishes to acknowledge the long-term support of the Oceanic Biology Program, Office of Naval Research.

AREA OF STUDY AND METHODS

The wood samples exposed in Monterey Bay were provided by J. D. Bultman and consisted of panels measuring 30 × 90 × 230 mm. These were cut from the heartwood of the four species of tropical trees referred to above and had been seasoned for one year. In addition, control panels of the same size of white oak (*Quercus* sp.) and douglas fir (*Pseudotsuga douglasi* Carr) were exposed along with the tropical woods.

The exposure site was under Municipal Wharf No. 2 in Monterey where the water depth is approximately 7 m at mean lower low water. This is the site where studies on growth rates and settlement times of *Bankia setacea* have been in progress since 1966. The physical parameters of the test site including temperature and salinity variations have been reviewed earlier (Haderlie & Mellor, 1973).

In the long-term exposures being reported on here the wood panels were exposed in Monel metal racks that held six panels each, one of each of the tropical woods plus one each of oak and fir. The panels were deployed in a vertical orientation with a space of 10 cm between each (Figure *1*) and the rack suspended from the wharf. When the study began in 1974 a total of three arrays of six panels each were employed, one array suspended 1.0 m below mean lower low water, a second at −3.5 m and a third near the bottom at −7.0 m. Two years after the initial exposure severe storm waves resulted in the lowest array being swept away and lost. The remaining two racks of panels were then placed on a heavy anchored array that rested on the bottom and was recovered with a winch on the wharf. These two sets of panels were exposed for an additional period of 5½ years at a position just above the bottom in a zone where previous studies indicated shipworm settlement and activity to be at a maximum level.

During the first four years the panels were recovered every third month and taken to the laboratory for examination, then returned to the sea for additional exposure. At each of the recoveries the fouling growth on each panel was removed and the panel scraped clean. During the remaining 3½ years the panels were recovered at intervals varying from six months to one year. The surviving panels were removed for the last time in early February 1982, and, after the fouling growth had been removed, they were examined and dried in an oven before being weighed.

RESULTS

Figure *2* shows one typical set of panels before exposure in Monterey in September 1974. The results after an initial four years' exposure were summarized by Bultman, Haderlie & DePalma (1980), and showed that the Panamanian woods were indeed resistant to attack by marine borers in Monterey harbor, for none of the experimental tropical woods showed any evidence of damage. Yet in the same rack douglas fir and white oak panels were damaged in less than one year at all three exposure depths, and all of the control panels were completely destroyed in less than three years. Figure *3* shows a typical fir panel after one year exposure. The oak survived attack only slightly better than the fir. Both *Limnoria quadripunctata* and *Bankia setacea* attacked the control panels at all three exposure depths, but *Limnoria* caused the greatest damage in panels initially exposed at shallow depths, whereas *Bankia* was responsible for most damage to panels exposed near the bottom. Adult *Limnoria* were often seen wandering over the surface of the tropical wood panels, yet after four years of exposure none of them had excavated burrows in the wood.

During the terminal 3½ years of this study the control panels, which were periodically replaced as the older panels were destroyed, were attacked as in the earlier period of exposure. The fir was destroyed within two years, the oak within three. Some of the tropical woods continued to resist any form of borer damage during this terminal period and thus survived intact for the full 7½ years (Figure *7*). Other panels, however, were eventually attacked moderately or fairly heavily. None, however, were destroyed and all retained structural integrity. Figures *4*, *5*, and *6* show representatives of undamaged and damaged tropical wood panels after final removal and drying. Each panel will be discussed briefly.

Panel 81 (cocobolo): During the fifth year of exposure this panel was penetrated by approximately six *Bankia setacea*, each of which grew to moderate size, then died within a year. No other borers entered the wood. The old bore holes in the panel were later eroded to larger size by nestlers. The panel decreased in weight from 576g at the beginning to 377g at the end, the loss due mainly to wood removed by *Bankia*.

Panel 82 (cocobolo): The panel survived intact with no evidence of any borer activity.

Panel 84 (guayacán): During the sixth year of exposure *Limnoria quadripunctata* attacked one face of the panel and a few live individuals were present in the burrows when the panel was removed at the end of the project. About four *Bankia setaceo* also penetrated the panel during the sixth year and created tunnels 10mm in diameter before dying within a year. Some of these tunnels were lined with layers of calcium carbonate up to 2mm thick, much heavier than seen in any *Bankia* burrows in fir and oak in this or other studies in Monterey. During the 7½ years the weight of this panel decreased from 602g to 410g, due mainly to the borers.

Panel 85 (guayacán): During the seventh year of exposure a few *Limnoria* burrowed into the panel face, but on removal of the panel no living gribbles were found and no *Bankia* burrows were present. The panel decreased very little in weight.

Panels 87 and 88 (laurel negro, see Figure 7): Both panels were undamaged with no evidence of borer attack.

Panels 90 and 91 (cedro espino): Both panels were intact with no evidence of borer damage. After 7½ years'exposure in sea water these two panels were still buoyant and displaced about the same amount of water as when initially exposed.

DISCUSSION

The numbers of samples of the four tropical woods exposed in Monterey were too small to draw firm conclusions. Yet it is obvious from the results discussed above that all four species of tropical woods tested are completely or partially resistant for extended periods of time to attacks by the two common wood borers found in Monterey harbor. It is remarkable that both laurel negro and cedro espino wood panels remained completely undamaged after such a long period of exposure in borer infested water. As has been pointed out (Bultman, Haderlie & DePalma, 1980), laurel negro should receive special attention as a possible marine construction timber in temperate waters in the future. In the tropical waters of the Panama Canal Zone laurel negro possesses no resistance to wood boring pholads such as *Martesia* (Southwell & Bultman, 1971), yet in the temperate waters on both coasts of North America and in the Mediterranean this wood has shown considerable resistance to damage by *Teredo*, *Bankia*, and *Limnoria*. Laurel negro is also highly resistant to termite attack (Bultman & Southwell, 1976). Unlike other borer resistant woods (such as cocobolo), laurel negro grows to large size trees and has strength properties similar to those of mahogany, yet the wood has a density similar to pine. The tree is grown widely as a reforestation and plantation tree in Central America (Johnson & Morales, 1972).

The results obtained with cocobolo and guayacán exposed in Monterey are similar to those obtained elsewhere; some panels show slight to moderate borer damage,while other seemingly identical panels show no damage. This indicates that the wood from different parts of the tree might contain different quantities of whatever material or fraction responsible for the resistance to borers. Only the heartwood of tropical woods is resistant, and newly formed heartwood is more resistant than older heartwood (Bultman, Haderlie & DePalma, 1980).

Attempts are now being made to extract and identify chemical components of the heartwood of tropical woods resistant to borers. From cocobolo the polyphenols obtusaquinone and p-cinnamylphenol have been extracted and these fractions seem to inhibit the phenoloxidase involved in the formation of the periostracum of molluscan borers (Waite & Wilbur, 1975). Obtusaquinone also appears to prevent the newly settled pediveliger larvae of wood boring molluscs from metamorphosing, and later inhibits the formation of calcified cones and pallets in these borers (Turner, 1976). In the future it might be possible to impregnate douglas fir, oak, or pine with extractives from tropical woods, or their synthetic analogs, and confer marine borer resistance to these commonly used construction timbers. Small wooden plaques of soft pine experimentally impregnated with obtusaquinone and exposed in Monterey harbor during this study resisted *Limnoria* attack for 18 months before being destroyed by the gribbles.

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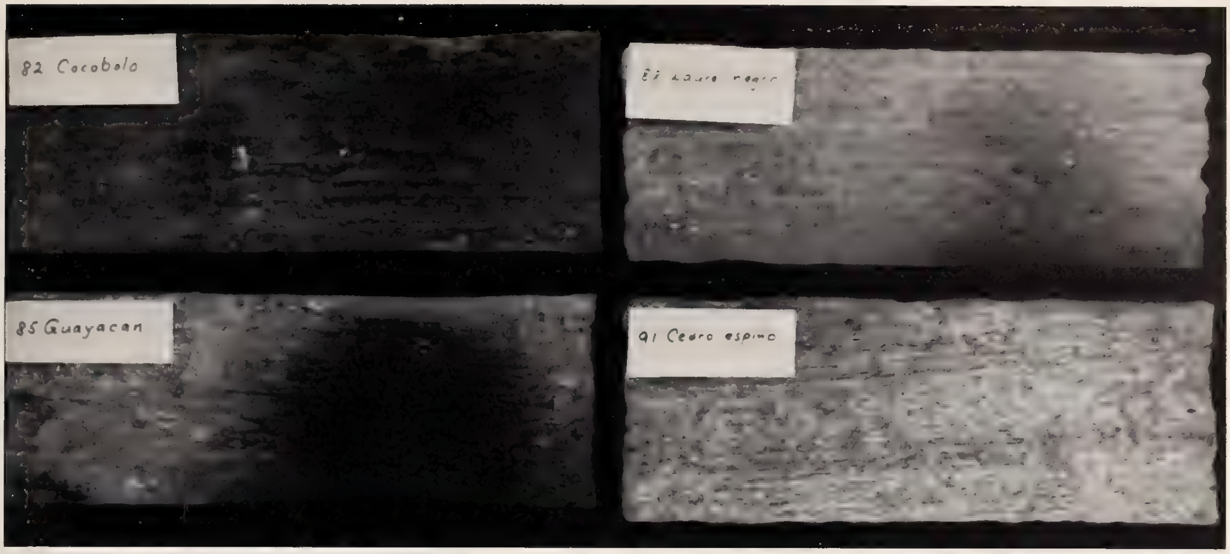

Figure *4*: Surviving panels of the set shown in Figure *2* after 7½ years exposure, February 1982. Only Panel 85 (Guyacán) was damaged, having been bored by a few *Limnoria quadripunctata*

Figure *5*: Cocobolo panel damaged by *Bankia setacea*

Figure 6: Guayacán panel damaged by *Bankia setacea* and *Limnoria quadripunctata*

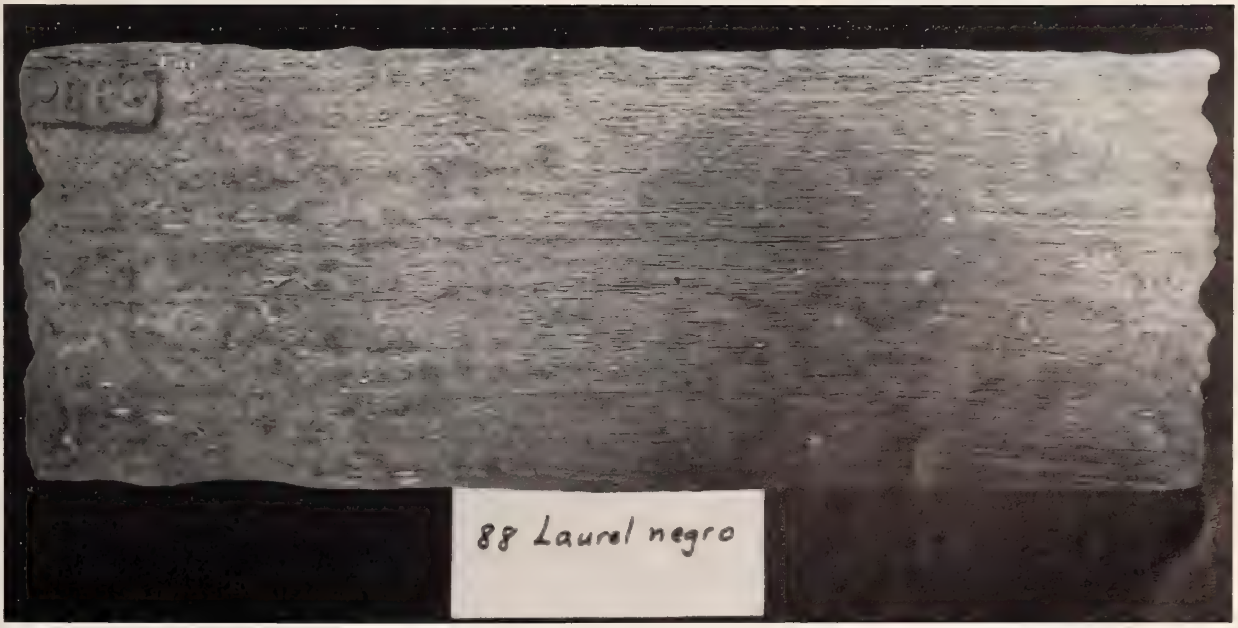

Figure 7: Laurel negro panel after 7½ years exposure showing no damage from borers

Conchological Redescriptions of *Mytilopsis sallei* and *Mytilopsis leucophaeta* of the Brackish Western Atlantic

(Bivalvia : Dreissenidae)

BY

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(1 Plate; 6 Text figures)

INTRODUCTION

The genus *Mytilopsis* Conrad, 1857 (type-species by M: *Mytilopsis leucophaetus* Conrad, 1831), one of the two extant dreissenid genera, is generally considered to comprise 9 extant species: *Mytilopsis adamsi* Morrison, 1946; *M. africana* (Van Beneden, 1835); *M. allyneana* Hertlein and Hanna, 1949; *M. cochleata* (Kickx, 1835); *M. domingensis* (Récluz, 1852); *M. leucophaeta* (Conrad, 1831); *M. sallei* (Récluz, 1849); *M. trautwineana* (Tryon, 1866) and *M. zeteki* Hertlein and Hanna, 1949. All members of the genus are mytiliform, byssate and epifaunal, and inhabit brackish waters of tropical, sub-tropical and, in two cases *(M. cochleata* and *M. leucophaeta)*, temperate latitudes. Most of the species are of New World geographic distribution, with 6 species occurring in the Americas, one in western Africa, one in northwestern Europe, and one in Fiji and eastern India.

Most species of *Mytilopsis* were described during the middle to late nineteenth century; many were redescribed several times, and there exist 66 synonyms. The descriptions and redescriptions, and their infrequently accompanying illustrations are of little value in species identification. With the possible exception of these by Récluz (1952), Hertlein & Hanna (1949) and Morrison (1946), any of the original descriptions can easily apply to a specimen of any species of the genus. Additionally, there has been little effort made to provide diagnoses for the species, except for the limited treatment of Récluz (1852), Morrison (1946) and Olsson (1961).

The purpose of this paper is to provide more precise definitions of the species of *Mytilopsis leucophaeta* and *M. sallei*, and to provide a means for workers in subtropical western Atlantic estuaries to easily distinguish one from another. The descriptions and discussion contained herein are based entirely on conchological characters.

A complete list of the materials examined by the authors in the course of this work may be obtained from the authors upon request and submission of a stamped, self-addressed legal sized envelope.

MATERIALS

Materials were examined from the following museums: Academy of Natural Sciences, Philadelphia, Pennsylvania (ANSP); British Museum (Natural History), London, England (BMNH); California Academy of Sciences, San Francisco, California (CAS); Los Angeles County Museum, Los Angeles, California (LACM); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM); as well as the private collections of one of us (DCM). All materials, with the exception of those of the senior author (DCM), consisted of dried shells. Shells of both *Mytilopsis leucophaeta* and *M. sallei* have been deposited as voucher specimens at the United States National Museum (USNM 818345 and 818346, respectively).

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REDESCRIPTIONS

Mytilopsis leucophaeta (Conrad, 1831)

(Figures 1, 2, and 7)

References and Synonymy:

Mytilopsis leucophaetus Conrad, 1831. Journ. Acad. nat. Sci. Phila. 6: 263; plt. XI, fig. 13
Mytilus cochleatus Kickx *in* Nyst, 1835. Bull. Acad. roy. Sci., Brux. 2: 235; figs. 1-3
Mytilina cochleata Cantraine, 1837. Ann. Sci. nat., 2nd ser. (Zool.) 7: 310
Mytilina cochleata Cantraine, 1837 (1838). Bull. Acad. roy. Sci., Brux. 4: 117
Dreissena cochleata Nyst, 1843. Coquilles de la Belgique: 264
Tichogonia cochleata Dunker, 1853. Zeitschr. Malak. 10: 91
Dreissenia cumingiana Dunker, 1855. Comm. de Septiferis: 14
Dreissenia cochleata Dunker, 1855. Comm. de Septiferis: 17
Mytilus americanus Reeve, 1858, Conch. Icon. 10(2): plt. X, fig. 43
Mytilus tenebrosus Reeve, 1858. Conch. Icon. 10:(2): plt. X, fig. 46
Mytilus cochleatus Reeve, 1858. Conch. Icon. 10(2): plt.X, fig. 50
Dreissena cochleata Fischer, 1858. Journ. Conchyl. 7: 129
Dreissena americana Fischer, 1858. Journ. Conchyl. 7: 131
Tichogonia cochleata Küster, 1889. Syst. Conch.-Cab. 8.3: 15; plt. 12, figs. 7, 8
Tichogonia americana Küster, 1889. Syst. Conch.-Cab. 8.3: 28
Congeria leucophaeta Dall, 1898. Trans. Wagner Free Inst. Sci. 3(4): 809 and *auct. sequ.*
Congeria cochleata Dall, 1898. Trans. Wagner Free Inst. Sci. 3(4): 809

Material Examined:

Fifty-five lots, comprising 1019 specimens; of these **Europe:** 2 lots, comprising 13 specimens, from Antwerp, Belgium. **United States:** 49 lots, comprising 980 specimens, from the Hudson River, Rockland County, New York, to the Colorado River, Cameron County, Texas. **Mexico:** 4 lots, comprising 26 specimens, from Tampico to Veracruz.

Comments: *Mytilopsis leucophaeta* was originally described by T. A. Conrad from shells attached to the oyster, *Crassostrea virginica* (Conrad, 1831). His original description is as follows:

> "Shell incurved, white, with a very rugose epidermis; anterior [ventral] side much depressed; hinge margin excavated, with the teeth obsolete; on the posterior [dorsal] side, under [posterior to] the beaks, is a pointed laminar tooth directed inwards. Cab. Academy, No. 1453. Inhabits the southern coast of the U.S."

This description is so poor that one cannot get an idea of the general shape of this animal. The accompanying figure is life size and nondescript, so that a reader has difficulty distinguishing *Mytilopsis leucophaeta* from other Dreissenidae or even Mytilidae based on the information provided by Conrad. Conrad (1831) even confused ventral with anterior and dorsal with posterior in his description, which have been corrected with bracketed comments. The description of Nyst (1835) for *M. cochleata* is far more complete in terms of characters discussed and detail of such. Nyst even attempted a diagnosis between *M. cochleata* and its supposed congeners, and provided the best illustrations of any species of *Mytilopsis* to date. Nyst, too, seems to have somewhat confused the anatomical directions of the mytiliform bivalve as can be seen in the following translation of his original description:

> "Type specimen: shell oblong, subcylindrical, slightly curved, depressed posteriorly [dorsally], compressed towards the upper edge [anteriorly] and slightly expanded at the posterior extremity of the cardinal ligament, covered with cob-webby threads, which causes it to appear finely and transversly striated and which gather [accumulate] with age in some of the species of curved lamellibranchs.
>
> The beaks are pointed, weakly curved, the shell is furnished in the interior with a septum-like lamina, such as in several species of the genus, but it is moreover furnished with a spoon shaped appendage, placed below [posterior to] the septum-like lamina in the direction of the upper [dorsal] edge.
>
> The right valve of this species is larger than the left; this character is most perceptible on the lower [ventral] edge. The shell is usually brown in color, ashen, and intersected by whitish zones; the young individuals sometimes appear zebra striped."

From the supplementary information presented in the paper, Nyst (1835) mentions that *Mytilopsis cochleata* was collected in the Escaut [Schelde] River, Antwerp, but from the presence of barnacles he presumed that *M. cochleata* was not a lotic species, but that it was probably introduced to the river by ocean going ships.

After examining topotypes of *Mytilopsis cochleata* (USNM 122466) as well as two lots from the British Museum (one

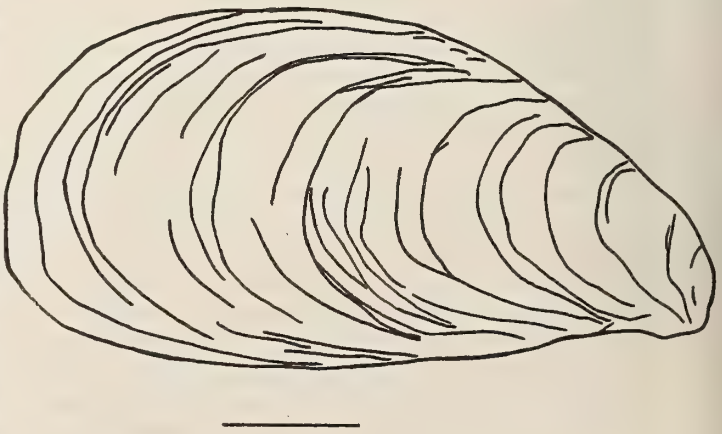

Figure 1

Exterior of the right valve of a specimen of *Mytilopsis leucophaeta* from Student Lake, Miami, Florida. (USNM 818345). Bar length equals 2.0mm

Explanation of figure abbreviations

AP — Apophysis
EVS — Extension of ventral shell margin
NYM — Nymph
PL — Pallial line
PAM — Posterior adductor muscle scar
PRM — Posterior retractor muscle scar
SEP — Septum

of which contained a specimen figured by REEVE, 1858), and over 60 lots of *M. leucophaeta* (including a virtual syntype, USNM 54227) from the United States National Museum, the Academy of Natural Sciences, Philadelphia, the Los Angeles County Museum, and the California Academy of Sciences we have concluded that *M. cochleata* and *M. leucophaeta* are synonyms. These nominal species are nearly identical in overall shape, color, size, and in the character states of the muscle scars, the ligament, the septum and the apophysis (Figure 2). Both species are also the only members of an overwhelmingly sub-tropical and tropical genus to range into temperate regions. Therefore, we have concluded that *M. cochleata* (Kickx, 1835) is a junior synonym of *M. leucophaeta* (Conrad, 1831), and have treated it as such herein. Further subjective synonyms are listed in the synonymy.

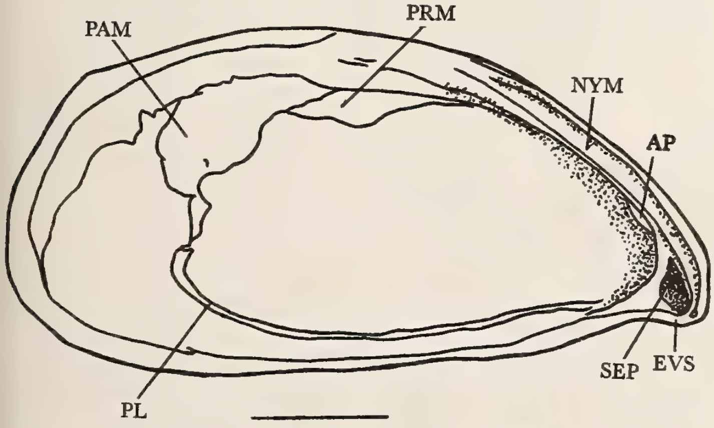

Figure 2

Interior of the left valve of a specimen of *Mytilopsis leucophaeta* from Student Lake, Miami, Florida. (USNM 818345). Bar length equals 2.0mm

REDESCRIPTION

Shell mytiliform, byssate; exterior bearing fine to medium rough concentric lines, periostracum cream colored to dark brown and heavy, yet easily broken (or eroded) off; shell sometimes marked with zig-zag lines, somewhat like *Dreissena polymorpha*, especially in juveniles. Shell inequivalve, the right valve slightly overlapping the left posteroventrally. General appearance of organism is long and wide, height to width ratio always less than 1.25:1 (for representative size measurements see Table 1).

Ventral margin of shell nearly straight, slightly convex one-third of the way from anterior to posterior margins in larger specimens; byssal notch slightly developed. Dorsal margin broadly convex in the area from the beaks to the posterior margin, at which point it changes direction, becoming only slightly curved and extending to the posterior margin; at this point the angle of the margin changes abruptly, and curves ventrally with a slight convexity down to join the ventral margin, where it becomes directed anteriorly rather abruptly. Small specimens appear to have more smoothly curving margins than larger specimens, which tend to appear very elongate and rectangular. Beaks well rounded to bluntly pointed and directed anteroventrally at an angle much less than 45°.

Shell interior white, with grayish areas postero-dorsally in some specimens. Pallial and extra-pallial regions porcellaneous; pallial line and posterior muscle scars glossy. Posterior muscle scars do not extend anteriorly to the posterior limit of the nymph. Anterior adductors attached to a shelf-like septum, which in this species is relatively short and small, appearing cup-like in the larger specimens, especially on the right valve. Left valve bears anteroventrally a well developed extension of the ventral shell margin which may act like a tooth. Anterior retractor muscles attached to an apophysis which in this species is

Table 1

Mean shell sizes and standard deviations from representative populations of *Mytilopsis leucophaeta*

Locality	N	Length (mm)	Height (mm)	Width (mm)
? Belgium (BMNH 1829)	5	21.48 ± 2.30	9.34 ± 0.89	7.96 ± 0.52
Galveston Bay, Texas (DCM)	12	8.38 ± 2.37	4.55 ± 0.87	4.15 ± 1.26
Lake Pontchartrain, Louisiana (DCM)	27	8.52 ± 2.17	4.37 ± 0.93	3.65 ± 1.01
Student Lake, Univ. of Miami campus, Coral Gables, Florida (DCM)	45	12.65 ± 4.56	6.93 ± 2.37	5.34 ± 2.05

Figure 3

Reported ranges of *Mytilopsis sallei* (■) and *Mytilopsis leucophaeta* (▲) in the Western Atlantic Province

closely associated with the septum, and is not closely associated with the hinge plate. Apophysis relatively small and rounded, but occasionally appearing almost pointed postero-dorsally; the apophysis does not extend posterior of twice the length of the septum.

Hinge plate low and wide, bearing a wide nymph which extends from the beaks to a point ⅓ to ⅖ of the way from anterior to posterior margins. Nymph bears a ligament of the same length. Anteriorly the hinge plate remains relatively high, causing the anterior end of the shell to appear rounded.

Range: Brackish waters in northern France, Belgium and Holland, and the Atlantic and Gulf of Mexico coasts of the Americas from the Hudson River estuary to Tampico, Mexico (Conrad, 1831; Nyst, 1835; Récluz, 1849; Dunker, 1853; Reeve, 1858; Fischer, 1858; Küster, 1889; Johnson, 1890; Pilsbry, 1911; Nylander, 1921; Rehder, 1937; Fairbanks, 1963; Morton, 1970; Swingle & Bland, 1974; Archambault-Guezou, 1976; Ristich, Crandall & Fortier, 1977; Wardle, 1980; and museum records examined by the authors) (Figures 3 and 4).

Type Locality: "Southern coast of the United States." (Conrad, 1831).

DISCUSSION

We suspect that Nyst (1835) was correct in presuming that *Mytilopsis leucophaeta* was introduced into the Escaut River, since the ranges of fossil and Recent species indicate that *Mytilopsis* is predominantly a New World group. The mode of introduction is unknown, although such things as ballast rocks in somewhat less than watertight wooden vessels seem to be likely candidates.

This species has been reported from both coastal lakes and streams along the Atlantic and Gulf coasts of the United States. *Mytilopsis leucophaeta* is a highly euryhaline species whose upstream limits are presumably controlled by the physiological tolerances of its larvae, and perhaps by

Figure 4

Reported ranges of *Mytilopsis sallei* (■) and *Mytilopsis leucophaeta* (▲) in the Eastern Atlantic, Indian and Eastern Pacific Provinces

the lack of high salinity pulses necessary to initiate spawning behavior (Siddall, 1980). These are only hypotheses, however, since the biology and natural history of *M. leucophaeta* are largely unknown. It is likewise not known what limits the seaward distribution of *M. leucophaeta.*

Mytilopsis sallei (Récluz, 1849)

(Figures 5, 6 and *8*)

References and Synonymy:

Dreissena sallei Récluz, 1849. Revue Zool. 2: 69
Dreissena sallei Récluz, 1852. Journ. Conchyl. 3: 255; plt. X, fig. 9
Dreissena domingensis Récluz, 1852. Journ. Conchyl. 3: 255; plt. X, fig. 8
Tichogonia pfeifferi Dunker, 1853. Zeitschr. Malak. 10: 88
Tichogonia rossmaessleri Dunker, 1853. Zeitschr. Malak. 10: 89
Tichogonia riisei Dunker, 1853. Zeitschr. Malak. 10: 91
Tichogonia sallei Dunker, 1853. Zeitscher. Malak. 10: 91
Dreissenia rossmaessleri Dunker, 1855. Comm. de Septiferis: 17
Dreissenia pfeifferi Dunker, 1855. Comm. de Septiferis: 17
Dreissenia gundlachii Dunker, 1855. Comm. de Septiferis: 18
Dreissenia sallei Dunker, 1855. Comm. de Septiferis: 18
Dreissenia moerchiana Dunker, 1855. Comm. de Septiferis: 18
Dreissena riisei Dunker, 1855. Comm. de Septiferis: 19
Dreissenia domingensis Dunker, 1855. Comm. de Septiferis: 20
Mytilus sallei Reeve, 1858. Conch. Icon. 10(2): plt. X, fig. 44
Mytilus rossmassleri [sic] Reeve, 1858. Conch. Icon. 10(2): plt. X, fig. 45
Mytilus domingensis Reeve, 1858. Conch. Icon. 10(2): plt. X, fig. 48
Mytilus morchianus [sic] Reeve, 1858. Conch. Icon. 10(2): plt. X, fig. 51
Dreissena roosmassleri Fischer, 1858. Journ. Conchyl. 7: 132
Dreissena pfeifferi Fischer, 1858. Journ. Conchyl. 7: 132
Dreissena gundlachi Fischer, 1858. Journ. Conchyl. 7: 132
Dreissena morchiana [sic] Fischer, 1858. Journ. Conchyl. 7: 132
Dreissena riisei Fischer, 1858. Journ. Conchyl. 7: 133
Dreissena domingensis Fischer, 1858. Journ. Conchyl. 7: 133
Dreissena sallei Fischer, 1858. Journ. Conchyl. 7: 133
Tichogonia sallei Küster, 1889. Syst. Conch.-Cab. 8.3: 17; plt. 12, figs. 13, 14
Tichogonia moerchiana Küster, 1889. Syst. Conch.-Cab. 8.3: 18; plt. 12, figs. 11, 12

Tichogonia riisei KÜSTER, 1889. Syst. Conch.-Cab. 8.3: 25; plt. 15, figs. 12, 13

Tichogonia domingensis KÜSTER, 1889. Syst. Conch.-Cab. 8.3: 26; plt. 15, fig. 14

Tichogonia rossmaessleri KÜSTER, 1889. Syst. Conch.-Cab. 8.3: 27; plt. 15, fig. 7

Tichogonia gundlachi KÜSTER, 1889. Syst. Conch.-Cab. 8.3: 29

Congeria rossmaessleri DALL, 1898. Trans. Wagner Free Inst. Sci. 3(4): 809

Congeria sallei DALL, 1898. Trans. Wagner Free Inst. Sci. 3(4): 809 and *auct. sequ.*

Congeria gundlachi DALL, 1898. Trans. Wagner Free. Inst. Sci. 3(4): 809

Mytilopsis allyneana HERTLEIN & HANNA, 1949. Bull. So. Calif. Acad. Sci. 48: 14

Material Examined:

Sixty-four lots, comprising 1844 specimens, of these **Florida:** 9 lots, comprising 213 specimens, from Tampa to Miami. **Caribbean Islands:** 29 lots, comprising 407 specimens, from Lyford Cay, Bahama Islands to Roseau, Dominica. **Western Atlantic Mainland:** 19 lots, comprising 1082 specimens, from Quintana Roo, Mexico to Barcelona, Venezuela. **Indo-Pacific:** 7 lots, comprising 82 specimens, from Viti Isle, Fiji and Visakhapatnam, India.

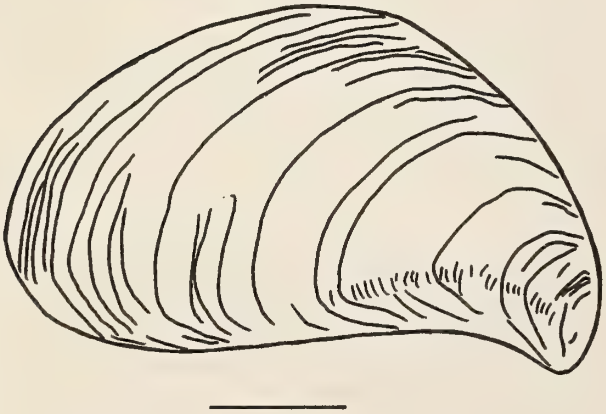

Figure 5

Exterior of the right valve of a specimen of *Mytilopsis sallei* from Laguna Bacalar, Mexico. (USNM 818346). Bar length equals 2.0mm

Comments: *Mytilopsis sallei* was originally described by C. A. Récluz from shells collected by August Sallé from the Rio Dulce, Guatemala (Récluz, 1849). The translation of the original description is as follows:

> "Shell oval-oblong, inequivalve towards the posterior end of the ventral region; beaks curved; valves slightly convex, chalky white below a rugose olivaceous colored epidermis: interior tinted with unequally concentric blackish zones. Length, 19-23mm. Height, 13-14mm."

Récluz' description, without illustrations, is very poor. The general shape of the animal is not even mentioned. That the means of attachment by byssus is not reported is not surprising since Récluz was probably given shells only, but one wonders why he did not attempt to draw conclusions about the mode of life of *Mytilopsis sallei* from its superficial similarity to *Mytilus.*

In 1852 RÉCLUZ described another species of *Mytilopsis* from the West Indian province, *M. domingensis* (RÉCLUZ, 1852). In this paper he again presented the description of *M. sallei,* and provided a diagnosis of sorts between *M. sallei* and its congeners in (at that time) *Dreissena.* The diagnosis is as follows:

> "This species, already conspicuous by the circumstance that it will be found boring, differs also from its congeners by its coloration, and by the rugosity of its epidermis. It has been brought back by Monsieur Sallé, to whom we dedicated it. We have already given a description of it in the *Revue Zoologique* of Monsieur Guérin, in 1849; but this species has not yet been illustrated, and we have had to recall the characteristics of it in depicting it on one of the plates of the Journal."

Unfortunately the illustration that Récluz refers to is of little value, since it depicts what we presume to be the type specimen at life size and only in an exterior view. The reference to boring is interesting, but unlikely to be correct. From our observations of *Mytilopsis sallei* in its habitat and those of MORRISON (1946) of *M. adamsi* in Panama, it appears that members of this genus have a tendency to nestle in small holes, but not to actually bore the holes.

RÉCLUZ (1852) also describes *Mytilopsis domingensis* in this paper, which has been translated into the following:

> "Small longitudinal shell, elongated, narrow, irregular, like most of its congeners, striated, or rather concentrically lined, but the epidermis does not show the lamellae like most of the other species. Its dorsal edge is generally angular towards the

Explanation of Figures *7* and *8*

Figure *7:* Scanning electron micrograph of the anterior hinge area of a specimen of *Mytilopsis leucophaeta* from Galveston Bay, Texas. (DCM) Bar length equals 500μm

Figure *8:* Scanning electron micrograph of the anterior hinge area of a specimen of *Mytilopsis sallei* from Laguna Bacalar, Mexico. (DCM) Bar length equals 500μm

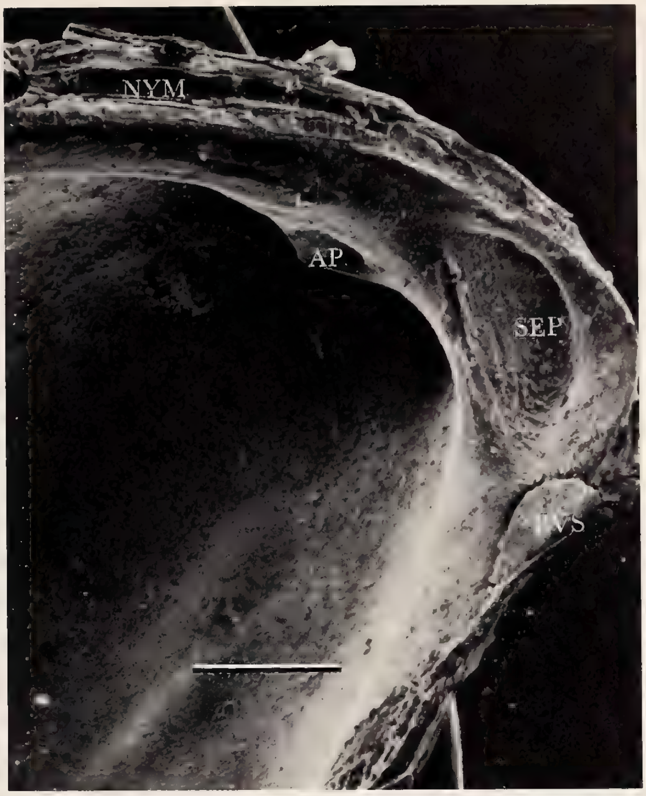

Figure 7

Figure 8

> center, and the ventral edge is sometimes straight, sinuous, concave, or protuberant. In this case, the right valve overlaps the left valve. Beaks projecting, curved toward the ventral side: the ventral side, closest to the beaks, bears an elongated aperture, narrow and linear, for the passage of the byssus. The general color of the species is of a more or less dark brown, frequently adorned with two longitudinal lines of yellowish-white. The interior of the valves has a blackish-violet tint. Length 22-24 mm. Height 10-13 mm. Width 8 mm."

The accompanying "diagnosis" for this species is as follows:

> "Our species has some relationship with *Dreissena cochleata* by its narrowness, but it differs from it [*D. cochleata*] by its dimensions, its irregularity, and its ever pronounced yellowish-white lines: it also differs from *D. cochleata* by its proportionately larger partition [septum], and by the lamella placed below the septum, [which is] always larger and less dentiform."

The information provided by Récluz for *Mytilopsis domingensis* is far better than that provided for *M. sallei*, and it demonstrates that, with respect to the shells, he had a good idea of the important characters and character states of the genus. It appears that his work is based on very few specimens however, and although Récluz does indicate some of the important characters in the 1852 descriptions, they are still somewhat ambiguous, especially considering the plethora of species which have been described since 1852. As a final comment on the 1849 and 1852 descriptions by Récluz, it is interesting to note that he, at least, does not confuse the anatomical poles of the Dreissenidae.

Based on examinations of specimens of *Mytilopsis sallei* from the type locality (ANSP 125268, CAS 46744), and specimens of *M. domingensis* from its type locality (USNM 215620), as well as over 60 lots of *M. sallei* and *M. domingensis* from the Academy of Natural Sciences, Philadelphia, California Academy of Sciences, Los Angeles County Museum and the United States National Museum we have concluded that *M. domingensis* and *M. sallei* are synonyms based on shell characteristics. We have therefore treated *M. domingensis* (Récluz, 1852) as a junior synonym of *M. sallei* (Récluz, 1849) herein. This conclusion is based on similarities in the shell character states of these nominal species, as well as the apparent limitation of *M. sallei*/*M. domingensis* to the tropical western Atlantic. Other nominal species which have been treated as junior synonyms of *M. sallei* in the present paper are listed in the synonymy, including *M. allyneana* Hertlein and Hanna (1949), which MORTON (1981) has recently synonomized with *M. sallei.*

REDESCRIPTION

Shell mytiliform, byssate; exterior bearing fine concentric lines, periostracum translucent to colored so that the shell appears white, cream colored or bluish-grey to medium brown; periostracum thin but not fragile, generally eroded anteriorly. Shell of very small specimens occasionally bearing brown zig-zag markings, while large specimens are never marked in this manner, but rarely bear a single light radial band. Shell inequivalve, the right valve overlapping the left postero-ventrally. General appearance of the animal is long, high and narrow; height to width ratio greater than 1.3:1 (for representative size measurements, see Table 2).

Ventral margin straight to slightly convex in its posterior half, slightly concave in its anterior half; byssal notch well developed and generally more pronounced on the right valve. Dorsal margin extending from beaks nearly vertically for a short distance, then curving smoothly posteriorly with a slight convexity to a point about one-half of the way from anterior to posterior, where the margin is directed more abruptly ventrally and joins the convex posterior margin, which in turn joins the ventral margin at an abrupt (about 90°), but somewhat rounded angle. Beaks bluntly to sharply pointed and directed antero-ventrally at an angle of more than 45°.

Table 2

Mean shell sizes and standard deviations from representative populations of *Mytilopsis sallei*

Locality	N	Length (mm)	Height (mm)	Width (mm)
Laguna Bacalar, Mexico 1976 collection (DCM)	50	12.71 ± 4.11	7.68 ± 2.31	5.34 ± 1.8
Laguna Bacalar, Mexico 1977 collection (DCM)	62	11.66 ± 3.49	7.23 ± 2.03	4.93 ± 1.53
Lake Izabal, Guatemala (USNM 684754, 684728, 684729)	58	18.67 ± 4.42	10.66 ± 2.16	7.56 ± 1.54
Robin's Bay, St. Mary, Jamaica (USNM 442006)	18	24.09 ± 3.24	11.51 ± 1.34	8.73 ±0.92
Roseau, Dominica (USNM 215620)	9	15.04 ± 6.32	7.94 ± 3.02	6.92 ± 2.99
Torbeck, Haiti (USNM 440374)	38	25.57 ± 3.49	12.58 ± 1.65	9.68 ± 1.31

Shell interior mottled gray-black and white to cream colored, bluish-gray or blue-black in the central portion; marginal areas white to bluish-gray (including hinge plate); interior sometimes bears a somewhat cancellate pattern of concentric dark bands and radial bands on a light background. Pallial region porcellaneous, extra pallial region glossy. Pallial line and posterior muscle scars also glossy; posterior muscle scars extend to anterior of the posterior limit of the nymph. Anterior adductor muscles attached to a shelf-like septum, which in this species is relatively flat, being nearly on the same plane as the hinge plate, but is overall relatively small. Left valve bears antero-ventrally a small extension of the shell margin, which extends over the right shell margin when the valves are closed. Anterior retractor muscles attached to an apophysis, located lateral to the septum near the dorsal shell margin; in this species the apophysis is well developed and not closely associated with the septum; the apophysis extends laterally well into the shell cavity, and posteriorly to twice the length of the septum, generally becoming pointed postero-ventrally and appearing hook-shaped; the apophysis in this species is generally closely associated with the hinge plate.

Hinge plate high, bearing a high nymph which extends from the beaks to a point ⅖ to ½ of the way from anterior to posterior margins; the nymph bears a ligament of the same length. Anteriorly the hinge plate becomes lower, so that the beaks remain relatively sharply pointed.

Range: Brackish waters in southern Florida, along the western Atlantic coast from Yucatan to Venezuela, and on many of the islands of the West Indies (Récluz, 1849, 1852; Dunker, 1853, 1855; Reeve, 1858; Fischer, 1858; Küster, 1889; Hinkley, 1920; Escarbassière & Almeida, 1976; Marelli & Berrend, 1978; and museum records examined by the authors). Introduced to Fiji and eastern India (Morton, 1980, 1981) (Figures 3 and 4).

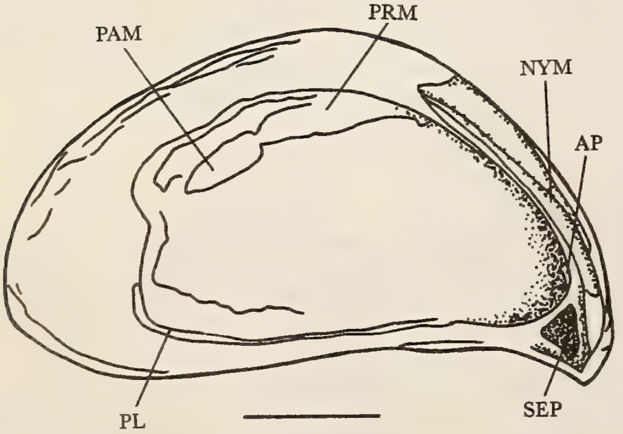

Figure 6

Interior of the left valve of a specimen of *Mytilopsis sallei* from Laguna Bacalar, Mexico. (USNM 818346). Bar length equals 2.0 mm

Type Locality: Mouth of the Rio Dulce, Guatemala (Récluz, 1849).

DISCUSSION

The range and distribution of *Mytilopsis sallei* are much less well known than those of *M. leucophaeta*, and consequently many of the records for *M. sallei* are undocumented and based on dried shells and old handwritten labels in museum drawers. If one accepts these records, however, *M. sallei* is seen to have a considerable range; essentially throughout the Caribbean and introduced to Fiji and India. It is an intriguing range since *M. sallei* is an estuarine inhabitant, and thus each of the island populations must be considered disjunct. Within its range, the distribution of *M. sallei* has not been examined in detail, but it is apparently found in coastal lakes (Marelli & Berrend, 1978) and streams (Hinkley, 1920; Escarbassière & Almeida, 1976), probably much like *M. leucophaeta* in the United States. Next to nothing is known about the life cycle of *M. sallei*, or the physical-chemical factors affecting such. The physiological tolerances of *M. sallei* and the factors affecting its distribution, both upstream and downstream, are likewise unknown.

CONCLUSIONS

There are two representatives of the genus *Mytilopsis* inhabiting the western Atlantic coast of the Americas; *M. leucophaeta* and *M. sallei*. The known geographic ranges of these mussels are as follows: *M. leucophaeta*, western Atlantic coast from the Hudson River estuary to southern Florida and along the Gulf of Mexico from Florida to Tampico, Mexico (*M. leucophaeta* has also been introduced into northwestern Europe); *M. sallei*, southern Florida, the Caribbean coast of Central and South America from Bacalar, Mexico to just east of Caracas, Venezuela, scattered throughout the West Indies, and also in Fiji and Visakhapatnam, India. Since *M. leucophaeta* and *M. sallei* are parapatric, with ranges overlapping in southern Florida, it is useful to be able to distinguish them from each other. From information provided in this paper it is clear that the two species differ in external shape, *M. leucophaeta* being rather elongated and having a height/width ratio of less than 1.25:1, whereas *M. sallei* appears higher, having a height/width ratio greater than 1.3:1, and is also concave ventrally with slightly recurved beaks, causing *M. sallei* to appear more "hatchet-shaped" as described by Olsson (1961). The interior of shells of *M. leucophaeta* and *M. sallei* are more distinctly different, with noticeable differences in the hinge plate, the septum, the apophysis, the position of the posterior muscle scars and the coloration and general appearance (glossy or porcellaneous) of the interior surface of the valves. The hinge plate of *M. leucophaeta* is lower, wider and shorter than that of *M. sallei*, extending for only one-third to two-fifths of the length of the shell, as opposed to a hinge plate that extends for two-fifths to one-half of the shell length in *M. sallei*. The septum of *M. leucophaeta* is more rounded anteriorly than that of *M. sallei*, and tends to appear more "cup-shaped" rather than being nearly on the same plane as the hinge plate as is that of *M. sallei*. The apophysis of *M. leucophaeta* is closely associated with the septum, and therefore less apparent than that of *M. sallei*. The apophysis of *M. leucophaeta* is also not closely associated with the dorsal hinge plate, as is that of *M. sallei*, and tends to be small and rounded in appearance as opposed to that of *M. sallei*, which is comparatively larger and almost always pointed or "hook-shaped" posteroventrally. The posterior muscle scars of *M. leucophaeta* do not extend anteriorly to the posterior limit of the nymph, whereas those of *M. sallei* do, reflecting the longer relative length of the *M. sallei* ligament and hinge plate. *M. leucophaeta* also tends to have a lighter colored shell interior than that of *M. sallei*, which is often bluish-gray to dark blue-gray or black. Finally, the extra pallial region of the *M. leucophaeta* shell interior is usually porcellaneous, whereas that of *M. sallei* is glossy.

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Emergence Pattern of Cercariae from *Oncomelania hupensis formosana*, Snail Host for Zoophilic Schistosomiasis japonicum

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(2 Text figures)

INTRODUCTION

Our experiments on immunological study of *Schistosoma japonicum* require hundreds to thousands of cercariae from snails *Oncomelania hupensis formosana* (Pilsbry and Hirase, 1905) each day. Thus, it became imperative to gain information on the following: optimal number of miracidia for exposure to *O. h. formosana* to produce the maximal emergence of cercariae; the incubation period for cercarial emergence; the mortality rate of snails at post exposure weeks; and the effect of temperature on the emergence of the cercariae. Hence this paper, which is a by-product of (and yet essential to) our current study of schistosome immunity.

In reviewing the literature, most of the study on the emergence of cercariae has been conducted on the snail hosts for *Schistosoma mansoni* (Gordon, *et al.*, 1934; Kuntz, 1946; 1947; Rowan, 1958; Asch, 1972; Nojima & Sato, 1978), and on *Schistosoma haematobium* (Gordon, *et al.*, 1934; Nojima & Sato, 1978), and on *Schistosoma douthitti* (Olivier, 1951). Fewer studies exist on cercarial emergence of *Schistosoma japonicum* from snail *Oncomelania hupensis quadrasi* (Bauman *et al.*, 1948; Pesigan *et al.*, 1958; and Nojima *et al.*, 1980), and on *Oncomelania nosophora* (Osaka, 1938; Komiya & Ishii, 1954; Gumble *et al.*, 1957; Okamoto, 1963). There exists only one paper on *Oncomelania hupensis hupensis* (Mao *et al.*, 1949); one on *Oncomelania hupensis formosana chiui* (Chiu, 1968), and again one on *O. h. formosana* with scanty information (which is more than a half century ago, Isobe, 1923).

Results on the role of light and temperature on the emergence of cercariae from *Oncomelania* snails have not been conclusive. However, all agreed that emergence of cercariae is reduced at 30°C and above. Isobe reported that the longest emergence period for *Oncomelania hupensis formosana* is at 18-19°C. A detailed report on the initial shedding of *Oncomelania hupensis quadrasi* cercariae has been provided by Pesigan (1958), but a similar report has not been found on *O. h. formosana.*

This paper concerns the methods and numbers of cercariae introduced to *Oncomelania hupensis formosana* to obtain the highest percentage of infected snails; the incubation period required for the initial emergence of cercariae; the mortality of the infected snails; and the periodicity of cercariae emerged from shedding and crushed snails. These data had not been found to be reported on *O. h. formosana.* This paper also compares the effect of temperatures on cercarial emergence with what had been reported earlier on *O. h. formosana* (Isobe, 1923).

MATERIALS AND METHODS

Oncomelania hupensis formosana collected from the fields at Changhua, Taiwan, were used throughout the shedding experiments. They were reared in either 13 cm clay saucers with mud mixture and water (Wagner & Chi, 1959) or in 20 cm glass bowls. The latter is a modified method from Institute of Parasitic Diseases, Shanghai, People's Republic of China, and was prepared by placing tightly packed mud on the entire floor covered by 2 cm of water with several pieces of broken clay pottery emerging above the water for egg laying and with moist rough paper towels lining the walls for food. A dry foam rubber strip bordered the circumference of the containers and extended 2 cm above the wall to prevent the snails from escaping. This eliminated the necessity of a cover and allowed greater air exchange. Such glass bowls housed up to 200 snails. Food for the snails consisted of rough paper towels and filter paper smeared with brewer's yeast, algae, and cereal powder. These snails were kept at 28-30°C and under continuous lighting.

Snails were exposed to miracidia hatched from eggs from livers of mice infected with Formosan strain of *Schistosoma japonicum.* They were exposed for 24 hours either (1) individually to 5-7 miracidia in a 2 cm watch glass, or (2) in small groups of 6 snails to 30-35 miracidia in a container of 1.5 cm diameter, 3.5 cm height, or (3) en masse of numerous snails to an undetermined number of miracidia (greater than 40) in an 8cm diameter by 9cm high container. After exposure, snails were placed in the 9cm petri dish with mud and water (usually 25 snails per dish) for the first 8 weeks. After that, they were prepared for cercarial shedding. Water was removed from the culture dish to discourage cercarial emergence and henceforth these snails were kept in moist mud.

Starting at 9 or 10 weeks after exposure, snails were checked every 1-2 weeks for shedding. The shedding procedure was as follows:

First day: Dry and dark—all exposed snails were isolated individually in a small vial with no water and placed in a dark environmental chamber at 30°C for 24 hours to induce shedding;

Second day: Wet and dark—water was added to each vial and the snails were kept in the dark for an additional 15 hours, in case shedding in the dark occurred;

Third day: Wet and light—at 3 a.m. the light was turned on in the environmental chamber since previous experiments seemed to indicate more cercariae emerged with light exposure. At 8:30 a.m., the snails were removed from the chamber for the first checking, followed by a second checking four hours later. Positive snails were identified and separated for further shedding at subsequent weeks. The surviving non-shedding snails were crushed at 15-17 weeks after exposure to detect any hidden infection.

To study the effect of temperature on the emergence of cercariae, fourteen known positive snails were kept at 26°C, but on checking days were placed in either one of the following three temperatures: 20-22°C, 26-28°C, or 31-32°C and checked for the emergence of cercariae for a 5-month experimental period.

RESULTS AND DISCUSSION

Of the 2182 snails that were individually exposed to 5-7 miracidia and survived 2 months after exposure, 84 became positive and first started to shed cercariae (initial shedding) between 11-20 weeks. A few (7 snails) showed initial shedding as early as the 9th week after exposure, our first checking schedule, and one snail as late as the 44th week. However, the number of snails that shed cercariae for the first time declined after 20 weeks. A somewhat similar pattern was exhibited in 21 positive snails from the 246 snails exposed in groups of 6 to 30-35 miracidia. In this group, the earliest initial shedding date was the 11th week after exposure and none shed after 19 weeks (Figure 1). With the en masse exposure group, only 3 snails out of 119 became positive and the number was too small to be significant. Thus, the initial shedding date could vary in a range from approximately 2 months after exposure to (rarely) 10 to 11 months.

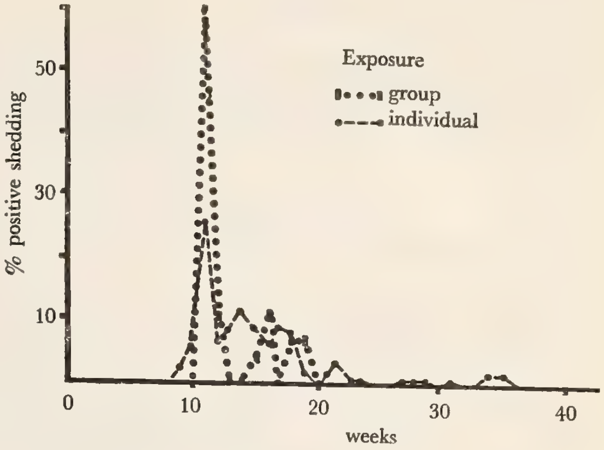

Figure 1

Percentage of positive snails exposed individually or in groups with initial shed various weeks after exposure

Such variation could be due to (1) the genetic variability of the individual snail, (2) parasites' variability, and (3) the length of time that these snails were in a desiccated condition. *Oncomelania* species are known to be able to survive in dry environments. Many are found to crawl up the dry wall of the culture dish and remain desiccated there until they regain moisture through the spraying of water or by being pushed back to the water. No doubt the development of sporocyst and production of cercariae could be delayed under such desiccated conditions. Whatever the cause may be, when the "incubation period" of infected snails could be as long as almost a year, it creates a difficult problem in schistosome control.

In comparing the three methods of exposure, the highest percentage of infected snails was obtained in small group exposure—8.5% (21/246). The percentages for the other exposure method were 3.8% (84/2182) for individually exposed snails, and 2.5% (3/119) for en masse. (Table 1). The overall percentage of shedding is small. Of course, it was not known if the snails that died were infected or not. The percentage of *Oncomelania hupensis formosana* snails that shed cercariae from previous findings from laboratory-raised snails has been higher, around 15% (Chi *et al.*, 1971). The lower infection rate could be due to the condition of the field snails. With the progression of time, we have noted a difference in the physical condition of the field snails received in regard to survival rate and fecundity. Previously the snails arrived with approximately 80% survival rate, and the reproduction continued; young snails appeared in about two to three months after arrival, and laboratory-raised snails were available for experi-

Table 1

Shedding results from snails under various exposure methods.

Exposure method	Number of snails Total	Surv. 2 mo.	+	% +
Individual 5-7 miracidia per snail	3523	2182	84	3.8
Small group 30-35 miracidia per 6 snails	345	246	21	8.5
En masse num. miracidia per num. snails	208	119	3	2.5
Total	4076	2547	108	4.2

ments. Currently the snails have arrived with only about 50% survival rate. The reproduction rate is slow and experimental snails would depend heavily on the replenishment by the field snails. Perhaps the field snails' being exposed to chemicals and molluscicides has resulted in reduced survival rate as well as greater resistance to schistosome infection. The high mortality rate of the laboratory-infected snails could also be attributed to the low infection rate as the infection was unknown in dead snails. Of the 1660 snails crushed, only 20 were positive. Most positive snails (12/20) were those crushed between 26 to 31 weeks and again (6/20) between 38-45 weeks after exposure. After that period (46-75 weeks), none were positive (Table 2).

Table 2

Number of crushed snails positive at various weeks after exposure.

Weeks after exposure	No. snails crushed	No. snails +	% +
14-15	28	0	0
16-21	none		
22-23	14	0	0
24-25	232	1	0.43
26-27	58	1	1.70
28-29	318	9	2.80
30-31	104	2	1.90
32-33	361	1	0.28
34-35	60	0	0
36-37	116	0	0
38-39	62	1	1.60
40-41	33	1	3.00
42-43	41	1	2.40
44-45	119	3	2.60
46-75	114	0	0
Total	1660	20	1.20

This seems to indicate that when snails harbor the cercariae, they have the tendency to shed them. It was only rarely that the snails retained the cercariae with no shedding activities.

About half of the positive snails repeated shedding over a 12-week experimental period. Out of a total of 53 snails known to be infected, 27 shed cercariae only once in 12 weeks. The other half exhibited multiple sheddings from two to five times. Similar results were exhibited by the group exposure method. Half of the snails only shed cercariae once; the other half showed multiple sheddings from two to four times.

Once the snails started shedding (in the 12-week experimental period), the number of cercariae emerging did not seem to decrease on later shedding dates, and the number of cercariae shed did not vary much between those exposed as a group or individually.

Of 73 positive snails over the two-day immersion period, most snails that shed did so on one day instead of two, and slightly more snails shed on the first day. The snails that shed on both days appeared to release more cercariae per day than those that shed on one day only. There was not much difference in degree of shedding between snails shedding on day one or day two.

As to the mortality of the snails that were exposed to miracidia, the heaviest toll began at 9 weeks after exposure and continued for 34 weeks (Figure 2). About 10% of the snails were found dead at every 2-week checking interval. En masse and small groups exposed snails had a higher mortality than individually exposed snails, especially in the early weeks (Figure 2). Whether the mortality rate is the result of harboring parasites, or the dryness in environment where the infected snails were kept before shedding induction, or the harassment of being submerged in water for two days during shedding checking dates, has not been determined.

As to the effect of temperature on cercarial emergence, *Oncomelania hupensis formosana* shed more cercariae at a cooler temperature of 20-22°C, an average of 135 cercariae per positive snail. At 26-28°C, the shedding is reduced and there was an average of 64.4 cercariae per snail. At 31-33°C the shedding is greatly reduced or completely stopped and only 0.76 cercariae per snail resulted. The reduced shedding at 30°C and above is in agreement with ISOBE (1923) and the MAO *et al.* (1949) working with *Oncomelania hupensis hupensis*, and BAUMAN *et al.* (1948) on *Oncomelania hupensis quadrasi*.

SUMMARY

The highest percentage of infected snails was obtained by exposing a small group of 6 snails to a total of 30-35 cercariae. The majority of the snails started shedding cer-

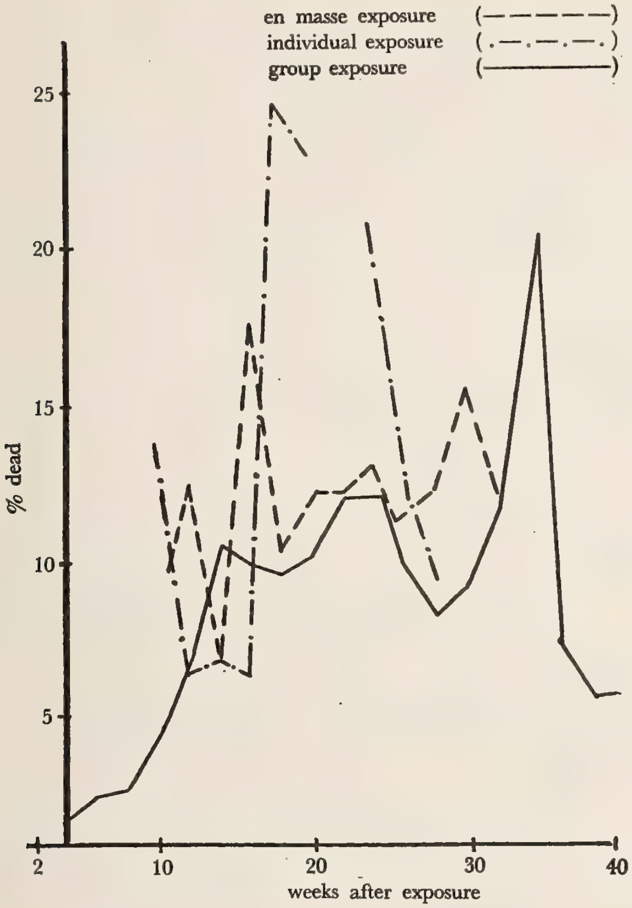

Figure 2

Mortality of snails exposed to miracidia by various methods (Individual vs. group vs. en masse exposure)

cariae at 10-11 weeks after exposure, but initial shedding ranged from 9 to 44 weeks. The number of snails that shed for the first time declined 20 weeks after exposure. The overall infection rate of *Oncomelania hupensis formosana* collected from the fields was about 5%. The snails that did not shed usually did not harbor cercariae. Only 20 of 1660 non-shedding snails crushed by 45 weeks after exposure were positive. When snails repeated shedding, the number of cercariae produced did not decrease. In a two-day shedding schedule, more snails shed on the first day. The mortality rate was highest for the majority of snails at 11 weeks after exposure.

ACKNOWLEDGMENTS

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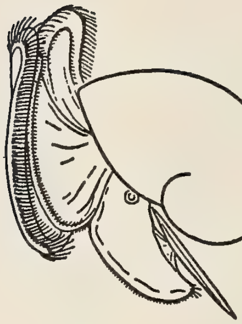

Systematics and Distribution of *Conus sanderi s. l.*

BY

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(2 Plates)

INTRODUCTION

In recent years 4 new species of *Conidae* were described from deep-water off the west coast of Barbados:

Conus sanderi Wils & Moolenbeek, 1979
Conus hunti Wils & Moolenbeek, 1979
Conus sorenseni Sander, 1982
Conus knudseni Sander, 1982

The species are obviously related, but scarcity of material has so far precluded a detailed study of their relationship. As already pointed out by Sander (1982) "further collections are required not only to describe the radula, operculum and soft parts of the living animals, but also to ascertain the extent of variation in the anatomy of the adult shells…" Rather than await the results of further collecting, the present authors have brought together more than 50 specimens of this species complex from various private collections. Examination of this rich material has led to a better understanding of the extent of variation within *Conus sanderi s. l.* and its distribution throughout the Western Atlantic.

Identification of *Conus sanderi s. l.*

First, the group of species should be well delimited. Wils & Moolenbeek (1979) and Sander (1982) briefly compared their nominal species with *Conus daucus* Hwass, 1792, *C. centurio* Born, 1778, *C. juliae* Clench, 1942, *C. villepini* Fischer & Bernardi, 1857, *C. amphiurgus* Dall, 1889, *C. attenuatus* Reeve, 1844, *C. mindanus* Hwass, 1792 and *C. jaspideus* Gmelin, 1791. In particular, confusion is possible with *C. villepini*, *C. centurio* and *C. daucus* (Figure *1*). The differences with these species will be further studied below.

1) *Conus villepini*

Some specimens of the group of nominal species here studied can be easily confused with *Conus villepini* (Figure *1*a). Wils & Moolenbeek (1979) list differences between *C. hunti* and *C. villepini* (*i. e.*, *C. villepini* is "more slender" …"larger"…"white with rows of large yellowish brown blotches") but these are insufficient for distinction between the specimens referred to above and *C. villepini*. Sander (1982) draws attention to the fact that *C. villepini* is "moderately light in weight" and this we feel is important as it reveals a different shell structure. However, the best differential character between *C. villepini* and species belonging to the *C. sanderi* complex is found in the morphology of the early whorls: in *C. sanderi s. l.* the earliest 2-4 postnuclear whorls are nodulose, in *C. villepini* the earliest 4-6 postnuclear whorls are ornamented with less numerous but larger nodules.

It is interesting to note that the pattern of the holotype of *Conus villepini* with irregular brown blotches is not typical for the species as known for instance from Florida, and it is legitimate to ask whether the *Conus* described by Fischer & Bernardi (1857) is not rather a specimen of *C. sanderi s. l.* It is a small specimen (32 mm) rather heavy ("solide"), collected near Marie Galante in the Eastern Caribbean. No mention is made of nodules on the spire whorls and these are often worn in specimens of *C. sanderi s. l.* On the other hand, the illustration of the holotype of *C. villepini* shows a cone with a rather straight spire (typical for specimens of the species traditionally known as *C. villepini*) and not concave as in most specimens of *C. sanderi s. l.* The present whereabouts of the holotype of *C. villepini* is not known. Until critical examination of the holotype, revealing it to be a specimen of the species here dealt with as *C. sanderi s. l.*, is possible, we prefer to maintain the well-known and established name *C. villepini* for the less heavy and larger species with 4-6 nodulose postnuclear whorls.

2) *Conus centurio*

Various rather large specimens of the group of species here studied are white with brown zigzag flammules reminiscent of the pattern of *Conus centurio* (Figure *1*c). They can be identified as not being this latter species by the spiral striae on the postnuclear whorls which are very weak or lacking in *C. centurio,* a feature already highlighted by Wils & Moolenbeek (1979) and Sander (1982) (Also in *C. knudseni* the postnuclear whorls are without distinct striae, but the pattern of this species does not lead to confusion with *C. centurio*). Furthermore, the spire of *C. centurio* is straight or only slightly concave in contrast to a concave spire in *C. sanderi s. l.*

3) *Conus daucus*

There is no doubt that *Conus daucus* without sculpture on the sides of the early whorls is a species distinct from *C. sanderi s. l.* However, the axial sculpture on the early postnuclear whorls in *C. sanderi s. l.* is sometimes worn and this may lead to confusion (Figure *1*e). Wils & Moolenbeek (1979) point to the higher spire and the lack of a pinkish protoconch in *C. sanderi,* but Vink (1979) has shown that the pattern and color of *C. daucus* shows much more variation than hitherto assumed (ranging from orange, orange/white to lilac, lilac/brown) and various color forms do not have a pinkish protoconch. Sander (1982) indicates that the shoulder in *C. daucus* is "broader, angulate to carinate, and slightly concave above." Indeed, most specimens of *C. sanderi s. l.* are more slender and where specimens of *C. sanderi s. l.* and *C. daucus* are of a similar triangular shape, the body whorl in *C. daucus* becomes convex somewhat lower below the shoulder than in *C. sanderi s. l.* Again the difference between the two species can best be seen from the postnuclear whorls, which in *C. daucus* immediately have larger tops than sides, whereas in *C. sanderi s. l.* high sides can be observed on the first three postnuclear whorls, the shoulder distinctly overhanging the suture of the next whorl.

Variation of *Conus sanderi s. l.*

In the first instance, an attempt was made to identify the material brought together with the 4 species recently named. For comparison the type material of *Conus sorenseni* and *C. knudseni* was available; specimens closely resembling the types of *C. sanderi* and *C. hunti* were found in the collection D. Hunt.

At first, difficulty was encountered in placing a number of large (up to 34 mm) white specimens with brown *centurio*-like and *villepini*-like markings, which, however, clearly belong to the *Conus sanderi* species complex. It was possible to identify these cones provisionally as *C. hunti,* and a number of such specimens can be put in a series showing the purplish background color gradually becom-

Explanation of Figures *1* to *3*

Figure *1:* Specimens of *Conus sanderi* Wils & Moolenbeek, 1979 resembling other species

a) 26.2 mm, coll. Vink, resembling *Conus villepini*

b) *Conus villepini* Fischer & Bernardi, 1857, 47.1 mm, Florida Keys

c) 31.9 mm, coll. Vink, resembling *Conus centurio*

d) *Conus centurio* Born, 1780, 48.4 mm, Trinidad

e) 25.0 mm, coll. Vink, resembling unusual colorform of *Conus daucus*

f) *Conus daucus* Hwass, 1792, 31.9 mm, Curaçao

Figure *2:* Transition of the colorform described as *Conus hunti* Wils & Moolenbeek, 1979 toward forms resembling *Conus villepini* Fischer & Bernardi, 1857 and *Conus centurio* Born, 1778

a) 22.9 mm, coll. Vink

b) 18.5 mm, coll. Hunt

c) 20.0 mm, coll. Hunt, resembling the holotype of the colorform described as *Conus hunti*

d) 29.1 mm, coll. Sander, resembling *Conus villepini*

e) 33.4 mm, coll. Vink, resembling *Conus centurio*

Figure *3:* Transition of *Conus sanderi* Wils & Moolenbeek, 1979 *s. s.* towards the colorform described as *Conus sorenseni* Sander, 1982

a) 22.8 mm, coll. Hunt, resembling the holotype of *Conus sanderi*

b) 22.3 mm, coll. Vink

c) 25.0 mm, coll. Vink

d) 16.3 mm, coll. Sander, paratype 1 of *Conus sorenseni*

e) 34.2 mm, coll. Zoological Museum, Copenhagen, holotype of *Conus sorenseni*

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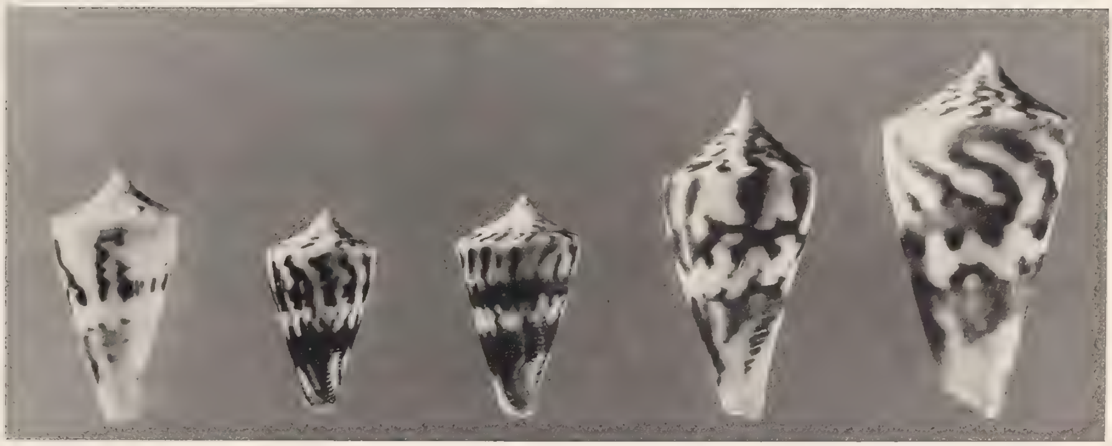

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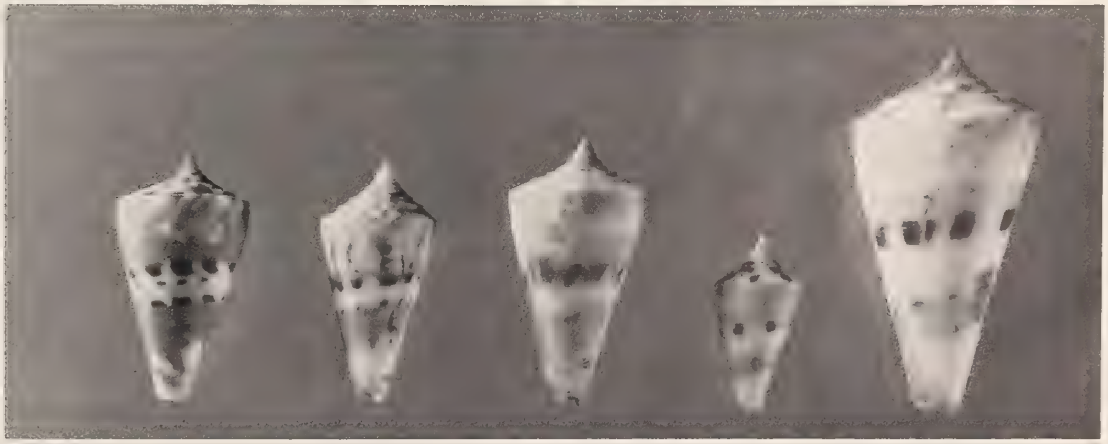

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ing more pale and finally white with increasing size (Figure *2*). The body whorls of some large specimens have spiral ridges (Figure *2*d), but most large specimens are smooth (Figure *2*e). It is apparent that Wils & Moolenbeek (1979) have only studied juvenile specimens of *C. hunti* with maximum size of 23 mm.

In *Conus sanderi s.s.* the observation can be made that the white zigzag streaks on the upper part of the body whorl sometimes merge into a whitish band, and in some specimens (Figure *3*b) also the base becomes white. The pattern can then be described as consisting of two yellowish orange bands bordering the white midbody band, with spiral lines of brown spots on the borders. On some specimens, in addition, other faint brown spotted lines are present. One specimen (Figure *3*c) with pinkish orange bands on a pinkish white background shows affinity with *C. sorenseni,* and, in fact, a number of specimens can be put in a series showing a typical *C. sanderi s.s.* gradually being replaced by the larger *C. sorenseni* with a white ground color (Figure *3*). There are no morphological differences between *C. sanderi s.s.* and *C. sorenseni;* we now consider the latter a form of *C. sanderi.*

As already observed by Wils & Moolenbeek (1979), the color pattern of *Conus hunti* is variable and "on the purplish ground colour sometimes only a few dark brown blotches are present." One such specimen, (Figure *2*a) with brown spots above the light midbody band and with 2 faint brown spotted lines below this band, somewhat resembles pinkish *C. sorenseni,* and we cannot but conclude that also *C. hunti* is to be considered a color form of *C. sanderi (C. sorenseni* in a way constituting a link between *C. sanderi* and *C. hunti).* It can be argued that *C. hunti* is quite distinct from *C. sanderi* and *C. sorenseni* with its brown axial flames, but then it should be noted that *C. sanderi* also shows zigzag orange streaks on the upper part of the body whorl which as Wils & Moolenbeek (1979) observed "continue on the spire as darker markings." It has been stated that *C. hunti* "has grooves all over the last whorl" whereas *C. sanderi* has spiral grooves on the base only, but this feature is not consistent in all specimens of *C. hunti* (some specimens even as small as 16 mm are smooth).

Of the nominal species of *Conus sanderi s. l., C. knudseni* is one of the rarest. Apart from the holotype and two paratypes, only two more specimens could be identified as belonging to this group. Sander (1982) described the color pattern of this *Conus* as white with two pale orange bands. One of the specimens identified as belonging to this group (Figure *4*a) has the orange upper band extending up to just below the shoulder with white blotches in the orange area. The pattern reminds one of some specimens of *C. sanderi s.s.,* but the rows of brown spots bordering the white mid area are missing. Nevertheless, under a lens spiral lines of orange dots can be observed. Sander (1982) pointed to the fact that *C. sanderi, C. hunti* and *C. sorenseni* all differ from *C. knudseni* in having prominent striae on the spiral whorls, which are nearly absent on the spiral whorls of the type specimens of *C. knudseni.* On the newly identified specimens, however, spiral striae are present, albeit somewhat obscured by strong though fine concave growth lines (concave, because they are the growth layers following the "notch" or apertural inset). In view of the large variability of *C. sanderi s. l.* now recognized, the fact that again two orange bands around a white midbody band can be observed with reduced orange dotted spiral lines, and the fact that the absence of striae on the spiral whorls does not seem to be consistent, we now conclude that *C. knudseni* is to be considered a form of *C. sanderi.*

Distribution of *Conus sanderi s. l.*

All nominal species of *Conus sanderi s. l.* are from Barbados. However, the species is not well known and specimens from other areas may well have been confused with *C. centurio, C. villepini* or *C. daucus.* There is evidence that *C. sanderi s. l.* occurs near Surinam and in Brazil.

1) Surinam

During dredging operations off the coast of Surinam in 1966, 1969 and 1970 only one specimen of *Conus daucus* was collected. This specimen of 28.5 mm was dredged from a depth of 94 m and pictured by Van Mol (1973: plt. 2, fig. 7). The specimen has the slender outline and triangular shape of *C. sanderi,* the profile of the early whorls is typical for this species and its color pattern resembles that of a specimen of *C. sanderi* from Barbados (Figure *3*b). In our opinion this specimen should be identified with *C. sanderi.*

2) Brazil

According to Van Mol, Tursch & Kempf (1967) *Conus daucus* is very rare in Brazil. They make the observation that adult Brazilian specimens seem to be very different from the typical form of *C. daucus.* However, not enough specimens could be examined to establish the existence of a well defined geographical variety. The specimen pictured by Van Mol *et al.* (1967: plt. 7, fig. 2) with the early postnuclear whorls forming a raised cone on a flat spire could well be *C. sanderi.* It is worth mentioning that the picture of the spire of *C. daucus* in Van Mol *et al.* (1967: fig. 7) which shows similarities with the spire of *C. sanderi* is replaced by a picture of a more typical spire of *C. daucus* in a later publication by Van Mol & Tursch (1968: fig. 1).

We studied a number of *Conus* specimens from Brazil, made available by Dr. L. R. Tostes, which in our opinion should be identified with *Conus sanderi* (Figure *5*b-e). All were dredged from deep-water off the coast of the State of Espirito Santo. They are slender with straight sides of the body whorl and angulated shoulders. The spire is concave and the postnuclear whorls have 4-5 striae. Typically, the early post nuclear whorls have higher sides than tops, but the axial sculpture is worn and only traces of it are visible on the two smallest specimens. Just as in typical *C. sanderi* the color pattern varies considerably, the ground color ranging from yellowish orange to orange red. There is a white midbody band, while white patches on the upper half of the body whorl sometimes form a second white band. One specimen (Figure *5*b) is only orange and white, much resembling a similar and somewhat unusual specimen from Barbados (Figure *5*a), but normally there are spiral lines of brown and white, the brown patches above the white midbody band being the most conspicuous. One specimen (Figure *5*c) shows a tendency to produce brown flames as in *C. hunti.*

Most specimens of *Conus sanderi* from Brazil are very large (up to 54mm) as compared to *C. sanderi s. l.* from type locality (up to 37mm). A similar situation was observed by Coomans, Moolenbeek & Wils (1979) in the case of *C. mindanus:* whereas the typical subspecies from Barbados *C. mindanus agassizii* Dall, 1886 only measures 30mm, specimens of *C. mindanus* are dredged off the State of Rio de Janeiro, Brazil, which measure 50mm or more. Also in the case of *C. cancellatus* Hwass, 1792 (still better known as *C. austini* Rehder & Abbott, 1951, a junior synonym) we see normal size specimens (up to 50mm) being replaced by very large specimens (70 to 80mm) in the South, dredged off the coast of the State of Espirito Santo (as pointed out by Vink (1982), these large specimens should not be identified with *C. capricorni* Van Mol, Tursch & Kempf, 1967). Possibly this tendency towards larger specimens in the South is related to a lower water temperature at these latitudes near the limit of their range.

CONCLUSIONS

Conus hunti, C. sorenseni and *C. knudseni* should all be considered forms of *C. sanderi,* which is a highly variable species. The species occurs in the Western Atlantic from Barbados to Brazil with records from off Surinam and off the State of Espirito Santo. Brazilian specimens are larger than typical *C. sanderi* from type locality.

ACKNOWLEDGMENT

The authors are grateful to Dr. L. R. Tostes from Rio de Janeiro and Mr. D. Hunt from Barbados for making available specimens from their collections for study. Dr. J. Knudsen of the Zoological Museum in Copenhagen kindly allowed us to photograph the type specimens of *Conus sorenseni* and *C. knudseni.*

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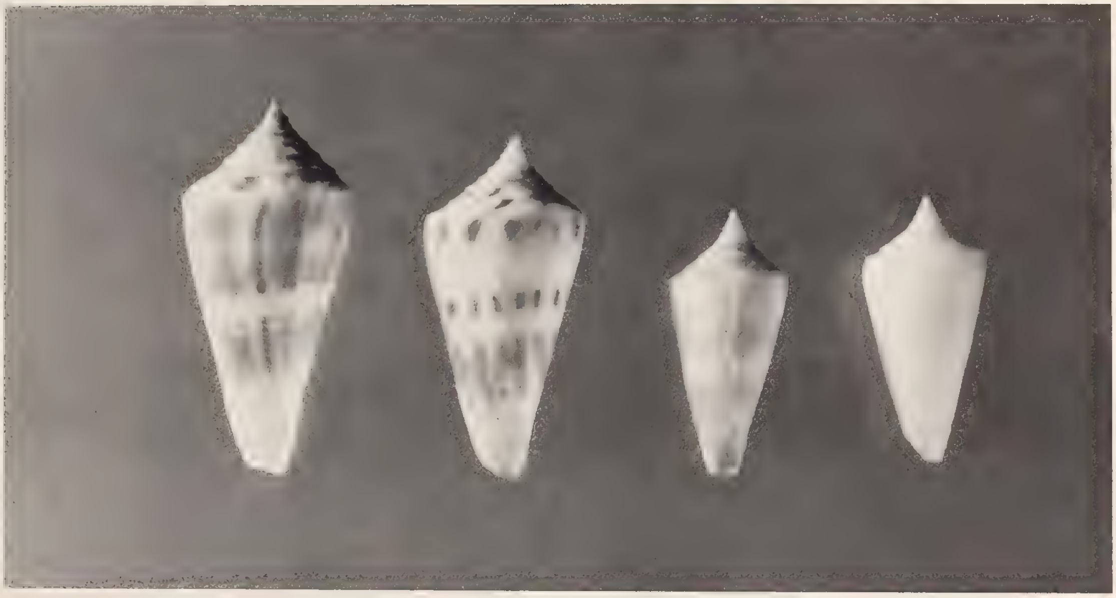
Explanation of Figures *4* and *5*

Figure *4:* The colorform described as *Conus knudseni* Sander, 1982
a) 32.0mm, coll. Vink
b) 29.0mm, coll. Vink
c) 22.4mm, coll. Sander, paratype 2 of *Conus knudseni*
d) 22.7mm, coll. Zoological Museum, Copenhagen, holotype of *Conus knudseni*

Figure *5:* Specimens of *Conus sanderi* Wils & Moolenbeek, 1979 from Barbados and Brazil, State of Espirito Santo
a) 36.7mm, coll. Sander, Barbados
b) 30.3mm, coll. Tostes, Brazil, resembling specimen *5*a
c) 44.9mm, coll. Vink, Brazil
d) 53.6mm, coll. Vink, Brazil
e) 48.6mm, coll. Tostes, Brazil



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5a 5b 5c 5d 5e

The genus *Chaetopleura* Shuttleworth, 1853

(Mollusca : Polyplacophora)

in the Warm-Temperate and Tropical Eastern Pacific, Southern California to Peru, with the Description of Two New Species

BY

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(4 Plates; 15 Text figures)

INTRODUCTION

In the course of investigating the chiton fauna of the eastern Pacific, it became apparent that a species of *Chaetopleura* described and illustrated a decade ago (Thorpe *in* Keen, 1971) had remained unnamed. In the process of providing the new species with a valid name, it was necessary to reconsider the prevailing understanding of other species in the genus, a process which eventually led to the discovery of a number of serious errors that had become ingrained in the literature of the group.

In carrying out of this review, I was favored by the availability of large collections of chitons from the tropical and warm-temperate eastern Pacific, particularly those in the repository of the California Academy of Sciences, San Francisco, (CAS), Stanford University (SU) [at CAS], Natural History Museum of Los Angeles County (LACM), Allan Hancock Foundation (AHF) [at LACM], San Diego Museum of Natural History (SDMNH), Academy of Natural Sciences of Philadelphia (ANSP), U.S. National Museum of Natural History (USNM), British Museum (Natural History) (BMNH), Muséum National d'Histoire Naturelle, Paris, (MNHN), and in the private collections of Laura B. Shy, Col. George A. Hanselman, and Antonio J. Ferreira (AJF-station numbers on file at CAS).

The following abbreviations for type designations are used: M = monotypy; OD = original designation; SD = subsequent designation.

The distinctions among the different species of *Chaetopleura* in the tropical and warm-temperate eastern Pacific were difficult to ferret out. In view of the unexpected conclusions of this investigation, a word is in order concerning methodology.

Initial endeavors to segregate specimens of *Chaetopleura* in accordance with named descriptions were, for the most part, fruitless. The original descriptions and stated differences among species of *Chaetopleura* with exclusive emphasis on tegmental sculpture and macroscopic girdle elements soon proved inadequate to unequivocal species assignment and taxonomic decisions. Several species of *Chaetopleura*, it was found, differ in characters which, being subtle, had been overlooked by earlier workers. Thus, a *tabula rasa* approach was adopted. The basic question raised: How many biological species of *Chaetopleura* can there be recognized in eastern Pacific collections?

Accordingly, every available specimen of *Chaetopleura* [the identification of the genus posed no serious problem] from the eastern Pacific was classified, at first, simply as "species A," "species B," "species C," etc. with no regard for museum (or collector's) label, geographic locality, or depth. The classification criterion was purely morphologic, based not only on the shell but on microscopic data derived from the examination of the mounted girdle and radula. With this approach, entailing the disarticulating of many specimens, consistent patterns eventually emerged which permitted the firm recognition of 5 species of *Chaetopleura* in the tropical and warm-temperate eastern Pacific. The nomenclatural problems involved in the subsequent naming of these species are treated in the systematic section of this paper.

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In the course of this investigation it became apparent that some anatomical features of chitons, particularly the radula, the mucro and what is here called the girdle bridges, had not been given adequate consideration by former workers.

The mucro has been considered in the descriptive anatomy of chitons at least since MIDDENDORFF (1847: 9). But its definition lacked precision. SMITH (1960: 46) defined it as the "point or projection in the tail valve, usually marking a separation between the configuration of the central and posterior areas." The problem, of course, is with the word "usually" for there are instances when the salient point on the valve does not coincide with the separation between the central and posterior areas, resulting in unclear descriptions. In view of the common usage of the terms mucro and postmucro (applied to the posterior area of the tail valve), it is here proposed that **mucro** be used for the median point on the tail valve where the central and posterior configurations (*i.e.*, sculptural patterns) meet, a point which is "usually" the salient point of the valve; and that the term **false mucro** be used for those situations, such as in the case of most specimens of *Chaetopleura lanuginosa*, where the prominence or salience of the tail valve is located in the postmucro (often strongly convex) area.

The **girdle bridges** refer to the tenuous prolongations of the girdle that extend between valves at the sutural joints and so bridge both sides of the girdle. In most species studied, when examined under the microscope, these girdle bridges are "empty," that is to say, they appear as amorphous, transparent cuticles devoid of scales, hairs, or spicular elements; but, by contrast, in a few species, such as *Calloplax janeirensis* (Gray, 1828) [see FERREIRA, 1978: 58] and some members of *Chaetopleura*, the bridges are packed with spicular elements throughout.

HISTORICAL SYNOPSIS

1853. SHUTTLEWORTH erected *Chaetopleura* to accommodate three species, "*Chiton rugosus* (Gray) Sowb., Ind. Oc. / *Chiton peruvianus* Lam., Chili / *Chiton gigas* Chemn., Cap. Bon Spei." The new genus was distinguished from *Acanthopleura* Gray, on the basis of the girdle elements, and defined "*Valvae transversae, externae; lamina insertionis valvarum terminalium plurilobata, posticae interdum subobsoleta, mediarum bilbata; limbus setis corneis obsitus*" (pp. 66-67).

1854. ADAMS & ADAMS defined *Chaetopleura* (with *Eudoxochiton* Shuttleworth, 1853, and *Craspedochiton* Shuttleworth, 1853, as synonyms): "Mantle beset with horny bristles. Shell with the valves external, broad, transverse; the hinder valve with the apex sub-central" (p. 475). They included 8 species in the genus, "*fulva*, Wood / *Hanleyi*, Bean / *Hennahi*, Gray / *laqueata*, Reeve / *nobilis*, Gray / *Peruviana*, Lam. / *rugosa*, Sow. / *Watsonii*, Sow." (p. 476).

1856. SHUTTLEWORTH described two new species of *Chaetopleura* from the Antilles, *Chiton (Chaetopleura) asper*, and *Chiton (Chaetopleura) candisatus*, observing that the latter has affinity to "*C. (Chaëtopleura) Hanleyi* Bean [1844]...(and) *C. (Chaetopleura) apiculato* Say" (p. 169).

1857. GRAY made no mention of *Chaetopleura*, placing *Chiton peruvianus* Lamarck in *Acanthopleura*.

1864. ADAMS & ANGAS described *Chaetopleura conspersa* from Port Lincoln, Australia.

1879. DALL, following Carpenter's unpublished manuscript, recognized *Chaetopleura* in the "Ischnoidea" group of "Regular Chitons," and explicitly designated *C. peruviana* as its type species. He diagnosed the genus, "*Testa Ischnochitoni similis; zona plus minusve pilosa. Branchiae ambientes*" (p. 329), adding a new species, *Chaetopleura gemma*, and bringing two others, *Chiton hartwegii* Carpenter, 1855 and *C. nuttallii* Carpenter, 1855, into it.

1892. PILSBRY recognized *Chaetopleura*, relating it to *Tonicia*, with the diagnosis, "Valves as in *Ischnochiton; eaves solid* [italics, Pilsbry's]; girdle leathery, more or less hairy; gills extending almost or entirely to the front end of the foot" (14: 27). PILSBRY (14: 28) considered the genus divisible into "several" groups of species, although he mentioned only two: 1) group of *C. peruviana*, "typical forms, rather large, and having very delicate sculpture," and 2) group of *C. gemma*, "having the lateral areas strongly raised and coarsely sculptured, the central areas also sculptured."

1899. PLATE erected Chaetopleurinae as a subfamily of Ischnochitonidae to accommodate the genera *Chaetopleura* and *Variolepsis* Plate, 1899.

1901. PLATE suppressed Chaetopleurinae, and placed *Chaetopleura* in Ischnochitoninae.

1929. THIELE defined *Chaetopleura:* "Surface of the shell with pustules, in the end valves and lateral areas in radial riblets or disorganized, in the central areas in longitudinal riblets. Upper side of girdle with small calcareous scale-like or cylindrical processes, larger spicules, or more or less elongated hairs" (p. 16, transl.). Based on the radula, Thiele distinguished two subgenera: 1) *Pallochiton* Dall, 1879, including *C. (P.) lanuginosa* (Dall, 1879), with a tricuspid major lateral tooth, and 2) *Chaetopleura s. s.*, including *C. (C.) peruviana* (Lamarck, 1819) with bicuspid major lateral teeth.

1955. BERGENHAYN placed *Chaetopleura*, *Dinoplax* Dall, 1882 and *Calloplax* Thiele, 1909, in the same family, Chaetopleuridae Plate, 1899.

1960. Smith accepted Bergenhayn's (1955) classification, and diagnosed *Chaetopleura:* "Small to medium sized, with valves somewhat as in *Ischnochiton,* ventral side porcelaneous, having rather sharp [insertion] teeth and squared sinus; eaves solid. Tegmentum usually sculptured with longitudinal beaded riblets on central areas, and pustules or pustulose ribs on lateral areas of intermediate and end valves, pustules being irregularly arranged in some groups" (p. 60).

1972. Kaas defined *Chaetopleura:* "Shell plates pustulate; on the end valves and lateral areas of the median valves the pustules are arranged in radial rows or scattered without order, on the central areas they are arranged in longitudinal rows. Upper side of girdle clothed with small scale-like or cylindrical calcareous corpuscules, between them spicules of different sizes" (p. 63).

1977. Van Belle defined the genus *Chaetopleura:* "Taille petite à moyenne, forme ovale, tegmentum pourvu de nodules radiaires ou placés sans ordre special, sinus subquadrangulaire et pourvu d'une plaque jugal, dents courtes et rugueuses" (p. 28).

SYSTEMATIC TREATMENT

POLYPLACOPHORA Gray, 1821

Neoloricata Bergenhayn, 1955

Ischnochitonina Bergenhayn, 1930

Chaetopleuridae Plate, 1899

Chaetopleura Shuttleworth, 1853

Definition: Small to large sized chitons. Tegmentum pustulose, with larger pustules arranged in quincunx or radial rows in the end-valves and lateral areas of intermediate valves, and smaller pustules in longitudinal rows or coalesced in riblets in the central areas. Insertion plates with rather sharp teeth; intermediate valves uni-slit. Eaves solid. Girdle covered with minute, simple, oval to spiculoid scales, with glassy, hyaline spicules and, in some species, horny hairs interspersed. Holobranchial, abanal gills. Radula median tooth wide, subquadrangular; major lateral teeth tricuspid or bicuspid.

Type species: *Chiton peruvianus* Lamarck, 1819, by SD (Dall, 1879).

Synonyms:

Choetopleura Shuttleworth, 1856 [nomen nullum]
Acanthopleura Gray, 1857 (not Guilding, 1829)
  Type species: *Chiton peruvianus* Lamarck, 1819, by SD, based on the first species listed by Gray (1857: 183) under this genus name (Ferreira, herein)
Pallochiton Dall, 1879
  Type species: *Pallochiton lanuginosus* Dall, 1879 by SD (Pilsbry, 1893)
Hemphillia Dall, 1879 (not Bland & Binney, 1872, a land slug)
  Type species: *Pallochiton lanuginosus* Dall, 1879, by M
Arthuria Dall, 1882
  Type species: *Arthuria filosa* Carpenter *in* Pilsbry, 1893c by SD (Pilsbry, 1893c)
Helioradsia Thiele, 1893
  Type species: *Chaetopleura gemma* Dall, 1879, by M
Helicoradsia Simroth, 1894 [*nomen nullum*]
Variolepsis Plate, 1899
  Type species: *Variolepsis iquiquensis* Plate, 1899, by OD
Typhlochiton Dall, 1921
  Type species: *Typhlochiton felipponei* Dall, 1921b, by OD
Chetopleura Ashby, 1929 [nomen nullum]

Remarks: In terms of species diversity, the genus *Chaetopleura* has a rather uneven world distribution: It is well represented in the faunas of the eastern Pacific, both sides of the Atlantic, and South Africa, but apparently absent in the Indo-Pacific and the otherwise chiton-rich waters of Australia, New Zealand, and Japan.

In the eastern Pacific, *Chaetopleura* ranges from Canada to Chile. In the area covered by this review, the tropical warm-temperate zones of the eastern Pacific, from Point Conception, California [34°27′N] to Punta Aguja, Peru [5°48′S], 5 species are here recognized:

Chaetopleura scabricula (Sowerby, 1832)
Chaetopleura lanuginosa Dall, 1879
Chaetopleura unilineata Leloup, 1954
Chaetopleura roddae Ferreira, spec. nov.
Chaetopleura shyana Ferreira, spec nov.

Key morphological characters in the differential diagnosis of these species are brought together in Table 1.

Chaetopleura scabricula (Sowerby, 1832)

Figures *1, 2, 3, 4,* 5, 6, 7, 8, *9,* and *11*

Chiton scabriculus Sowerby (1st) *in* Broderip & Sowerby, 1832: 28—Sowerby (1st and 2nd), 1840: 8, no. 100; fig. 21—Reeve, 1847; plt. 15, sp. & fig. 81—Pilsbry, 1892, 14: 33 (as syn. of *Chaetopleura lurida* (Sowerby, 1832))—Keen, 1958: 524 (as syn. of *C. lurida*)—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)

"*Chaetopleura lurida* (Sowerby)" *ex auttore* treating Panamic species. Pilsbry, 1892, 14: 33-35; plt. 12, figs. 53-54—Steinbeck & Ricketts, 1941: 552; plt. 27, fig. 3 [Reprinted, 1971]—Keen, 1958: 524; Amphineura, sp. & fig. 35—Thorpe *in* Keen, 1971: 877-878, Polyplacophora, sp. & fig. 41—Abbott, 1974: 401—Smith, 1977: 217, 243, 246. [Not *Chiton luridus* Sowerby (1st) *in* Broderip & Sowerby, 1832: 26]

"*Chiton columbiensis* Sowerby, 1832" Sowerby (2nd), 1840: 8, no. 99, fig. 15 (as syn. of *C. spinulosus* Gray and *C. luridus* Sowerby)—Pilsbry, 1892, 14: 34-35; plt. 12, figs. 51-52 (as var. of *C. lurida*)—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*). [Not *Chiton columbiensis* Sowerby, 1832]

Table 1

Key characters in the differential diagnosis of *Chaetopleura* species of the tropical eastern Pacific. (* character present)

Characters / Species	Body: Width/ length <0.60	Body: Height/ length <0.20	Mucro posterior	Postmucro convex	Girdle with hairs	Girdle bridges with spicules	Radula bicuspid
Chaetopleura scabricula		*			*		
Chaetopleura lanuginosa			*	*		*	
Chaetopleura roddae						*	
Chaetopleura unilineata							*
Chaetopleura shyana	*	*		*		*	

"Chiton catenulatus Sowerby, 1832." Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*) [Not *Chiton catenulatus* Sowerby, 1832]

"Chiton jaspideus Gould 1846" Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Abbott, 1974: 401 (as syn. of *C. lurida*). [Not *Chiton jaspideus* Gould, 1846 (= *Chaeotopleura hennahi* (Gray, 1828) *fide* Smith, 1977)]

Lepidopleurus bullatus Carpenter, 1857a: 252, *nomen nudum;* 1857b: 195-196—Brann, 1966: 45; fig. 254—Keen, 1968: 434; plt. 59, fig. 95—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 243 (as syn. of *C. lurida*)

Chaetopleura bullata (Carpenter). Pilsbry, 1892, 14: 31-32.

Chaetopleura (Chaetopleura) bullata (Carpenter). Keen, 1958: 524; Amphineura, sp. & fig. 33, 33a

Lepidopleurus bullatus calciferus Carpenter, 1857a: 252, *nomen nudum;* 1857b: 196—Brann, 1966: 45; fig. 245b—Keen, 1968: 434; plt. 59, fig. 96—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 243

Chaetopleura bullata calcifera (Carpenter). Pilsbry, 1892, 14: 32—Keen, 1958: 524, Amphineura, sp. & fig. 33, 33a

Ischnochiton parallelus Carpenter, 1864a: 314 (Reprinted, 1872: 213); 1864b: 618 (Reprinted, 1872: 104)—Keen, 1958: 524 (as syn. of *C. lurida*)—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 246 (as syn. of *C. lurida*)

Chaetopleura lurida var. *parallela* (Carpenter). Pilsbry, 1892, 14: 34; plt. 12, fig. 50

Chaetopleura parallela (Carpenter). Dall, 1921: 193—Oldroyd, 1927: 889-890—Smith, 1947a: 18; 1947b: 4—Palmer, 1945: 100; 1958: 267—Abbott, 1974: 401 *("lurida?")*

Ischnochiton prasinatus Carpenter, 1864a: 315 (Reprinted, 1872: 213); 1864b: 618 (Reprinted, 1872: 104)—Keen, 1958: 524 (as syn. of *C. lurida*)—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 246 (as syn. of *C. lurida*)

Chaetopleura lurida var. *prasinata* (Carpenter). Pilsbry, 1892, 14: 34

Chaetopleura prasinata (Carpenter). Dall, 1921: 193—Oldroyd, 1927: 889—Burch, 1942: 7—Smith, 1947a: 18; 1947b: 4-5—Palmer, 1958: 267—Abbott, 1974: 407 *("lurida?")*

Choetopleura [sic] *dacrydigera* Rochebrune, 1882: 193

Nomenclatural Comments: Sowerby (1st of name) *in* Broderip & Sowerby, 1832, described three tropical eastern Pacific species of chitons referable to *Chaetopleura, Chiton luridus* (p. 26), *C. scabriculus* (p. 28), and *C. columbiensis* (p. 58). But the descriptions, except for the girdles differentially characterized as *"velutino"* in *C. luridus, "piloso"* in *C. scabriculus,* and *"granoso"* in *C. columbiensis,* left the species virtually indistinguishable among themselves. Further information about these species was imparted by Sowerby *(op. cit.)* on associating, on the basis of the girdle, *C. luridus* with *C. limaciformis,* and *C. columbiensis* with *C. dispar, C. rugulatus* and *C. punctulatissimus,* and on describing *C. catenulatus,* despite its *"laevi"* girdle, as a species which "in general appearance...resembles *Chit. luridus"* (1832: 104). When first figured by Sowerby (1833, *Conchological Illustrations, Chiton,* figs. 20, 21, and 15, respectively, *fide* Corrected List of Figures, 1840: 9) in the colored drawings of the day, the three species, *C. luridus, C. scabriculus,* and

Explanation of Figures *1* to *4*, *9* to *11*, *19*

Figure *1: Chaetopleura scabricula* (Sowerby, 1832). Specimen 22 mm long (AJF 307, Playa La Angosta, Acapulco, Mexico)

Figure *2: Chaetopleura scabricula* (Sowerby, 1832). Specimen 16 mm long (AJF 305, Zihuatanejo, Mexico). Lateral areas and girdle

Figure *3: Chaetopleura scabricula* (Sowerby, 1832). Specimen 16 mm long (AJF 307). Tegmental surface of valves i, ii, and viii

Figure *4: Chaetopleura scabricula* (Sowerby, 1832). Same specimen as in Fig. *3*. Articulamental surface of valve viii

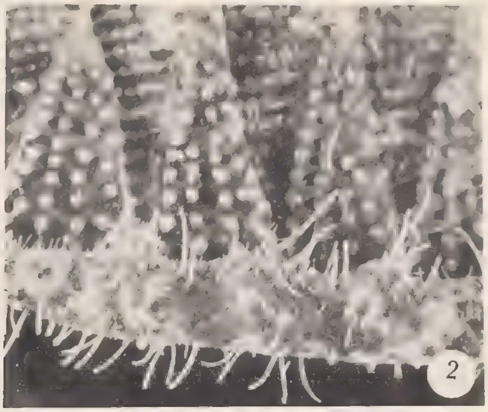
Figure *9: Chaetopleura scabricula* (Sowerby, 1832): *Chiton scabriculus* Sowerby, 1832 **lectotype** (BMNH 1980113)

Figure *10: Chiton columbiensis* Sowerby, 1832. **Lectotype** (BMNH 198111)

Figure *11: Chaetopleura scabricula* (Sowerby, 1832): *Choetopleura dacrydigera* Rochebrune, 1882, holotype (MNHN)

Figure *19: Chaetopleura lanuginosa* (Dall, 1879): *Pallochiton (Arthuria) filosus* Carpenter in Pilsbry, 1893, **lectotype** (BMNH 1980115)


1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9


10


11


19

C. columbiensis, retained their apparent similarity with no feature standing out to permit ready differential diagnosis. Reeve's (1847) illustrations of the species (plt. 15, figs. 85, 81, and 82, respectively) failed to elucidate the diagnostic problems involved and, instead, compounded the difficulties by figuring as *C. luridus* a specimen other than Sowerby's, and pointing out that the sculpture of *C. columbiensis* "is very similar to that of *C. luridus.*"

Despite the ambiguities, Pilsbry (1892), following Carpenter's unpublished manuscript, concluded for the synonymity of these three species and adopted the name *"Chaetopleura lurida"* for the common "hairy" chiton of the eastern tropical Pacific, an action which has been accepted uncritically to this day.

Examination of Sowerby's type material, on loan from the British Museum (Natural History), brought to light the fact that the single specimen labeled *Chiton luridus* in the H. Cuming collection and regarded as "? holotype;... syntype," although a *Chaetopleura*, does not correspond to *"lurida"* of authors. From the shell alone, this "syntype" of *luridus* could qualify as either one of two other species of *Chaetopleura* in the area; but without the microscopic study of the radula (no longer available in the specimen), girdle elements, and girdle bridges, the biological species corresponding to Sowerby's *C. luridus* remains undeterminable. Thus, the nominal species *C. luridus* Sowerby, 1832, is here suppressed as a *nomen dubium*, and the biological species known heretofore as *"Chaetopleura lurida"* of authors given the next available name, *scabriculus* Sowerby, 1832.

It must be added that the type specimens of *C. scabriculus* agree unequivocally with both, Sowerby's (1832) description and illustration of the species and the current concept of *"lurida"* of authors. The name *columbiensis* is here suppressed, also, as a *nomen dubium.*

Type Material: *Chiton scabriculus* Sowerby, 1832: **Lectotype** (BMNH 1980113) and **paralectotypes** (BMNH 1980114) herein designated; locality, *"ad littora* Americae centralis (Guacomayo and Puerto Portrero)."

Lepidopleurus bullatus Carpenter, 1857: Holotype (BMNH, Tablet no. 902, Mazatlan Colln.); locality, "Mazatlan," Sinaloa, Mexico [23° 13′ N; 106°25′ W].

Lepidopleurus bullatus calciferus Carpenter, 1857: Holotype (BMNH, Tablet no. 903, Mazatlan Colln.); locality, "Mazatlan," Sinaloa, Mexico [23° 13′ N; 106°25′ W].

Ischnochiton parallelus Carpenter, 1864a: Lectotype (USNM 4017; Redpath Museum, Montreal, Canada, no. 46) designated by Smith (1977); locality, Cabo San Lucas, Baja California Sur, Mexico [22°50′ N; 109°55′ W].

Ischnochiton prasinatus Carpenter, 1864: Holotype (USNM 15892); locality, Cabo San Lucas, Baja California Sur, Mexico [22°50′ N; 109°55′ W].

Choetopleura dacrydigera Rochebrune, 1882: Holotype (Muséum National d'Histoire Naturelle, Paris); locality, "Amérique Central," here restricted to the eastern Pacific.

Type Locality: Here restricted to Puerto Portrero, Costa Rica (10°28′ N; 85°47′ W).

Original Description: *"Chit. testá ovali, planiuscula, cinereá, albido-variegatá; valvá anticá, areis lateralibus valvarum intermediarum et parte posticá valvae posticae radiatim scabroso-lineatis; valvis intermediis et parte anticá valvae posticae longitudinaliter sulcatis; limbo piloso, cinereo, rufoarticulato: long.* $1^{1}/_{10}$, *lat.* $^{9}/_{20}$ *poll.,"* under the classifying heading of *"Ligamento marginis piloso."* (Sowerby *in* Broderip & Sowerby, 1832: 28).

Description: Medium sized, carinate chitons (Figures *1, 2, 3,* and *4*). Color variable, gray to brownish green predominating, occasionally with suffusions of red or patches of cream. Largest specimen examined, 38 mm long (LACM 65-13, Islas Tres Marias, Mexico). Body width/length, mean 0.61; height/length, mean 0.15. Tegmentum pustulose; on end valves and lateral areas of intermediate valves, round pustules, about 100 μm in height and diameter, usually well defined in radial rows (14-24 on anterior valve, 10-16 on posterior valve, 4-6 on lateral areas); on central areas of intermediate valves, pustules appreciably smaller (about 30-50 μm in height and diameter), often coalescing into granose riblets (15-25 per side); on valve ii jugal tract of riblets fans out forward outlining wedge-like figure. Mucro central or slightly anterior; postmucro area straight to slightly concave. Posterior edge of valves iii to vii, straight, *i.e.*, not beaked or angled. Articulamentum bluish-white. Insertion teeth well defined, followed by slit-rays; slit formula range 9/11-1-8/13, mode 10-1-9. Sutural laminae subtriangular on valve ii, subrectangular on posterior valves. Relative width of sinus (width of sinus / width of sutural lamina) on valve viii, mean 0.30. Width of valve i / width of valve viii, mean 1.12. Gills, about 30 plumes per side, holobranchial, abanal. Girdle's upper surface (Figure 5) covered with

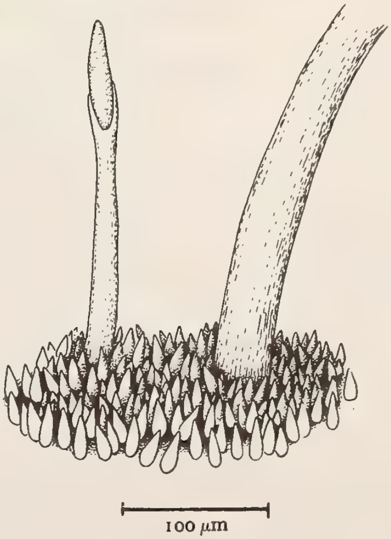

Figure 5

Chaetopleura scabricula (Sowerby, 1832). Specimen 16 mm long (AJF 307, Playa La Angosta, Acapulco, Mexico). Girdle's upper surface scales and hair simple, chaffy scales [not unlike those of lepidochitonids], often triangular in outline, about 25 × 10µm, and abundant, conspicuous, golden-brown, corneous, not dendritic hairs, up to 1mm long in an average specimen (up to 2mm in large ones) and about 50µm thick, randomly (*i. e.*, not bunched up in tufts) distributed; bridges' (Figure 6) outer ⅓ or ¼ packed with transparent, slender (150 × 15µm) spicules, close together in palisade, but empty of spicular elements in their middle ½ or ⅓; undersurface (Figure 7) paved with transparent, rectangular (35 × 25 µm) scales with convex, protuberant outer edge and concave inner edge.

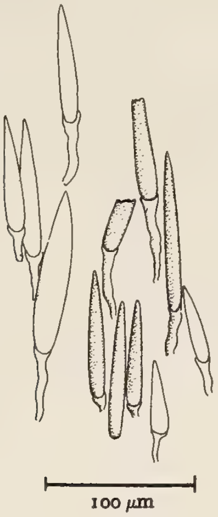

Figure 6

Chaetopleura scabricula (Sowerby, 1832). Same specimen as in Figure 5. Spicules from the outer ¼ of girdle's bridges

Radula (Figure 8) comprises about 35 rows of mature teeth. In a disarticulated specimen (AJF 307, Playa La Angosta, Acapulco, Guerrero, Mexico), 16mm long, median tooth rectangular, 250µm long, 160µm wide at anterior blade; first lateral teeth cup-shaped with thickened anterior edge; major lateral teeth with long protuberance at inner side of distal end, and tricuspid head, 280µm long (at middle cusp), 180µm wide; outer marginal teeth elongate, about 220 × 140µm.

Distribution: The geographic range of *Chaetopleura scabricula* extends from the central part of the Gulf of California, Mexico, to northern Colombia. Northernmost verified record in the Gulf of California, Bahía de San Francisquito, Baja California, Mexico [28°26′N; 112°53′W] (CASG 23779); southernmost verified record, Gorgona Id., Colombia [2°58′N; 78°11′W] (LACM-AHF 405-35). Many collecting records in between suggest a continuous distribution: Partida Id. (AJF 62), Espiritu Santo Id. (LACM-AHF 510-36); AJF 76; AJF 77; AJF 161; AJF 162), Ballena Id. (AJF 638), Cerralvo Id. (AJF 475), Bahía de los Muertos (AJF 599; AJF 639), Bahía Ventana (AJF 57; AJF 58), Los Frailes (AJF 471); Bahía Pulmo (AJF 474), Mazatlan (AJF, Mar. 1971), Manzanillo (Shy Coll.), Puerto Vallarta (AJF 430; AJF 431; AJF 432), Tres Marias Is. (LACM 65-13), Zihuatanejo (AJF 303; AJF 305), Acapulco (AJF 307), Puerto Escondido (AJF 300), Puerto Angel (AJF 302), Mexico; Zacatillo (AJF 13), Las Tunas (AJF 15), El Salvador; Tortugas Is. and Guanacaste Penins. (AJF on R/V *Searcher*, 1972), Costa Rica; El Velero (AJF 133), San Juan del Sur

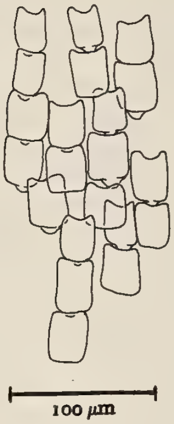

Figure 7

Chaetopleura scabricula (Sowerby, 1832). Same specimen as in Fig. 5. Girdle's undersurface scales

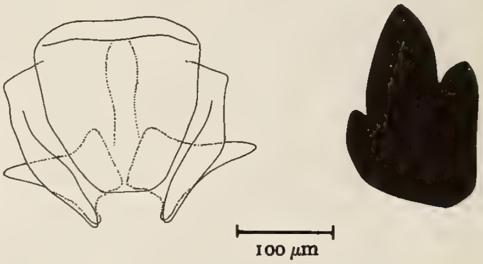

Figure 8

Chaetopleura scabricula (Sowerby, 1832). Same specimen as in Fig. 5. Radula's median tooth, first lateral teeth, and head of major lateral tooth

(B. Keagan Coll.), Nicaragua; Perlas Is. (LACM 10800; LACM 10833; LACM 10848), Punta Mala (AJF 219), Veracruz (AJF 221), Contadora Id. (AJF 224), Bique (LACM 72-75), Perico Id. (LACM 70-17), Panama; Punta San Francisco (CAS 010088), Punta Cruces (CAS 010092), Port Utria (LACM-AHF 413-35), Colombia. *Chaetopleura scabricula* has been collected also at the oceanic islands of Revillagigedos, Mexico [19° N; 11° W], at San Benedicto (AJF 518), and Socorro (LACM H-2459; LACM 71-26; AJF 497; AJF 503).

Chaetopleura scabricula seems to be confined to the intertidal and shallow subtidal zones, 0-30 m.

Remarks: *Chaetopleura scabricula* displays considerable intraspecific variation in color, and number and size of tegmental pustules. Specimens from the Revillagigedos Archipelago, Mexico, have a remarkably subdued tegmental sculpture: All 36 specimens of *C. scabricula* from 7 collecting sites at Socorro and San Benedicto islands (ANSP 72501; LACM 71-26; AJF 496, 497, 503, 504, and 508, aboard R/V BAJA EXPLORADOR, Nov. 1979) show only few and relatively small tegmental pustules conferring the specimens an almost smooth, rather than scabrous appearance. Since careful comparisons revealed no other morphological differences (in the articulamentum, slits, girdle elements and bridges, gills, or radula) between Revillagigedos' and mainland's specimens there seemed to be no need to introduce a new name for the population. Although the observed differences would suffice to erect a subspecies, the Revillagigedos population is here recorded simply as a variation, albeit extreme, of *C. scabricula.*

As mentioned above, the type material of *Chiton luridus* Sowerby, 1832, is limited to a single specimen in the H. Cuming Collection (BMNH 19826). It is accompanied by a pink museum label which reads, in part "? Holotype / Figd. Syntype.../ Loc. Stae. Elenae (published) / It was found on stones in five fathoms water / Coll. Cuming Acc. 1829." The specimen, dry, flat, well preserved, soft parts removed, measures 27.7 × 17.0 × 6.4 mm, including girdle; articulamentum white to which a small piece of paper is glued, reading "296..."; strongly carinate; tegmentum uniformly brick-red; lateral areas of intermediate valves with about 8 radial rows of pustules; central areas with 13-15 longitudinal rows of smaller pustules; mucro central, prominent; postmucro concave. Girdle with no hairs or other visible ornamentations; under transmitted light microscopy (×40) many glassy, pointed, slightly curved spicules up to 300 mm in length are seen, but no hairs or scars indicating the presence of hairs (such as would be expected in specimens of *C. lurida* of authors). The specimen does not correspond to the concept of *"luridus"* of authors and, since the radula and girdle bridges are not available for study, cannot be related with certainty to other biological species in the area. Thus, *Chiton luridus* Sowerby becomes a *nomen dubium.* The type status of this particular specimen is also open to question for two reasons, 1) study of the original labels demonstrates that mixing-up with specimen(s) of *columbiensis* did occur some time in the past, and 2) the specimen, in my opinion, is not the specimen in fig. 20 of SOWERBY's (1833: plt. 40) *Conchological Illustrations.* Although the museum label accepts the specimen as "syntype" and Sowerby's figured specimen (S. Morris, *in litt.,* 18 March 1982), the specimen differs from SOWERBY's (1833: fig. 20) in color [the specimen is solid red, the figure is mottled greenish brown] and measurements [in SOWERBY's (1832) text, it reads 30 × 15 mm; in SOWERBY's (1833) fig. 20, it measures 27 × 15 mm; the examined "syntype" specimen measures 27.7 × 17 mm, *i.e.,* considerably *wider* than reported or figured]. The specimen does correspond to *C. luridus* in REEVE's (1847: fig. 85b, plt. 15).

The type material of *Chiton scabriculus* Sowerby, 1832 is accompanied by a blue museum label which reads, in part, "Syntypes / Central America (Guacomayo + P. Portrero) / H. Cuming colln. / 5 specs. Acc. no. 1892 P.Z.S. 1832: 28 / Fig. in Sow.: Conc. Illust. sp. 100 f. 21 (spec. meas. 2.8 cm = fig.) / Reeve: Conc. Icon., 4 pl. 15 fig. 81 (largest spec.)." It consists of 5 specimens, dry, well preserved, soft parts removed; light brown mottled with white and dark brown; moderately carinate, not beaked; posterior edges of valves iii to vii essentially straight; lateral areas with 6-8 radial rows of pustules; central areas with 15-25 longitudinal rows of smaller pustules, many coalescing into ridges or riblets; mucro central or slightly anterior; postmucro area straight or slightly concave. Girdle, under transmitted light microscopy (× 40), shows several long, non-dendritic hairs. In all respects, the specimens agree with Sowerby's description of *Chiton scabriculus* and the current understanding of *"Chaetopleura lurida"* of authors. The largest specimen (Figure *9*), illustrated in Reeve (1847, plt. 15, fig. 81), measuring 34.5 × 22.5 × 5.7 mm, is here designated **lectotype** (BMNH 1980113); the other 4 specimens in the lot are here designated **paralectotypes** (BMNH 19800114).

The types of *Chiton columbiensis* Sowerby, 1832, are accompanied by pink museum labels reading, in part, "Loc. Sinu panamae—published / Found under stones at low water / Coll. Cuming Acc. 1829." The lot comprises 4 specimens, dry, flat, well preserved, soft parts removed; strongly carinate; light brown with brighter, reddish dots at posterior edge of valves of larger and smaller specimens; lateral areas with 8-10 radial rows of pustules; central areas with 12-16 longitudinal rows of smaller pustules; mucro, central in the three larger specimens, definitely anterior in the smallest specimen. Girdle, under transmitted light microscopy (× 40), shows no hairs, spicules, or traces of their former presence. The largest specimen, measuring 30.3 × 18.5 × 5.8 mm, conforms with SOWERBY's illustration (1833: fig. 15) [SOWERBY's text (1832: 58) and illustration

(1833: fig. 15) agree on the measurements, 32 × 19mm] and Reeve's (1847: plt. 15, fig. 82); it is here designated **lectotype** (BMNH 198111). The other specimens, 23.5mm, 22.8mm and 22.5mm long are designated **paralectotypes** (BMNH 1980112). The smallest specimen in the group does not appear to be conspecific with the others; it differs in body proportions (width / length ratio, 0.73), and anterior mucro. Since the radulae are no longer available and elements of girdle and bridges could not have been studied without disarticulating the specimens, the name *columbiensis* becomes a *nomen dubium.* Conchologically, the type specimens of *C. columbiensis* could well belong to the same biological species as the type specimen of *C. luridus* here examined, but are sufficiently different from *"luridus"* of authors to dispel the notion of synonymity erroneously entertained since Pilsbry (1892).

Upon examination of type material, *Lepidopleurus bullatus* Carpenter, 1857, *L. b. calciferus* Carpenter, 1857, *Ischnochiton parallelus* Carpenter, 1864, and *I. prasinatus* Carpenter, 1864, have been regarded as synonyms of *"Chaetopleura lurida"* of authors by Smith (1977). Examination of photographs of the type specimens, in the CASIZ Color Slide Series, corroborates the synonymy.

Choetopleura dacrydigera Rochebrune, 1882, based on a single specimen from "Amerique Centrale," was left unfigured. Rochebrune (1882) did not specify whether the specimen came from the Atlantic or the Pacific side of Central America, an omission which has rendered the name taxonomically useless. Examined on a loan (MNHN), the museum label reads, *"Chaetopleura dacrydigera* Rochbr. 1882 / = *C. lurida* Sow. / Amerique Centrale / Bull. Soc. Philom. Paris 1882: 193," and on the top corner, "XV.III. Type" on a red background. The dry, flat, well preserved specimen measures 20mm in length, 13mm in width (including girdle), 4.1mm in height [Rochebrune's (1882: 193) given dimensions are 22mm long, 14mm wide]. Soft parts removed, articulamentum bluish white. Girdle's hairs have fallen off, leaving obvious scars and traces of their former presence clearly visible under microscopic examination (× 40) with transmitted light. The specimen agrees in every respect with the current concept of *Chaetopleura scabricula.* Since there is no such species on the Atlantic side of Central America (or elsewhere), its locality must be restricted to the eastern Pacific, as already suspected by Thiele (1909).

Thorpe's (*in* Keen, 1971) and Abbott's (1974) placement of *Chiton jaspideus* Gould, 1845 in the synonymy of *C. lurida* of authors was in error. Upon examination of the holotype, Smith (1977) concluded that *C. jaspideus* is a junior synonym of *C. hennahi* (Gray, 1828). Study of several lots of *C. hennahi* from Peru and color slides of the holotype of *Chiton jaspideus* (CASIZ Color Slides Nos. 2199-2200) confirmed Smith's (1977) view.

The placement of *Chiton catenulatus* Sowerby, 1832, in the synonymy of *C. lurida* by Thorpe (in Keen, 1971) is also incorrect. The study of the types of *C. catenulatus* (BMNH 198032) revealed the two species to be not only distinct but not even congeneric (Ferreira, in press).

Chaetopleura scabricula is readily distinguished from other species of *Chaetopleura* in the tropical eastern Pacific by the presence of corneous hairs in the girdle. It differs clearly from the three other hairy *Chaetopleura* species in the south eastern Pacific, *C. hennahi, C. peruviana,* and *C. fernandensis,* in the characteristics and distribution of the hairs as well as in the body proportions, tegmental sculpture, and mucro.

Chaetopleura lanuginosa (Dall, 1879)

(Figures 12, 13, 14, *15, 16, 17, 18,* and *19*)

Pallochiton lanuginosus Dall, 1879: 297; plt. 3, fig. 21 (radula); 1882: 287—Pilsbry, 1893, 14: 257-258; plt. 56, figs. 1-11—Dall, 1921a: 193—Oldroyd, 1927: 893-894—Burghardt & Burghardt, 1969: 33 [as *"languinosus,"* typ. err.]

Chiton (Pallochiton) lanuginosus (Dall). Orcutt, 1885: 544

Explanation of Figures *15* to *18, 38, 39, 48, 49*

Figure *15: Chaetopleura lanuginosa* (Dall, 1879): *Chaetopleura (Pallochiton) euryplax* Berry, 1945, paratype (USNM 658237). Tegmental surface of valve i

Figure *16: Chaetopleura lanuginosa* (Dall, 1879). Same specimen as in Fig. *15.* Valve viii

Figure *17: Chaetopleura lanuginosa* (Dall, 1879). Same specimen as in Fig. *15.* Valve viii

Figure *18: Chaetopleura lanuginosa* (Dall, 1879). Same specimen as in Fig. *15.* Valve viii

Figure *38: Chiton lividus* Middendorff, 1847. **Holotype** (Zoological Institute, Academy of Sciences, Leningrad, USSR). Tegmental surface of valves

Figure *39: Chiton lividus* Middendorff, 1847. **Holotype.** Articulamental surface of valves. [Photographs for Figs. *38* and *39* provided through the courtesy of Prof. B. Sirenko, Zoological Institute, Leningrad, USSR]

Figure *48: Chaetopleura thouarsiana* Rochebrune, 1882. Type specimen (MNHN)

Figure *49: Chaetopleura biarmata* Rochebrune, 1882. Type specimen (MNHN)


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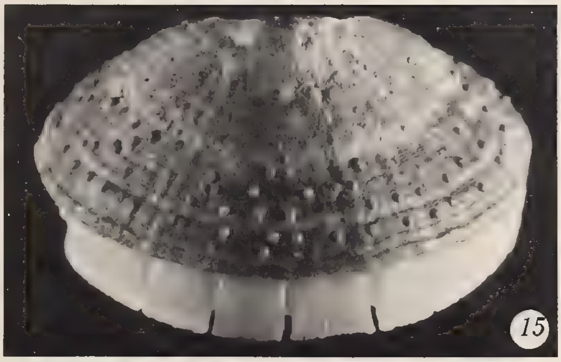
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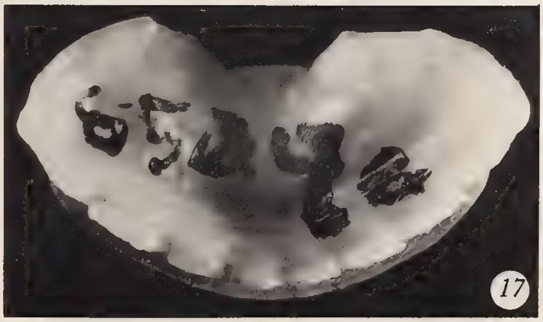
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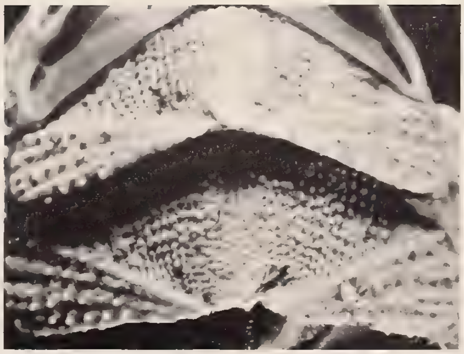
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Chaetopleura (Pallochiton) lanuginosa (Dall). Smith, 1947a: 18; 1947b: 5 [as *"languinosa,"* typ. err.]—Palmer, 1958: 268; plt. 27, fig. 7

Arthuria filosa Carpenter *in* Dall, 1882: 287 *(nomen nudum)*

Pallochiton (Arthuria) filosus Carpenter *in* Pilsbry, 1893, 14: 258-259

Nuttallina magdalena Dall, 1919: 502—Smith, 1961: 82, 86; 1977: 217, 244 (as possible syn. of *Chaetopleura lanuginosa)*

Chaetopleura magdalena (Dall). Keen, 1958: 524, Amphineura sp. & fig. 36—Abbott, 1974: 401

Tonicia mixta Dall, 1919: 515-516 [in part]—Smith, 1977: 217, 245-246 [Not *"Chaetopleura mixta* (Dall)" of authors treating Panamic species]

Chaetopleura raripustulosa Pilsbry *in* Pilsbry & Lowe, 1932, 84: 129 *(nomen nudum)*—Steinbeck & Ricketts, 1941: 549—Smith, 1961, **30**(4): 83 (as syn. of *Chaetopleura euryplax* Berry, 1945)

Chaetopleura (Pallochiton) euryplax Berry, 1945: 491-492; figs. 1-9—Keen, 1958: 525, Amphineura sp. & fig. 38—Smith, 1961, **30**(4): 83-86; plt. 8, fig. 2 (with *C. raripustulosa* Pilsbry, 1932, as syn.)

Chaetopleura euryplax Berry. Thorpe *in* Keen, 1971: 877, Polyplacophora sp. & fig. 40—Abbott, 1974: 401

Nomenclatural Comments: The species name *lanuginosus* was first published by Dall (1879) with the description and illustration of the radula; further details of the species, assigned to *Pallochiton* Dall, 1879, were later (Dall, 1882) given but no type was specified. Pilsbry (1893) described and figured the species as if new and, like Dall, attributed it to Carpenter's unpublished manuscript. Thus, an equivocal situation arose. Palmer (1958), in a mood of uncertainty, summed it up by pointing out that if the species were judged to be of Dall a series of 5 specimens in the Carpenter Collection of the Redpath Museum (Redpath Museum no. 66) constituted its type material whereas if judged to be of Pilsbry the type lot would be the one studied by Pilsbry at the Academy of Natural Sciences of Philadelphia (ANSP 35684). The question is resolved on the realization that in accordance with Articles 16, 17 and 14b of the International Code of Zoological Nomenclature (ICZN), the authorship of the name *lanuginosus* is clearly Dall's as already indicated by Boss *et al.* (1968) and Davis *et al.* (1979).

Type Material: *Pallochiton lanuginosus* Dall, 1879: **Lectotype** (ANSP 35684) and **paralectotypes** (ANSP 353937) herein designated.

Pallochiton (Arthuria) filosus Carpenter *in* Pilsbry, 1893: **Lectotype** (BMNH 1980115), and **paralectotype** (BMNH 1980116) designated herein; locality, "unknown" (Pilsbry, 1893, 14: 259).

Nuttallina magdalena Dall, 1919: Lectotype and paralectotypes (USNM 217924), designated by Smith (1977: 244-245); locality, "Magdalena Bay, Lower California," Mexico [28°40′ N; 112°00′ W].

Tonicia mixta Dall, 1919: Lectotype (USNM 110345), designated by Smith (1977: 245-246), and one **paralectotype** here designated [the other specimen in the lot proved to be of a different species]; locality, "Angeles Bay, Gulf of California," Mexico [29°00′ N; 113°30′ W].

Chaetopleura (Pallochiton) euryplax Berry, 1945: Holotype (S. S. Berry Collection, Cat. No. 8943), and paratypes (Berry Colln., Cat. No. 8564; SDNH Type series no. 5; USNM 658237); locality, "Bahía de Adair, Sonora, Mexico," [31°30′ N; 113°50′ W].

Type Locality: Point Abreojos, Baja California, Mexico [26°44′ N; 113°40′ W] (Dall, 1879: 343).

Description: Dall's (1879) original description of *Pallochiton lanuginosus* was limited to the radula, "Minor lateral normal, bialate; major lateral tridentate, shaft normal Fig. 21" (p. 297). For practical purposes, the species remained unrecognizable until Pilsbry (1893) provided a full account of it, based on Carpenter's unpublished manuscript. To Pilsbry's (1893) description, and to Berry's (1945) later account of *Chaetopleura euryplax*, the following observations should be added:

Large sized chitons; largest specimen examined, 60 mm long (AJF Colln., Bahía San Quintín, Baja California, Mexico, intertidally, *leg.* A. J. Ferreira & W. E. Dailey, 15 Oct. 1971). Carinate; posterior edge of intermediate valves straight but with tendency to beak. Body width / length, mean 0.62; height / length, mean 0.21. Width of valve i / width of valve viii, mean 1.07. Color variable with brown tones predominating. Tegmentum pustulose; on end-valves and lateral areas of intermediate valves, relatively few round pustules (up to 150 μm in diameter) in ill-defined radial rows or as if randomly placed; on central areas, smaller, often elongated pustules in longitudinal rows (about 15 per side) that tend to arch as they diverge forward. Mucro posterior; postmucro area strongly convex, often incurving forward, with prominent, almost terminal, sometimes recurved, pointing upward false mucro. Articulamentum white, posteriorly covered by forward reflecting tegmentum. Sutural laminae subtriangular on valve ii, subrectangular on valves iii to viii. Relative width of sinus (width of sinus / width of sutural laminae) on valve viii, mean 0.33 (n = 10). Insertion teeth well defined; slit formula range 8/11-1-7/9, mode 9-1-9. In anterior valve, insertion teeth tend to be fluted on outer surface and thickened at edges (a feature reminiscent of *Callistochiton);* in posterior valve, teeth relatively shorter, incurved forward, buttressed by strong transversal callus (a feature reminiscent of *Acanthopleura* and *Nuttallina*). Eaves solid. Gills, about 30 plumes per side, holobranchial, abanal. Girdle's upper surface (Figure 12) covered with juxtaposed, spiculoid scales, about 50 × 10 μm, and abundant, randomly distributed glassy spicules, about 500 × 30 μm, mostly straight and pointed; bridges (Figure 13) crowded with long, pointed, glassy spicules, up to 200 μm long, 15 μm thick, disposed mostly in palisade; undersurface

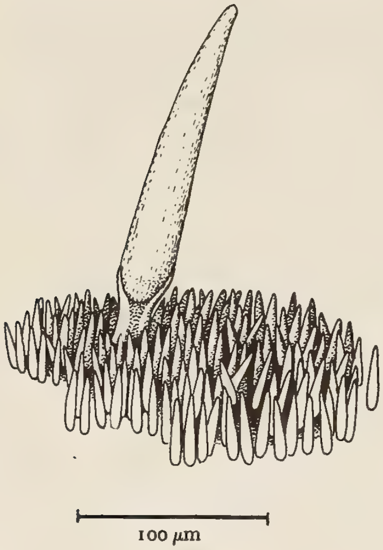


Figure 12

Chaetopleura lanuginosa (Dall, 1879). Specimen 24mm long (LACM 38-3, Magdalena Bay, Baja California, Mexico). Girdle's upper surface scales and spicules

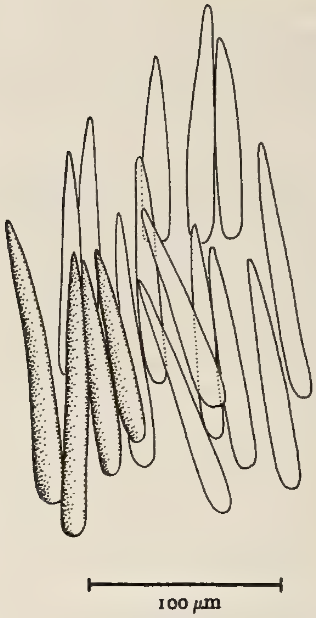


Figure 13

Chaetopleura lanuginosa (Dall, 1879). Same specimen as in Fig. 12. Spicules on the girdle's bridges

paved with flat, transparent, rectangular scales, about 50 × 20μm, identical to those seen in *Chaetopleura scabricula*. Radula (Figure 14) of a specimen 24mm long (LACM 38-3), measures 8.0mm (33% of specimen's length) comprising 35 rows of mature teeth; median tooth rectangular, 150μm wide at anterior blade; first lateral teeth 160μm long; major lateral teeth with tricuspid head, about 165μm wide.

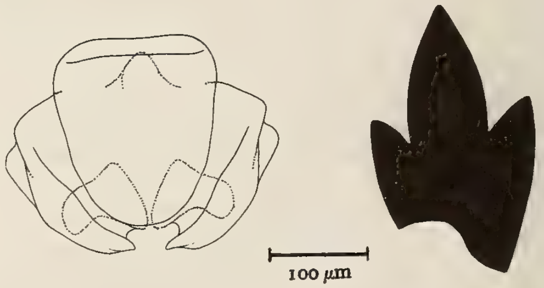


Figure 14

Chaetopleura lanuginosa (Dall, 1879). Same specimen as in Fig. 12. Radula's median tooth, first lateral teeth, and head of major lateral tooth

Distribution: *Chaetopleura lanuginosa* is present in the quasi tropical waters of the Gulf of California, and in the warm-temperate waters of the Pacific coast of the Baja California peninsula. The two populations seem to be discontinuous. On outer Baja California, *C. lanuginosa* ranges from southern California to Bahía Magdalena; northernmost verified record, Ensenada, Baja California, Mexico (31°55′ N; 116° 50′ W) (LACM 66-5, *leg.* J. H. McLean, 9 June 1966, intertidally) [a single specimen, 8.6mm long, *leg.* Paul J. & Antonio J. Ferreira, 8 April 1974, intertidally, at White's Point, San Pedro California, 33°42′ N, AJF 147, identified as a juvenile of *C. lanuginosa*, constitutes a record so far uncorroborated]; southernmost verified record, Marry Channel, Bahía Magdalena, Baja California, Mexico (23° 30′43″ N; 111°50′01″ W) (LACM-AHF 1718-49). Between these two extreme points, the species has been collected at many other sites such as Punta Banda (CASG 43929), Ensenada (LACM 65-53), Camalu (LACM 66-2), Bahía San Quintín (AJF Colln.), Guerrero Negro (L. Shy Colln.), and Bahía Magdalena (LACM 38-3; LACM 66-8; LACM 71-14; LACM 66-232; LACM A-1207; LACM A-2777; LACM-AHF 1718-49; LACM-1721-49; CASG 10223).

In the upper Gulf of California, *Chaetopleura lanuginosa*, hitherto known as *"euryplax,"* has been found from San Felipe [31°03′ N; 114°49.3′ W] (LACM 61-6; LACM P465.62; CAS 010086; AJF 27), Bahía de los Angeles (LACM-AHF 700-37), to Bahía de Concepcion [26°40′ N; 111°50′ W] (LACM A.6542; SDNH 23648) on the Baja California side; and Bahía de Adair (LACM P.465.62), Guaymas (G. A.

Hanselman Colln.; L. Shy Colln.; LACM-AHF 1039-40) and Bahía Topolobampo, Sinaloa [25°37′N; 109°03′W] (LACM 59-9), on the mainland side.

Apparently, *Chaetopleura lanuginosa* is not present in the lower Gulf; a single specimen, 4.4mm long, of what seems to be a juvenile of *C. lanuginosa* was collected 12km NE of Cabo San Lucas, Baja California (CAS 010090) but given its small size,the identity remains uncertain.

Judging from the collections, *Chaetopleura lanuginosa* is predominantly a species of the intertidal zone; however, its bathymetric range is known to extend from 0 to 91m (L. Shy Colln., SE of San Antonio Point, Guaymas, Sonora, Mexico, *leg.* L. Shy, November 1978).

Remarks: The original specimen, or the radula upon which Dall (1879) introduced the species *Chaetopleura lanuginosa* could not be found at the U.S. National Museum (Dr. J. Rosewater, *in litt.,* 3 Oct. 1980) and is presumed lost. But a lot in the Academy of Natural Sciences of Philadelphia (ANSP 35684) has been regarded as part of the original series used by Dall and, as such, syntypic material (Mary A. Garback, Collection Manager, ANSP, *in litt.,* 3 March 1981). The 5 specimens in the lot are accompanied by a red-dotted cardboard label which reads "*Pallochiton lanuginosus* Cpr. / Type 35684 / Pta. Abreojos / Henry Hemphill ! L. Cal." Four of the specimens are preserved dry, flat, entire except for removed soft parts. They are 39, 42, 46, and 47mm long. The smallest and the largest specimens seem to be the ones illustrated by Pilsbry (1893) in plt. 56 as fig. 1 and fig. 4, respectively. The fifth specimen in the lot, disarticulated and segregated in a separate vial, is estimated to be 40mm long; slit formula, 9-1-11. The specimens correspond in every respect to the description provided by Carpenter *in* Pilsbry (1893: 257), and to the current understanding of the species. Palmer (1958: 268) stated that the specimen in plt. 56, fig. 4 of the Manual of Conchology (Pilsbry, 1893: 14) had been selected by Pilsbry as lectotype; but Pilsbry's action not being known otherwise, a lectotype designation seems in order. Accordingly, the disarticulated specimen in the lot, comprising loose valves and a dry girdle, already segregated, is here designated **lectotype** (recatalogued, ANSP 353937), and the other 4 specimens, **paralectotypes** (ANSP 35684).

Nuttallina magdalena Dall, 1919, was equated with *Chaetopleura lanuginosa* by Smith (1977) upon examination of the type material (CASIZ Color Slides Nos. 3137-3139 and 3262-3263). Smith's action is here corroborated.

The placement, herein, of *Tonicia mixta* Dall, 1919, in the synonymy of *Chaetopleura lanuginosa* culminated an interesting phase of this work. Smith (1977) recognized *Tonicia mixta* as a member of the genus *Chaetopleura* (an action first taken by Keen, 1958), and described its type material as consisting of two specimens, "an entire specimen with all valves in place" which he designated as lectotype, and "another that has been disarticulated" which he designated as paralectotype (p. 245). Smith's observations were documented with photographic color slides (CASIZ Color Slides Series Nos. 2178, 2183, and 2184).

However, attentive study of Smith's color slides disclosed that the two syntype specimens of *Tonicia mixta* photographed by Smith are not conspecific. From the color slides it is apparent that the entire specimen designated by Smith as lectotype of *mixta* (Color Slide No. 2183) is conspecific with *Chaetopleura lanuginosa* (Dall, 1919), whereas the disarticulated specimen designated as paralectotype (Color Slides Nos. 2178 and 2184) corresponds, indeed, to the concept of *"C. mixta"* of authors treating the Panamic species.

To resolve this matter, the type material of *Tonicia mixta* (USNM 110345) was re-examined on a loan. And another puzzle came to light: The Museum catalogue indicates that the lot consists of 4 specimens when, in fact, only 3 specimens are present (Dr. J. Rosewater, *in litt.,* 29 Aug. 1979). Now, since Smith *(op. cit.)* reported solely on 2 specimens in the lot, "one entire and another disarticulated," it became perplexing to realize that the syntype lot of *T. mixta* studied anew comprises one more specimen than Smith mentioned, and one less than listed in the Museum catalogue. Dall (1919) provided no clue to the number of specimens present in the original lot.

Here examined, the three specimens in the type lot of *Tonicia mixta* Dall, 1919 (USNM 110345) are preserved dry, two entire and curled, one disarticulated. The two entire specimens agree in every respect with the present interpretation of *Chaetopleura lanuginosa* Dall, 1879: both light brown with creamy stripe, very sparse pustules on end valves and lateral areas of intermediate valves, posterior mucro, markedly convex postmucro area forming false mucro, girdle with long (up to 350μm) hyaline spicules. The disarticulated specimen (loose valves only, no girdle or soft parts) corresponds to the concept of *C. mixta* of authors: valves markedly carinate, jugal angle about 90°, round pustules (about 120μm in diameter and height) in quincunx on valve i, sparser and larger (about 150μm in diameter and height) on well defined and elevated lateral areas, central areas with 11-13 longitudinal rows per side of smaller (about 100μm in diameter, less in height) pustules, mucro central, postmucro straight at about 45° angle, no false mucro, width of valve i larger than valve viii (6.3mm and 5.3mm, respectively), white articulamentum except for brown discolorations at posterior end of valves ii-vii, slit formula 12-1-11 [in some valves there are minute notches at the edge of the insertion teeth which, on a superficial examination, could be mistaken for extra slits, a mistake which Dall (1919) obviously made on describing the species]. The two entire specimens, very similar to each other, clearly differ from the disarticulated one in the following points which bear stressing: 1) pustules much sparser on end valves and lateral areas of intermediate valves (about 4 pustules/mm^2 in the entire specimens *vs.* 14 pustules/mm^2 in the disarticulated one), 2) lateral areas much less elevated, 3) tegmental surface smoother, almost shiny, 4) central areas with only 8 rows (instead of 11-13) of pustules per side, 5) mucro posterior, and 6) postmucro convex with posterior, almost terminal false mucro.

Unfortunately, Smith (1977), as first reviser, overlooking as Dall (1919) did, that he had before him specimens of two different species, designated as lectotype of *Tonicia mixta* a specimen that must now be referred to *Chaetopleura lanuginosa;* in so doing, he occasioned the name *mixta* Dall, 1919, to fall into the synonymy of *C. lanuginosa,* and unwittingly left *"Chaetopleura mixta"* of authors without a name.

Hence, the status of the specimens in the type lot of *Tonicia mixta* Dall, 1919, appears as follows: Of the two entire specimens, the "most curled" one (for lack of any other tenable distinction) is the lectotype as designated by Smith (1977) and determined by direct comparison with Smith's color slides of the specimen (CASIZ Color Slide No. 2184); the "less curled" one, a paralectotype as here designated. The disarticulated specimen is to be disregarded as not conspecific.

On describing *Chaetopleura euryplax* in the upper Gulf of California, Berry (1945) observed that the species was similar to *C. lanuginosa* although "critical inspection shows them to differ in one way or another at almost every point" (p. 492). The assumed differentiating characters were "1) the much longer and proportionately less deeply slitted insertion plates, particularly those of valve i, 2) the convex and more pointed tail valve, with its narrower, square sinus and wider, fewer, more oblique and much less forward-projecting teeth, 3) the generally sparse sculpture, especially the much less numerous lirae of the pleural regions" (*op. cit.,* p. 492). The results of this study fail to support Berry's contention. The examination of large collections of specimens from the Gulf of California, including many topotypes and a paratype of *C. euryplax* (USNM 658237) (Figures *15, 16, 17,* and *18*), revealed no substantial morphological differences from specimens collected on the outer coast of Baja California, except for slightly larger sizes and less accentuated tegmental sculptures.

Pallochiton (Arthuria) filosus Carpenter *in* Pilsbry, 1893, is based on two specimens, at one time part of the H. Cuming Collection (nos. 23 and 28, *fide* Pilsbry, 1893), now at the British Museum (Natural History). The specimens are well preserved, soft parts removed, dry, exactly the same size (29 × 15 × 6 mm), partly disarticulated (valves i, ii, and vii are loose, the others in place, in both specimens). But they differ in color: the darker, brown specimen is here designated **lectotype** (BMNH 1980115) (Figure *19*), the other, light beige, is designated **paralectotype** (BMNH 1980116). They conform in every respect to the description given by Pilsbry (1893), and are morphologically indistinguishable from outer Baja California specimens of *Chaetopleura lanuginosa.*

Chaetopleura roddae Ferreira, spec. nov.

(Figures *20, 21, 22,* 23, 24, 25, *26,* and *27*)

"Chaetopleura..." Thorpe *in* Keen, 1971: 877, Polyplacophora, sp. & fig. 39

Diagnosis: Medium sized chitons, carinate, grayish brown to orange or pink. Tegmentum with round pustules in quincunx on end valves and lateral areas of intermediate valves, in longitudinal rows on central areas. Mucro central; postmucro area convex but with no false mucro. Girdle with abundant glassy, whitish spicules. Insertion teeth of posterior valve directed outwardly, not incurved forward. Radula major lateral teeth, tricuspid.

Type Material: **Holotype** (CAS 028808); **paratypes** (CAS 028809; LACM 1977; USNM 784716; ANSP A9868).

Type Locality: Salinas, Ecuador (2°12′ S; 80°58′ W), intertidal zone.

Explanation of Figures *20* to *22, 26, 27, 40* to *43*

Figure *20: Chaetopleura roddae* Ferreira, spec. nov. **Holotype** (CAS 028808). Tegmental surface of valve i

Figure *21: Chaetopleura roddae* Ferreira, spec. nov. **Holotype** (CAS 028808). Tegmental surface of valve viii

Figure *22: Chaetopleura roddae* Ferreira, spec. nov. **Holotype** (CAS 028808). Articulamental surface of valve viii

Figure *26: Chaetopleura roddae* Ferreira, spec. nov. **Paratype** CAS 028809), 20.5 mm long

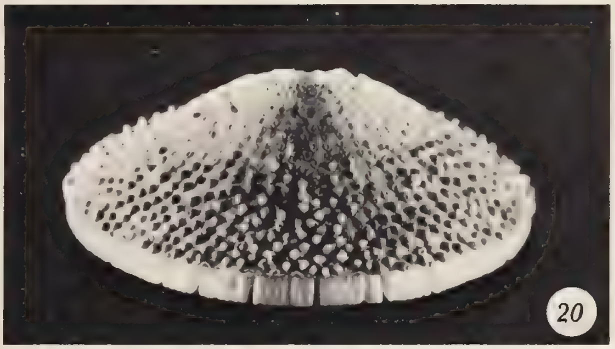
Figure *27: Chaetopleura roddae* Ferreira, spec. nov. Close-up of same paratype as in Fig. *26*

Figure *40: Chaetopleura fernandensis* Plate, 1899. **Lectotype** (Zoologisches Museum, Humboldt Universität, Berlin, DDR). Anterior valves

Figure *41: Chaetopleura fernandensis* Plate, 1899. **Lectotype.** Intermediate valves

Figure *42: Chaetopleura fernandensis* Plate, 1899. **Lectotype.** Posterior valves

Figure *43: Variolepsis iquiquensis* Plate, 1899. **Lectotype** (Zoologisches Museum, Humboldt Universität, Berlin, DDR)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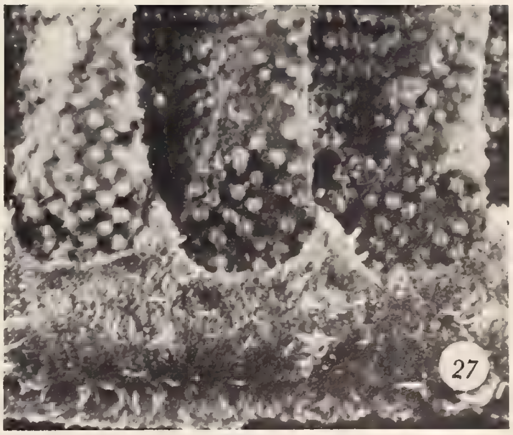
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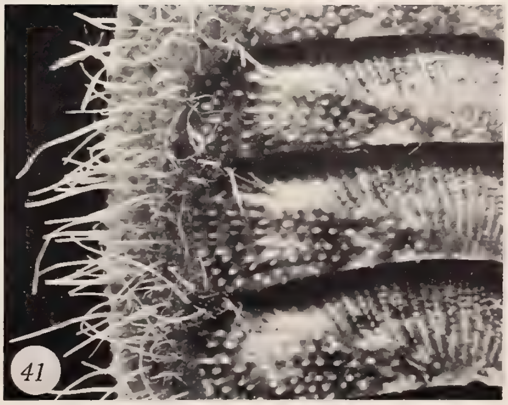
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Description: **Holotype** (Figures *20, 21, 22*) The specimen, preserved in alcohol and fully extended, 33.6mm long (including girdle), 23.5mm wide (at the iv level), is the second largest in a lot of 9 specimens collected at Salinas, Ecuador, in the intertidal zone (LACM 70-9, *leg.* J. H. McLean, 5-6 March 1970). Carinate, jugal angle about 110°; posterior edge of intermediate valves straight, not beaked. Color, mottled grayish brown and cream. Girdle, 3.0mm wide, dark orange brown against which whitish spicules stand out conspicuously. Tegmentum markedly pustulose; on end-valves and lateral areas of intermediate valves, pustules (about 150-170µm in diameter and height) mostly in quincunx or ill-defined radial rows, stand about 150µm apart from each other; on central areas of intermediate valves, smaller pustules (100-120µm in diameter and height), round to elongate, flat topped, in longitudinal rows (about 20 per side) crowded at jugum. Lateral areas, moderately elevated in valve ii, progressively less elevated in posterior valves, only defined by differences in sculptural features on valve vii. Mucro central, not prominent; antemucro area somewhat inflated; postmucro area markedly convex but without false mucro. Articulamentum bluish white. Insertion teeth well defined; posterior valve with teeth directed outwardly and no transversal callus; slit formula 9-1-8. Eaves solid. Gills, about 30 plumes per side, holobranchial, abanal. Width of valve i / width of valve viii = 10.0mm / 8.7mm = 1.15. Relative width of sinus on valve viii (width of sinus / width of sutural laminae) = 1.2mm / 4.5mm = 0.27. Sutural laminae subtriangular on valve ii to subrectangular in posterior valves.

Girdle's upper surface (Figure 23) covered with juxtaposed, spiculoid scales (40-60µm long, 5-10µm wide), with abundant glassy, whitish, curved, pointed spicules (up to 500µm in length, 45µm in thickness) interspersed; bridges (Figure 24) crowded with slender, pointed, glassy spicules, up to 250µm long, 18µm thick, disposed in palisade; undersurface paved with flat, transparent, rectangular scales, 45 × 20µm, identical to those seen in *Chaetopleura scabricula.* Radula (Figure 25) 11.0mm long (30% of specimen's length) comprises some 30 rows of mature teeth; median tooth rectangular, about 300µm long, 250µm wide at anterior blade; first lateral teeth about 250µm long; second lateral teeth with tubercle (about 120 × 60µm) at inner edge, near upper end, and tricuspid head about 400µm long (at longest middle cusp) and 250µm wide; outermarginal teeth elongate, 300 × 150µm.

Paratypes (Figures *26* and *27*): Varying in length from 34.6mm to 10.2mm, and in color from drabby gray to brown mottled with cream and bright red areas on valves i and iv. A paratype, 19.7mm long, disarticulated for study, shows features much like the holotype; girdle 2.1mm wide, slit formula 9-1-9, 25 gill plumes per side, radula 6.7mm long with 30 rows of mature teeth.

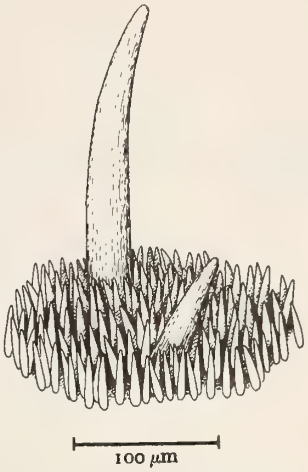

Figure 23

Chaetopleura roddae Ferreira, spec. nov. **Holotype** (CAS 028808). Girdle's upper surface scales and spicules

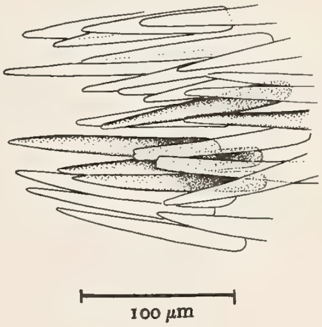

Figure 24

Chaetopleura roddae Ferreira, spec. nov. **Holotype.** Spicules of the girdle's bridges

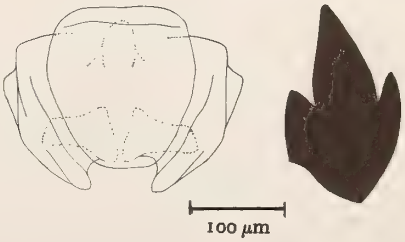

Figure 25

Chaetopleura roddae Ferreira, spec. nov. **Holotype.** Radula's median tooth, first lateral teeth, and head of major lateral tooth

Individual Variation: Among 86 specimens of *Chaetopleura* ***roddae*** examined, from 22 lots, largest specimen is 42 mm long (LACM 10846, Venado Island, Panama, *leg.* E. Bergeron, 16 Sept. 1966). Color varies from drabby grayish brown often mottled with cream or light green to uniform bright orange, rose, or pink. Girdle's glassy spicules usually abundant (by comparison to specimens of other species of *Chaetopleura* bearing such spicules) but varying appreciably in number from specimen to specimen. Body proportions: width/length, mean 0.61, height/length, mean 0.21 (n = 20). Slit formula range 8/10-1-7/8, mode 8-1-8; width of valve i/width of valve viii, mean 1.14; relative width of sinus on valve viii, mean 0.33 (n = 6).

Distribution: The known geographical range of *Chaetopleura roddae* extends between latitudes 8° N and 3° S. Northernmost record, Fort Kobbe, Panama (8°55′ N; 79° 35′ W) (LACM 10820); southernmost record, Bocapan, Tumbes Prov., Peru (3°44′ S; 80°46′ W) (LACM 72-81). Specimens have been examined from sites in Panama (LACM 65-22; LACM 75-54; LACM M-864; LACM 10787; LACM 10810; LACM 10820; LACM 10821; LACM 10843; LACM 10844; LACM 10846; LACM 10848; LACM 10849; LACM-AHF 451-35; LACM-AHF 863-38), Ecuador (LACM 70-9; LACM 70-13; LACM 209-34; LACM-AHF 210-34), and Peru (LACM 72-83). Bathymetrically, *C. roddae* ranges from the intertidal zone to 54-90 m (LACM-AHF 863-38, Bahía Honda, Panama).

Remarks: *Chaetopleura roddae* is remarkably similar to *C. lanuginosa* with which it must be assumed closely related. The two species are allopatric, and live some 4000 kms apart. They have the same body proportions (Table 1), the radulae are identical, and the girdles are indistinguishable for practical purposes (the same spiculoid processes, glassy spicules, and bridges with densely packed slender spicules in a palisade). They differ most in the shape of the posterior valve, a difference large and consistent enough to warrant considering them as distinct biological entities at the species level. In contrast with *C. lanuginosa*, specimens of *C. roddae* have convex postmucro area on tail valve ["the posterior margin swollen" in Thorpe's (*in* Keen, 1971) description of "39. *Chaetopleura*..."] but without forming a false mucro; mucro central (instead of posterior): insertion teeth directed outward (not recurved forward) and not buttressed by callus. Other smaller and subtler features of *C. roddae* that separate it from *C. lanuginosa* are the presence of more abundant glassy spicules in the girdle, more abundant and more crowded tegmental pustules, and less accentuated (less elevated) lateral areas in valves iii to vii.

Chaetopleura roddae is sympatric with *C. lurida* in Panamá, and specimens of the two species have been collected together, side-by-side, at the same site.

This new species of *Chaetopleura* is here named ***roddae*** after Dr. Peter U. Rodda, Department of Geology, California Academy of Sciences, who, in the course of the years, has fostered and promoted my interest in taxonomy and critically and cheerfully encouraged my work with chitons.

Chaetopleura unilineata Leloup, 1954

(Figures *28, 29,* 30 and 31)

Chaetopleura unilineata Leloup, 1954: 1-6, figs. 1, 2
"Chaetopleura mixta (Dall, 1919)" *ex auttore* treating Panamic species. Keen, 1958: 524, Amphineura, sp. & fig. 37—Thorpe *in* Keen, 1971: 879, Polyplacophora, sp. & fig. 42—Abbott, 1974: 401. [Not *Tonicia mixta* Dall, 1919, = *Chaetopleura lanuginosa* (Dall, 1879)].

Nomenclatural Comments: As mentioned before, the biological species known heretofore as *"Chaetopleura mixta* (Dall, 1919)" became without a name when *C. mixta* proved to be an objective synonym of *C. euryplax* Berry, 1945, itself a junior synonym of *C. lanuginosa* (Dall, 1879). The first available name for this common tropical species is *Chaetopleura unilineata* Leloup, 1954.

Diagnosis: Medium size chitons, carinate, beige to pink or orange. Tegmentum with pustules in quincunx on end valves and lateral areas of intermediate valves, in longitudinal rows on central areas. Mucro central to slightly anterior; postmucro, concave. Girdle with minute oval scales, and conspicuous glassy spicules; girdle bridges with no spicules. Posterior valve with insertion teeth directed outward, *i. e.*, not incurved forward. Radula major lateral teeth, bicuspid.

Type Material: *Chaetopleura unilineata* Leloup, 1954: Holotype (Institut Royal des Sciences Naturelles de Belgique, Bruxelles).

Type Locality: "Machalillo [= Machallila], Ecuador," [1°29′ S; 80°46′ W], at 5-8 m of depth.

Description: In the description of *Chaetopleura unilineata* Leloup (1954) made no mention of the characteristics of the girdle bridges or the radula. Examination of the holotype provided the much needed additional information. The girdle bridges, clearly recognized in the alcohol-preserved specimen, are "empty" and show no spicules or any other ornamentation. The radula has rectangular median teeth with small blade at anterior end, and major lateral teeth with empty bicuspid heads. The gills, holobranchial and abanal, comprise about 22 plumes per side.

Supplementary Observations: Among 161 specimens of *Chaetopleura unilineata* examined, from 41 lots, largest specimen is 32 mm long (L. Shy Colln., Punta Jualapan, Manzanillo, Colima, Mexico, *leg.* L. Shy, Jan. 1976, at 31m). Specimens (Figures *28, 29*) carinate, jugal angle about 100°; posterior edge of intermediate valves, straight, not beaked or angled. Color variable, from beige-brown to uniformly bright red or orange, often with wide creamy stripe along jugum (also a common color pattern of *C. lanuginosa).* Body width / length, mean 0.64; height / length, mean 0.23. Tegmentum pustulose. On end valves and lateral areas, pustules usually round, large (about 120-140µm in diameter and height, mostly in quincunx, varying in number from abundant and crowded to sparse and irregularly placed; on central areas, pustules often elongate, smaller (about 50µm in diameter, less in height) in well spaced longitudinal rows (6-15 per side), crowded at jugum. Mucro central to slightly anterior; postmucro concave. Articulamentum white, often with transversal brown discolorations in posterior half of valve. Slit formula range 6/13-1-8/14, mode 11-1-12. Width of valve i / width of valve viii, mean 1.20; relative width of sinus on valve viii, mean 0.31. Girdle's upper surface (Figure 30) covered with minute, nippled, ovoid scales (40 × 18 µm), and slightly curved, pointed, thin (15-20µm) glassy spicules varying in number from few to very abundant, and in length from inconspicuous to 500µm; girdle bridges, empty; undersurface with translucent, colorless rectangular scales like in *C. scabricula.* In a specimen 18mm long (CASIZ 010091, Punta Colorado, Guaymas, Mexico), the radula (Figure 31) 5.5mm long (33% of specimen's length) comprises 30 rows of mature teeth; median tooth rectangular, about 180µm wide, 200µm long, with small blade at anterior end; first lateral teeth about 150mm long; major lateral teeth with bicuspid head (180µm long, 130µm wide), outer cusp larger and longer; spatulate teeth, about 300µm long, with only moderate flexure; outer marginal teeth, elongate, 150 × 90µm.

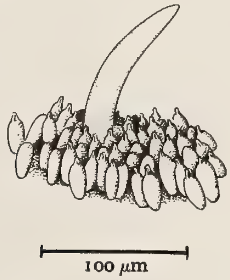

Figure 30

Chaetopleura unilineata Leloup, 1954. Specimen 18mm long (CAS 010091, Punta Colorada, Guaymas, Sonora, Mexico). Girdle's upper surface scales and spicules

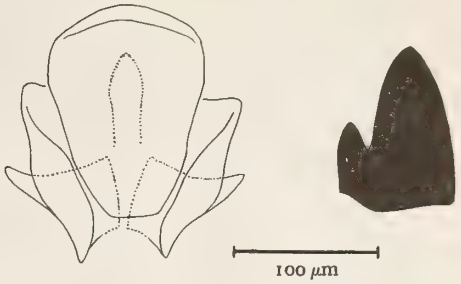

Figure 31

Chaetopleura unilineata Leloup, 1954. Same specimen as in Fig. 30. Radula's median tooth, first lateral teeth, and head of major lateral tooth

In the extremes of intraspecies variation, two forms of *Chaetopleura unilineata* may be distinguished, 1) often in bright tones of orange or red, with end valves and lateral areas crowded with numerous, conspicuous, quincuncially arranged pustules and crowded longitudinal rows of smaller pustules on central areas, and 2) drab brown color specimens, often with wide creamy stripe along jugum, with few, scattered pustules on end valves and lateral areas, and widely spaced longitudinal rows of smaller pustules on central areas. These variations in color and tegmental sculpture caused considerable confusion in the investigation of the species [at one time in this study these two morphs were even regarded as different species], particularly since, on a superficial examination, specimens of the latter form may not be readily separable from specimens of *C. lanuginosa* (with exactly the same color pattern and tegmental sculpture) collected at the same site. No relationship was found between the two morphs of *C. unilineata* and geography or depth.

Distribution: *Chaetopleura unilineata* ranges from the head of the Gulf of California to northern Peru. Northernmost verified record, San Felipe, Baja California, Mexico (31°00′ N; 114°52′ W) (AJF Colln., and many others); southernmost record, Sechura Bay, Peru (5°39.5′ S; 81°01′ W) (LACM-AHF 845-38, 1 specimen at 17m). The species has been collected at many sites in between; in the Gulf of California, at Willard Id. (LACM-AHF 1063-22), Tiburon Id. (LACM 67-18), Puertecitos (LACM 69-22; LACM 69-26), Guaymas (CASG 60520; CASG 60521; CAS 010091; CAS 010113; L. Shy Colln.); Bahía de los Angeles (L. Shy Colln.), Topolobampo (CAS 010115), Mazatlán (CAS 010114), La Paz (LACM 66-30); and further south, at Manzanillo, Colima (L. Shy Colln.), Bahía Tenacatita, Jalisco, Mexico (LACM 38-6; LACM 38-7; LACM-AHF 272-34), Gulf of Fonseca, Nicaragua (CAS 010085), Bahía Jobo, Bahía Ballena, and Bahía Cocos, Costa Rica (LACM 72-19; LACM 72-45; LA-

CM 72-58; LACM-AHF 116-33; AJF Colln., R/V *Searcher* sta. 394), Taboga Id., Secas Is., Cape Mala, Tolita Is., Panamá (LACM 66-42; LACM 10787; LACM-AHF 251-34; LACM-AHF 960-39), Vijía, Colombia (Universidad del Valle Colln., Cali, Colombia), and Bahía Santa Elena, Ecuador (LACM-AHF 209-34).

Bathymetrically, *Chaetopleura unilineata* has been collected from the intertidal zone to 90m (CAS 010113, off Cabo Haro, Guaymas, Sonora, Mexico, *ex* Myra Keen, *Ariel* Exped., 28 August 1962).

Remarks: The holotype of *Chaetopleura unilineata* initially deposited in the Zoologische Museum of Hamburg has been granted to the Institut Royal des Sciences Naturelles de Belgique, Bruxelles (Dr. Wilfrida Decraemer, *in litt.,* 7 December 1981). The type material consists of a single specimen preserved in alcohol, and two slides. The specimen is accompanied by two old labels: one, typed, stating "Chaetopleura unilineata Type / Det. E. Leloup 1954," another, handwritten, adding "28. Machalillo Ecuador / 5-8m Tiefe / Kpt. R. Paessler leg. 4.12.1912 / ded. 28.II.1913 / 1 stck." The specimen is partly disarticulated; valves i, ii, vii, and viii loose; valves iii, iv, v, and vi in place but longitudinally broken on the left. Girdle and soft parts in place except for two loose fragments of the girdle. The two slides accompanying the specimen bear fragments of the girdle's upper and under surface scales; a companion label reads "32 Moll. Mod. II / D2 I.G.: 11.365 / Chaetopleura unilineata Leloup, 1954 / Machalillo-Ecuador (Zool. Mus. Hamburg, 1912) / Det.: Dr. E. Leloup, 1954." The specimen corresponds in every respect to LELOUP's (1954) description and illustrations except for the length reported as 7.5mm, but here measured (including girdle) as near 8.5mm. A fragment of the anterior part of the radula, almost loose, was detached and mounted on a glass slide for microscopic examination (A. J. Ferreira, 27 January 1982).

In the available maps, the locality "Machalillo, Ecuador" could not be found; Machalilla, instead, was located and is here assumed to be the place given by LELOUP (1954) as the collecting site for the type specimen of *Chaetopleura unilineata.*

LELOUP *(op. cit.)* did not differentiate *Chaetopleura unilineata* from other species of *Chaetopleura* in the eastern Pacific but compared it, instead, with *C. asperrima* (Gould, 1852) from southern Brazil, and *C. asperior* (Carpenter *in* Pilsbry, 1892) from east Asia.

Chaetopleura unilineata is sympatric with two other species of *Chaetopleura, C. lanuginosa* in the northern half of its range and *C. roddae* in the southern half. As mentioned above, *Chaetopleura unilineata* may be easily confused with *C. lanuginosa* on account of their similar tegmental sculpture and color pattern. However, the two species differ clearly in 1) shape of posterior valve (mucro posterior, postmucro strongly convex with false mucro in *C. lanuginosa;* mucro central to slightly anterior, postmucro concave with no false mucro in *C. unilineata*), 2) insertion teeth of posterior valve (recurved forward, buttressed by transversal callus in *C. lanuginosa;* directed outward, with no callus in *C. unilineata*), 3) girdle bridges (with abundant, slender spicules densely packed in palisade in *C. lanuginosa;* empty of spicules or other elements in *C. unilineata*), 4) radula's major lateral teeth (tricuspid in *C. lanuginosa;* bicuspid in *C. unilineata*), and 5) although less reliably, slit formula (9-1-9 in *C. lanuginosa;* 11-1-12 in *C. unilineata*).

In the southern part of the range, *Chaetopleura unilineata* may be confused with *C. roddae* Ferreira on account of similarities in 1) color, 2) tegmental sculpture, 3) central mucro, and 4) posterior valve's outward directed insertion teeth. However, the two species differ sharply in 1) girdle's upper surface scales (ovoid in *C. unilineata;* spiculoid in *C. roddae*), 2) girdle bridges (empty in *C. unilineata;* densely spiculated in *C. roddae*), and 3) radula's major lateral teeth (bicuspid in *C. unilineata;* tricuspid in *C. roddae*).

Explanation of Figures *28, 29, 32, 36, 37, 44* to *47*

Figure *28: Chaetopleura unilineata* Leloup, 1954. Specimen 19mm long (L. Shy Colln., Smith Id., Bahía de los Angeles, Gulf of California, Mexico). Close-up of anterior valves

Figure *29: Chaetopleura unilineata* Leloup, 1954. Same specimen as in Fig. *28.* Close-up of posterior valves in profile

Figure *32: Chaetopleura shyana* Ferreira, spec. nov. **Holotype** (CAS 028810). Tegmental surface of valves i, ii, vii, and viii

Figure *36: Chaetopleura shyana* Ferreira, spec. nov. **Paratype** (AJF Colln.), 14.5mm long

Figure *37: Chaetopleura shyana* Ferreira, spec. nov. Close-up of same paratype as in Fig. *36*

Figure *44: Chaetopleura benaventei* Plate, 1899. **Lectotype** (Zoologisches Museum, Humboldt Universitat, Berlin, DDR)

Figure *45: Ischnochiton (Trachydermon) asperior* Carpenter *in* Pilsbry, 1892. **Holotype** (USNM 24121)

Figure *46: Ischnochiton (Trachydermon) asperior* Carpenter *in* Pilsbry, 1892. **Holotype.** Tegmental surface of valves i, vii and viii

Figure *47: Ischnochiton (Trachydermon) asperior* Carpenter *in* Pilsbry, 1892. **Holotype.** Articulamental surface of valves i, vii, and viii


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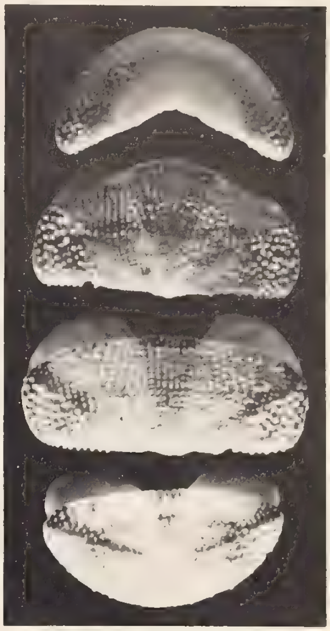
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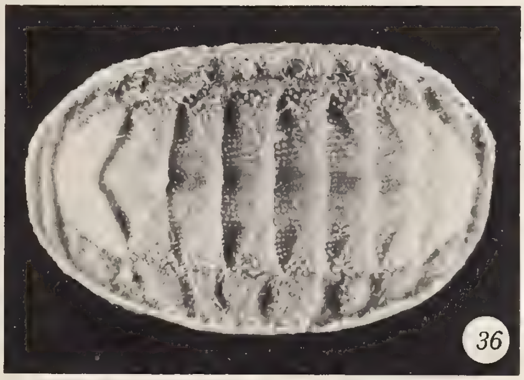
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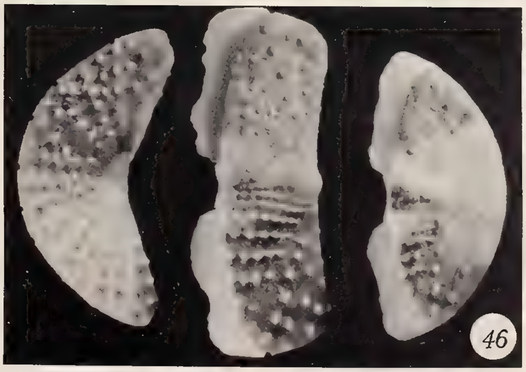
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Chaetopleura shyana Ferreira, spec. nov.

(Figures *32,* 33, 34, 35, *36,* and *37*)

Diagnosis: Medium sized chitons, relatively elongate, round back, golden brown. Tegmentum with abundant but small pustules; on end valves and lateral areas of intermediate valves, pustules arranged in quincunx; on central areas, pustules arranged in longitudinal rows, about 15 per side. Mucro central; postmucro area convex, semilunar. Girdle with abundant glassy spicules. Radula major lateral teeth, tricuspid.

Type Material: **Holotype** (CAS 028810); **paratypes** (CAS 028811; LACM 1978; USNM 784717; ANSP 355041; and in the private collections of L. B. Shy, and A. J. Ferreira).

Type locality: Isla Pata, Bahía de los Angeles, Baja California, Mexico (29°00′ N; 113°30′ W).

Description: **Holotype** (Figure *32*) Selected from a lot of 15 specimens collected at Isla Pata, Bahía de los Angeles, Baja California, Mexico, under rocks at mid-low tide (L. Shy Colln., lot no. 11, *leg.* L. Shy, May 1976). Specimen perfectly flat, preserved dry, 19.1mm long (including girdle), 10.3mm wide (at valve iv), 2.4mm high. Round back. Golden brown color. Posterior edge of intermediate valves straight, not beaked. Tegmentum pustulose; on end valves and lateral areas of intermediate valves, pustules are numerous, about 90-110μm in diameter, 120-140μm in height, rather close together (less than 90μm apart), quincuncially disposed; on central areas, pustules smaller (about 70-80μm in diameter and height) disposed in longitudinal rows (about 15-18 per side), less apparent at the jugum. Lateral areas well defined, moderately elevated. Mucro well marked, central; postmucro area convex with no false mucro but round, semicircular posterior edge. Articulamentum white. Insertion teeth well defined; slit formula 10-1-8. Eaves slightly spongy. Width of valve i / width of valve viii = 5.1mm / 5.3mm = 0.96. Sutural laminae subtriangular on valve ii, subrectangular in posterior valves. On valve viii, relative width of sinus, 0.83.

Girdle's upper surface (Figure 33) covered with ovoid but elongate scales, about 70 × 10μm with abundant, slightly incurved, pointed glassy spicules, up to 300 × 30μm, randomly placed; bridges (Figure 34) with abundant, slender, transparent spicules, up to 120 × 15μm, in palisade;

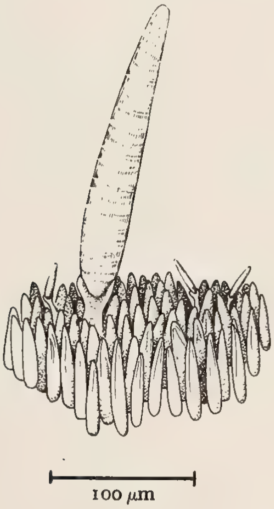

Figure 33

Chaetopleura shyana Ferreira, spec. nov. **Paratype** (CAS 028811), 20 mm long. Girdle's upper surface scales and spicules

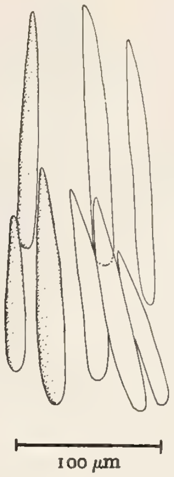

Figure 34

Chaetopleura shyana Ferreira, spec. nov. Same **paratype** as in Fig. 33. Spicules in the girdle's bridges

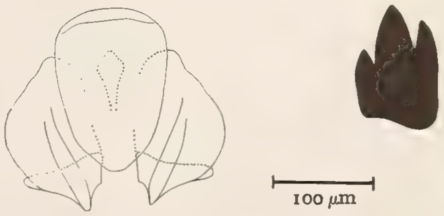

Figure 35

Chaetopleura shyana Ferreira, spec. nov. Same **paratype** as in Fig. 33. Radula's median tooth, first lateral teeth, and head of major lateral tooth undersurface with flat, transparent, rectangular scales, about 50 × 25 μm, identical with those seen in the other species of *Chaetopleura* in the tropical eastern Pacific. Radula (Figure 35), 6.5 mm long (30% of specimen's length), comprising about 30 rows of mature teeth; median tooth rectangular, about 150 μm in width at anterior blade, 180 μm in length; first lateral teeth, about 140 μm long with thickened anterior edge; major lateral teeth with protuberance at upper inner level and tricuspid head, 150 μm long at the middle, longest cusp, 150 μm wide; outer marginal teeth elongated, about 180 × 90 μm.

Paratypes (Figures *36* and *37*), in color and general features, very similar to the holotype. Body width / length, mean 0.55; height / length, mean 0.13. Slit formula range 9/11-1-8/9, mode 9-1-9.

Individual Variation: There is little variation among 39 specimens of *Chaetopleura shyana* examined, from 5 lots; largest specimen (a paratype), 27.2 mm long.

Distribution: *Chaetopleura shyana* is known only from a few localities in the Midriff area of the Gulf of California. Aside from the type locality, at Bahía de los Angeles, Baja California [29°00′ N; 113°30′ W], the species has been collected only on the northeast side of Turner Id., south of Tiburon Id. [28°43′ N; 112° 19′ W] (CAS 010093 & CASG 42540, *leg.* D. D. Chivers, April & May, 1966, respectively, in the intertidal zone), and at Isla Partida, Islas de San Lorenzo [28°44′ N; 113°00′ W] (CAS 010089 & CAS 009412, *leg.* D. D. Chivers, 29 April 1966). All specimens have been collected in the intertidal to shallow subtidal zone.

Remarks: *Chaetopleura shyana* differs from the other 3 species of *Chaetopleura* in the Gulf of California (*C. lurida*, *C. lanuginosa*, and *C. unilineata*) in the body proportions (Table 1), and in its brown golden color, round back, and smaller but more numerous granules in the tegmentum. The shape of the tail valve is also distinctly different for its semicircular outline, and convex, semilunar postmucro area. The species seems to have a remarkably narrow geographical distribution, amounting to less than 1° of latitude.

The species is here named ***shyana*** after Laura B. Shy, Westminster, California, enthusiastic chiton worker who not only collected and generously provided the type material but first recognized the species as new, pointing out my initial error in identification.

OTHER SPECIES OF *Chaetopleura*

To preclude confusion in the identification of *Chaetopleura* species in the eastern Pacific, attention was also given to species outside the study area.

In the cold waters of the northeastern Pacific, *Chaetopleura gemma* Dall, 1879 (often cited, erroneously, as *"gemmea"* by authors after Pilsbry, 1892) poses no diagnostic problems given its very different characteristics in shape, size, and sculpture. Length up to 20 mm; largest specimen examined, 17.8 mm long. Tegmentum bright or orange with grayish to black tail valve. Lateral areas with 4-7 tubercular ridges; central areas with 10-15 beaded longitudinal riblets, obsolete at jugum; posterior valve depressed, mucro inconspicuous. Slit formula, 9/12-1-7/8. Geographic range: Vancouver Island, British Columbia, Canada to Magdalena Bay, Baja California, Mexico (Burghardt & Burghardt, 1969). Northernmost verified record, Nanoose Bay, Vancouver Id., Canada (49° 16′ N; 124° 12′ W) (LACM A-8881.65); southernmost verified record, San Juanico Bay, Baja California, Mexico (26° 15′ N; 112°27′ W) (LACM 71-80). Bathymetric range, 0 to 22 m (LACM A-8881.65).

Chiton lividus Middendorff, 1847a, described from Sitka, Alaska, [further described: in Middendorff, 1847b: 124-125; plt. 13, figs. 3, 4 (reprinted: Pilsbry, 1892, 14: 76; plt. 6, figs. 22-24)] was assigned to *Chaetopleura* by Thiele (1910: 76). The species has not been recognized by subsequent workers treating northeastern Pacific species. The holotype, at the Zoological Institute, Academy of Sciences, Leningrad, USSR, has been studied by Prof. B. Sirenko who offered the opinion that "... *Chiton lividus* Middendorff is *Chaetopleura angulata* (Spengler, 1797)... the first label was lost and the second was in error... *Chaetopleura angulata* is (an) Atlantic species..." (B. Sirenko, *in litt.*, 24 Jan. 1981). Photographs of the specimen, kindly provided by Prof. Sirenko and, with his permission, here reproduced (Figures *38* and *39*) clearly demonstrate the correctness of Prof. Sirenko's opinion.

In the southeastern Pacific, along the Peru-Chile coast, several species of *Chaetopleura* have been described:

Chaetopleura hennahi (Gray, 1828) is a relatively large chiton; largest specimen examined, 52 mm long (LACM 72-78, Isla Chincha Norte, Peru, *leg.* J. H. McLean & V. Alamo, 1 Apr. 1972). Specimens carinate, bright-red to brown; tegmental pustules subdued (in lateral areas, about 90 μm in diameter); mucro anterior; postmucro moderately concave. Girdle with abundant, corneous, rather thin hairs, rarely exceeding 800 μm in length. Body width / length, mean 0.73; height / length, mean 0.20; slit formula range 8/15-1-11/12; width of valve i / width of valve viii, mean 0.99; relative width of sinus on valve viii, mean 0.31. Radula averages 53% of specimen's length and 48 rows of mature teeth, with tricuspid major lateral teeth. Northernmost verified record, Ancon, Peru [11°47′ S] (LACM 74-21).

Chaetopleura peruviana (Lamarck, 1819) is a medium sized chiton; largest specimen examined, 35 mm long (LACM 74-21). Girdle profusely beset with very long (up to 2-3 mm), thick, coarse, corneous hairs, usually dark-red in color, not only interspersed throughout girdle but in girdle bridges, protruding at sutures and extending over valves (specimens as small as 13 mm long already show this unique characteristic). Tegmentum pustulose but sculpture very subdued; mucro anterior; postmucro straight to slightly concave. Body width / length, mean 0.66; height / length, mean 0.22; radula major lateral teeth, bicuspid (*fide* THIELE, 1929: 16). Northernmost verified record, Ancon, Peru [11°47′ S] (LACM 74-210).

Chaetopleura fernandensis Plate, 1899, is based upon 26 specimens collected at Bahía Padres, Juan Fernandez Id., Chile. A type specimen, here designated **lectotype**, examined on loan from the Zoologisches Museum, Humboldt Universität, Berlin, DDR; preserved in alcohol, relatively flat, 27 mm long, 16 mm wide, 4 mm high (Figures *40, 41* and *42*); it bears two holes pierced in girdle, one in front, another in back, suggesting that at some time it might have been string-attached to a tag. In color, light brown mottled with white; subcarinate; posterior edge of valves straight, except for discrete beak. Anterior valve with 50-60 radial rows of pustules (about 150 μm in diameter and height); lateral areas with 10 radial rows of similar pustules; postmucro area with some 40 radial rows of less well defined pustules; central areas with smaller pustules in longitudinal rows (about 25 per side) extending to the jugum; jugal area of valve ii with wedge-shaped area defined by forward diverging rows of pustules. Girdle with very abundant, light golden, corneous hairs interspersed, but no hairs coming out of sutures; holobranchial, abanal. In all respects, the specimen conforms well with the description given by PLATE (1899). PLATE *(op. cit.)* distinguished *C. fernandensis* from *C. peruviana* by the color of the hairs (light golden in *C. fernandensis*, dark red in *C. peruviana*) and their distribution (present at the sutures, between the valves in *C. peruviana*, not present at sutures in *C. fernandensis*). LELOUP (1956) regarded the two species as synonymous. Until more material from Juan Fernandez Id. is available for study, a conservative stand is here recommended, and *C. fernandensis* accepted as a valid species.

Variolepsis iquiquensis Plate, 1899, is based upon 3 specimens collected at Iquique, Chile, at 30 m depth. A type specimen, here designated **lectotype**, was examined on loan from the Zoologisches Museum, Berlin, DDR. Preserved in alcohol, somewhat curled, the specimen (Figure *43*) measures an estimated 8 mm in length, 5 mm in width; golden brown color suffused with darker brown at the sides; carinate; posterior edge of intermediate valves iii to vii, straight, except for discrete beak. On anterior valve, pustules (about 100 μm in diameter) in about 10 poorly defined radial rows; on lateral areas, about 3 radial rows of similar pustules; on central areas, smaller pustules (ca. 60 μm in diameter) in longitudinal rows (6-7 per side) widely separated by smooth areas about four times the diameter of the pustules; jugal area, smooth (*i.e.*, without pustules). Girdle with abundant white, glassy spicules, about 100 μm in length. Holobranchial, abanal. LELOUP (1956), in the material from the Lund University Chile Expedition, 1948-49, found no specimens of *C. iquiquensis*, and MARINCOVICH (1973), treating the mollusks of Iquique made no mention of the species. However, from the examination of this type specimen, which agrees with PLATE's (1899) description, the species is regarded as valid, and distinct from *C. peruviana, C. hennahi*, and possibly *C. benaventei.*

Chaetopleura benaventei Plate, 1899, is based upon 5 specimens from Talcahuano and Iquique, Chile. A type specimen, here designated **lectotype**, examined on loan from the Zoologisches Museum, Berlin, DDR; preserved in alcohol, somewhat curled, is an estimated 12 mm long (Figure *44*). Golden brown flecked with darker brown; carinate; posterior edge of intermediate valves iii to vii straight except for very slight beak; mucro central; postmucro concave. Pustules, about 100 μm in diameter, in about 20 radial rows on anterior valve, 4-5 rows on lateral areas of intermediate valves; on central areas smaller pustules (ca. 70 μm in diameter) in longitudinal rows (about 10 per side) which tend to converge forward; jugum mostly smooth, *i.e.* without pustules or riblets. On valve ii, longitudinal rows of pustules do not form a wedge-like figure (a distinction from *C. iquiquensis*). Girdle with relatively long and thin (up to 1 mm long, 0.03 mm thick) horny golden hairs. The specimen agrees with PLATE's (1899) description. The species was not reported by LELOUP (1956) or mentioned by MARINCOVICH (1973). Despite some similarities to *Chaetopleura iquiquensis*, the species is accepted here as valid.

Chaetopleura savatieri Rochebrune, 1891b, *C. ahnni* Rochebrune, 1884, *C. hahni* Rochebrune, 1889, and *C. frigida* Rochebrune, 1889, are junior synonyms of *Plaxiphora carmichaelis* (Gray, 1828) [Ferreira, 1982]; *C. lactica* Dall, 1919 = *Mopalia acuta* (Carpenter, 1855) [*fide* SMITH, 1977]; and *C. rosetta* Berry, 1907, a *nomen nudum*, ? = *Dendrochiton thamnoporus* Berry, 1911 [*fide* SMITH, 1977].

In the Atlantic, *Chaetopleura angulata* (Spengler, 1797) [= *Chiton ferruginoseus* Spengler, 1797, *Chiton lusitanicus* Tilesius, 1802, *Chiton fulvus* Wood, 1815, *Chiton tehuelchus*, Orbigny, 1841, and *Typhlochiton felipponei* Dall, 1921] has been recognized along the coasts of Portugal and Spain as well as in South America from Cabo Frio, Brazil, to Patagonia (BULLOCK, 1972). *Chaetopleura apiculata* (Say *in* Conrad, 1834) [= *Chiton (Chaetopleura) candisatus* Shuttleworth, 1856] is a common chiton in the Caribbean region. *Chaetopleura spinulosa* (Gray, 1828), *C. isabellei* (Orbigny, 1841), *C. asperrima* (Gould, 1852), and *C. carrua* Righi, 1970 [names which may represent a single biological species] were described in southern Brazil and Uruguay. *Chaetopleura reesi* Salisburg, 1953 [= *Chiton viridis* Spengler, 1797, *fide* KAAS, 1972] was described from Grand Cayman Island, Caribbean Sea. *Chaetopleura veneris* Rochebrune, 1884 [= *Plaxiphora* sp. *fide* KAAS & VAN BELLE, 1980], from Patagonia, and *C. armillata* Carpenter *in* Pilsbry, 1892, from "Is. Gorriti" [? Uruguay], have remained unrecognized by subsequent authors.

In South Africa, *Chaetopleura* is represented by *C. papilio* (Spengler, 1797) [= *Chiton watsoni* Sowerby, 1840, and *Chaetopleura destituta* Ashby, 1931, *fide* BARNARD, 1963], *C.*

pertusa (Reeve, 1847) [= *Chiton pustulatus* Kraus, 1848, and *Chaetopleura destitua* Sykes, 1903a (not Ashby, 1931), *fide* Barnard, 1963], *Chaetopleura pomarium*, Barnard, 1963, *C. angolensis* Thiele, 1910, and, possibly, *Tonicia gambiensis* Rochebrune, 1881a [*fide* Thiele, 1901].

In the western Pacific, *Chaetopleura asperior* (Carpenter *in* Pilsbry, 1892) described upon a single specimen from "East Asia" has not been recognized by authors treating the eastern Asia chiton fauna (Sykes, 1903b; Leloup, 1952; Wu, 1969 & 1975). The holotype (USNM 24121) (Figures *45*, *46* and *47*) is accompanied by a museum label that reads, in part, "... Trachydermon asperior Cpr. / Type / ? Hong Kong, Stimpson." An older label adds, in a different handwriting, the word "Chaetopleura!" The single specimen, dry, well preserved, flat, corresponds to that described and illustrated by Pilsbry (1892, 14: 77; 1894, 15: 74; plt. 15, figs. 38-41). Valves i, vii, and viii, loose; the others and soft parts in place. Girdle with straight or slightly curved, simple, not dendritic hairs, up to 1mm long and 0.03mm thick. Slit formula, 8-1-9.

Chaetopleura thouarsiana Rochebrune, 1882, described from Kamchatka, proved to be a *Mopalia*, possibly *M. ciliata* (Sowerby, 1840). The type specimen (Figure *48*), examined on loan (MNHN), is accompanied by a label which reads, in part, "Chaetopleura thouarsiana Rochbr. 1882 / = Mopalia ciliata Sow. / = M. wosnessenskii Midd. / Kamchatcka...," and "Type" on a red background after the words "M. du Petit Thouars XIV 303." The specimen, well preserved, dry, flat, measures 25 × 14 × 4mm; it shows signs of having been glued to paper or cardboard; valves i and v, broken but in place. It agrees with Rochebrune's (1882) description of the species, and the current interpretation of *Mopalia ciliata*.

In Australia no species of *Chaetopleura* have been reported except for *C. conspersa* Adams & Angas, 1864 [= *Plaxiphora albida* (Blainville, 1825) *fide* Iredale & Hull, 1926] and *C. biarmata* Rochebrune, 1882.

Chaetopleura biarmata Rochebrune, 1882, was described as a Polynesian species from "Port du Roi Georges." The type specimen (Figure *49*), examined on loan (MNHN), is accompanied by a Museum label which reads, in part, "Chaetopleura biarmata Rochebrune, 1882 / Quoy & Gaimard / Port du Roi Georges." Three other labels add no further information except a date, "1829." The specimen, fairly well preserved in alcohol, a bit curled, measures about 18mm in length; soft parts intact except for a slit through which the radula had been removed. Only 4 valves present, 2 in place (iii and iv), 2 loose (? ii and v); girdle with short glassy spicules, interspersed. The specimen agrees with Rochebrune's (1882) description, but the locality ["Port du Roi Georges" = ? King George Sound, SW Australia] is questionable, for there has been no other report of *Chaetopleura* in Australian or Polynesian waters. Thus, the species remains a *nomen inquirendum*.

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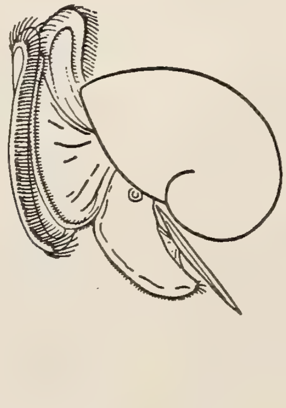

Eye of the Mussel, *Mytilus edulis* Linnaeus: Electrophysiological Investigations

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(1 Plate; 1 Text figure)

INTRODUCTION

Many scientists (see reviews by Bullock & Horridge, 1965) have conducted anatomical studies with the light microscope on the cerebral eyes of the adult mussel, *Mytilus edulis* Linnaeus, 1758; but none have investigated the eye's electrophysiological behavior. Recently Rosen *et al.* (1978) have conducted an electron microscopical investigation on these eyes. They found anatomical features that suggest that the eyes of the adult mussel are functional. The presence of axons and synthesizing organelles and that the structure of the eye is that of a photosensitive organ indicate sensory activity to them. Field (1922), Bayne *et al.* (1976), and others also have concurred from their anatomical studies that the eye is functional. Bayne (1964) has demonstrated that eye-veliger larvae and pediveliger larvae respond behaviorly to light. However, no behavioral responses indicative of light sensitivity during simple field and laboratory experiments on adult mussels were observed by Rosen *et al.* (1978). Harger (1968) reports that the other senses predominate over that of light sensitivity during competitive interactions with mussels.

In consideration of the findings of Rosen *et al.* (1978) and Harger (1968), a vital question arises. Are the cerebral eyes of an adult mussel electrophysiologically active and if they are: what is their behavioral role? We adopted this study to answer the above questions.

METHODS AND MATERIALS

Adult specimens of the mussel, *Mytilus edulis*, were collected at Ocean Beach, New London, Connecticut and then transported to the Biological Engineering Laboratory of the University of Connecticut.

In preparation, the valves of the mussel were pried apart and then the anterior and posterior adductor muscles were cut. A wood applicator stick was placed between the valves near the edge of the mantle in order to maintain a valve separation angle ranging from 90-100°. This angle facilitated the photo-stimulation of either eye and its electrophysiological recording.

White light stimuli were produced by a tungsten filament, battery operated, microscope lamp; duration of stimuli was produced by an electromechanical photographic shutter. Intensity was controlled by a series of Wratten neutral density filters and monitored by a Metrologic Radiometer.

The light was focused onto the preparation with a fiber optic tube. The fiber optic tube is a bundle of glass fibers, each 0.003 inches in diameter, transmitting wavelengths from 320 nm to 2000 nm. The stimulating apparatus formed a circular spot of uniform light about 60 μm in diameter when a single optical fiber was used.

The electro-mechanical shutter was controlled by a Wavetek signal generator. The shutter drive also produced a cue signal that followed its output for triggering purposes.

Since the preparation was usually under several millimeters of sea water, it was not considered necessary to heat-filter the light from the lamp.

For recording, a section of the optic nerve was drawn "en passant" into a polyethylene suction electrode. The optic nerve was severed near the cerebral ganglion.

The signal from the suction electrode was fed to a low-noise differential preamplifier (PAR-CR4A) with a gain of 10000 and a band pass of 300 Hz to 3 kHz. The output of the preamplifier and the cue signal from the electromechanical shutter were displayed on a Tektronix-565 oscilloscope and recorded on a four channel Hewlett Packard model-3960C Instrumentation recorder.

For data analysis, a nerve spike discrimination process was accomplished by a window circuit which produced a standard pulse when the base-to-peak amplitude of a spike was between two adjustable voltage levels. By adjusting these levels, spikes from one of a number of active fibers recorded with the suction electrode could be counted. It was usually found most convenient to use only the lower level of the window and thus count only the largest spikes. The output of the window was fed into an event counter (Data Precision—Model 5740).

RESULTS

Cessation of white-light stimulation of the eye caused a discharge of spikes in the optic nerve. A representative recording of this activity is shown in Figure *1*. The lower trace shows spikes occurring after a preceding light was turned off. Only spikes with amplitudes exceeding a preset threshold voltage were counted in this experiment. The upper trace represents the output of a pulse-height window circuit.

Several features of the response in Figure *1* are typical of our observations: (1) Spikes appear only in response to the cessation of the light, (2) there is a latent period before the first spike (approximately 166ms here), (3) spikes from a single fiber occur transiently (there is little or no on-going activity if the preparation has been in total darkness for 3 minutes), and (4) the spikes occur with regular interspike intervals, seldom exceeding an instantaneous rate of 300 per second. Stimulus parameters are defined in this report as those properties of the illumination that determine the characteristics of the OFF-RESPONSE.

The first stimulus parameter to be investigated was light intensity. In Figure 2 a graph of the responses to flashes of constant duration at seven intensities are shown. Each point on the graph is an average of 3 different mussels taken over 10 off-responses each. At the lowest intensity (0.003μW/cm^2) spike activity is almost non-existant with no synchrony between spikes and stimulus. Over the range from 0.003μW/cm^2 to 0.003mW/cm^2 of stimulus intensity, the response grows approximately as the logarithm of the flash intensity. From 0.003mW to 0.5mW/cm^2 of stimulus intensity, the response falls approximately as it rose. At a stimulus intensity of 0.003mW/cm^2, the photoreceptor is very active.

Looking at the latency versus stimulus curve, also in Figure 2, one sensed that over the range from 0.06μW/cm^2 to 0.003mW/cm^2 of stimulus intensity, the latent period to the first spike decreases approximately linearly. Similar to the response intensity series plot, the system seems to be extremely sensitive at 0.003μW/cm^2 of stimulus intensity where the shortest latency exists at 6ms. As the stimulus intensity increases from 0.003mW/cm^2 to 0.005mW/cm^2 the latency slowly increases.

DISCUSSION

The authors realize that this study is not complete if one considers characterizing the photoreceptor to such stimulus parameters as duration, background intensity, and spectral variation. However, the study does prove that the photoreceptors of *Mytilus* are electrophysiologically active. It was found that the receptors produce spike characteristics that are dependent on preresponse (stimulus) parameters. In other words, the photoreceptors of *Mytilus* are OFF-RECEPTORS (responding to the cessation of stimulation). There are other reported examples of OFF-RECEPTORS in the eyes of pelecypod molluscs (Kennedy, 1960, surf clam; Barber & Land, 1967, cockle; Mpitsos, 1973, file clam; Wiederhold *et al.*, 1973; quahog clam).

The results can be compared with Kennedy's (1960) for *Spisula*, and Wiederhold's *et al.* (1973) for *Mercenaria*. In *Spisula*, the off-response using white light grows over the lowest 2 log units of stimulus intensity and then decreases over 2 log units. The off-response in *Mytilus* follows a similar pattern. In both *Spisula* and *Mytilus* their visual systems are very sensitive to a specific stimulus intensity. A difference between these results *(Spisula* and *Mytilus)* and Wiederhold *et al.* (1973) is that *Mercenaria* has a monotonic growth of responses with intensity. In *Spisula* and *Mercenaria* the latency to the off-response is a monotonically decreasing function of stimulus intensity. In *Mytilus*, the latency follows inversely the stimulus intensity.

The present study provides insight to the possible behavioral function of the photoreceptors of *Mytilus*. One possibility is that they function in protection from predatory attack. This is based on the fact that the photoreceptors respond to cessation of illumination or to shadows. Another possible function of the eyes of *Mytilus* is presented by Elvin (1976). He demonstrated that neurosecretory release by the cerebral ganglion in sexually mature specimens of *Mytilus* is enhanced by the presence of light. He suggested that the eyes of *Mytilus* may function in some long term response, such as mediating photoperiod in the reproductive cycle. This suggested function of the eyes is highly possible, since the optic nerve innervates directly

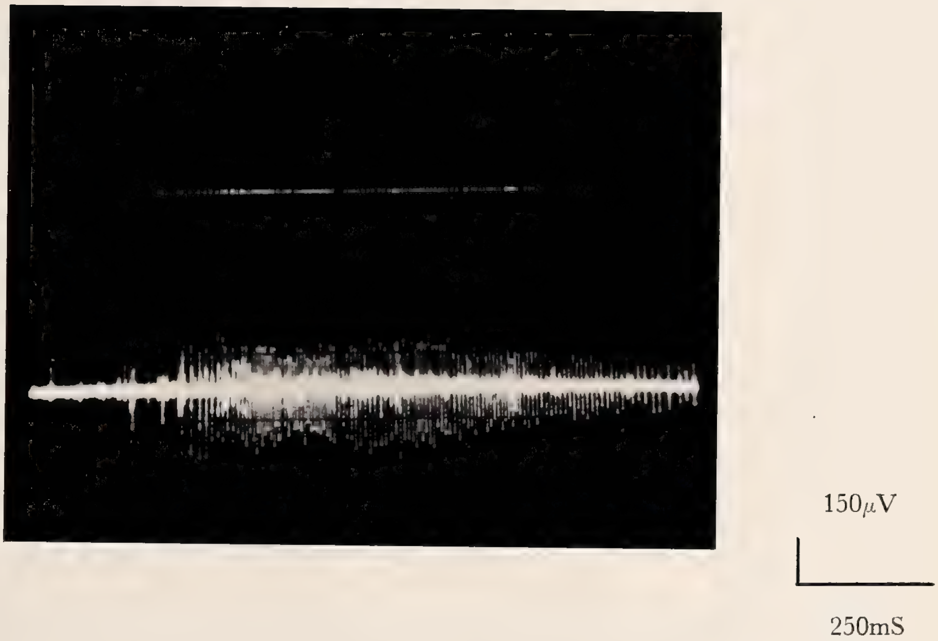

Figure *1*

Sample recording with suction electrode of spikes from a strand of *Mytilus* optic nerve in response to turning off a spot of white light directed on the eye. Lower trace: electrode output showing spikes from many different fibers. Dotted trace: window circuit output. All spikes with positive peak amplitudes above 75μV were accepted by the window circuit. Both traces were initiated with the turning off of a preceding light. Light stimulus: 0.8μW/cm^2. Light was on for 30 seconds before trace begins

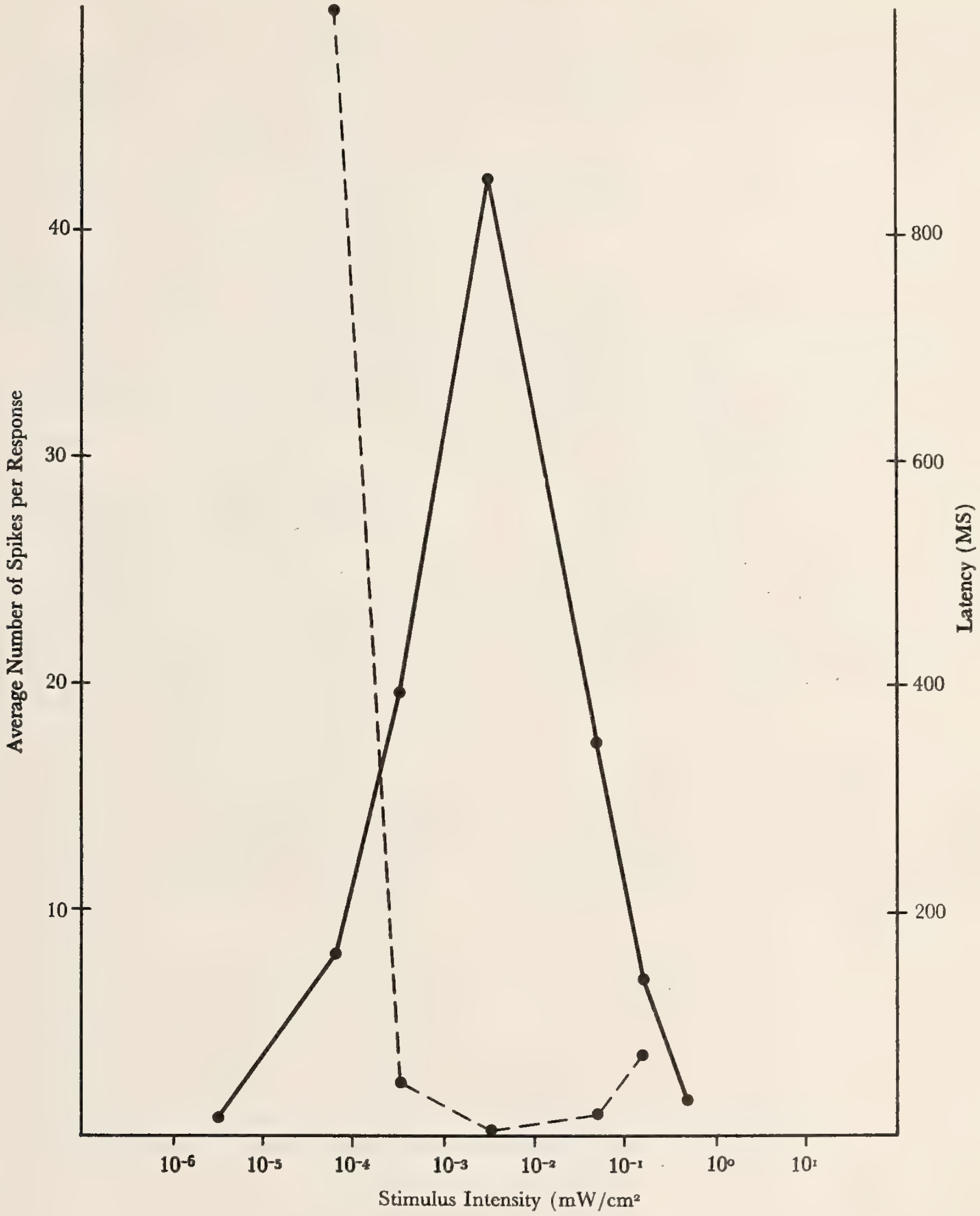

Figure 2

Composite plot of a response-intensity series and a latency-intensity series. Each point on graph is an average of 3 different mussels taken over 10 off-responses. Light is turned off at the beginning of the oscilloscope trace. White light stimulus. Multiunit recording. Spot diameter 60μm. Flash duration 60 seconds. In each case the off-response was monitored for 2 minutes the cerebral ganglion. Finally, the eye may function in some integrative aspect with other receptors within the mussel. For example, the response of the eye may be used in modifying the sensitivity of the equilibrium receptors (statocysts) in *Mytilus.*

An offshoot of this study is the adding of information to a pool of existing knowledge concerning behavioral function and photoreceptoral structure.

Land (1968) concluded from behavioral and electrophysiological data that eyes with ciliary photoreceptors typically respond to cessation of illumination or to shadows and usually function in protection from predatory attack. In contrast, eyes with rhabdomeric photoreceptors typically respond to the onset of illumination and function by monitoring light intensity. Vanfleteren & Coomans (1976) considered this correlation between photoreceptor type and ocellar function as a generalization with a few known exceptions.

However, in *Mytilus,* Rosen *et al.* (1978) have shown the receptor to be rhabdomeric in structure and we have demonstrated that the eye is an off-receptor. It seems we have found another exception to Land's (1968) and Vanfleteren & Coomans' (1976) theory.

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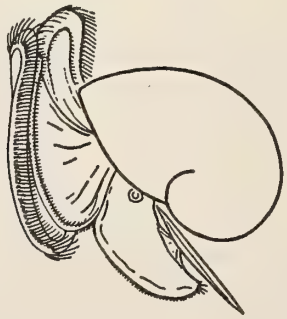

The Topography, Formation and Role of the Home Depression of *Collisella scabra* (Gould)

(Gastropoda : Acmaeidae)

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(1 Plate)

INTRODUCTION

MANY SPECIES OF patellacean limpets have been reported to form depressions (home scars) on various substrata (GRAY, 1833; GRANT, 1933; POWELL, 1973; BRANCH, 1975; VERMEIJ, 1978). These depressions are typically formed by homing and/or territorial species, and are thought to aid in resistance to desiccation. Although the role of these depressions has been discussed frequently, the mode of formation has not been examined rigorously. Instead, there exist three alternative explanations, all of which appear to be based, at best, on single observations or the intuition of the observer.

The earliest explanation of the formation of home depressions is that of GRAY (1833: 800) who proposed that they were "produced by the dissolution of the surface onto which it [the limpet] is affixed." DALL (1870), after examining the home depressions of the pulmonate limpet *Trimusculus reticulatus* (Sowerby), concluded that home depressions were excavated by the radula. HAWKSHAW (1878) advocated a third alternative—that home depressions are formed by abrasion of the substratum by the shell edge. All three explanations have had numerous proponents, but the working of the shell edge against the substratum has become the most popular (DAVIS & FLEURE, 1903; HYMAN, 1967: 346; YONGE & THOMPSON, 1976: 59).

The topography of the home depression has been discussed by several workers including GRAY (1833), DALL (1870), and LINDBERG (1976). However, the relationship between home depression contours and the mechanism of their formation has seldom been considered (but see BATE, 1850). The formation of home depressions by working the shell edge against the substratum can be rejected for two reasons. First, the home depression consists of two levels, a shallow, outer depression that corresponds to the shell's aperture, and a deeper, inner depression that corresponds to the limpet's foot (Figure *1-2*). Because of the inner depression's smaller diameter and greater depth, it appears physically impossible for the shell edge to be responsible for its formation. Moreover, it would also appear to be physically impossible to form an outer crenulate margin by working the shell edge against the substratum. Secondly, few substrata are less resistant than the shell edge. The hardness of the limpet shell (calcium carbonate) is approximately 3 units on the Mohs Hardness Scale. This is quite low and exceeds only minerals such as talc and gypsum. Basalts, cherts, and most of the individual grains that make up well indurated coarse clastic rocks typically exceed 5 units on the Mohs scale. Thus, the shell edge would be inefficient in excavating home depressions except for clay- and mud-stones or substrata from which the cement has been leached, such as friable sandstones. This leaves radular excavation or dissolution of the substrata as viable explanations.

The surface of the home depression on less resistant substrata (*e.g.,* mollusc shells, mudstones and claystones) is covered with numerous radular striations (Figure *3*). Moreover, the radular teeth of patellacean limpets are capped with goethite ($Fe_2O_3 \cdot H_2O$) which has a hardness of approximately 5 units on the Mohs scale (LOWENSTAM, 1962; POWELL, 1973). While this explanation appears to be better supported, it is not totally sufficient because home depressions are formed on substrata that exceed 5 units on the Mohs scale.

We became interested in the possible role of secretions in home depression formation for two reasons. First, if the home depression is excavated by the radula, there must be a template on the substratum that enables the limpet to

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distinguish the home site from adjacent areas. Because the limpet excavates these areas to different depths (Figure *2*), it must be able to discriminate the region where the shell rests (shell platform) from the area under its foot (foot depression). Secretions from the mantle and foot were likely candidates because they could impregnate the substratum while the limpet was on the home depression and then be chemically sensed when the limpet was excavating. Secondly, we considered the possibility that secretions might weaken more resistant substrata so that they could be excavated by the radula.

While reviewing the literature on biological erosion we became aware of M. R. Carriker's work on the mechanism of borehole excavation by predatory gastropods (see review by Carriker & Williams, 1978). We noted several similarities between boreholes and home depressions and adapted several of Carriker's experiments to our study. A paper by Grenon & Walker (1978), describing the pedal gland systems of two patellacean limpets, focused our attention on the possible role of the pedal glands in home depression formation, and we repeated several of their experiments on a local species that forms home depressions, *Collisella scabra* (Gould).

In this paper we report on the topography, formation, and role of the home depression of *Collisella scabra*, including the mechanism of excavation, and characteristics and sources of secretions that cause dissolution of calcium carbonate substrata. Examples of nonpatellacean home depressions also are discussed.

MATERIALS AND METHODS

Topography:

Home depressions of *Collisella scabra* were examined on shells of the molluscs *Mytilus californianus* (Conrad) (n = 50) and *Lottia gigantea* (Sowerby) (n = 135) collected from Southeast Farallon Island, California (37°42′ N; 123°00′ W) and on *L. gigantea* shells from Isla de Guadalupe, Mexico (n = 25) (29°00′ N; 118°20′ W) and from San Nicolas Island, California (n = 100) (33°16′ N; 119°30′ W).

To characterize the secretions available for forming home depressions, experiments were conducted using the following four techniques: calcium carbonate etching, carbonic anhydrase histochemistry of the foot and mantle, mucopolysaccharide histochemistry of the foot and mantle, and pH measurements from the sole of the foot. All experiments utilized *Collisella scabra* collected at Santa Cruz, California (36°58′ N; 122°10′ W).

Calcium Carbonate Etching:

Large crystals of calcium carbonate (icelandic spar) were cleaved into 30 smaller blocks. The blocks were examined under a dissecting microscope at 30×, and a specimen of *Collisella scabra* was placed on the smoothest, least fractured side of 20 of the blocks. Several wraps of thread kept the limpet on the block. The remaining 10 blocks had empty *C. scabra* shells affixed to them as a control. Each block was then placed in a petri dish containing filtered seawater and held at 10° C for 8 hours.

Carbonic Anhydrase Histochemistry:

Sagittal and transverse sections of the head, foot, and mantle of 15 specimens of *Collisella scabra* were cut at 10 μm with a cryostat. Sections were post-fixed in cold acetone (−20° C), transferred to acetone at 18° C for 2 hours, and tested for carbonic anhydrase activity following the technique of Pearse (1968: 1365). Control sections were incubated in the presence of acetazolamide (Diamox sodium salt).

Mucopolysaccharide Histochemistry:

Seven specimens of *Collisella scabra* were relaxed in a 1:1 solution of seawater and 7% magnesium chloride to obtain a flat foot surface, and then fixed in 4% buffered neutral formalin. The head, foot, and mantle tissues were embedded in paraffin and sagittal and transverse sections cut at 10 to 15 μm. Four histochemical tests, all based on Pearse (1968), were performed: (1) Alcian Blue pH 1.0 (AB 1.0); (2) Alcian Blue pH 2.5 (AB 2.5); (3) Alcian Blue-Critical Electrolyte Concentration (AB-CEC), and (4) Alcian Blue pH 2.5-Periodic Acid-Schiff (AB-PAS). The first three tests (AB 1.0, AB 2.5, and AB-CEC) are

Explanation of Figures *1* to *7*

Figure *1:* *Collisella scabra* home depression on the shell of *Lottia gigantea.* Isla de Guadalupe, Mexico Bar = 3 mm

Figure *5:* Sagittal section through the foot of *Collisella scabra* stained with Alcian Blue-Periodic Acid-Schiff. Mucocytes and ducts containing acidic mucopolysaccharides are stained dark Bar = 25 μm

Figure *6:* Home depressions of *Sabia conica* on *Turbo* sp. Indo-Pacific Bar = 5 mm

Figure *7:* Home depression of *Haliotis cracherodii* on sandstone. San Nicolas Island, California Bar = 5 cm

Figure *2:* *Collisella scabra* home depression on *Lottia gigantea.* Southeast Farallon Island, California. sp = shell platform, fd = foot depression Bar = 0.5 mm

Figure *3:* Radular striations. *Collisella scabra* home depression on *Lottia gigantea.* Southeast Farallon Island, California Bar = 1 mm

Figure *4:* Dissolution of calcium carbonate substratum by foot secretions from *Collisella scabra* Bar = 5 mm

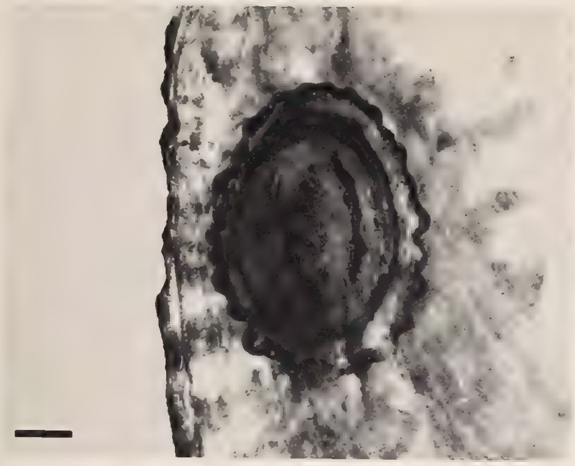

Figure *1*

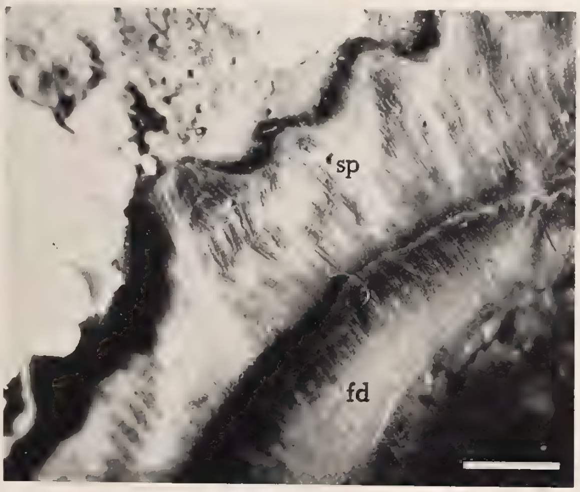

Figure *2*

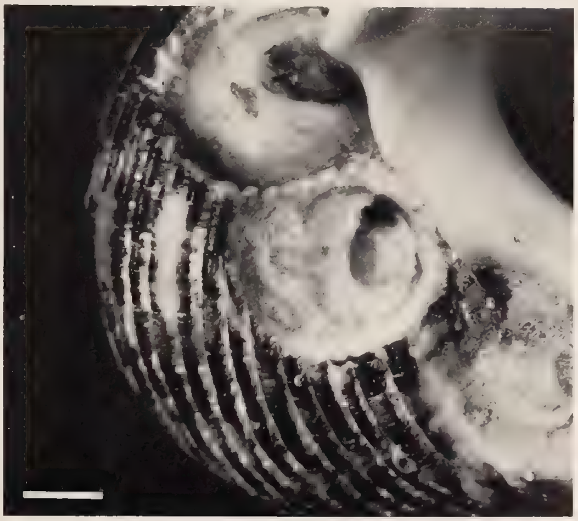

Figure *6*

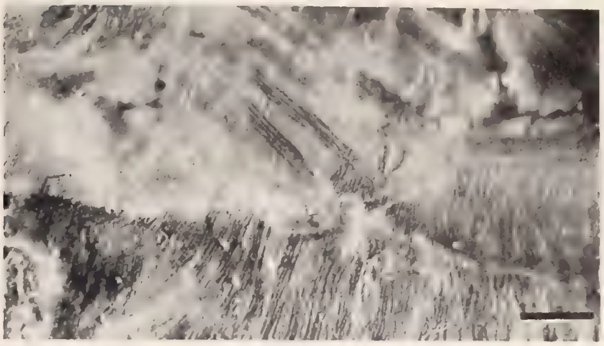

Figure *3*

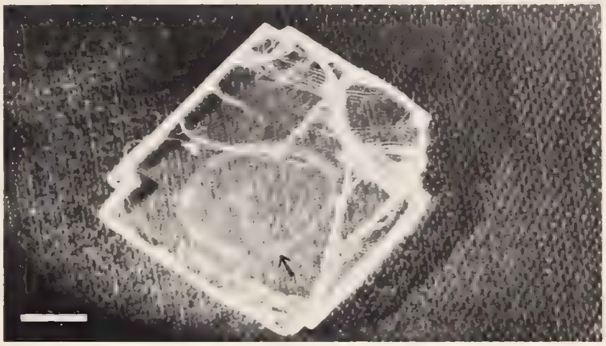

Figure *4*

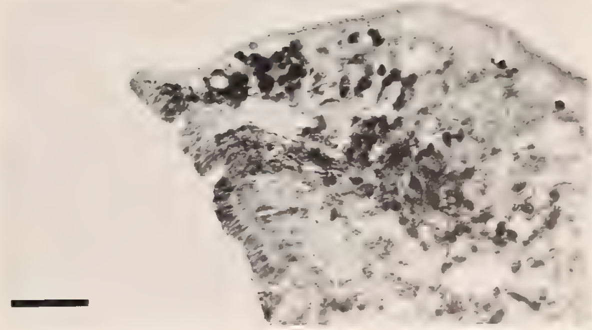

Figure *5*

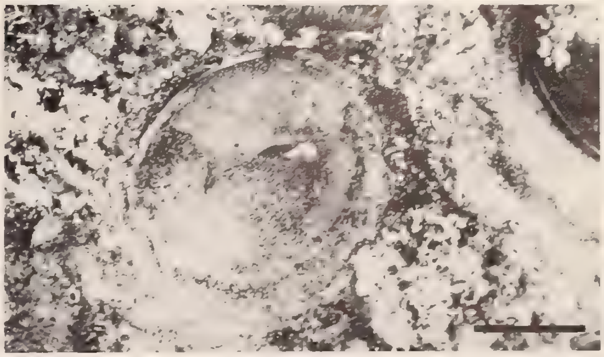

Figure *7*

selective stains for sulfated, acidic mucopolysaccharides. Test four (AB-PAS) differentiates between neutral and acidic mucopolysaccharides.

pH of the Foot of *Collisella scabra:*

We collected 43 intertidal specimens of *Collisella scabra,* ranging between 10 mm and 24 mm in length, and measured the pH of the sole of the foot at the anterior edge and center with a 1.2 mm diameter pH probe (Microelectrodes, Inc., MI-410) connected to a digital pH meter (Orion Research, model 601A). All measurements were concluded within 2 hours of removing the limpets from the substratum.

RESULTS

Topography:

The home depression is composed of two distinct levels (Figures *1, 2*). The outer level or shell platform conforms to the crenulate shell margin of *Collisella scabra* and the inner, deeper depression corresponds to the limpet's foot dimensions. The bottom of the foot depression is convex, with the center almost level with the shell platform. The surface of the home depression is covered with fine striations that correspond to the configuration of the first and second lateral teeth of the radula (Figure *3*).

Calcium Carbonate Etching:

When the limpets were removed and the calcium carbonate blocks viewed under a dissecting microscope, etchings corresponding to the limpet's foot areas were found on the surfaces of the 20 experimental blocks. Dissolution was strongest on the periphery and weakest in the center (Figure *4*). No evidence of dissolution was found under the mantle regions after 8 hours or under the shells of the control group.

Carbonic Anhydrase Histochemistry:

Carbonic anhydrase activity, as indicated by brown-black deposits of cobalt-sulphide, was found in the mantle edge of *Collisella scabra,* but not in the foot tissues. Control sections lacked such deposits in the mantle edge.

Mucopolysaccharide Histochemistry:

Based on position and specific staining, seven different mucopolysaccharides were identified; 5 in the foot (G1-G5) and 2 in the mantle edge (G6 and G7). Table 1 presents the results of the tests.

The pedal glands that contain mucopolysaccharides occur at three levels; in the ventral epidermis, in the lower half of the foot, and in the upper half of the foot. The glands in the upper half of the foot contain neutral, nonsulfated, hexose-containing mucoid substances. The remaining four types of mucopolysaccharides are divisible into two groups (1) neutral, nonsulfated mucopolysaccharides, and (2) acidic, sulfated mucopolysaccharides. Both groups occur in both the ventral epidermis and in the lower half of the foot. Those in the lower half of the foot are most abundant in the periphery. The mucocytes in the lower half of the foot that contain acidic mucopolysaccharides are consistently larger than those containing neutral mucopolysaccharides.

pH of the Foot of *Collisella scabra:*

The pH of the anterior margin of the foot of *Collisella scabra* ranged from 2.5 to 6.4 ($\bar{x} = 3.6 \pm 0.6$ SD). The center of the foot ranged from pH 2.6 to 6.6 ($\bar{x} = 3.9 \pm 0.7$ SD). There was no significant difference between the anterior margin and the center region (t-test value = 1.932, d.f. = 84, $P < 0.1$).

Table 1

Histochemical reactions of mucocytes in the foot (G1-G5) and mantle (G6 and G7) of *Collisella scabra.*

	Glands						
Histochemical tests	G1	G2	G3	G4	G5	G6	G7
AB pH 1.0	–	+	–	++	–	+++	–
AB pH 2.5	–	+++	–	+++	–	++	–
AB-PAS	+++(r)	+++(b)	+++(r)	+++(b)	+(r)	+++(b)	+++(r)
AB-CEC 0.1 M-$MgCl_2$	–	++	–	+++	–	++	–
AB-CEC 0.2 M-$MgCl_2$	–	+	–	++	–	+	–
AB-CEC 0.5 M and above- $MgCl_2$	–	–	–	–	–	–	–

Reactions: – = negative, + = weak, ++ = moderate, +++ = strong
Colors: b = blue (acidic), r = red (neutral)

DISCUSSION

The results of the etching experiment clearly indicate that secretions from the foot of *Collisella scabra* cause dissolution of calcium carbonate. These secretions do not contain carbonic anhydrase, but rather sulfated, acidic mucopolysaccharides. The pattern of dissolution on the blocks (Figure *4*) is identical to the gross distribution of the acidic pedal mucocytes; they are most abundant on the periphery and fewest in the center (Figure *5*). This pattern corresponds to the depth pattern found in the inner, foot region of home depressions on calcium carbonate substrata.

The results of histochemical tests indicate that both carbonic anhydrase and acidic mucopolysaccharides are present in the mantle edge. When *Collisella scabra* is on its home site the mantle edge is placed against the substratum, as evidenced by the irregular growth of the shell edge of specimens on granitic rocks.

From these data we infer the following mechanism and sequence of events in home depression formation by *Collisella scabra.* Adhering to a specific site, *C. scabra* impregnates the substratum with acidic mucopolysaccharides secreted from the foot. Secretions from the mantle edge, acidic mucopolysaccharides and/or carbonic anhydrase, also impregnate the substratum. These areas are then recognized by the limpet, and scraped with the radula. If the substratum undergoes dissolution, the depth and complexity of the home depression are increased. If the substratum is harder than the radular teeth or does not undergo dissolution, the shell edge conforms to the substratum and no home depression is formed.

This compound chemical-mechanical method of excavation is similar to the method used by predatory gastropods to bore holes through the shells of their prey (Carriker, 1969). The major differences are that predatory gastropods are thought to soften the substratum with a combination of acid, chelator, and possibly an enzyme secreted from an accessory boring organ (Carriker & Williams, 1978).

Carriker *et al.* (1967), studying the accessory boring organ of *Urosalpinx cinerea* (Say), recorded pH levels of between 3.8 and 4.1 when the microelectrode bulb was completely enveloped by the accessory boring organ. This is close to the mean pH of *Collisella scabra* foot secretions.

Pedal glands secreting acidic mucopolysaccharides are not unique to *Collisella scabra.* They have been reported previously in other patellacean limpets that form home depressions, as well as those that do not (Fretter & Graham, 1962; Grenon & Walker, 1978) and have been reported in many other prosobranch molluscs (Fretter & Graham, 1962).

We propose that gastropods with acidic mucopolysaccharide pedal secretions have the potential to form home depressions. The only requirement is that they invariably return and/or adhere to a specific site (*e.g.*, have homing behavior). Once the mollusc homes, the secretions will impregnate the substratum at the home site. If the substratum undergoes dissolution a home depression will be formed. The rate and complexity of formation will depend on the mineralogy of the substratum, but will be enhanced if the mollusc acquires a second behavior pattern and removes the softened material with the radula.

The similarity of home depressions among prosobranch taxa suggests that this mechanism may be common. The home depression of the pulmonate limpet *Trimusculus reticulatus* on calcium carbonate substrata is multi-contoured and covered with radular striations, and the pedal gland system is similar to that found in *Collisella scabra* (Dwyer, 1979). This method of forming home depressions may also occur in the families Siphonariidae (Willcox, 1905; Voss, 1959; Cook, 1969), Hipponicidae (Figure *6*), Coralliophilidae (Robertson, 1970), Capulidae (Orr, 1962), Calyptraeidae (Ulbrick, 1969) and Haliotidae (Figure *7*).

The results of histochemical tests enabled us to rule out carbonic anhydrase as an agent of dissolution in the formation of the inner foot depression, but other enzymes or chelating substances may also be present.

The life histories of most species that form home depressions may be used as an argument against the presence of enzymes and chelating substances because of the chemical specificity of these substances. Most of these species have planktic larvae that have little or no control over the geographical region in which they will eventually settle. Thus, there is no guarantee that the substratum will be chemically similar between generations and selection for enzymes or chelating substances that act on specific substrata appears very unlikely. The fact that home depressions are formed on such diverse substrata as shells, basalts and wood strongly suggests that the substance that serves as a template and the mechanism of depression formation is of a very general nature.

Homing and home depressions typically have been associated with resistance to desiccation (Fretter & Graham, 1962; Haven, 1971). However, Wolcott (1973: 413), in a study of the physiological ecology of five northeastern Pacific acmaeid species (including *Collisella scabra*) suggested that "...the advantage of homing may be primarily related not to desiccation but to some other environmental factor, *e.g.*, dislodgment by wave impact or injury by waveborne sand..."

Branch (1975) suggested that home depressions have different functions in different species, including protection from predation and desiccation. Vermeij (1978: 143) proposed that the ability of epizoic limpets to excavate home depressions on molluscan hosts has a geographical component associated with predation pressure.

We also infer that the primary role of the home depression is not to prevent desiccation but rather dislodgment.

Home depressions are formed by subtidal species that are in no danger of desiccation, including *Capulus danieli* (Crosse) (Orr, 1962), *Crucibulum spinosum* (Sowerby) (Ulbrick, 1969), and *Pectinodonta maxima* (Dautzenberg) (Wolff, 1979). Also, typically intertidal species, including *Collisella scabra*, form home depressions even when they are completely submerged in tide pools, or occur subtidally (see also Branch, 1975; MacKay & Underwood, 1977).

When on its home depression, *Collisella scabra* is virtually immovable because the crenulated edges of the shell and home depression function like a lock and key, preventing lateral movement. Furthermore, the recessed shell platform makes the limpet less vulnerable to prying or stabbing predators such as shore birds and possibly fishes (*cf.* Vermeij, 1978: 143).

In addition to providing protection from predation, the home depression may allow smaller species to occur on the territories of larger agonistic species by preventing the smaller species from being shoved off the substratum.

Wright (1977, 1981) measured the shear force exerted by the territorial limpet *Lottia gigantea* on other species of limpets. He found that *L. gigantea* exerted a maximum shear force of 2.8kg when attempting to dislodge intruders from its territory and that 2.0kg was required to displace moving *Collisella scabra*. However, the force required to displace *C. scabra* from home depressions typically exceeded 5.0kg and on several occasions the shells of *C. scabra* or the substratum broke before the limpet was dislodged.

SUMMARY

1. The complexity of the home depression of the limpet *Collisella scabra* rules out its formation by the shell edge.

2. We have identified and characterized secretions from the foot (acidic mucopolysaccharides) and mantle edge (acidic mucopolysaccharides and carbonic anhydrase) that are capable of penetrating calcium carbonate substrata and causing dissolution.

3. We believe that these secretions impregnate the substratum and serve as templates for radular excavation of the home depression and that their ability to cause dissolution aids in home depression formation on certain types of substrata.

4. Observations of nonpatellacean home depressions suggest that this method of formation may also occur in other prosobranch taxa.

5. We suggest that the primary role of the home depression is to resist dislodgment rather than prevent desiccation.

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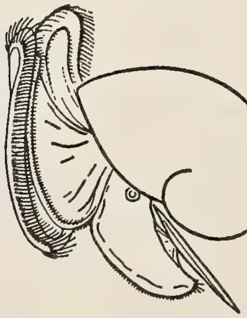

The Role of the Home Scar in Reducing Water Loss During Aerial Exposure of the Pulmonate Limpet, *Siphonaria alternata* (Say)

BY

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(4 Text figures)

INTRODUCTION

PREVENTING THE DESICCATION of body fluids during low-tide aerial exposure is one of the most crucial problems facing intertidal organisms. Intertidal gastropods have evolved various mechanisms that help them avoid severe desiccation. For example, the prosobranch limpet *Acmaea digitalis* (Eschscholtz, 1833) forms a mucous sheet between its shell margin and the substrate during low tide (WOLCOTT, 1973). Nonpatelliform snails use opercula to protect themselves from potentially harmful ambient conditions (MAYES, 1962).

Both prosobranch and pulmonate limpets return to depressions termed 'home scars' before or shortly after rocks begin to dry (ORTON, 1929; HEWATT, 1940; OHGUSHI, 1954; JESSIE, 1968; COOK, *et al.*, 1969; COOK, 1970). This pattern of behavior has traditionally been used as indirect evidence that limpets return to scars to minimize desiccation and subsequent lethal or debilitating effects (BORLAND, 1950; DAVIES, 1969; HAVEN, 1971; WOLCOTT, 1973; BRANCH, 1975; COOK, 1976). There have been no direct measurements of body fluids in limpets on and off scars.

In this study, we examine the hypothesis that homing to a scar provides protection against desiccation at low tide. We describe activity and homing patterns in *Siphonaria alternata* (Say, 1822) to determine whether these limpets appear to avoid drying conditions, and we report the first direct comparisons of water loss in homing and non-homing limpets. We have used the chloride concentrations of pulmonary fluids as reliable field measurements of desiccation. Our results show how these concentrations change during low tide exposure in both homing limpets and animals kept from homing, and identify in laboratory and field experiments the consequences that various amounts of water loss may have for individual limpets.

METHODS

Site Description: Field experiments were conducted on the southwest corner of West Summerland Key, Florida (see STEPHENSON & STEPHENSON, 1950, plate 10) during July and August 1979, and during the summer of 1980. West Summerland Key belongs to the upper Keys, those islands which stretch from Key Largo to Big Pine Key and are composed of the Key Largo limestone (HOFFMEISTER & MULTER, 1968).

A well-developed rocky intertidal zone borders the oceanside of West Summerland Key. It averages 8 m in width, measured from low spring tide to high spring tide, and experiences the semi-diurnal tides that are common to the Atlantic coast. The tidal amplitude at West Summerland is 0.76 m at spring tide. Surface erosion here has led to a severely pinnacled and honeycombed rock surface, especially along the lower intertidal zone.

Siphonaria alternata occur on the lower platform and in the yellow zone (see STEPHENSON & STEPHENSON, 1950). They occupy a band approximately 2 m wide along the entire intertidal zone, which we term the *Siphonaria* band. Limpets are distributed unevenly in densities averaging 200/m^2.

Labelling Procedure: A population of 20 limpets covering 2.0 m^2 of substrate was labelled by attaching a small bit of heavy typing paper numbered with black India ink to each limpet's shell with a cyano-acrylate-containing adhesive (crazy glue).

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The Undisturbed Behavior of *Siphonaria alternata*: On July 1, 1979, observations of the natural behavior of limpets within the labelled population were begun and continued daily throughout the next 2 weeks. The frequency, duration, and distance of flood and ebb tide grazing excursions were observed. The wetness of home scars (which was visually determined) of limpets initiating and terminating both flood and ebb tide grazing excursions was noted at the time of exit and reentry. The process of resettling onto a home scar by a limpet was also closely observed. Both outbound and homeward journeys of several limpets were mapped for evidence of trail following.

Chloride Concentration as Indicator of Desiccation: We used measurements of the chloride concentration of lung fluids as a simple field assay of water loss without the use of a field balance. This technique is an extension of WOLCOTT's (1973) finding that the chloride concentration of extracorporeal water in prosobranch limpets increases linearly as limpets lose water. Since the lung cavity in siphonariids is an extension of the mantle cavity (YONGE, 1951) and there is laboratory evidence that siphonariids are perfect osmometers (*i. e.,* their internal fluids closely follow external conditions; MCALISTER & FISHER, 1968), changes in lung chloride should mirror water loss.

To confirm that lung fluid concentrations and body weight changes give comparable estimates of water loss, twenty limpets were placed, ventral surface up, on a paper towel to drain off external water; additional blotting was unnecessary. Limpets were transferred individually to numbered, tared watch glasses and wet weights obtained. The limpets were then desiccated at 34°C for 15 h in still air, and weighed again. One microliter samples of mantle cavity fluids were taken by inserting a 1 μl capillary tube ("Microcap") into the pneumostome so that the tube filled with fluid. Chloride concentrations of these samples were determined with a Buchler-Cotlove chloridometer that had been standardized with a 1 mM NaCl solution. The limpets were then placed in an oven and dried to constant weight to obtain dry weights.

Percent total body water loss as determined both by weight and changes in the chloride concentrations of the pulmonary fluids were calculated and compared to one another. Since the chloride concentration of pulmonary fluids of freshly collected limpets in seawater equalled that of the seawater (see Results), the initial chloride concentration of limpets was assumed to be 0.63 eq. Cl^-/L, the chlorinity of seawater at West Summerland Key.

The Wilcoxon Signed Rank statistic was used to compare the two groups of percentages.

The Effect of the Home Scar on Desiccation: Half of the limpets of a labelled population were removed from their home scars by carefully wedging a sharp knife between the shell margin and the substrate and lifting the limpet off the rock surface. Each of the 'non-homing' limpets was then replaced onto the substrate 3 cm east of its own home scar (to cancel any tendency to bias the experiment by choosing a particular substrate configuration) and "corralled" into place with a clay ring. These rings did not contact the shell and allowed the limpets several millimeters of movement in any direction. The remaining control limpets ('homing limpets') were also removed from their home scars and replaced directly onto them again. These procedures were completed within 10 minutes after the labelled population had been exposed by an ebb tide; however, if the substrate began drying before the manipulations were completed, the limpets were wetted repeatedly with seawater.

Both homing and non-homing limpets were exposed during the following low-tide. The procedure was repeated daily until 8 groups receiving varying amounts of exposure were accumulated. A range of exposures from 1 to 8 h was obtained. Humidity and wind conditions remained constant during these experiments. Temperatures ranged from 29° to 32°C, and cloud cover was virtually non-existent.

After exposure, limpets were blotted dry to remove any external water from the ventral surface and lung fluids of both homing and non-homing limpets were sampled. The sampling procedure for all the limpets on a given tide required approximately 20 minutes to complete. Non-homing limpets were always sampled first, so that control limpets experienced slightly longer exposure than experimentals. Thus, our estimates of water loss by experimental limpets, in comparison to controls, may be conservative. In the field, each sample was added to individual vials containing a solution of 1 ml 0.5 M HNO_3 and 1 ml distilled water. The vials were transported to the laboratory for titration on the Buchler-Cotlove chloridometer.

The Effect of the Home Scar on Survival: To determine the effect of the home scar on survival of limpets, the limpets in the previous experiment were carefully replaced after the low tide exposure onto their home scars in the same orientation in which they were found. Scars were first wetted with seawater. The limpets were then replaced, and enough seawater splashed over them so that they could clamp down onto the substrate. The number of vacant scars which belonged to homing and non-homing limpets were counted the next day.

The Effect of Desiccation and Responsiveness: To determine the effect of desiccation on responsiveness, 30 limpets were transported in seawater to the laboratory and placed on individual watch glasses. The limpets were then desiccated in still air at 24°C. Every hour, two limpets were removed and tested for a response by slightly pricking the mantle tissue with a straight pin. A positive response was defined

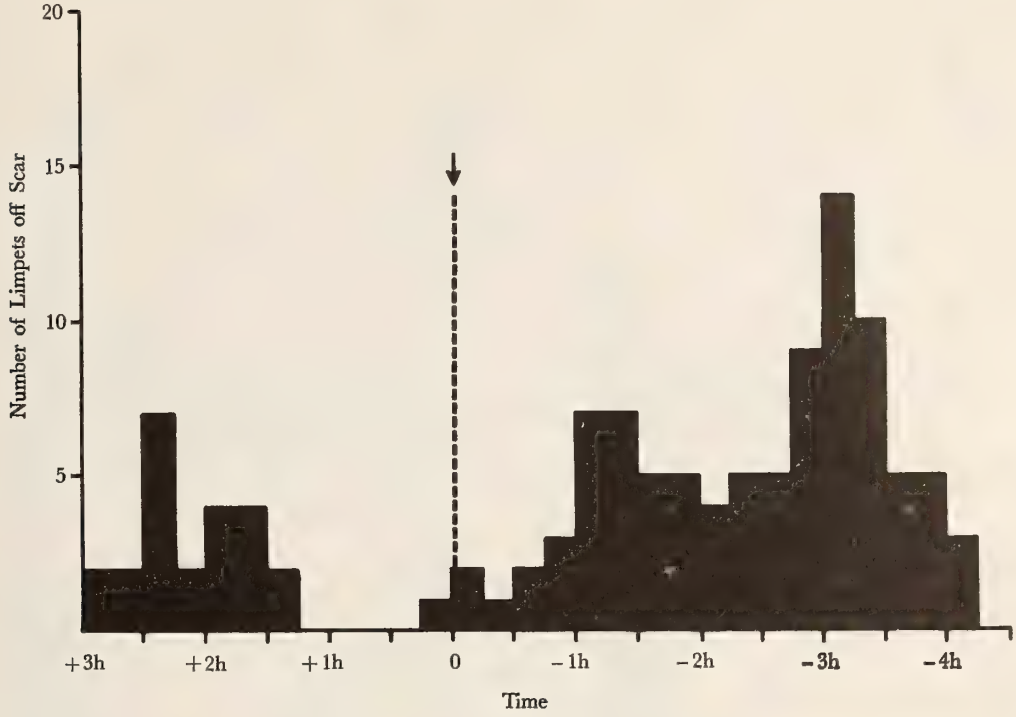


Figure 1

Number of limpets off scars throughout a complete tidal cycle. Data include 3 repeated observations of 21 limpets throughout 3 complete tidal cycles (low-flood-high-ebb-low). Positive numbers along abscissa designate time before dead high tide, negative numbers designate time after dead high tide. Arrow indicates dead high tide

as the retraction of the mantle away from the edge of the shell. After testing for a response, the chloride concentration of the pulmonary fluid of the limpet was determined. The experiment was conducted until limpets no longer responded to tactile stimulation.

Water Loss and Survival in 'Less Manipulated' Limpets: On a few occasions, it was possible to interfere with homing in a less disruptive way, by corralling animals away from home scars without picking them up. The chloride concentrations of these corralled limpets were compared to those of normally homing limpets. Time, effort, and sample size constraints made this technique impractical for the bulk of the work.

On a separate occasion, we blocked the scars of 9 limpets while the animals were grazing by placing a piece of modelling clay directly onto the unoccupied scar. Survival and subsequent behavior of these limpets were followed for 15 days to collect data on mortality and the ability of 'untouched' animals to establish a new home site.

RESULTS

The Undisturbed Behavior of *Siphonaria alternata:* Grazing excursion activity is distributed bimodally throughout a complete tidal (low-flood-high-ebb-low) cycle (Figure 1). In most cases, limpets restricted their movements to flood and ebb tides; however, occasional grazing excursions occurred during high tide.

Flood tide grazing excursions: Figure 2a shows the wetness of home scars of limpets initiating a flood tide grazing excursion. Although most limpets did not vacate their scars until the tide line was just above their scars and they were well submerged, it was not always necessary for a limpet to be completely submerged before beginning a grazing excursion. Complete drenching by an occasional wave was often enough to initiate a grazing excursion when the tide line was still below the *Siphonaria* band.

Following a flood tide grazing excursion, most limpets returned to their scars after the scars had been submerged

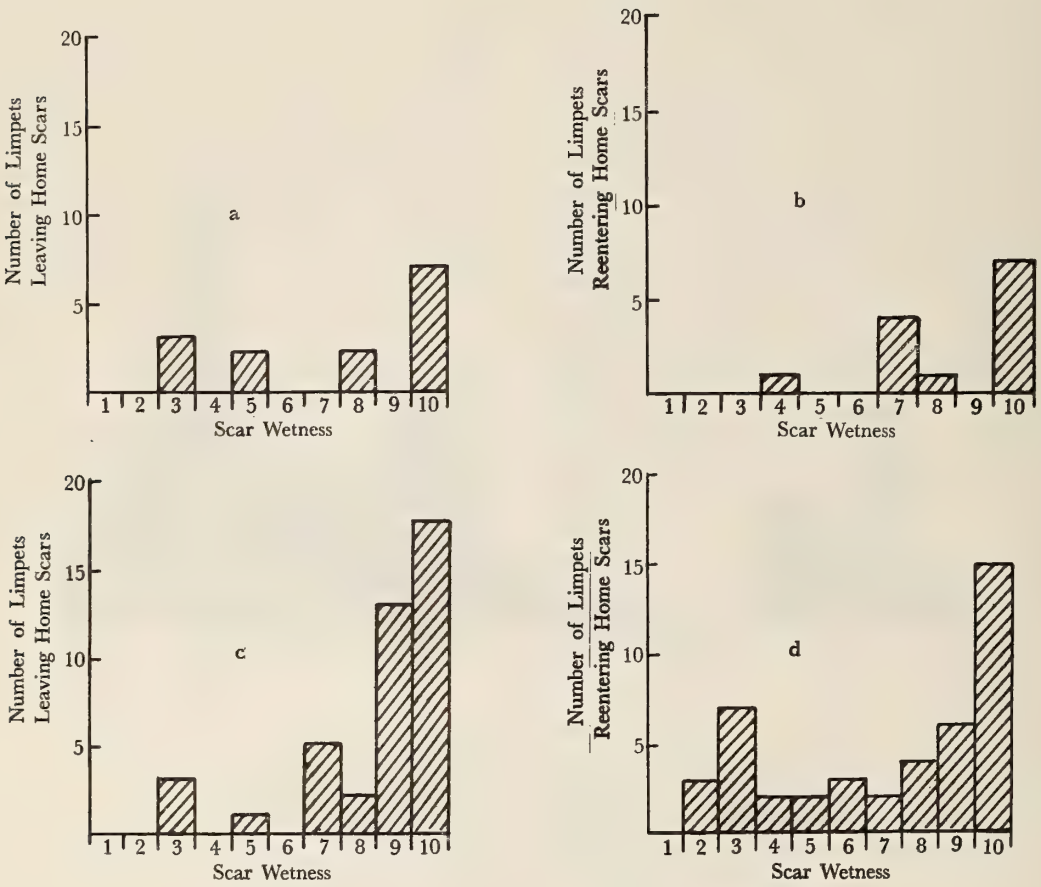


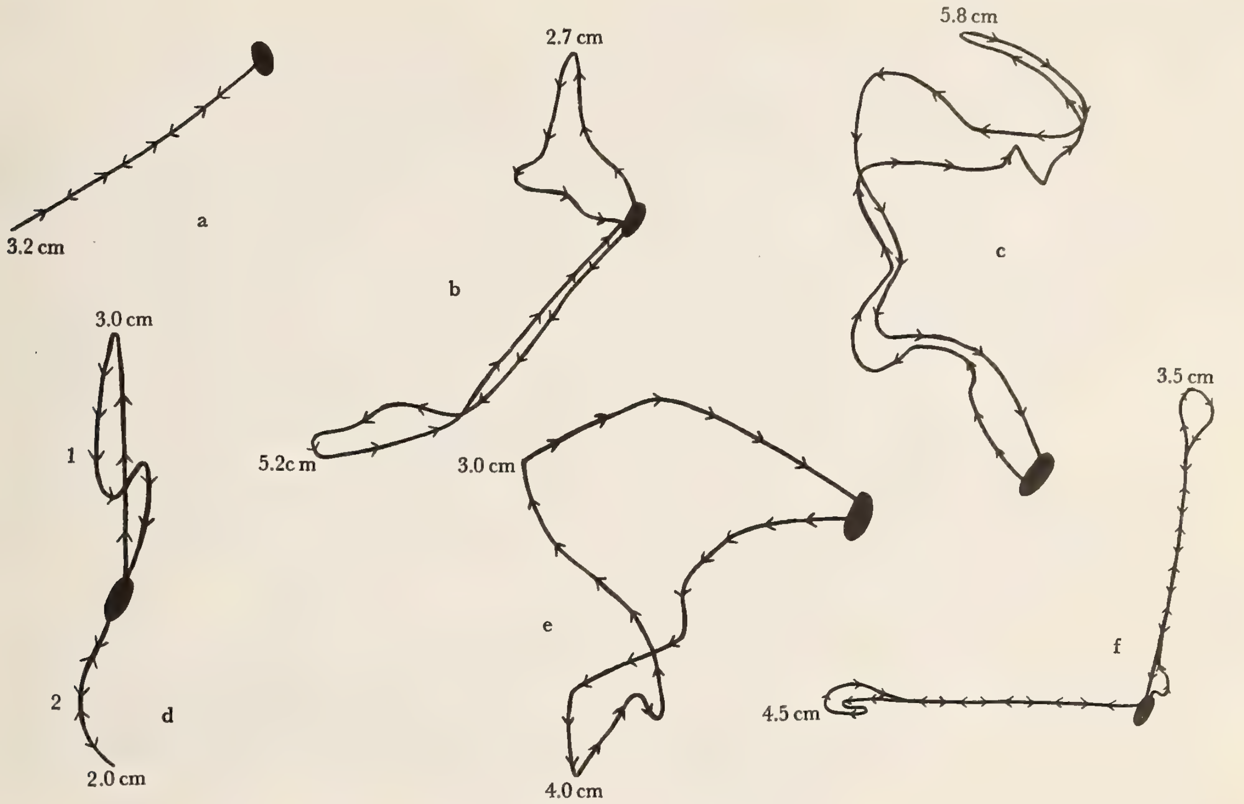
Figure 2

a) Wetness of home scars of limpets initiating flood tide grazing excursions, N = 16; b) wetness of home scars of limpets completing flood tide grazing excursions, N = 13; c) wetness of home scars of limpets initiating ebb tide grazing excursions, N = 42; d) wetness of home scars of limpets completing ebb tide grazing excursions, N = 44. Abscissa scale: 1-dry, 2-damp, 3-exposed but wet, 4-intermittent wave action (infrequent submersion by a wave followed by 1-1.5 min of exposure), 5-continuous wave action (frequent submersion by waves followed by 0.5-1.0 min. exposure), 6-intermittent submersion (home scars in small pools above tide line would become infrequently submerged as these pools were filled by unusually high waves; the pool would drain slowly, keeping the home scar submerged until the pool emptied completely), 7-intermittent exposure (tide line above home scar, home scar occasionally exposed by unusually shallow wave trough), 8-partial submersion (water line partially covering home scar), 9-wave surge (home scar completely submerged but experiencing wave surge), 10-submerged, no wave surge

by the incoming tide (Figure 2b). However, several limpets which had left their scars relatively early (*i. e.,* just after being splashed and wetted by a wave while still exposed), returned to their home scars before the scars became completely submerged.

Flood tide grazing excursions ranged in duration from 3 to 158 min (39.52 min (X) ± 35.14 (S.D.); N = 21). The distance that a limpet wandered from its home scar during a flood tide excursion ranged from 1.2 to 6.4cm (3.54cm ± 1.46; N = 18).

Ebb tide grazing excursions: Limpets beginning ebb tide grazing excursions vacated their scars primarily while their scars were still submerged (Figure 2c), although limpets would exit their scars as long as the immediately surrounding substrate remained wet.



Figures 3a-f

Grazing excursion maps. a. limpet #40, flood tide, 4-VII-1979; b. limpet #40, ebb tide, 6-VII-1979; c. limpet #5, ebb tide, 11-VII-1979; d. limpet #5, ebb tide, 14-VII-1979; e. limpet #5, ebb tide, 15-VII-1979; f. limpet #40, flood tide, 2-VIII-1979. Numbers along limpet trails indicate distance (cm) from home scar at that point

Figure 2d shows that almost as many limpets returning from ebb tide grazing excursions re-entered home scars that were submerged (conditions 9 and 10) as re-entered scars that were exposed (conditions 1 through 8). All limpets re-entered their scars before the scars, or the substrate over which the limpets grazed, were completely dry.

Ebb tide excursions ranged from 11 to 103 min (44.68 min ± 21.00; N = 28) in duration. Limpets wandered from 1.0 to 9.3 cm (4.70 cm ± 2.25; N = 28) away from their home scars while grazing at ebb tide.

Trail following and scar re-entry: Figure 3 contains maps of several grazing excursions. Direct trail-following, as described by Cook (1971), while returning to the home scar is depicted in 3a, 3f, and in the second excursion of 3d. Maps 3b and 3c depict cases in which limpets returned to their home scars along paths which were parallel to, but separate from their outbound paths. Map 3e depicts a case in which trail-following is lacking altogether.

Normally, limpets fit into scars so that the outlines of their shells and scars are closely matched. When re-entering scars, limpets rotated within them until this orientation was achieved. Once oriented, the limpets lowered their shells and clamped down tightly onto the substrate. If the fit between the shell margin and the substrate was not exact, a limpet would lift its shell off the substrate, readjust its position, then lower its shell to the substrate again, and clamp down. Limpets remained sessile until the next grazing excursion.

Chloride Concentration as Indicator of Desiccation: In comparing the chlorinity of lung fluids against weight loss as an indicator of water loss, we found no significant difference between between the values for percent body water lost provided by these two methods (Wilcoxon Signed Rank statistic; $P > 0.488$; by weight loss, $\bar{x} = 49.3\% \pm 12.1$; by chloride concentration, $\bar{x} = 50.1\% \pm 13.1$; $N = 18$ for each case). This comparison included a range of values from 30 to 73%.

After complete desiccation of limpets in a drying oven, dry weights revealed that water represents 51% (50.8% ± 5.6, N = 14) of the total weight of *Siphonaria alternata.*

The Effect of the Home Scar on Desiccation: Figure 4 and Table 1 show the effect of different amounts of daytime, low tide exposure on the chloride concentration of pulmonary fluids of homing and non-homing limpets. Both groups of limpets showed increasing chloride concentrations with increased exposure. Non-homing limpets had significantly higher chloride concentrations than homing limpets in populations exposed for 5 to 8h (in all cases, $P \leq 0.03$; Wilcoxon Rank Sum test). There was a marginal difference between the chloride concentration of homing and non-homing limpets in the populations exposed for less than 4h ($P > 0.05$).

Samples taken from seven undisturbed, submerged limpets yielded a value of 0.62 ± 0.036 eq. $\mathrm{Cl^-}$/L (N = 5). This value is not significantly different from the chloride

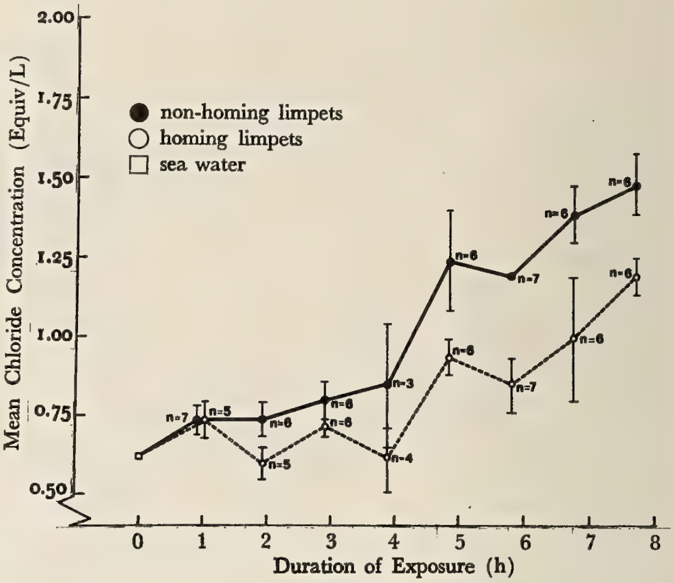


Figure 4

The relationship between increasing low tide exposure and the chlorinity of pulmonary fluids from populations of homing and non-homing limpets. Vertical bars are standard errors

Table 1

Mean Values of the chloride concentration of pulmonary fluids expressed as eq. $\mathrm{Cl^-}$/L ($\mathrm{Cl^-}$/L), percent total body water loss (% T.B.W.L.) and size (cm) of homing and non-homing limpets within populations experiencing 1-8h of daytime, low tide exposure. Success of reattachment following desiccation expressed as the number of limpets desiccated/the number of limpets reattached (Reatt.) is also shown.

	Homing limpets				Non-homing limpets			
Exposure	$\mathrm{Cl^-}$/L	% T.B.W.L.	Size (cm)	Re-attachment	$\mathrm{Cl^-}$/L	% T.B.W.L.	Size (cm)	Re-attachment
1	0.74	32	1.13	3/6	0.74	32	1.39	6/7
2	0.60	17	1.20	3/7	0.74	32	1.25	5/7
3	0.72	31	1.12	4/7	0.80	37	1.22	6/7
4	0.62	19	1.30	4/4	0.85	41	1.23	1/3
5	0.94	47	1.12	3/6	1.25	60	1.18	3/6
6	0.85	41	1.20	5/7	1.20	59	1.20	0/7
7	1.00	51	1.32	4/6	1.40	64	1.33	2/7
8	1.20	59	1.15	4/6	1.50	67	1.15	0/6
$\bar{x}$	0.80	37	1.20	63[1]	1.06	49	1.24	44.0[1]
S.D.	0.21	15.0	0.08	17.9[1]	0.31	15.0	0.08	34.7[1]

[1] expressed as %.

concentration of the ambient seawater (0.63 eq. Cl^-/L; t-test; $P < 0.05$).

Distinct gaps existed between the substrate and the shell margins of non-homing limpets. This was not true for limpets which could return to their scars.

The Effect of the Home Scar on Survival: A *G*-test (Sokal & Rohlf, 1969) revealed an overall relationship between non-homing and successful reattachment ($P < 0.01$; Table 1). Individually, within the populations exposed for 4, 6 and 8h, the inability to home significantly lowered re-attachment ($P < 0.033$, 0.002, 0.006,respectively). Variation within the small samples involved might have prevented significance within the remaining populations. In both experimental and control limpets, the ability to re-attach is significantly reduced when mean chloride concentrations exceed 1 eq. Cl^-/L ($P < 0.01$; χ^2 comparison of frequencies above and below 1 eq. Cl^-/L).

Table 2

Presence (+) or absence (−) of a response from limpets containing pulmonary fluids of increasing chlorinity to mechanical stimulation.

Limpet no.	Equiv. Cl^-/L	Response	Limpet no.	Equiv. Cl^-/L	Response
1	0.54	+	21	0.80	+
2	0.54	+	22	0.80	+
3	0.56	+	23	0.82	+
4	0.57	+	24	0.82	+
5	0.58	+	25	0.87	+
6	0.59	+	26	0.88	+
7	0.61	+	27	0.90	+
8	0.62	+	28	0.92	+
9	0.63	+	29	0.94	−
10	0.64	+	30	0.96	+
11	0.65	+	31	1.00	+
12	0.66	+	32	1.06	+
13	0.66	+	33	1.12	+
14	0.67	+	34	1.20	−
15	0.69	+	35	1.20	−
16	0.69	+	36	1.20	−
17	0.70	+	37	1.30	−
18	0.74	+	38	1.34	−
19	0.78	+	39	1.40	−
20	0.79	+			

The Effect of Desiccation on Responsiveness: Table 2 compares chloride concentrations of lung fluids with responsiveness of *Siphonaria* in the laboratory. No limpets responded to mechanical stimulation of the mantle after their lung fluids reached a concentration of 1.20 eq. Cl^-/L, although one limpet failed to respond at 0.94 eq. Cl^-/L.

Water Loss and Survival in 'Less Manipulated' Limpets: Following 8h of exposure during a midday low tide, limpets which had been corralled away from their home scars, but not removed from the substrate, contained significantly higher chloride concentrations than limpets on scars (Mann-Whitney U test; $P = 0.01$; Table 3). Chloride concentrations of corralled limpets in this experiment could not be distinguished from those of non-homing limpets exposed for the same duration, but which had been removed from the substrate (Wilcoxon Rank Sum test; $P > 0.05$; see Table 1).

Table 3

Chloride concentrations of homing limpets and limpets corralled by modeling clay fences (but not removed from the substrate) at end of grazing paths.

Sampling conditions	N of limpets	Mean limpet size size (cm)	Mean chloride concentration (equiv. lb.)
Limpets on scars	8	1.4	1.1779
Limpets kept at end of grazing paths by modeling clay fences	12	1.3	1.4004

Limpets prevented from homing by pieces of modelling clay placed directly on their scars showed no mortality after 15 days of scar blockage. All limpets were successful in using other pits and depressions in the eroded substate as 'surrogate' home scars. The contours of the surrogate scars apparently matched those of the shell margins closely enough to prevent severe water loss at low tide.

DISCUSSION

Behavioral Observations: Our observations of the behavior of *Siphonaria alternata* in the Florida Keys confirm previous observations of this pulmonate limpet in Bermuda with respect to movement in relation to tide level (Cook & Cook, 1978). Both the timing of movement and the condition of home scars at the time of return from grazing forays support the idea that one function of homing behavior is to retard water loss during low tide aerial exposure. On rising tides, the animals do not initiate excursions until they are either dampened or submerged, and on ebbing tides they return to scars before either the scar or the substrate over which they were grazing becomes dry.

How limpets time journeys so that they return home before scars dry out remains to be investigated, but evidently they can manage this over a fortnightly range of tidal amplitudes (*cf.* Cook & Cook, 1978).

In laboratory and field experiments, Cook (1971) demonstrated that pulmonate limpets utilize mucous trails in homing. The occasional failure to return along outbound paths which we report may mean that limpets sometimes prefer trails laid down on previous excursions. In the laboratory, trails can remain effective for at least 48h (Cook, 1970). There is no conclusive evidence that siphonariid limpets can use clues other than mucous trails in homing behavior (Cook, 1969, 1971).

The Role of the Home Scar in Reducing Desiccation: The results of our experiments clearly show that homing behavior and subsequent 'clamping down' onto snugly fitting home scars reduce water loss at low tide. A similar effect has been reported by McAlister & Fisher (1968) for *Siphonaria pectinata* (Linnaeus, 1758). They found that limpets in the laboratory clamped onto glass plates so that there was relatively little moist surface area exposed; this behavior retarded the osmotic dehydration of these limpets when submerged in tanks of hypertonic seawater. Freshly collected limpets whose shell margins were irregular lost more water under such experimental conditions than those limpets whose shell margins had been allowed to grow and conform to the smooth glass surfaces before being used in the experiment.

Our laboratory and field data indicate that limpets lose muscular control and so become increasingly vulnerable to dislodgement by waves and predators as the chloride concentrations of body fluids approaches 1.20 eq. Cl^-/L (59% of total body water lost). These values are similar to those reported for other pulmonate limpets (*Siphonaria aspera*, Allanson, 1958; *S. pectinata*, McAlister & Fisher, 1968), and suggest that homing should have immediate value during low tides which expose limpets for 5h or longer, when desiccation of non-homing limpets exceeded this critical level (see Figure 4). Limpets which do not have access to scars during these periods face a critical situation unless they can locate "surrogate scars" on pitted rocks. In our study, limpets survived for at least a fortnightly cycle of tidal amplitude after their scars had been artificially blocked. Such survival resulted from the availability of suitable crevices at the study site.

In situations where such refuges are not available, survival of non-homing limpets is more likely to be affected. In Bermuda *Siphonaria alternata* occurs on limestone benches which generally lack the pitted topography which characterizes the Keys limestone. These animals typically have a homing failure rate of about 1% (Cook, unpublished). We have observed that 33% of the limpets which failed to home during observation periods of 2-35 days disappeared, in contrast to a loss rate of 3% for animals which homed successfully. A number of the limpets which subsequently disappeared had distinct gaps between shells and the substrate after they had "lost" their scars, suggesting that desiccation had become increasingly likely.

Access to a scar may make little difference during prolonged periods of aerial exposure. During our long-term study of *Siphonaria alternata* populations in Bermuda, we have found two occasions when limpets which were normally in permanently wet high level pools experienced at least 12 hours of exposure, due to neap tides which prevented exchange of ocean water; the pools dried out completely. In both cases, nearly all of the resident limpets appeared severely desiccated and were only feebly attached to their scars. These animals subsequently vanished. Although prolonged periods of aerial exposure can occur in the Florida Keys (at least up to 72h; Verderber, personal observations), we have no information on the survival of *S. alternata* under these conditons.

We can not rule out other functions of home scars. Other possibilities which have been suggested include protection from aquatic and/or terrestrial predators (Branch, 1975; Giesel, 1970; Cook, 1980), protection from dislodgement by waves (Wolcott, 1973), or by aggressive actions of other limpets (Wright, 1977), protection of soft parts from abrasion by sand (Wolcott, 1973), and reduction of intraspecific competition (Beckett, 1968; Breen, 1971; Branch, 1975; Underwood, 1976; Mackay & Underwood, 1977). The occupancy of scars during high tide suggests that limpets might be using home scars to increase tenacity (limpets off scars are more easily removed from rocks than those on scars) in avoiding aquatic predators.

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The genus *Praticolella* in Texas

(Polygyridae : Pulmonata)

BY

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(18 Text figures; 6 Maps)

The Texas species of *Praticolella* differ from most of our land snails in that there are no genetic barriers between species. The barriers are geographical and ecological. Species will hybridize freely when brought into contact. Selection in hybrid populations has resulted in the development of three species. This occurred during the Pleistocene, as shells from that period are identical with those found today. This type of speciation is rare in animals. It was made possible in this case by the presence of nearby empty niches into which the hybrids could move, and to which they became adapted. At the present time. *P. berlandieriana* and *P. trimatris* appear to be geographically isolated from each other and from their parent species, as I have seen no evidence of hybridization. Each is remarkably uniform in shell size and shape, and with only small variations in banding. There is a small amount of hybridization between *P. taeniata* and its parent species, but this is not producing a significant effect on the species. The shells show little variation in size and shape. There is considerable variation in the basal bands. This is due in part to the fact that the basal bands are quite variable in *P. griseola* and because *P. candida* is without basal bands.

Praticolella griseola (Pfeiffer, 1841)
(Figures 1-3; Map 1)

Helix griseola Pfeiffer. 1841. Symbolae Hist. Hel. 1: 41; Conchyl. Cab. Helix, p. 342, plt. 60, figs. 17, 18; Monog. Hel. Viv. 1: 337

Praticolella griseola (Pfeiffer). 1940. Pilsbry. Acad. Nat. Sci. Philadelphia, Mono. no. 3, 1: 690

Praticolella campi Clapp & Ferriss. 1919. Nautilus, 32: 78; plt. 6, figs. 1-4. Pilsbry. 1940. Acad. Nat. Sci. Philadelphia, Mono. no. 3, 1: 693

Description: Shell depressed-globose, somewhat fragile, glossy, first two whorls translucent, brownish, later whorls opaque-white, with a translucent brownish band above the periphery; umbilicus small, partly covered by the reflected lip; nuclear whorls with fine irregular pitting, later whorls with irregular, weak growth wrinkles; whorls well rounded with moderately deep sutures; last whorl descending behind the lip, contracted behind the lip; aperture oblique, lunate, about as high as wide; peristome narrowly reflected, white, somewhat thickened; base usually with about five narrow, translucent bands, but may be completely white, or completely translucent.

Diameter 10-14 mm, height 8.4-10.5 mm, aperture width 5.5-7 mm, aperture height 5.2-6.8 mm, whorls 5.3-5.5.

Distribution: In Texas it is known only from Cameron and Willacy counties. It also occurs in Mexico and south into Nicaragua. In Texas it is found near the coast, usually on the stems of grasses around the margins of brackish marshes. It has been reported as introduced into southern Florida, but this account is of a closely related species, probably native of Mexico, which I have not been able to identify.

Remarks: *Praticolella griseola* can be distinguished from the other Texas species by the narrow, reflected lip. It is one of the three parent species. Its principal contribution to hybrids is the basal bands, and it also contributed the broad, supraperipheral band, and sometimes the narrow, reflected lip.

Praticolella pachyloma (Menke in Pfeiffer, 1847)
(Figures 4-6; Map 3)

Helix pachyloma Menke in Pfeiffer. 1847. Zeitschr. für Malak., 4: 32

Praticolella pachyloma (Mke.). 1915. Vanatta. Proc. Acad. Nat. Sci. Philadelphia, p. 195; fig. 2. 1956. Pilsbry & Hubricht. Nautilus 69: 96

Praticolella berlandieriana pachyloma ('Menke' Pfeiffer). 1940. Pilsbry. Acad. Nat. Sci. Philadelphia, Mono. no. 3, 1: 697

Description: Shell solid, depressed globose-conic, rather dull, subtranslucent, very pale, grayish, frequently with a narrow, reddish band above the periphery; umbilicus small, partly covered by the expanded lip; nuclear whorls nearly smooth, later whorls with irregular, weak growth wrinkles, and sometimes with traces of spiral striae above;

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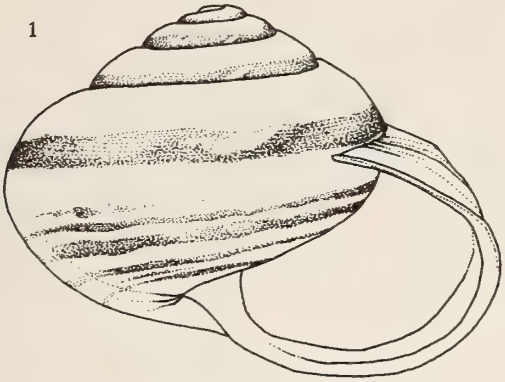

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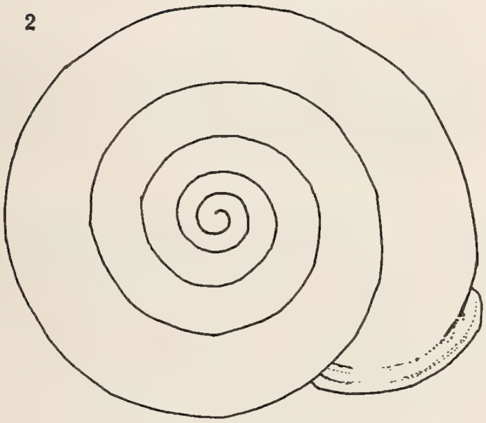

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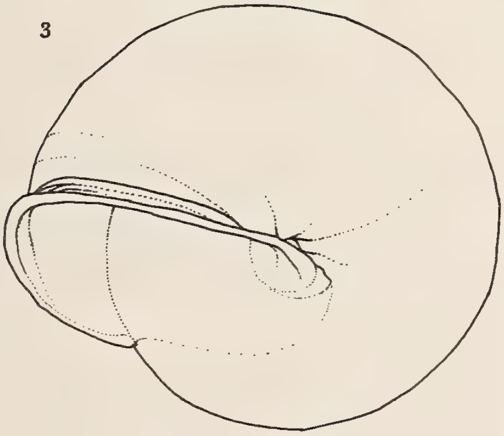

Figures 1-3

Praticolella griseola (Pfeiffer). Cameron Co.: 4 miles northeast of Rio Hondo (198753 FMNH).

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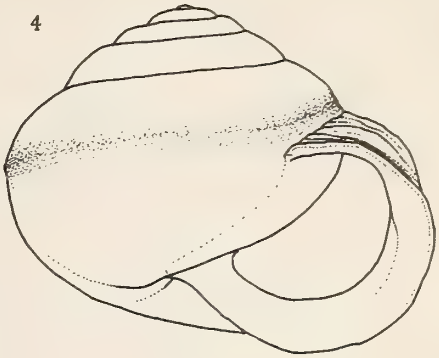

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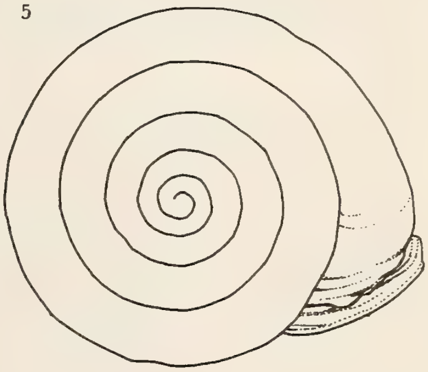

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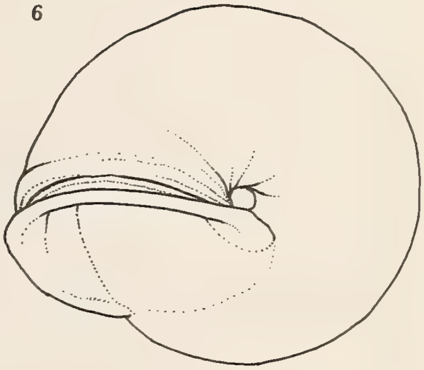


Figures 4-6

Praticolella pachyloma (Menke in Pfeiffer). Jim Wells Co.: Alice (198751 FMNH).

whorls well-rounded with deep sutures, last whorl descending behind the lip; contracted behind the lip; aperture oblique, about as high as wide; peristome expanded, heavily callused within, white.

Diameter 8.5-11mm, height 7.5-9mm, aperture width 3.2-4.8mm, aperture height 3.8-5mm, whorls 5-5.2.

Distribution: Restricted to Texas, where it is found north of the ranges of *Praticolella griseola* and *P. candida* and east of the range of *P. berlandieriana;* its northern limit is in the vicinity of Dallas and Fort Worth.

Remarks: *Praticolella pachyloma* is one of the three parent species. It can be easily recognized by the absence of any opaque, white pigment on the shell. To hybrids it contributed its more globose shape, its narrow supraperipheral band, and a reduction in the white pigment, and above all, its tolerance of dry habitats, which became amplified in the hybrids, enabling them to enter habitats in which none of the parent species could survive.

Praticolella candida Hubricht, spec. nov.

(Figures 7-9; Map 2)

Description: Shell depressed-conic, somewhat fragile, glossy, first two whorls translucent brownish-gray, later whorls opaque-white, sometimes with a broad brownish-gray band above the periphery; umbilicus small, partly covered by the expanded lip; nuclear whorls with fine irregular pitting, later whorls with irregular growth wrinkles; whorls well-rounded with deep sutures, last whorl descending in front, contracted behind the lip; aperture oblique, lunate, about as high as wide; peristome expanded, white, strongly thickened within.

Diameter 11.9mm, height 8.9mm, aperture width 4.6mm, aperture height 4.5mm, whorls 5.5. Holotype.

Diameter 9.7mm, height 7.3mm, aperture width 3.6mm, aperture height 3.6mm, whorls 4.8. Smallest paratype.

Diameter 12.4mm, height 8.7mm, aperture width 4.4mm, aperture height 4.4mm, whorls 5.2. Largest paratype.

Type locality: San Benito, Cameron Co., Texas. Holotype 198745, and Paratypes 198746, Field Museum of Natural History (FMNH); other paratypes 14363, collection of the author.

Distribution: In Texas it occupies a narrow belt between the ranges of *Praticolella berlandieriana* and *P. trimatris* on the west and *P. taeniata* on the east. It is widely distributed in northeastern Mexico.

Remarks: *Praticolella candida* has been confused with *P. berlandieriana* from which it differs in being usually more depressed, in frequently lacking the brownish-gray band above the periphery, and in being whiter, without the radial translucent streaks found on the base of *P. berlandieriana.* In the type lot there are 167 unbanded shells and 100 banded shells. The banded shells average a little larger, with higher spires, a heavier callus on the lip, and in having a more robust appearance. Most of the unbanded shells which I have examined showed repaired breaks in the shells; these repairs were not as common in banded shells. *Praticolella candida* is one of the three parent species. To hybrids it contributed the white color, the broad supraperipheral band and the expanded lip.

Praticolella berlandieriana (Moricand, 1833)

(Figures 10-12; Map 4)

Helix (Helicogena) berlandieriana Moricand. 1833. Mem. Soc. Physique d'Hist. Nat. de Geneva, 6: 537, plt. 1, fig. 1

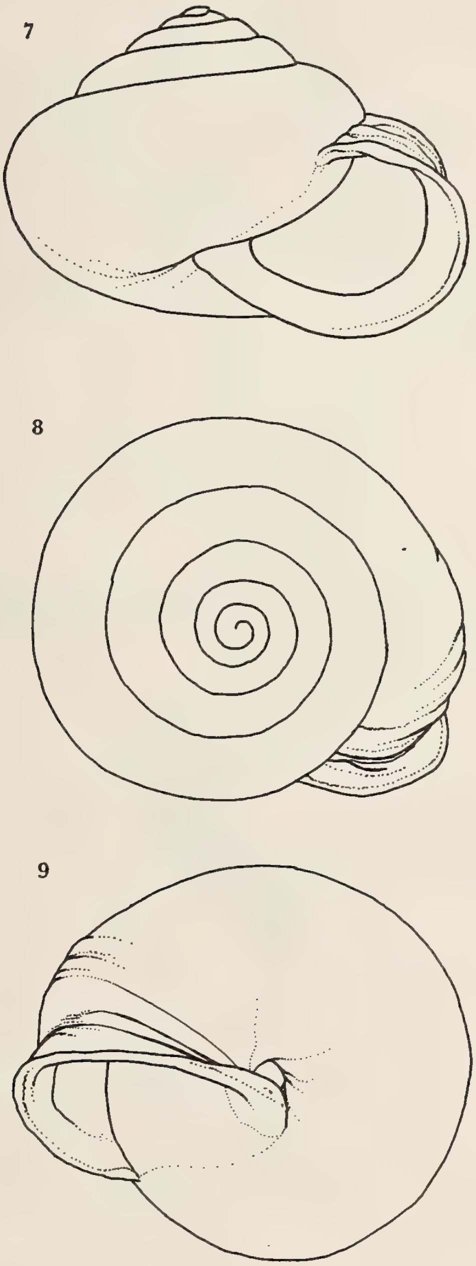
Praticolella berlandieriana (Moricand). 1940. Pilsbry. Acad. Nat. Sci. Philadelphia, Mono. no. 3, 1: 694

Description: Shell solid, depressed globose-conic, glossy, first two whorls translucent brownish-gray, later whorls whitish, usually with a narrow translucent grayish band above the periphery, base often with irregular radial translucent streaks or sometimes totally translucent; umbilicus small, partly covered by the expanded lip; nuclear whorls with fine irregular pitting, later whorls with irregular, weak growth wrinkles; whorls well rounded with deep sutures; last whorl descending in front, contracted behind the lip; aperture oblique, lunate, somewhat quadrate, about as high as wide; peristome expanded, heavily callused within, white.

Diameter 9-11.5mm, height 7.3-8.2mm, aperture width 3-4.2mm, aperture height 3.2-4.1mm, whorls 5-5.3.

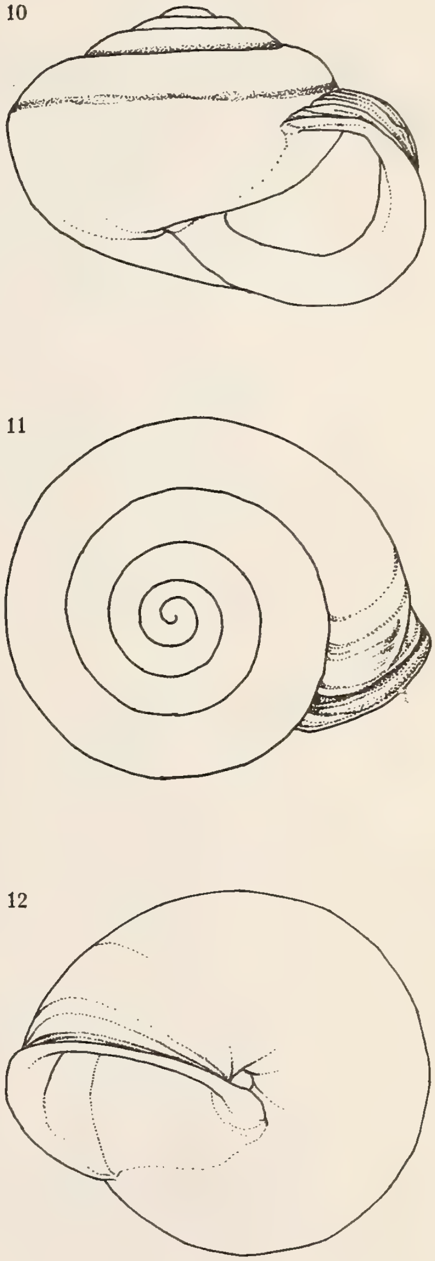
Distribution: Restricted to Texas where it occurs west of the range of *Praticolella pachyloma* and north of the range of *P. trimatris.* The range extends onto the Edwards Plateau as far west as Real County.

Remarks: *Praticolella berlandieriana* is a selected stock derived from hybrids between *P. pachyloma* and *P. candida.* This hybridization took place a long time ago as Pleistocene fossils are not distinguishable from Recent shells. I have seen no evidence of recent hybridization between *P. berlandieriana* and any other species. From *P. candida,* which has been confused with it, *P. berlandieriana* differs in having the white pigment reduced so that it is not uniformly distributed over the base, and in having a usually narrower translucent band above the periphery. It is nearly always banded, whereas *P. candida* is more often without the band.



Figures 7-9

Praticolella ***candida*** Hubricht. Holotype.



Figures 10-12

Praticolella berlandieriana (Moricand). Milan Co.: near Brazos River, 4.7 miles northeast of Gause (198749 FMNH).

Praticolella trimatris Hubricht, spec. nov.

(Figures 13-15; Map 6)

Description: Shell depressed-conic, dull, nuclear whorl translucent, brownish-gray, later whorls also translucent brownish-gray, but with a narrow, opaque, whitish band around the periphery, and a broader whitish band below the suture; umbilicus small, partly covered by the expanded lip; nuclear whorls with fine irregular pitting, later whorls with irregular growth wrinkles; whorls well-rounded with moderately deep sutures; last whorl descending at the lip, contracted behind the lip; aperture oblique, lunate, somewhat quadrate, about as high as wide; peristome expanded, white, strongly thickened within.

Diameter 9.5mm, height 7.7mm, aperture height 4.0mm, aperture width 4.0mm, whorls 4.9. Holotype.

Diameter 9.6mm, height 7.1mm, aperture width 4.6mm, aperture height 3.7mm, whorls 4.6. Paratype.

Diameter 10.2mm, height 8.9mm, aperture width 4.6mm, aperture height 5.0mm, whorls 5.3. Paratype.

Type locality: Hidalgo, Hidalgo Co., Texas. Holotype 198747, and Paratypes 198748, FMNH; other paratypes 14110, collection of the author.

Distribution: In Texas it is found in the Lower Rio Grande Valley south of the range of *Praticolella berlandieriana* and west of the range of *P. candida.* It also occurs in adjacent Mexico.

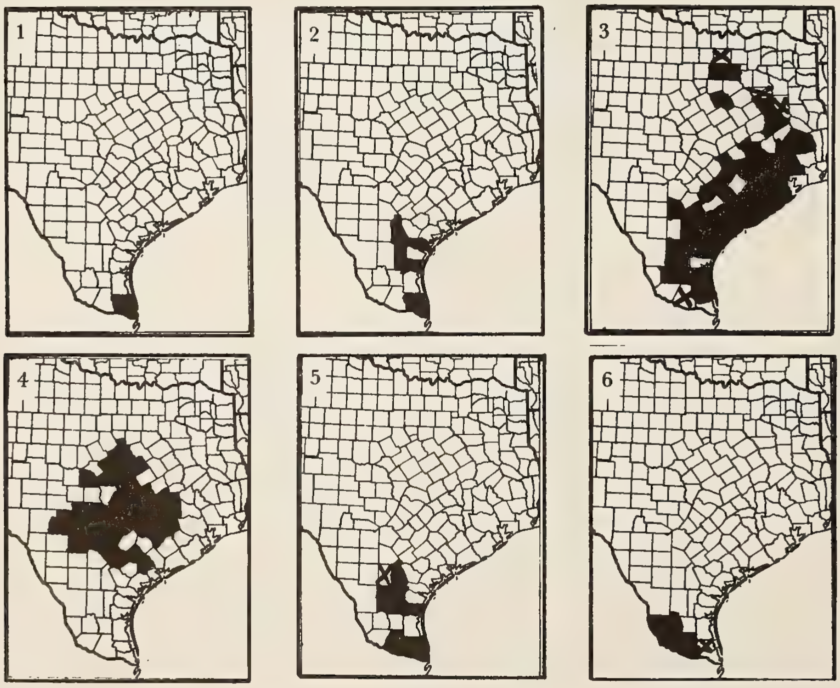
Remarks: *Praticolella trimatris* is a selected stock from a three-way hybrid between *P. pachyloma, P. griseola,* and *P. candida.* This hybridization occurred a long time ago, as Pleistocene shells are not distinguishable from Recent shells. I have seen no evidence of recent hybridization between *P. trimatris* and any other species; but along the railroad, 2.4km (1.5 miles) north of Raymondsville, Willacy Co., Texas, where *P. pachyloma* reaches its southern limit, it has hybridized with *P. taeniata* and produced *P. trimatris*-like shells.

Praticolella taeniata Pilsbry, 1940

(Figures 16-18; Map 5)

Praticolella berlandieriana taeniata Pilsbry, 1940. Acad. Nat. Sci. Philadelphia, Mono. no. 3, 1: 696.

Description: Shell depressed-conic, somewhat fragile, glossy, first two whorls translucent brownish-gray, later whorls opaque-white, usually with a broad brownish-gray



Map 1. *Praticolella griseola* (Pfeiffer). 2. *P. candida* Hubricht.
3. *P. pachyloma* (Menke in Pfeiffer). 4. *P. berlandieriana* (Moricand).
5. *P. taeniata* Pilsbry. 6. *P. trimatris* Hubricht.
Solid black = found living, X = fossil only.

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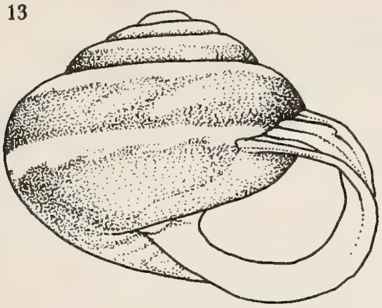

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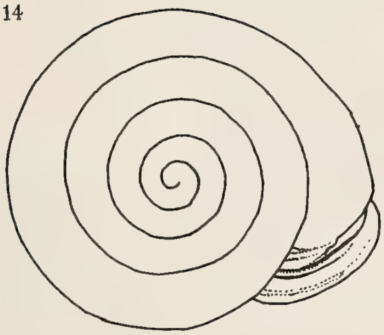

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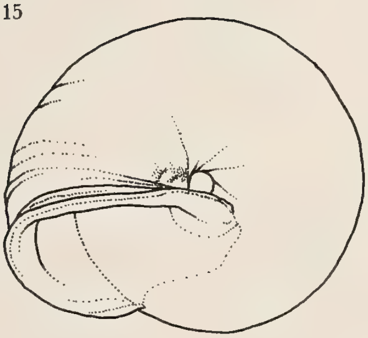

Figures 13-15

Praticolella trimatris Hubricht. Holotype.

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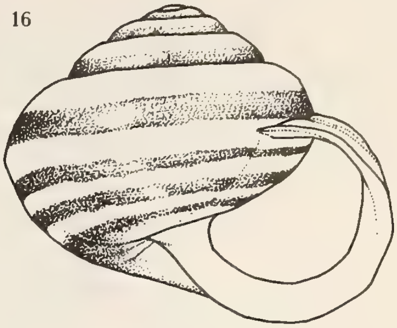

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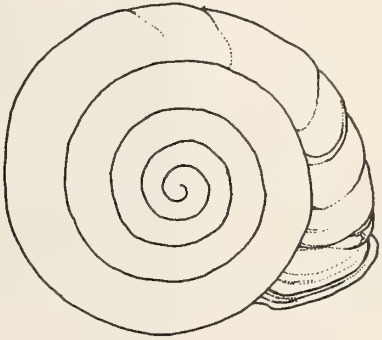

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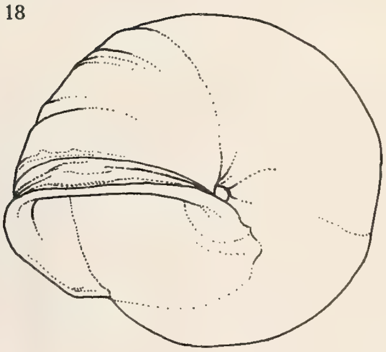

Figures 16-18

Praticolella taeniata Pilsbry. Cameron Co.: near Arroyo Colorado, 1.5 miles southeast of Harlingen (198755 FMNH). Drawings by Linnea Lahlum, courtesy of Field Museum of Natural History.

band above the periphery, and with one or more bands of varying width on the base; umbilicus small, partly covered by the expanded lip; nuclear whorls with fine, irregular pitting, later whorls with irregular growth wrinkles; whorls well-rounded with deep sutures; last whorl descending in front, contracted behind the lip; aperture oblique, lunate, about as high as wide; peristome expanded, white, thickened within.

Diameter 9.7-13.7 mm, height 7.5-10.2 mm, aperture width 4.5-5.5 mm, aperture height 4.3-6.2 mm, whorls 5.0-5.7.

Distribution: Found in southern Texas between the ranges of *Praticolella griseola* and *P. candida.* It also occurs in northeastern Mexico.

Remarks: *Praticolella taeniata* is a population derived from hybrids between *P. griseola* and *P. candida.* From *P. griseola* it received its basal bands, and from *P. candida* its general shape, expanded lip, and heavier white pigment. There appears to have been very little selection for the shell characters except the expanded lip. The reflected lip was found only in a lot which showed recent hybridization with *P. griseola.* There is some evidence of recent hybridization with both *P. griseola* and *P. candida.* It would perhaps be more appropriate to consider *P. taeniata* a hybrid swarm rather than a species.

Occurrence of a Brush Border in the Caecum (Appendix) of Several *Teredo* and *Bankia* species

(Teredinidae : Bivalvia : Mollusca)

BY

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AND

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(2 Plates)

INTRODUCTION

It has long been known that many members of the Teredinidae, a family of wood-boring molluscs commonly called shipworms, possess a large caecum (appendix) (Sigerfoos, 1908; Potts, 1923; Lazier, 1924) whose function has been a matter of debate among researchers. Although many investigators feel that this organ is the primary site of wood digestion by these animals (Lazier, 1924; Liu & Townsley, 1968; Cutter & Rosenberg, 1972; Rosenberg & Cutter, 1973), others believe that the histological structure of the caecum does not suggest an absorptive function (Saraswathy & Nair, 1971; Morton, 1970; 1978), and that the caecum probably stores fragments of wood too large to be digested intracellularly, for later elimination through the intestine (Morton, 1970; 1978).

The caecum is the largest of the digestive organs and has a large, double-coiled, ventral typhlosole extending throughout its length. The typhlosole affords a large surface area for absorption and is well supplied with aerated blood furnished by a large artery originating from the heart to the anterior end of the caecal typhlosole (Lazier, 1924; Saraswathy & Nair, 1971).

The makeup of the epithelial surface of the caecum appears to be a point of disagreement among researchers. Many studies indicate the caecum to be totally or partially ciliated (Sigerfoos, 1908; Nair, 1957; Saraswathy & Nair, 1971). Lazier (1924) did not find any ciliated cells or even the types of cells that would normally bear cilia. Finding no evidence of ciliary action in the caecum, Lazier concluded that material is moved in and out of the caecum by muscular contraction.

Turner (1966) has proposed that in the Teredinidae, the relative size of the caecum has an inverse relationship to the size and development of the gills, which are important in typical eulamellibranch ciliary feeding. This infers that the caecum evolved to become a larger organ as the species became more specialized and more dependent upon wood, and less upon plankton and detritus as primary food sources.

The caecum is always found filled with large quantities of wood during the life of an actively boring individual (Potts, 1923; Lazier, 1924; Turner, 1966; Turner & Johnson, 1971; Morton, 1970; Saraswathy & Nair, 1971). Sigerfoos (1908), Potts (1923), Lazier (1924), and Lane (1959) all noted that planktonic remains were rare or absent in the caecum and other digestive organs. This evidence supports Turner's (1966) proposal.

There is much biochemical evidence that wood digestion occurs in the caecum (Miller & Boynton, 1926; Greenfield, 1953; Greenfield & Lane, 1953; Liu & Townsley, 1968; Cutter & Rosenberg, 1972); however, much of this evidence is circumstantial. The enzymes involved may have been produced in the anterior portions of the digestive system and shunted to or concentrated in the caecum. There is also evidence that wood digestion occurs elsewhere (Potts, 1923; Deschamps, 1953; Greenfield & Lane, 1953).

The purpose of this study was to investigate the ultrastructure of the caecum and to speculate as to the organ's probable function, if any, in digestive processes.

MATERIALS AND METHODS

Three species of shipworms were examined in this study. Adult, wood-boring specimens of *Teredo bartschi* Clapp, 1923 were obtained from pieces of submerged wood (casuarina) collected from wood pilings in Sebastian Inlet, Indian River, Florida. Wood planks containing adult teredinids of the species *Bankia setacea* (Tryon, 1863) were collected from waters off Monterey, California. Pine blocks infested with *Teredo navalis* Linnaeus, 1758 were collected from the waters off the Woods Hole Oceanographic Institute, Woods Hole, Massachusetts. Live animals were removed from the collected wood, identified (Turner, 1966), and carefully dissected. The caeca were excised and cut into small (1-2 mm) pieces. In some cases the animals were fixed before dissection.

Tissues for light microscope examination were fixed in Hollande's fixative for 48 hours and dehydrated using increasing concentrations of ethanol. After dehydration was complete, tissues were embedded in polyester wax and serially sectioned (5-6 μm sections) using a rotary microtome. Sections were stained with 2% aqueous methylene blue for two minutes, dehydrated, and permanently mounted on standard microscope slides.

Caeca from liver specimens of *Teredo navalis* were excised, cut into small (1mm) pieces and fixed in 2% glutaraldehyde in Pipes buffer which was previously filtered through an 0.45 μm Millipore membrane filter (Millipore Co., Bedford, Massachusetts). Tissues were dehydrated in an acetone-distilled water series. Critical point drying was accomplished in liquid CO_2. Tissues were then mounted and viewed under an AMR scanning electron microscope (Harvard Museum of Comparative Zoology, Cambridge, Massachusetts).

RESULTS

Figure *1*, a low power micrograph, shows a typical cross section of the caecum of *Teredo bartschi*. Figure *2* shows the presence of a "brush" (microvillar) border on the caecal wall of *Bankia setacea*.

A scanning electron micrograph, Figure *3*, of a cross section of the caecum of *Teredo navalis* shows this layer to be a microvillar border. Microvilli and ciliated tracts can be seen at the stomach-caecal orifice as shown in Figure *4*. Figure *5* shows the extension of the brush border into the intestine, in which the epithelial cells not only bear microvilli, but also much larger cilia.

DISCUSSION

The caecum (appendix) of several species of teredinids has been described by Morton (1970) and by Saraswathy & Nair (1971) as being lined by flat, non-ciliated epithelial cells, although ciliated columnar epithelial cells were observed in certain regions, especially mid-dorsally. This is in great contrast to the original description by Sigerfoos (1908), who found the caecum of all the animals he studied to be completely ciliated. Morton (1970), Saraswathy & Nair (1971), and Dean (1978) concluded that the caecum acts as a storage organ wherein wood fragments abraded during boring activities are sorted and temporarily stored, possibly for later digestion in other organs such as the digestive diverticula.

Sigerfoos (1908) presumed that digestion and absorption of nutrients occurs in the caecum because of the large surface area afforded by the size of the organ itself, by its large double-coiled typhlosole, and because of the ade-

Explanation of Figures *1* to *4*

Figure *1*: *Teredo bartschi*, cross section of caecum. Note the large ventral typhlosole (t), and the numerous wood fragments (wf) in this organ. Because the intestine loops around the caecum, two portions of the intestine (i) are seen in each cross section. (g: Gonads) Bar represents 160 μm

Figure *2*: *Bankia setacea*, caecal wall. Arrows indicate brush (microvillar) border Bar represents 5 μm

Figure *3*: *Teredo navalis*, microvilli on the caecal wall White bar represents 1 μm

Figure *4*: *Teredo navalis*, ciliated tracts (c) and microvilli (mv) at the stomach-caecal orifice White bar represents 10 μm

Through an unfortunate error the figures in this article have all been numbered incorrectly and also placed in an incorrect sequence. The figure numbered *5* should actually be numbered figure *1*. Similarly the figures numbered *1*, *2*, *3*, and *4* should be figures *2*, *3*, *4*, and *5*, respectively.

Although incorrectly placed, the figure explanations are correctly numbered. Also the references to the figures in “Results“ are to the correct figures.

We offer our sincere apologies for this misadventure to the authors and the readers.

The Editor.

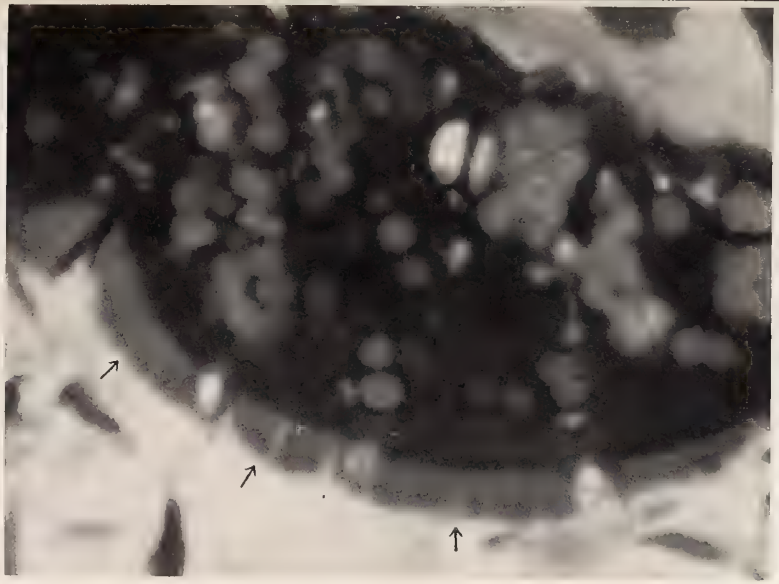

Figure *1*

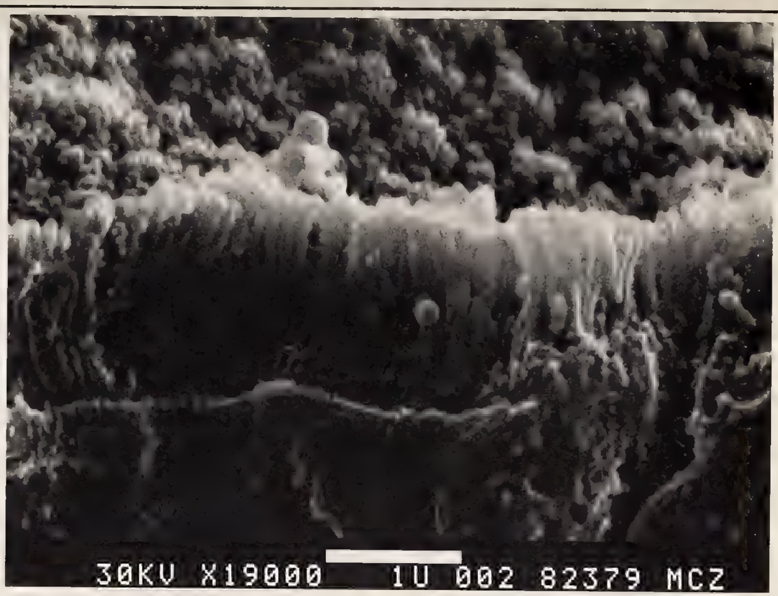

Figure *2*

Figure *3*

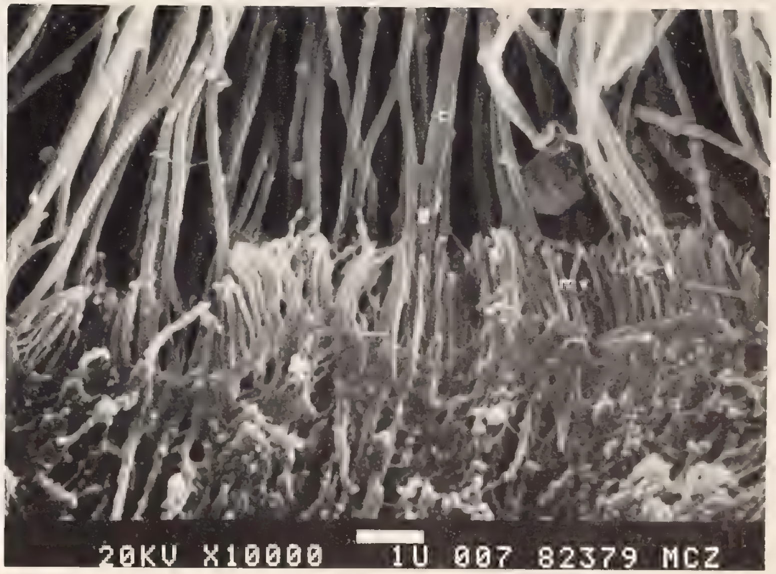

Figure *4*

quate amount of aerated blood supplied to the caecum by the so-called caecal artery.

Figure *1* shows the epithelial cells of the caecum to be flat and non-ciliated, but close examination of these cells (Figure *3*) reveals that these cells possess a microvillar border, which appears to line the entire internal surface of the caecum. Ciliated tracts also appear to be present in the caecum (Figure *4*) but appear to be limited mainly to the stomach-caecal orifice.

The fact that cilia were confined to small, specific regions in the caecum coincides with the descriptions of Lazier (1924), Morton (1970; 1978), and Saraswathy & Nair (1971). However, the presence of a microvillar border in this organ has not been noted in the literature. Morton (1970; 1978) did note a brush border on cells of the secondary ducts of the so-called particle-digesting portion of the digestive diverticula, in which he assumed that these microvilli were involved in the absorption of nutrients.

The discovery of a microvillar border in the caecum is of major importance in the understanding of this organ. It appears to be generally accepted that microvilli are associated with absorption of nutrients and facilitation of enzymatic processes in the digestive tracts of many animals (Berridge & Oschman, 1972). The occurrence of a microvillar border in the caecum suggests that this organ is not a site of temporary storage of wood as previously thought (Morton, 1970; 1978; Saraswathy & Nair, 1971; Dean, 1978), but is a location where a significant amount of nutrient absorption takes place, as Sigerfoos (1908) & Lazier (1924) had originally proposed. The fact that cellulases and other enzymes, and various metabolic intermediates have been found in this organ (Miller & Boynton, 1926; Boynton & Miller, 1927; Greenfield & Lane, 1953; Liu & Townsley, 1968; Liu & Walden, 1970; Cutter & Rosenberg, 1972) would further support this proposed function of the caecum. Turner & Johnson (1971) have shown that shipworms remain alive when removed from the wood until the caecum has emptied. This suggests that nutrients are still being absorbed and extracted from the wood in the caecum, where it is most likely enzymatically degraded.

Further, it should be noted that microvilli are also found interspersed with cilia in the intestine (Figure *5*). The fact that microvilli are found in areas of the digestive diverticula (Morton, 1970; 1978), the caecum, and the extremely long, looped intestine has interesting ramifications. Morton & McQuiston (1974) have shown that a quick turnover of wood fragments occurs in the gut, particularly the caecum, and wood digestion is generally accepted as being a slow process. This extended microvillar border would allow for maximum absorption of nutrients from the breakdown of abraded wood, which may not remain in the digestive tract for a significant amount of time, and would thus be advantageous to the animal.

SUMMARY

The ultrastructure of the caecum of the teredines *Teredo bartschi*, *T. navalis* and *Bankia setacea*, was examined. A microvillar border was found to be associated with the epithelial cells of the caecum. It is suggested that this organ has an absorptive function, rather than being a site of temporary storage of wood fragments.

ACKNOWLEDGMENTS

The authors would like to thank Roy L. Hughes; E. C. Haderlie of the Naval Postgraduate School, Monterey, California; and Carl Berg of the Woods Hole Oceanographic Institute for their help with collection of the animals and for their suggestions and interest in this project.

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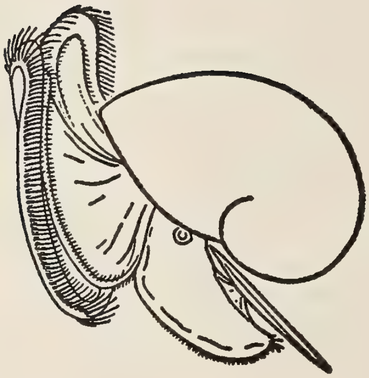

Figure 5

Teredo navalis, cross section of the intestine. Note the presence of both cilia and microvilli. White bar represents 1 μm

A Description of a New Species of Enoploteuthid Cephalopod, *Abralia siedleckyi* spec. nov., with Some Remarks on *Abralia redfieldi* G. Voss, 1955

(Cephalopoda : Enoploteuthidae)

BY

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(8 Text figures)

INTRODUCTION

The Open Ocean Expedition of R/V *Professor Siedlecki* to the South Atlantic waters in 1978 collected more than 2500 specimens of cephalopods. Some of them appeared to be new species; among them were three specimens of *Abralia*.

Besides this, the only other species of *Abralia* collected by R/V *Professor Siedlecki* in 1978 was *Abralia redfieldi* G. Voss, 1955, which was not previously recorded in the South Atlantic Ocean. Three hundred sixteen specimens of this species, also mature males, were collected at the seven stations.

Additional material concerning this species was collected by R/V *Professor Bogucki* east of Recife (Brazil) in 1977 (five specimens).

The localities of new *Abralia* species and new distribution of *A. redfieldi* are illustrated in Figure 1.

METHODS

Measurements were taken of squids which had been kept for two years in 70% ethyl alcohol.

A 1mm ruler and 0.1mm caliper were used for routine measurements. Microscopic observations and measurements were made by means of an MB-30 PZO microscope, MST 131 PZO stereomicroscope and Carl Zeiss micrometric microscope.

The surfaces of the eyeball photophores were calculated by use of equations $S = \pi ab$ (ellipse) and $S = 0.785D^2$ (circle).

The following abbreviations were used:

DML — dorsal mantle length, defined as in G. Voss (1963: 11-12);
VML — ventral mantle length (G. Voss, *loc. cit.*);
HL — head length, measured from nuchal cartilage to V-shaped juncture between arms I;
HW — greatest width of head across eyes;
FL — greatest length of fins, parallel to body's axis;
FN — length of fins from anterior border of juncture between fins to the apex of the mantle;
FWL — greatest width across both fins;
MW1-MW3 — widths of mantle, defined as in Roper *et al.* (1969: 297);
A1-A4 — lengths of arms I-IV p., respectively, measured from first basal sucker to tip of arm. Left arms are usually measured;
TL, TR — lengths of left and right tentacular arms, measured from base to the tip of dactylus;
CL — club length, measured from first carpal knob or sucker to the tip of dactylus;
GL — gladius length;
H1-H4 — number of hooks on arms I-IV, respectively. Hooks on the left arms are usually counted, except in mature males, where both ventral arms are examined.

The measurements and indices for spermatophores were used after N. Voss (1969: 735).

Tail is defined here as distal end of a body cone without fins or their rudiments.

MATERIAL AND DESCRIPTIONS

Abralia siedleckyi spec. nov.; Figures 2-7, Table 1.

Holotype: male, fully mature (V;[1]), DML = 31mm; R/V *Professor Siedlecki*, Sta. 98/43: 39°05′08″S; 13°43′E (start), 39°00′S; 13°44′E (end); sea depth 1910m, catch depth 500m; dawn, 3 July 1978; midwater trawl 110 feet [33m] with 6mm codend mesh.
Coll. number: SFI IXEN 212.
Collector: M. Lipiński.

Paratypes: male, fully mature (V), DML = 30mm, R/V *Professor Siedlecki* Sta. 98/43; female, fully mature (V), DML = 33mm, same.
Coll. numbers: SFI IXEN 213-214.
Collector: M. Lipiński.

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[1] According to maturity scale proposed by Lipiński (1979).

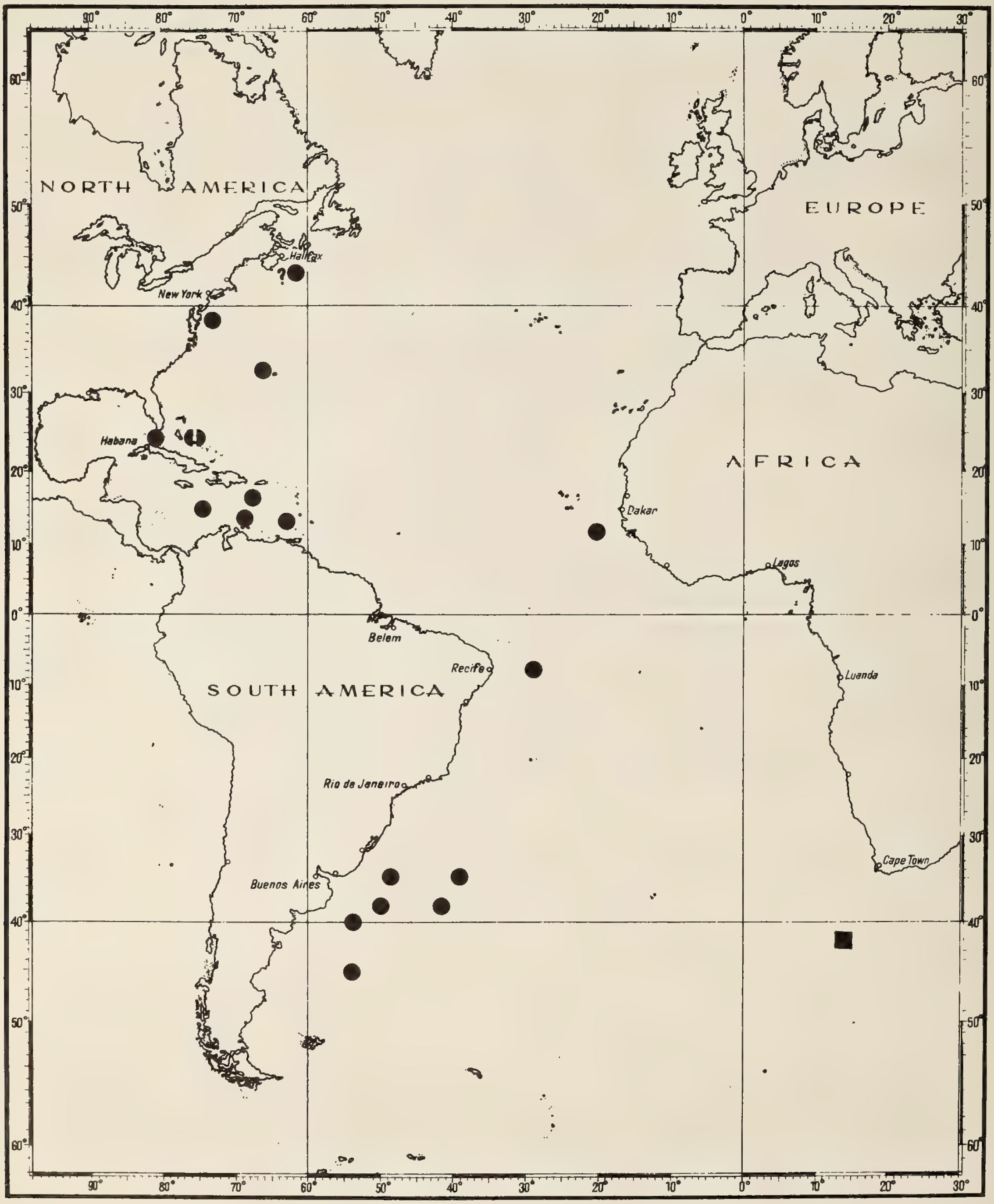


Figure 1

Distribution of the *Abralia* species described in the paper: *Abralia redfieldi* G. Voss, 1955 (●; ◐—location of the type), and *A. siedleckyi* Lipiński, spec. nov. (■). Most northerly findings of *A. redfieldi* are according to AMARATUNGA *et al.* (1980: 17)

Description: The mantle is fairly short (present range of DML within the genus: 21-62mm) and conical, widest at the anterior margin (MWlI = 42%). The antero-dorsal margin is projected forward and forms a distinct obtuse angle. The antero-ventral margin is excavated beneath the funnel with marginal acute angles. The posterior end of the mantle is bluntly pointed, but there is no tail. The gladius shows through the mantle dorsally as a dark line.

The fins are large (FLI = 64-67%; FWLI = 103-106%), their antero-lateral margins are convex, the postero-lateral margins concave and pointed laterally. The anterior lobes project antero-laterally, beyond the mantle.

The head is fairly narrow and long (HWI = 27%, HLI = 39%). Proximally, there are three nuchal folds.

The buccal membrane connectives typical.

The eyes are large but not prominent, the anterior sinus is inconspicuous. The light organs on the eyeball are invisible through the muscles and skin (there are no ventral windows). On the dorsal side of the head there are two characteristic windows, completely devoid of chromatophores, otherwise completely covering the head. Under the skin and thin wings of the cartilaginous skull there are large, oval optic glands.

The funnel is large; it projects about one-third beyond the ventral mantle margin; the funnel groove has an inconspicuous lateral fold. The mantle-funnel locking apparatus is simple, consisting of a straight groove on the mantle. The funnel organ consists of a prominent dorsal pad with long apical papilla and broad shoulders with conspicuous lateral ridges, which continues to ⅕-⅙ of the fleshy arms. Ventral pads large, oval.

The arms are of moderate length, arm formula 4.2.3.1. Arms I-III are keeled; longest keel on III; IV lacks keel. The arms are stout and strong, gradually becoming slender. On their proximal two-thirds, the arms bear two rows of hooks: I-12-14; II-12-14; III-12-14; IV-11 (hectocotylized) and 11-16 (normal). Distally the hooks are followed by many biserial rows of small oval to round suckers that gradually become minute. The suckers and hooks are bordered on either side, on arms I-III, by a protective membrane between conspicuous trabeculae. This membrane is very low and inconspicuous dorsally and well-developed ventrally, especially on arms II-III. Arms IV have very low rudimentary protective membranes from which the ventral is better developed, and bear a well-developed swimming membrane on its dorso-lateral surface.

The tentacles are long and slender, slightly flattened laterally, length more than 100% of DML. Clubs small, very slightly expanded, with three hooks on the right club (armature of the left club incomplete). The basal hook is the smallest, the middle – the largest. The two distal hooks are long, thin, flattened laterally. Dorsally to the hooks are two regular rows of suckers; first (marginal) row contains only three relatively large suckers, next row – five similar suckers. Suckers on the dactylus small, tetraserial. Carpus bears four small suckers and three flat, inconspicuous knobs. Protective membrane on the dorsal side broad and fleshy, broadest at the attachment of the largest hook. Protective membrane on the ventral side thin, paper-like, broadest at the attachment of the proximal hook, then gradually becomes very low and inconspicuous.

In the male, the left ventral arm is hectocotylized. Proximally there are 10 normal hooks; eleventh small hook lies dorsally at the beginning of the large, ventral flap. This flap is semicircular and does not continue to the tip of the arm. It lies at the beginning of the distal half of the arm and occupies about 20% of the arm length. The dorsal flap lies distally to the ventral one. It is small (about 9% of the arm length), semicircular, diagonally set on the oral surface of the arm. It does not continue to the end of the arm. The remaining part of the hectocotylized arm (about 29% of the arm length) is devoid of suckers to the tip; it bears well-developed protective membranes (the ventral one is better developed).

As in the other members of the genus, there are very distinct photophore patterns; photophores are mainly placed on the ventral parts of the arms IV, head, eyeballs, funnel and mantle.

The photophore pattern on the ventral part of the **eyeballs** is most distinct and constant in all cases. There are five photophores: posterior extra large, oval, creamy white, with inconspicuous ventral and dorsal sinuses; small, round, orange; small-medium, round, red; small, round, orange; anterior small-medium (little, or not larger than medial), round, or slightly oval, creamy white, with no sinuses. The large, posterior photophore is 11-13 times larger than the anterior.

The **eyelid** bears the following pattern of photophores: on the ventral side (below the sinus) 16 larger and 15 small black photophores alternately, then above the sinus three oblique black photophores; dorsally 12-16 black, small photophores.

The photophores on the bases of **arms** I-III are few; same on the base of swimming keel on arms III. Bases of arms IV with 9-10 ventrally set, slightly irregular, oblique rows of all three kinds of photophores; marginal rows more regularly set than medial ones. Only second dorsal row continues to the arm tip; ventral row ends subterminally, and first dorsal row ends much earlier.

The dorsal side of the **head** has only a few very small, irregularly set photophores. The ventral surface of the head covered with ten white photophores, arranged in the regular pattern; an additional such photopore lies at the base of each arm IV, near conjunction between them. The

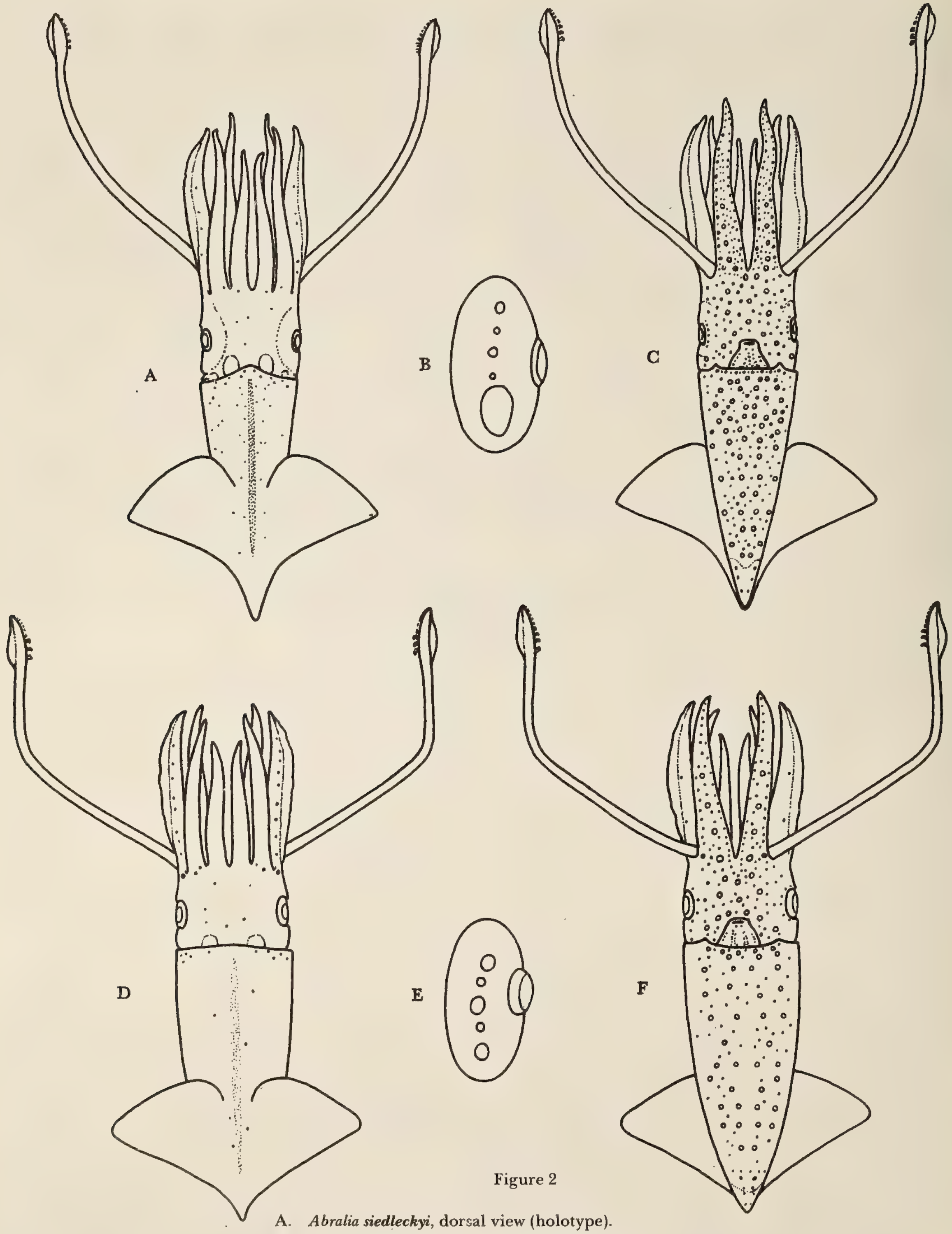


Figure 2

A. *Abralia siedleckyi*, dorsal view (holotype).
B. Same, left eyeball; C. Same, ventral view;
D. *A. redfieldi*, dorsal view (R/V *Prof. Siedlecki*, Sta. 10/5, DML = 30mm, female); E. Same, left eyeball; F. Same, ventral view

photophores of two other types are fairly irregularly dispersed. There are about 40 larger photophores and twice as many smaller ones.

Funnel has four regular multiple bands of photophores; there are 30-36 black photophores in each medial band, and only 4-6 in the marginal ones. There is one white photophore anteriorly in each marginal band and ⅓ the way down each medial one. Lateral bands biserial.

Mantle is dorsally covered with very small photophores, widely set in about 8-14 longitudinal rows; photophores in the first row are most regularly arranged.

The skin on the dorsal surface of the fins is damaged, but there still remain a few small black photophores.

Ventrally, the mantle is covered with numerous photophores of all three usual types. The first proximal row and white photophores are set in orderly arrangement,

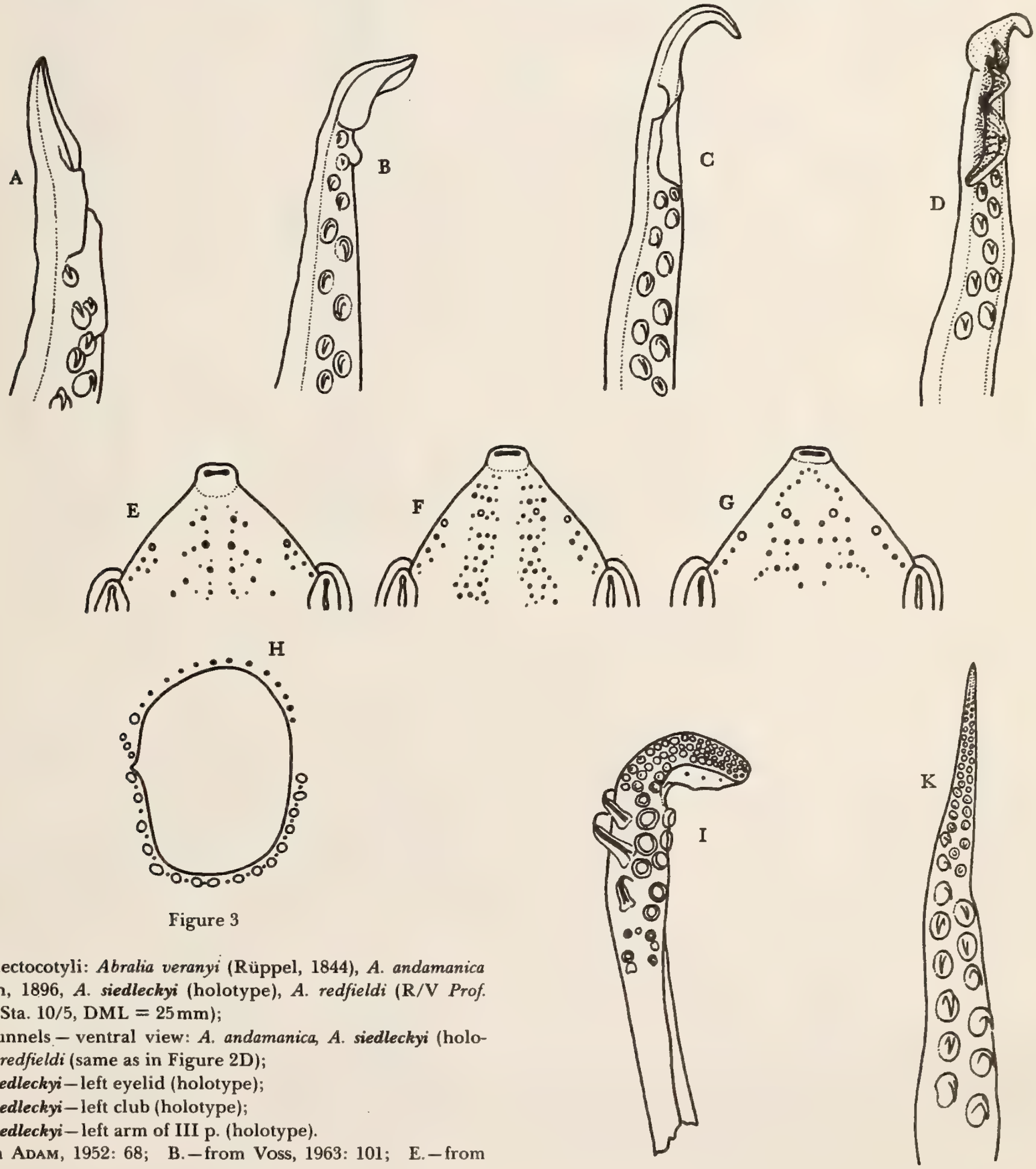


Figure 3

A-D. Hectocotyli: *Abralia veranyi* (Rüppel, 1844), *A. andamanica* Goodrich, 1896, *A. siedleckyi* (holotype), *A. redfieldi* (R/V *Prof. Siedlecki*, Sta. 10/5, DML = 25mm);
E-G. Funnels — ventral view: *A. andamanica*, *A. siedleckyi* (holotype), *A. redfieldi* (same as in Figure 2D);
H. *A. siedleckyi* — left eyelid (holotype);
I. *A. siedleckyi* — left club (holotype);
K. *A. siedleckyi* — left arm of III p. (holotype).
A. — from Adam, 1952: 68; B. — from Voss, 1963: 101; E. — from Sasaki, 1929: 243, and Voss, 1963: 101, modified

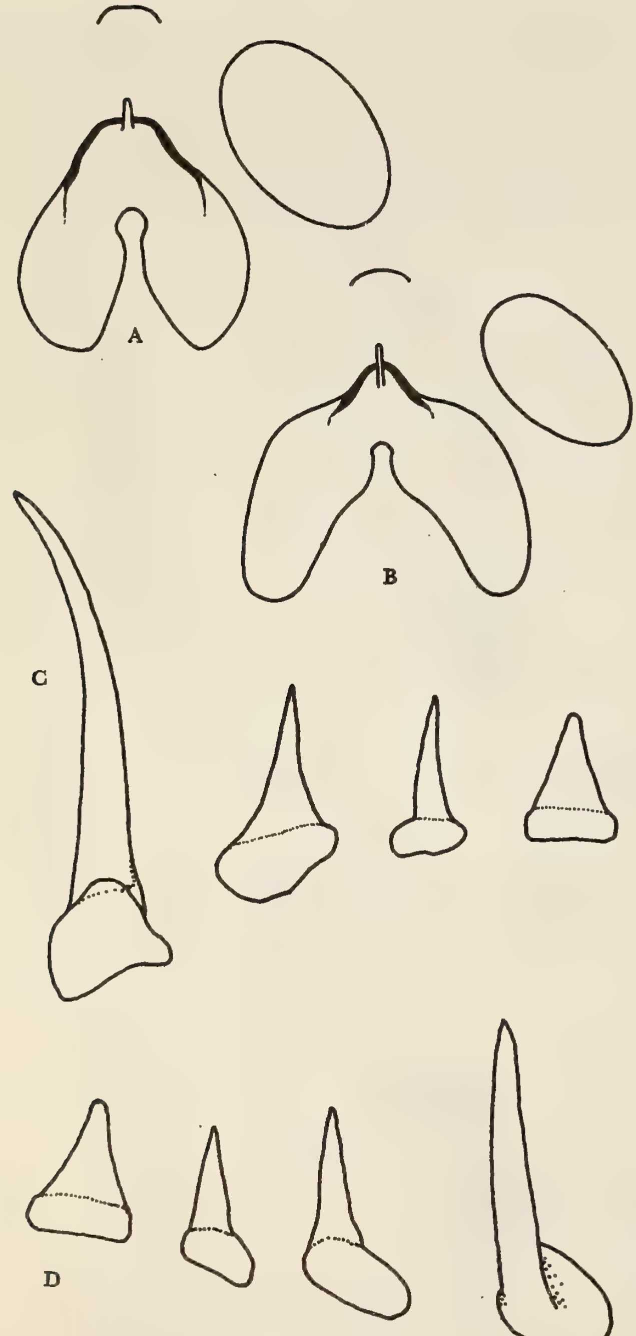


Figure 4

A-B. Funnel organs: *A. siedleckyi* (holotype), *A. redfieldi* (same as in Figure 2D);
C. *A. siedleckyi*—radula (paratype, DML = 31 mm, male);
D. *A. redfieldi*—radula (R/V *Prof. Siedlecki,* Sta. 10/5, DML = 29 mm, female)

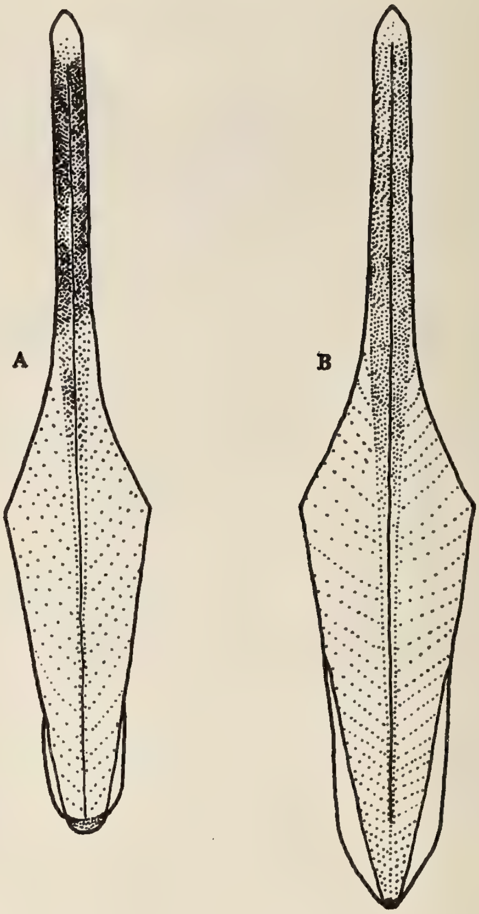


Figure 5

A. *Abralia redfieldi*—gladius; B. *A. siedleckyi*—gladius

others are irregular. The first row consists of bigger black photophores inter-spaced with smaller ones; the white photophores are regularly set in 14-15 transverse rows. There is no ventral midstripe devoid of light organs.

Ventral surface of the distal tip of the mantle is semi-gelatinous, devoid of chromatophores, with only two lateral bands of widely spaced black photophores.

Spermatophores small, numerous. SpMI = 16.2%; CBI = 46.2%; SpWI = 1.2%; EjAI = 37.6% (Figure 7).

Gladius (Figure 5) occupy about 84% of DML and do not enter the gelatinous cone.

Table 1

The measurements of the *Abralia siedleckyi* Lipiński, spec. nov. and *Abralia redfieldi* G. Voss, 1955 specimens.

Feature	Species																				
	Abralia siedleckyi			*Abralia redfieldi* (R/V *Professor Siedlecki,* 1978)																	
	Holo-type	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂
DML	31	30	33	24	25	30	27	23	23	28	26	27	24	25	26	24	26	24	22	25	24
VML	28	28	31	22	24	29	26	22	21	27	25	26	22	24	25	22	24	22	20	23	22
HL	12	12	12	11	11	13	11	10	10	11	10	12	11	14	11	8	11	9	9	10	10
HW	8	8	7	8	9	11	8	9	7	10	8	7	7	8	8	7	8	7	7	6	8
FL	20	20	21	13	13	17	14	13	12	14	14	15	12	12	14	11	12	11	11	11	12
FN	16	16	17	10	10	14	12	9	10	13	12	12	11	11	11	9	10	10	9	9	9
FWL	32	31	35	22	22	26	24	23	21	24	22	21	21	25	22	22	25	23	21	23	20
MW_1	13	13	13	10	10	13	10	10	10	11	10	10	9	10	10	9	11	10	10	10	10
MW_2	10	11	11	9	9	11	9	10	8	10	10	10	9	9	8	8	10	9	8	9	9
MW_3	8	8	9	8	8	10	8	9	7	9	8	8	8	8	8	6	8	8	6	7	9
A_1	15	16	13	8	8	12	10	10	9	10	9	10	10	11	9	8	10	9	9	9	10
A_2	20	19	16	10	11	11	11	11	9	11	9	12	12	13	15	9	11	12	10	11	12
A_3	17	16	14	8	8	11	10	8	6	10	9	11	10	14	16	11	12	12	12	12	12
A_4	19	20	18	9	12	12	11	11	9	11	10	11	12	13	16	11	13	14	14	12	13
TL	—	52	—	25	30	37	27	23	30	30	29	35	31	30	30	27	29	28	29	28	27
TR	48	—	—	28	27	—	31	25	29	30	29	35	30	29	—	24	26	25	25	24	25
CL	4	—	—	2	4	5	2	3	4	3	4	3	2	4	4	3	5	3	4	4	3
GL	—	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H_1	14	14	12	13	11	13	12	13	13	16	13	13	11	12	11	15	12	12	13	14	16
H_2	13	14	14	16	13	12	12	14	15	14	15	12	12	13	12	11	13	14	13	13	15
H_3	13	12	14	13	12	12	12	11	16	13	12	12	11	11	14	16	11	12	11	12	12
H_4^3/	11/16	11/14	12	14	11	16	15	10	11	15	15	14	10	10	13	9/13[1]	0/14	9/12	11/12	9/14	10/13

[1] In the case of mature males, both arms were investigated (upper—hectocotylized).

Vane broad, long (⅔ of GL); conus small, rather sharp. The walls of vane are set at angle of 90° or slightly less.

Radula (Figure 4c) contains seven rows of unicuspid teeth.

Beaks (Figure 6c-d) strong, enoploteuthid-like. Lower beak has conspicuous ridge on the lateral wall.

Color in the 70% ethyl alcohol: dark grayish-brown.

Etymology: The specific name was given in honor of the late Professor Michal Siedlecki, Polish marine biologist.

Holotype and paratypes are located at Museum, Sea Fisheries Institute, 81-345 Gdynia, Al. Zjednoczenia 1, Poland.

Abralia redfieldi G. Voss, 1955; Figures 2-8, Table 1.

Material examined: A. eight males, maturity II-V, DML range 23-27 mm; 20 females, maturity II-III, DML range 23-30 mm; R/V *Professor Siedlecki,* Sta. 10/5, 45°06′1″S; 54°02′02″W (start), 45°10′3″S; 54°04′4″W (end); depth of catch 45-55 m; 9 May 1978; midwater trawl 110 feet [33 m], codend with 6 mm mesh liner; total number of specimens in the sample: 242.

Data from other stations, where *Abralia redfieldi* was caught were as follows:

- Sta. 3/3: 35°04′1″S; 39°22′8″W (start), 35°04′2″S; 39°18′9″W (end); depth of catch 300 m; day, 4 May 1978; gear as Sta. 10/5; 20 specimens;
- Sta. 11/6: 45°33′S; 54°01′W (start), 45°38′8″S; 54°01′1″W (end); depth of catch 320 m; night, 10 May 1978; gear as Sta. 10/5; 4 specimens;
- Sta. 39/14: 40°01′2″S; 53°45′5″W (start), 39°59′S; 53°42′W (end); depth of catch 720 m; dawn, 22 May 1978; gear as Sta. 10/5; 1 specimen;
- Sta. 44/17: 37°55′3″S; 49°51′1″W (start), 37°55′2″S; 49°48′1″W (end); depth of catch 640 m; night, 23 May 1978; gear as Sta. 10/5; 4 specimens;
- Sta. 49/18: 38°02′S; 42°03′W (start), 38°01′9″S; 41°58′2″W (end); depth of catch 230 m; night, 25 May 1978; gear as Sta. 10/5; 21 specimens;
- Sta. 57/21-59/23. Central position: 34°58′S; 48°34′W; depth 24-210 m; night, 29-30 May 1978; gear as Sta. 10/5; 24 specimens.

Coll. numbers: SFI IXE 210-211(M).

Collector: M. Lipiński.

B. four males (some with spermatophores), and one immature female (III); DML range 25-27 mm (males), and 30 mm (female); R/V *Professor Bogucki,* Sta. 2: 7°26′S; 28°28′W (central position); depth of catch 70 m; day, 2 December 1977; midwater trawl 110 feet, codend with 6 mm liner.

Coll. numbers: SFI IXE 205-209.

Collector: W. Ślósarczyk.

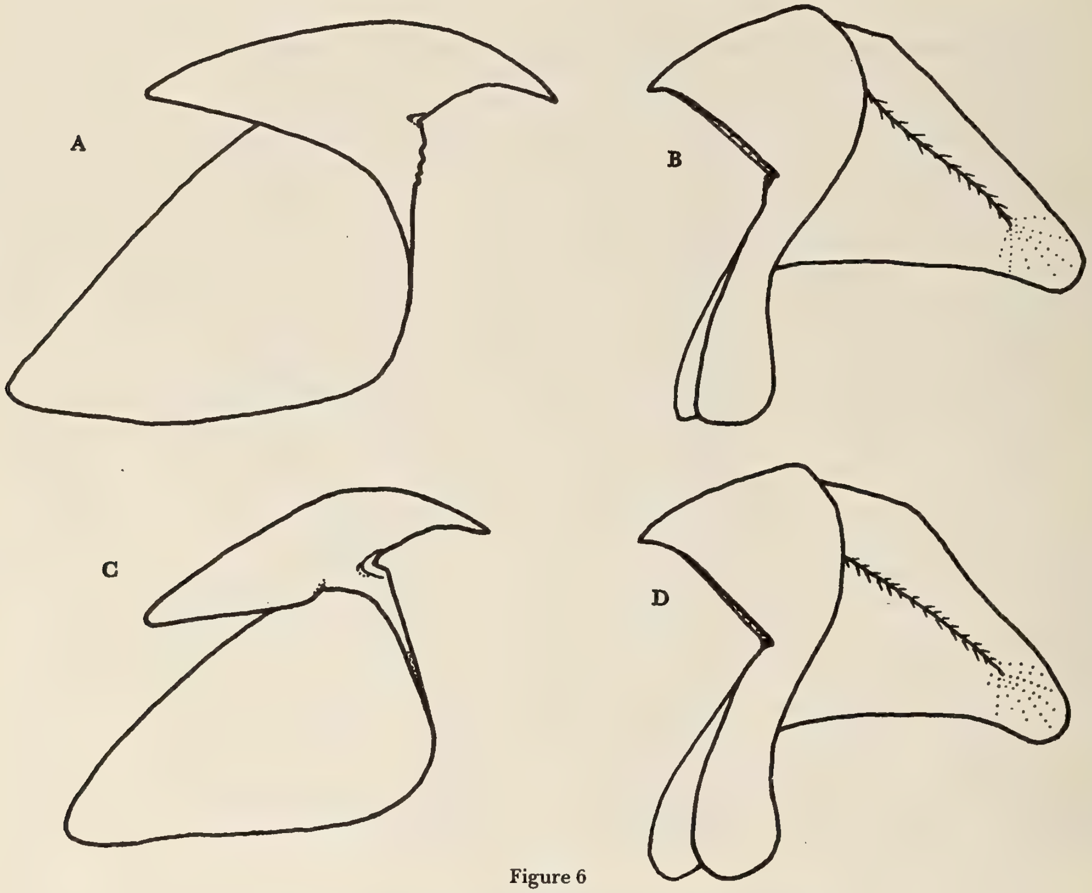


Figure 6

A-B. *Abralia redfieldi*—upper and lower beak (same as in Figure 4D);
C-D. *A. siedleckyi*, upper and lower beak (same as in Figure 4C)

Description: The mantle is fairly short and conical, widest at the anterior margin (MW1I = 37-48%). The antero-dorsal margin is fairly straight, with no distinct angle. The antero-ventral margin is excavated beneath the funnel with acute marginal angles. The posterior end of the mantle is bluntly pointed, with a very small tail (5-6% of DML). The gladius shows through the mantle dorsally as a dark line, but is not protruding.

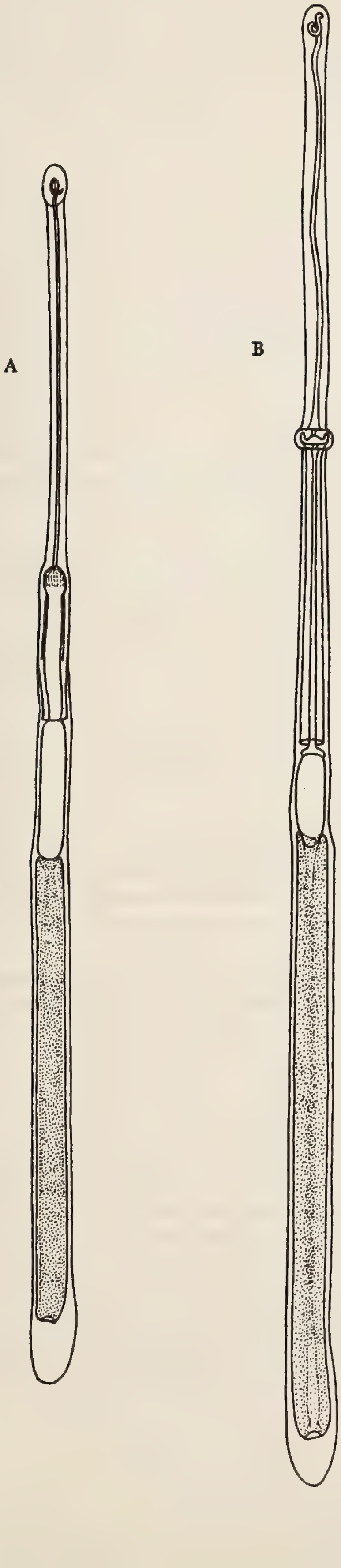
The fins are fairly short (FLI = 46-57%) but broad (FWLI = 83-100%), their antero-lateral margins are convex, the postero-lateral margins concave and rounded laterally. The anterior lobes ("ears") project forward, within the contour of the mantle.

The head is compact, squarish (HWI = 27-39%, HLI = 36-46%). Proximally, there are three nuchal folds. The buccal membrane connectives typical.

The eyes are large, but not prominent; anterior sinus is inconspicuous. The eyeball light organs are clearly visible through muscles and skin; small ventral windows present. Dorsally there are clear windows, with only tiny chromatophores; under these windows are large optic glands.

The funnel is large, projecting about one-fourth beyond the ventral mantle margin; the funnel groove has conspicuous, small lateral fold. The funnel-mantle locking apparatus is typical. The funnel organ consists of a prominent dorsal pad with filamentous papilla. Shoulders short; arms long, bean-shaped. Short, inconspicuous lateral ridge projects from papilla to beginning of arms. Ventral pads large, oval.

The arms are of moderate length; arms II-IV almost equal, arms I usually shorter. Arms I-III are keeled; IV



lacks keel. All arms are stout and strong, gradually becoming slender, and bear on their proximal two-thirds the following number of hooks, arranged biserially: I—11-16; II—12-16; III—11-16; IV—9-10 (hectocotylized) and 10-16 (normal). Distally, hooks are followed by 7-10 pairs of small oval to round suckers which gradually become minute. The suckers and hooks bordered on either side of arms I-III by a protective membrane between conspicuous trabeculae. This membrane is fairly low dorsally and well-developed ventrally. Arms IV have very low rudimentary protective membranes (ventral one is better developed), and bear well-developed swimming membrane on their dorso-lateral surface.

The tentacles are long and slender, slightly flattened laterally, length more than 100% of DML. Clubs small, slightly expanded, with three ventral hooks almost equal in size (the middle hook is slightly larger than the marginal ones). Dorsally to the hooks there are two rows of suckers: first lateral row contains four relatively large suckers, next —four smaller suckers. At the base of the first (proximal) hook there is one medium sucker. Suckers on the dactylus tetraserial, proximally medium, then gradually become small. Carpus bears four small suckers and 6-7 flat knobs. Protective membrane on the dorsal side of the manus broad and fleshy; on the ventral side thin, paper-like.

In the male the right ventral arm is hectocotylized(2). Proximally there are 9-10 normal hooks; eleventh small hook sometimes present in the younger animals at the base of the first flap. The distal half of the arm is occupied by three flaps: two proximal ones large, spoon-shaped, located medially on the oral side with oblique, thick, muscular base (immature males have these flaps directly on the ventral side); distal flap located dorsally, small, semicircular, does not extend to the arm tip. Proximally to the last flap lies semioval, ventral fold of swimming membrane. The tip of the hectocotylized arm is devoid of suckers (immature males have several pairs of small suckers on this part of arm). Approximate proportions of the main parts of hectocotylized arm are as follows: hooks 50% of arm length; flaps 33%, suckerless tip 17%.

The photophore pattern on eyeballs, arms IV, head, funnel and mantle is very distinctive.

On the **eyeballs** are five fairly widely spaced light organs in the following order: medium, small, medium, small, medium. All these organs are round, red-green or red-yellowish. Medium photophores are 2.5-3.0 times greater than small ones. The pattern described is the same in all cases investigated.

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[2] Description of hectocotylus is based only on the mature males with spermatophores in the Needham's sac.

← Figure 7

A. Spermatophore of *Abralia siedleckyi* (holotype);
B. Spermatophore of *A. redfieldi* (R/V *Prof. Siedlecki* Sta. 10/5, DML = 25mm)

In the ventral half the **eyelid** bears 15-16 larger photophores irregularly spaced with smaller ones; dorsal part has smaller widely-spaced photophores, plus one bigger and one smaller just below the sinus.

The photophores on the bases of **arms** I-III are few; usually there are no photophores on I, two small black photophores on II, one large white and several small black photophores on III. A few photophores on the base of the swimming keel on III (usually eight on the dorsal and two at the base of the ventral side). These photophores are fairly regularly spaced. Bases of arms IV have five regular rows of photophores of all three kinds (Sasaki, 1929: 245). First dorsal row is long; second is very short; third extends to the arm's tip; next is very short; ventral one is long. The white photophores on the arms IV are very large.

Dorsally, **head** has 0-3 irregularly spaced very small photophores, deeply embedded in the tissue. The ventral surface of the head covered with twelve white photophores, arranged in regular pattern; additional ones are at the base of each arm IV. The other two kinds of photophores are arranged in 10-12 irregular longitudinal rows.

Funnel has four regular multiple bands of photophores; there are 19-22 black photophores of two kinds in each medial band and a single row of three larger black photophores in each marginal one. There is one white photophore anteriorly in each lateral band and in the proximal ⅓ of each medial band.

Mantle and **fins** dorsally covered with a few very small photophores, especially near the gladius and anterior border of the mantle; last ones are regularly spaced in two rows. Ventrally, the mantle is covered by numerous photophores of all three usual types. The anterior row contains photophores fairly irregularly arranged. There are six longitudinal, broad, irregular multiple bands of photophores of all three types; sometimes these bands are indistinct, but there always remains the medial midstripe devoid of photophores. The large white photophores are set in 12-15 transverse rows (in the middle of VML somewhat irregularly set).

Ventral surface of the distal tip of the mantle is semigelatinous, devoid of chromatophores, with only two lateral strips of widely-spaced black photophores.

Spermatophores small; SpMI = 40.2%, CBI = 28.5%, SpWI = 3.6%, EjAI = 31.3%; the structure of spermatophores is very different from that of *Abralia siedleckyi* (Figure 7).

Gladius (Figure 5a) occupy about 89% of DML and do not enter the gelatinous cone. Vane broad, long (⅔ of GL); conus small, rounded. The walls of vane are set at angle of 90° or slightly less.

Radula (Figure 4d) contains seven rows of unicuspid teeth.

Beaks (Figure 6a-b) strong, enoploteuthid-like. Lower beak has conspicuous ridge on the lateral wall.

The whole body is covered with thin, whitish, gelatinous envelope, not mentioned by G. Voss (1955: 99-102).

The length frequency of *Abralia redfieldi* from the R/V *Professor Siedlecki* (Sta. 10/5) is presented in Figure 8.

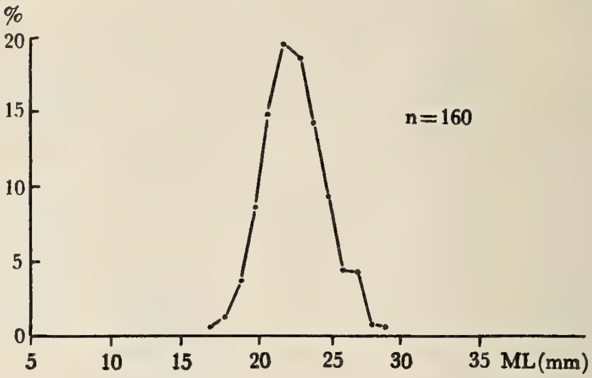

Figure 8

Length frequency distribution of *Abralia redfieldi* from South Atlantic waters (R/V *Prof. Siedlecki*, Sta. 10/5, 9 May 1978)

DISCUSSION

Abralia siedleckyi spec. nov. and *A. andamanica* Goodrich, 1896 are undoubtedly closely related, and as substantial variation of the latter species was reported, a problem exists in respect to the systematic status of *A. siedleckyi*.

Abralia andamanica could probably be split into the following subspecies:

- *A. andamanica andamanica* Goodrich, 1896 (Andaman Sea, Philippines; Goodrich, 1896; G. Voss, 1963: 99-105);
- *A. andamanica robsoni* Grimpe, 1931 (Japan; Sasaki, 1929: 242-245; Grimpe, 1931; 150 and 164; G. Voss, *loc. cit.;* Okutani, 1974: 38);
- *A. andamanica* subspec. A (Hawaiian Islands; Okutani, 1974: 33);
- *A. andamanica* subspec. B (Galapagos Islands and 30° north to Marquesas Islands; Okutani, 1974: 34-38).

The differences between these subspecies concern the following features: body proportions, tentacular armatures, photophore arrangement on the mantle, head, arms and eyeballs, and shape of hectocotylus.

Abralia siedleckyi has similar body proportions as *A. andamanica* subspec. B (the individual illustrated by Okutani, *op. cit.:* (Figure 2), but differs from all other described or illustrated forms of *A. andamanica* by the following characteristics:

- size and shape of photophores on the eyeballs (Figure 2b);
- shape of hectocotylus (Figure 3b-c);
- proportions of manus/dactylus (Figure 3i).

In all known subspecies of *A. andamanica* the anterior and posterior photophores of the eyeballs are larger than the other three and are of different shape; *i.e.*, external photophores are elongate oval. *A. **siedleckyi*** has an anterior photophore of similar shape and only slightly larger than the medial one. I consider this characteristic alone to be a species-level difference. This view is supported by other differences between *A. andamanica* subspecies and *S. siedleckyi:*

- all forms of *A. andamanica* have dactylus much longer than manus;
  A. siedleckyi has dactylus only slightly longer;
- all forms of *A. andamanica* have hectocotylus with ventral flap slightly longer, equal or much shorter than dorsal;

Abralia siedleckyi has ventral flap three times longer. Other differences between these species concern the probable distribution of photophores on the funnel and eyelid, shape of the funnel organ, and spermatophores; unfortunately, these characteristics have not been described or illustrated for all *A. andamanica* subspecies.

Okutani (1974) described morphological changes with growth concerning *Abralia andamanica?* subspec. B; the present material was insufficient to point out the differences between *A. andamanica* subspecies and *A. siedleckyi* in growth sequences, therefore only adults of these species were compared.

Abralia redfieldi is now known from 43° N to 45° S (Amaratunga *et al.*, 1980: 17; G. Voss, 1955: 99; Nesis, 1975: 260-261; Cairns, 1976: 244; Lu & Roper, 1979: 5; and present material). This species was found only once in the eastern Atlantic, near Dakar (Lu & Clarke, 1975: 372). Such distribution may indicate that *A. redfieldi* is a relatively "young" species, developed in Caribbean center of evolution.

ACKNOWLEDGMENTS

I am most grateful to Dr. Kir N. Nesis of the Institute of Oceanology, AS USSR (Moscow), and Gilbert L. Voss of RSMAS, University of Miami, (Miami), who were so kind as to read and give their comments on the manuscript; Dr. Martina A. Roeleveld of the South African Museum (Cape Town) and Dr. Takashi Okutani of the National Science Museum (Tokyo), who helped me with literature problems; Dr. Wiesław Ślósarczyk of the Sea Fisheries Institute (Gdynia), who supplied some specimens of *Abralia redfieldi*. The cooperation of Dr. Andrzej Karabin of Polish Academy of Sciences (Warsaw) concerning illustrations is greatly appreciated.

This contribution is from the Sea Fisheries Institute, Gdynia, Poland.

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NOTES & NEWS

Ashmunella angulata Pilsbry, 1905
Ashmunella esuritor Pilsbry, 1905
Ashmunella lenticula Gregg, 1953
Ashmunella lepiderma Pilsbry and Ferriss, 1910 and
Ashmunella varicifera (Ancey, 1901)
Re-Established as Valid Species

BY

WALTER B. MILLER

PILSBRY (1940) REVIEWED the various populations of *Ashmunella* Pilsbry & Cockerell, 1899, of the Chiricahua Mountains and the Huachuca Mountains of Arizona. He was particularly perplexed by the apparently minor differences among populations in the degree of shell peripheral angulation and in the proportions and spacing of the basal teeth. He decided that "it may be well to recognize the local diversity by the use of subspecific names." Accordingly he recognized five subspecies of *Ashmunella proxima* Pilsbry, 1905, in the Chiricahuas and five subspecies of *Ashmunella levettei* (Bland, 1882) in the Huachucas.

BEQUAERT & MILLER (1973), on the basis of additional collections, made additional revisions to the genus resulting in reducing *Ashmunella angulata* Pilsbry, 1905, and *A. lepiderma* Pilsbry and Ferriss, 1910, to subspecies of *A. proxima*. They synonymized *A. lenticula* Gregg, 1953, with *A. proxima angulata*. They reduced *A. esuritor* Pilsbry, 1905, to a subspecies of *A. chiricahuana* (Dall, 1895), and *A. varicifera* (Ancey, 1901) to a subspecies of *A. levettei*. The underlying philosophy in these changes was that the rather minor morphological differences of the presumed subspecies could not be indicative of a sufficiently different genome to cause reproductive isolation, the *sine qua non* of a biological species.

From 1973 to the present, the author and his graduate students have attempted to obtain additional information on the degree of speciation in many populations of *Ashmunella*. REEDER & MILLER (1974), REEDER *et al.* (1975), and REEDER (1975) provided cytotaxonomic data based on karyotypes. TRIFAN (1976) and FAIRBANKS (1979) provided information based on electrophoresis of foot proteins. Finally, Babrakzai and Miller (in press) showed conclusively, as a result of hybridization studies coupled with examinations of the C-banded and G-banded chromosomes of the hybrids, that the apparently minor differences in morphology were nevertheless accompanied by major genetic differences, as exhibited by chromosomal rearrangements, sufficient to interfere with normal synapsis and gametogenesis. In other words, the genetic differences in the presumed subspecies studied are indeed sufficient to cause reproductive isolation, and the relatively minor morphological differences exhibited in the shell characters are but "the tip of the iceberg" of genetic differences.

Accordingly, it has become apparent to the author, as a result of the excellent and painstaking work of his former graduate students, that the following taxa are good species, reproductively isolated from other taxa:

Ashmunella angulata, A. esuritor, A. lenticula, A. lepiderma, and *A. varicifera.*

ACKNOWLEDGMENT

Noorullah Babrakzai, H. Lee Fairbanks, Richard L. Reeder, and Donna Trifan, through their graduate and postgraduate research, have provided the basic data which allowed me to make the specific determinations expressed in this paper.

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THE CONCHOLOGICAL CLUB
OF SOUTHERN CALIFORNIA

sent a very generous contribution to the Veliger in memory of

John E. Fitch

who died on September 30, 1982. Mr. Fitch is best known among malacologists for several papers on mollusks and especially the "Fish Bulletin No. 90" of the California Department of Fish and Game, entitled *Common Marine Bivalves of California.* He was the world authority on otoliths of fossil cephalopods and fish. For a number of years he was Research Director of the Department of Fish and Game.

The Executive Board of the California Malacozoological Society joins the members of the Conchological Club of Southern California in extending condolences to his family.

The Nominal Cancellariid Genus *Panarona* Petit, 1975

BY

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THE GENUS *Panarona* Petit, 1975 was proposed on the premise that a valid type designation had been made by Kobelt (1878: 102) for *Narona* H. & A. Adams, 1854 which changed the commonly accepted concept of that genus. This has now been found to be incorrect. The consensus of systematists consulted is that Kobelt's type designation was for a vernacular group and not for the genus *Narona.* Fortunately, no papers have been written on Panamic Cancellariidae since the unnecessary proposal of *Panarona,* and this correction is being published to prevent propagation of this nominal taxon. *Panarona* is a junior synonym of *Narona* H. & A. Adams, 1854.

The genus-level taxa *Narona* and *Hertleinia* are correctly used by Keen (1971) and the earliest known type designations for these taxa are as follows:

Narona H. & A. Adams, 1854, Genera of recent mollusca 1: 277.
Type, by SD, Jousseaume, 1887, *Cancellaria clavatula* Sowerby, 1832.
Hertleinia Marks, 1949, Journal Paleont. 23: 457.
Type, by OD, *Cancellaria mitriformis* Sowerby, 1832.

The writer is greatly indebted to Drs. A. Myra Keen, Harald A. Rehder and Harold E. Vokes, and to Mr. Lee A. Schremp for their reviews of the literature involved and for their discussions of the status of *Panarona.*

For pertinent literature citations refer to PETIT, 1975, The Veliger 17(4): 387-388.

Important News

At its regular Annual Business Meeting on October 13, 1982, the Executive Board of the California Malacozoological Society, Inc. decided to adjust the subscription rate for Members ("dues") to conform with the U. S. Postal regulations pertaining to second class mailing privileges to the required minimum of 50% of the regular subscription rate, while holding the latter to the current $37.50 per volume-year (July 1 to April 1). This means that the "dues" will increase a minimal 25¢ to $18.75. On the other hand, the Society is forced to increase the mailing charges for members and subscribers to $3.25 for all domestic address and to $6.00 for all foreign addresses (including Canada and Mexico). The initiation fee for new members remains at US$2.00; the reinstatement fee, due if membership renewals are not made to reach the Society on or before April 1 preceding the start of the new volume will also remain at US$1.00. Reinstatement is not possible if application is not made within 11 months after original renewal was due. A new application for membership and the payment of a new initiation fee will be required.

Similarly, the need to include a self-addressed, stamped envelope or (in the case of foreign members) the envelope and two International Postal Reply Coupons, was reaffirmed.

In view of the deplorable fact that the postal services throughout the world seem to become ever more expensive and also more unreliable, members are urged to lodge complaints for intolerable delays in deliveries of their journals with their local postmasters. Most likely, this will not result in better service, at least not immediately, but it may be hoped that in the long run it will lead to some improvement. Complaints to the Society cannot lead to any improvement, since we already do more than the requirements of the postal service in respect to second class mailings stipulate.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

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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.

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 First Interstate Bank (formerly United California Bank). This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable, except as indicated elsewhere in this section.

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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.

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$25.00 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.

We think it important to bring to the notice of all our actual and potential correspondents that the postal fee for registered articles is the highest in the world: $3.25, regardless of destination. Further, to certain countries it is not possible to have mail pieces insured or registered. In the cases where the prospective recipient desires our communications sent as registered article, we must expect advance payment of that fee. We are unable to return manuscripts (either for reworking or with the recommendation that they be submitted elsewhere) other than by ordinary surface mail. In view of the ever more deteriorating postal services in most countries, we can obviously not assume any responsibility for the safe delivery of any items we must dispatch. Our responsibility must and does end with our delivery to the post office of any item.

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It seems necessary to bring the following points to the notice of prospective authors:

All manuscripts submitted for inclusion in The Veliger are subject to review by at least two scientists; acceptance is entirely on the basis of merit of the manuscript. Although many scientific journals assess page charges, the Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought.

Similarly, while it was hoped at the "birth" of The Veliger, that a modest number of reprints could be supplied to authors free of charge, this has not as yet become possible. We supply reprints at cost. Unfortunately, in recent years it has become "fashionable" for some authors and some institutions to ignore paying for reprints ordered and supplied in good faith or to delay payment for a year or more. This causes financial losses to the Society since our debts are paid promptly. Since the Society is in fact not making any profit, it is necessary to introduce a policy which, it is hoped, will protect us against negligence or possible dishonesty. In the case of manuscripts from sources outside of the United States, if a manuscript is accepted, we will inform the author of the estimated cost of reprints and require a deposit in U. S. funds to cover these costs. If such a deposit is not made, we will not supply any reprints. In the case of non-payment by domestic authors or institutions, we will pursue legal recourses.

Sale of C. M. S. Publications:

Effective September 1, 1981, all back volumes still in print, both paper covered and cloth bound, will be available only from "Seashell Treasures Books," 646 30th Street, San Diego, California 92102. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Pisor at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from "Seashell Treasures Books" are as follows:

Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:
[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]
Supplement to Volume 6: out of print.
Supplement to Volume 7: available again; see announcement elsewhere in this issue.
Supplement to Volume 11:
[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]
Supplement to Volume 14:
[The Northwest American Tellinidae by Dr. E. V. Coan]
Supplement to Volume 16:
[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]
[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]
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, Mon-

terey, CA(lifornia) 93940.

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 through Volume 6: $9.00 each.
Volume 7 through Volume 12: $12.00 each.
Supplement to Volume 6: $3.00; to Volume 18: $6.00
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, 359 Roycroft Avenue, Long Beach, California 90814.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from "Seashell Treasures Books," 646 30th Street, San Diego, CA 92102. Orders should be sent directly there.

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 may be obtained by sending a self-addressed, stamped envelope to the Veliger, 1584 Milvia Street, Berkeley, CA(lifornia) 94709. Foreign correspondents should enclose one international postal reply coupon. Requests for the list, for which return postage is not provided, will be ignored.

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.

IMPORTANT NOTICE

Effective immediately, Manuscripts and correspondence pertaining to them should be sent to Dr. D. W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616. All business correspondence (subscription orders, membership applications, payments for them, changes of address, as well as any other correspondence not pertaining to the editorial activity) should be sent to C. M. S., Inc., Post Office Box 9977, Berkeley, CA 94709.

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 $400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, $400.-). 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 insist on these conditions; however, the exorbitant inother countries must be provided. We regret that we must creases 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.

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, devises 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.

A. M. U.

AMERICAN MALACOLOGICAL UNION

The American Malacological Union will hold its 52nd Annual Meeting at the University of Washington, Seattle, Washington, August 7-13, 1983. The meeting will include contributed papers and posters, exhibits, field trips, workshops, and several symposia. Symposium topics include molluscan nerve cells and their roles in behavior and in nervous system organization, organized by Prof. Dennis Willows; molluscan extinctions in the geologic record and at the present time, organized by Prof. Geerat Vermeij; and avian molluscivores, sponsored by the Western Society of Malacologists, which will be meeting with the AMU this year. Additional information and registration forms are available from Alan J. Kohn, Department of Zoology, University of Washington, Seattle, WA 98195.

W. S. M.

WESTERN SOCIETY OF MALACOLOGISTS

The 16th Annual Meeting of the Western Society of Malacologists will be held jointly with the American Malacological Union in Seattle, Washington, August 7th to 13th, 1983, on the campus of the University of Washington.

The meeting will feature symposia and contributed papers on molluscan topics, exhibits, shell and book auction, and field trips. All interested persons are invited to attend. For further information contact Mrs. Katharine Stewart, 19 La Ranchera, Carmel Valley, CA 93924.

Applications for membership should be sent to Mrs. Margaret Mulliner, 5283 Vickie Drive, San Diego, CA

92109. Dues are: Regular Members, $7.50 (with additional Family Members $1.00 each), and Student Members $3.00. Regular and Student Members receive the Annual Report containing the published proceedings of the annual meeting.

BOOKS, PERIODICALS, PAMPHLETS

of Sea and Shore

The Winter Issue of this popular quarterly has just arrived. As usual, it contains several popular accounts of shelling trips and shell shows. There are also two articles dealing with chitons. We are particularly pleased with a strong warning against the use of formalin for preserving shelled mollusks. The author of that article, Mrs. Paula Mikkelsen has rendered a valuable service to traveling conchologists, not only by mentioning the deleterious effect of the formalin, but also of the restrictions air travelers must expect when attempting to bring material with them onto the plane.

R. Stohler

Thais

No. 3 of "Publicaciones Diversas de la Sociedad Panameña de Malacología" by M. C. Avilés E., L. E. Sánchez & R. Caicedo. 71 pp.; 12 full-page "plates" of diagrams 30 December 1981

This is an apparently complete list of molluscan taxa down to the family level. Several "accepted" classifications are presented for comparison, leaving to the reader which one to accept.

No price is indicated; however, those interested may obtain additional information by writing to Professor M. C. Avilés E. at Apartado 6-593, Zona Postal El Dorado, Panama, Rep. de Panama.

R. Stohler

Annual Report of the Western Society of Malacologists

Volume 14; 32 pp.; 1 photograph. 13 July 1982

This volume contains abstracts or titles of papers presented at the 14th meeting of the Society in San Diego, California, June 23 to 26, 1981. The photograph is of a group of the participants at the meeting.

It is a pleasure to see the variety of subjects discussed and especially the greater emphasis on paleontological aspects than has been the case in the past.

R. Stohler

Estudios sobre los efectos del aislamiento en poblaciones de gasteropodos terrestres asturianos. II. Análisis de las diferencias intraspecificas.

by Emilio Anodon & Nuria Anodon. 357-387; 10 figs. in text; Revista de la Facultad de Ciencias, Universidad de Oviedo. N. S. "Volumen Extraordinario" 1978

This is a concluding report on a comparative study between neighboring populations of land mollusks that are, however, separated by an effective barrier and have been so separated, apparently, for at least 10000 years.

Differences in morphology and in banding were analyzed. While significant differences were observed in several species, none could be discerned in *Helix (Cryptomphalus) aspersa.* The authors discuss the results and causes of the differences and conclude that possibly the *"effet du fondateur"* coupled with the isolation of the populations may explain the differences. On the other hand, there seems to be no possible explanation for the extreme intrapopulational variation in banding in *Helicella itala.*

R. Stohler

Una nueva especie de *Doto* del Norte de Espana

by J. A. Ortea. pp. 389-392; 1 page figs. Revista de la Facultad de Ciencias, Universidad de Oviedo. N. S. "Volumen Extraordinario" 1978

Doto arteoi is described as new with Artedo as the type locality. The species was associated with the hydroid *Laomedea.*

R. Stohler

The Acknowledgment section was inadvertently omitted from the article on the family Lepidochitonidae by Antonio J. Ferreira. We enclose a supplementary page with the missing part.

ACKNOWLEDGMENTS

For the loan of types and other specimens in their charge, I wish to express my appreciation to Dr. Peter U. Rodda and Dr. Welton L. Lee, California Academy of Sciences, San Francisco; Dr. James H. McLean and Gale Sphon, Natural History Museum, Los Angeles; Dr. Hans Bertsch, Natural History Museum, San Diego; Dr. LouElla Saul, University of California, Los Angeles; Dr. Joseph Rosewater, National Museum of Natural History, Washington, D.C.; Dr. Robert Robertson and Melanie Miller, The Academy of Natural Sciences, Philadelphia; Dr. John S. Pearse, David Lindberg, and Douglas Eernisse, University of California, Santa Cruz; Dr. D. Idler and Gordon Chaisson, Memorial University of Newfoundland, St. John's, Newfoundland; Dr. Ian McTaggart Cowan, University of British Columbia, Vancouver; Aileen Blake, Mollusca Section, British Museum (Natural History); Dr. David Heppell, Royal Scottish Museum, Edinburgh; D. J. Waterman, The Crescent Museums, Scarborough Borough Council, Yorkshire; Dr. B. Sirenko, Zoological Institute, Academy of Sciences USSR, Leningrad; Dr. Rafael Contreras Rengifo, Universidad del Valle, Cali, Colombia; Dr. Jørgen Knudsen, Zoologisk Museum, Copenhagen; Dr. R. Kilias, Zoologisches Museum, Berlin, DDR; Piet Kaas, Rijswijk, Netherlands; Richard A. Van Belle, Sint-Niklaas, Belgium; Col. George A. Hanselman, San Diego, California; William Old, Jr., American Museum of Natural History, New York; and Dr. Kenneth J. Boss, Museum of Comparative Zoology, Cambridge, Massachusetts.

For valuable assistance in several phases of this work, thanks are due to Dr. Robert Melnikoff and the late Dr. Paul O. Weiss, San Jose, California; and to Dustin D. Chivers, Dalene Drake, and Chet Chaffee, California Academy of Sciences.

Drawings of radulae and girdle elements are credited to Barbara Weitbrecht, California Academy of Sciences, who played an important part, also, in several other aspects of this study.

I am particularly grateful to Dr. Barry Roth and Dr. Daphne F. Dunn, California Academy of Sciences, for their ever attentive interest, advice, and critical readings of the manuscript.

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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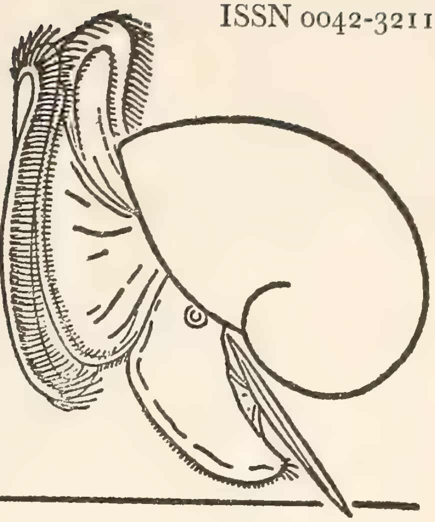

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Contents — *Continued*

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

The Eastern Pacific Donacidae

BY

EUGENE COAN

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Golden Gate Park, San Francisco, California 94118

(7 Plates)

As I prepared my discussion of the two northwest American species of *Donax* (Coan, 1973b), I became aware that the nomenclature of the tropical eastern Pacific species was in a confused state and deserved critical attention. After examining the available type material of these species, as well as several large collections, I am now prepared to offer a revision of the family. I have also included information about the two species that occur in California.

The first two global reviews of the Donacidae were those of Reeve (1854-1855) and Sowerby (1866). Tryon (1869) gave a listing of the species, and Römer (1869a) treated the species of *Iphigenia.* Küster & Römer (1841-1870) also monographed the family, with all of the text issued by the latter (Römer, 1869b-1870). Finally, Bertin (1881) monographed the family. Significant treatments of the tropical eastern Pacific species were those of Hertlein & Strong (1949), Keen (1958), Olsson (1961), and Keen (1971). A list of the species occurring in Peru was published by Peña (1971). A review of the western Atlantic species of *Donax* was prepared by Morrison (1971).

It is important that such common and ecologically significant taxa as the Donacidae be brought up to date taxonomically. Otherwise, a great deal of confusion can occur in ecological and biogeographic studies. The errors in such studies cited in the discussions below also serve to show how important it is to retain voucher specimens in major institutions.

CONVENTIONS AND ABBREVIATIONS

In the following treatment, the correct name is followed by a synonymy, information on type specimens and localities, a description, notes on distribution, and, if necessary, an additional discussion.

The synonymies include all major accounts about the species, but not minor mentions in the literature. The entries are arranged in chronological order under each species-name, with changes in generic allocation and other notes provided in brackets.

The following are the abbreviations of institutions used in the text:

AMNH	– American Museum of Natural History
ANSP	– Academy of Natural Sciences of Philadelphia
BM(NH)	– British Museum (Natural History)
CAS	– California Academy of Sciences
LACM	– Los Angeles County Museum of Natural History
MCZ	– Museum of Comparative Zoology, Harvard University
MNHN	– Muséum National d'Histoire Naturelle, Paris
SBMNH	– Santa Barbara Museum of Natural History
SDNHM	– San Diego Natural History Museum
USNM	– United States National Museum of Natural History

The following are the other abbreviations used in the text:

auctt.	– of authors
Co.	– County
Coll.	– Collection
ex...MS	– from the manuscript of...
fig(s).	– figure(s)
h	– height (maximum ventral-dorsal dimension perpendicular to maximum length)
in litt.	– in correspondence
km	– kilometer(s)
l	– length (maximum anterior-posterior length)
M	– Monotypy
m	– meter(s)
mm	– millimeter(s)
Mus.	– Museum
non	– not of
OD	– Original Designation
pair	– the two valves of one individual
plt(s).	– plate(s)
Prov.	– Province
SD	– Subsequent Designation
sd	– standard deviation (based on measurements of 10 or more randomly selected adult specimens)
th	– thickness (maximum thickness of closed, paired valves)
var.	– variety
= ...	– junior synonym of ...

The term "**lectotype** herein" means that the lectotype is designated in this paper.

Donacidae Fleming, 1828

There are two genera in the Donacidae of the eastern Pacific—*Donax* and *Iphigenia.* (Some authors have recognized *Amphichaena* as a separate genus, but I rank it here as a subgenus of *Donax.*) The large shells of *Iphigenia* lack the radial structure and sculpture of *Donax. Iphigenia* also has scarcely evident lateral teeth, whereas *Donax* has prominent laterals.

For a listing of the genera of the Donacidae, see Keen (1969).

Donax Linnaeus, 1758

[Type species: *Donax rugosus* Linnaeus, 1758; by SD of Schumacher, 1817]

Radial sculpture and structure present, sometimes evident only as marginal crenulations; one or two lateral teeth prominent. All species marine.

In my 1973 paper, I gave a brief bibliography of papers on the functional morphology of *Donax.* In addition to those cited there, relevant works include Turner & Belding (1957), Wade (1967a,b; 1969), Penchaszadeh & Olivier (1975), and Ansell (1981).

Subdivision of *Donax* into meaningful subgenera is a task that remains for someone willing to make a study of all of the world's species. The roster of named subgenera is surprisingly brief, and there are some eastern Pacific species that have no convenient subgeneric homes. The naming of new subgeneric units must also await a global review.

As explained by Keen (1971: 236), the word "donax" in Latin is a masculine noun, which determines its usage as a scientific name. Thus, species-names in *Donax* that are adjectives must have masculine endings. Unfortunately, many early authors considered "donax" to be feminine. Here, the correct adjectival terminations are used, following the instructions of Article 30 (as revised in 1972) of the "International Code of Zoological Nomenclature." In the synonymies, the original, incorrect spellings are given in brackets. Thus, *Donax "contusa"* becomes *D. contusus.*

Some authors assumed that the masculine equivalent of *-fera* was *-ferus,* whereas it is simply *-fer.* For example, Olsson's (1961) usage of *Donax dentiferus* should have been *D. dentifer.*

Finally, some species-names are nouns in apposition and do not change with the gender of the generic name. For this reason, *Donax navicula* and *D. scalpellum* are correct.

A Key to the Eastern Pacific Species of *Donax*

(1a) Rib interspaces with fine punctations (over all or part of shell) 2
(1b) Punctations not present 8
(2a) Shell very short (l/h = 1.3); sculpture low . . . . *D. obesus*
(2b) Shell not so short (l/h = 1.4-1.9) (*D. ecuadorianus,* the next shortest species—1.4— has heavy sculpture) 3
(3a) Shell elongate (l/h = 2.0) and generally flat (th/h = 0.59), though variable in shape . . *D. culter*
(3b) Shell not so elongate (l/h = 1.4-1.5), more inflated (th/h = 0.61-0.74) 4
(4a) Sculpture rugose . . . . *D. ecuadorianus*
(4b) Sculpture subdued 5
(5a) Pattern of punctations dipping toward ventral margin near anterior end . . . . . *D. obesulus* (part)
(5b) Punctations regularly deployed in interspaces . . 6
(6a) Punctations present near posterior end . . . . *D. punctatostriatus*
(6b) Punctations replaced by fine concentric lines near posterior end 7
(7a) Less inflated (th/h = 0.67); sculpture prominent to ventral margin; Mexico & Central America . . . . *D. caelatus caelatus*
(7b) More inflated (th/h = 0.73); sculpture obsolete near ventral margin; South America . . . . *D. caelatus rothi*

Explanation of Figures *1* to *5*

Figures *1* to *2*: *Donax (Chion) punctatostriatus* Hanley. Figure *1*: lectotype (herein) of *D. punctatostriatus* Hanley, length 35.5 mm. Figure *2*: lectotype (herein) of *D. sowerbyi* Bertin, length 23.6 mm

Figure *3*: *D. (Chion) caelatus caelatus* Carpenter, lectotype (herein), length 35.0 mm

Figures *4* to *5*: *D. (Chion) caelatus rothi* Coan, new subspecies. Figure *4*: holotype, length 21.5 mm. Figure *5*: a paratype, length 19.8 mm

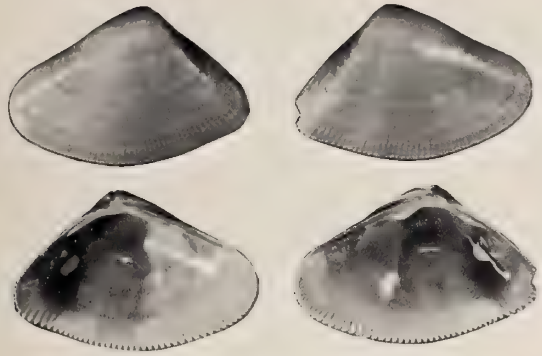


Figure *1*

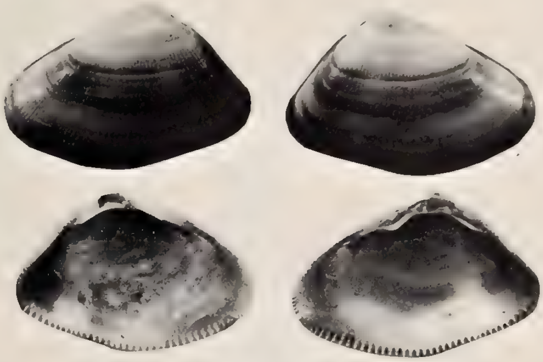
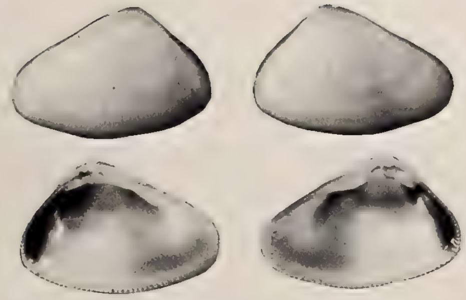


Figure *2*


Figure *3*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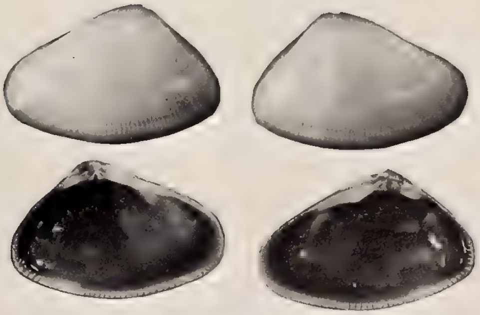
Figure *5*

(8a) Shell with a sharp carina or ridge setting off posterior slope 9
(8b) No such carina or ridge present 10
(9a) Shell very elongate (l/h = 2.3) . . . . . . *D. transversus*
(9b) Shell not so elongate (l/h = 1.7) . . . . *D. carinatus*
(10a) Shell elongate (l/h = 1.9-2.6) 11
(10b) Shell not elongate (l/h = 1.3-1.7) 13
(11a) Both lateral hinge teeth evident; well separated, equidistant from cardinals 12
(11b) Posterior lateral tooth scarcely evident; anterior lateral very close to cardinals . . . . *D. kindermanni*
(12a) Ventral edge flexed; periostracum smooth but not shiny; shorter (l/h = 1.9) . . . . . *D. californicus*
(12b) Ventral edge not flexed; periostracum very shiny; longer (l/h = 2.3) . . . . *D. gracilis*
(13a) Shell high (l/h = 1.3) 14
(13b) Shell elongate (l/h = 1.5-1.7) 15
(14a) Shell thin; sculpture fine; laterals thin, elongate, laterally directed . . . . *D. dentifer*
(14b) Shell thick; sculpture heavy; laterals thick, short, more ventrally directed . . . . *D. asper*
(15a) Shell relatively smooth 16
(15b) Shell with conspicuous radial sculpture . . *D. assimilis*
(16a) Shell elongate (l/h = 1.7); flat (th/h = 0.60) . . . . . . *D. marincovichi*
(16b) Shell shorter (l/h = 1.5); inflated (th/h = 0.72-0.74) 17
(17a) Cardinal teeth of left valve of equal size; anterior lateral more distant, elongate; California and Baja California . . . . *D. gouldii*
(17b) Posterior cardinal of left valve smaller; laterals equidistant; South America . . . *D. obesulus* (those lacking pits)

(Chion) Scopoli, 1777

[**Type species:** *Donax denticulatus* Linnaeus, 1758; by M]

Relatively thick-shelled; interspaces between radial ribs with punctations or concentric striations. The valves close tightly; periostracum not very adherent. The pallial sinus reaches anteriorly past the beaks.

The left valve has a large anterior cardinal, a small posterior cardinal, and a conspicuous lateral on each side. The right valve has a large posterior cardinal and a small, thin anterior cardinal; there are large grooves for the laterals of the left valve, and the ventral edges of these grooves (here called "submarginal ridges") are often swollen into lateral teeth.

Most eastern Pacific species belong to this subgenus, the type species of which is from the Caribbean. The habitat, behavior, and anatomy of *D. denticulatus* have been discussed by Wade (1967a, 1969) and by Trueman (1971).

Donax (Chion) punctatostriatus Hanley, 1843

(Figures *1, 2*)

Donax punctatostriatus Hanley, 1843
Hanley, 1843a-1844: 84-85; 9 (plt. expl.); plt. 14, fig. 24 [as *D. "punctato-striata"*]
Hanley, 1843b: 5
Reeve, 1854: plt. 3, figs. 16a, b
Carpenter, 1857b: 232, 241, 246, 285, 304
Carpenter, 1857c: 44-46, 548
Carpenter, 1864b: 537, 541, 665 [1872: 23, 27, 151]
Sowerby, 1866: 210; plt. 2 [= 281], figs. 49, 50
Tryon, 1869: 113 [as = *D. radiatus* Valenciennes]
Römer, 1870: 57-59; 119 (plt. expl.); plt. 10, figs. 4-10
Bertin, 1881: 95
Hertlein & Strong, 1949: 255-256; 258 (plt. expl.); plt. 1, fig. 17
Keen, 1958: 186, 187; fig. 455
Olsson, 1961: 341-342; 534 (plt. expl.); plt. 61, fig. 6 [Olsson's figs. 6a & 6b are of *D. caelatus*]
Keen, 1971: 239, 241; fig. 598
Donax punctostriatus, punctatoradiatus, punctatostriatis, auctt., spelling errors
Donax sowerbyi Bertin, 1881
Bertin, 1881: 85; plt. 4, figs. 2a-c
Keen, 1958: 184 [as = *D. assimilis*]
Keen, 1971: 237 [as = *D. panamensis*]

Type Material & Localities:

D. punctatostriatus—BM(NH) 1912.6.18.27, **lectotype** herein, pair; length, 35.5 mm; height, 23.0 mm; thickness, 13.9 mm (Figure *1*).

"China" (Hanley, 1843a); not certain (Hanley, 1843b); Mazatlán, Sinaloa, Mexico (23°12′ N; 106°24′ W) (Reeve, 1854).

D. sowerbyi—MNHN, pair, **lectotype** herein; length, 23.6 mm; height, 15.5 mm; thickness, 10.8 mm (Figure *2*).

A second specimen in the MNHN is a **paralectotype**. A specimen illustrated by Sowerby (1866: 307-308; plt. 1, fig. 21) as *D. assimilis* and cited by Bertin (1881) would also be a paralectotype; this figure appears to be of a *D. dentifer*. The MNHN specimens were from an unknown locality and were purchased from Sowerby, but it seems most appropriate to restrict the concept of the taxon to the material Bertin actually had in hand.

Description: Medium-sized for genus, to 48 mm in length CAS 024441; "Lower California," Mexico); rhomboidal to elongate-rhomboidal, length 1.5 times height (sd, ±0.1); somewhat inflated, thickness 0.61 times height (sd, ±0.03); anterior end longer, slightly produced; posterior end slightly truncate ventrally; posterior slope often set off by an angle (more rounded in some); beaks not conspicuously inflated; external ligament short; ventral end flexed a little anterior of midline.

Surface relatively smooth, with incised striae; striae with radial punctations, which are sometimes larger and more elongate toward ends of shell; traces of dark periostracum present at shell margins.

Left valve with lateral teeth close to cardinals, the posterior a little more distant. Right valve with sockets for laterals, their ventral margins (submarginal ridges) swollen into teeth.

White to tan externally, sometimes with radial rays (especially in material from the Pacific Coast of Baja California). Internally purplish, often darker toward posterior end.

Distribution & Habitat: Isla Cedros (about 28°3′ N; 115° 11′ W) (USNM 13660; ANSP 52963); Laguna San Ignacio (26°45′ N; 113° 15′ W) (USNM 105618), Baja California Sur, throughout the Gulf of California, to Manzanillo, Colima (19°3′ N; 104°20′ W) (CAS 024813), Mexico; intertidal area to about 5 m.

Records from farther north, including California (Dall, 1916, 1921), are not confirmed by any material in museum collections. I doubt that the species is established north of Laguna San Ignacio; the more northerly records probably represent stray settlings.

Records from farther south in Mexico and from Central America are based on *Donax caelatus.* Records from South America are based either on *D. obesulus* or on *D. caelatus rothi.*

I have seen 189 lots.

Donax (Chion) caelatus caelatus Carpenter, 1857

(Figure *3*)

Donax punctatostriatus "var." caelatus Carpenter, 1857
Carpenter, 1857b: 246 [*nomen nudum*]
Carpenter, 1857c: 46-47, 548 [as a "var." of *D. punctatostriatus*]
Bertin, 1881: 101
Keen, 1958: 621 [as = *D. punctatostriatus*]
Olsson, 1961: 342
Palmer, 1963: 312
Keen, 1968: 399; 402 (plt. expl.); plt. 56, fig. 34 [as = *D. punctatostriatus*]
Keen, 1971: 239 [as = *D. punctatostriatus*]
Donax punctatostriatus, auctt., non Hanley, 1843
Olsson, 1961: 534 (plt. expl.); plt. 61, figs. 6a, b

Type Material & Locality:

D. punctatostriatus caelatus—BM(NH) Mazatlán Coll. 1857.6.4.-168, a closed pair, **lectotype** herein; length, 35.0 mm; height, 22.8 mm; thickness, 15.2 mm (Figure *3*).
Same lot, 2 paralectotypes; tablet 168*, 2 more paralectotypes. Mazatlán, Sinaloa, Mexico (23°12′ N; 106°25′ W); F. Reigen; 1848-1850.

Description: Medium-sized for genus, to 49 mm in length (CAS 024812; Manzanillo, Mexico), smaller towards Central America; elongate-rhomboidal, length 1.5 times height (sd, ±0.1); somewhat inflated, thickness 0.67 times height (sd, ±0.04); anterior end longer, more so than in *Donax punctatostriatus,* slightly produced; posterior end somewhat truncate ventrally; angle setting off posterior slope sharper than in *D. punctatostriatus;* beaks somewhat inflated; ventral edge flexed a little anterior to beaks, less so than in *D. punctatostriatus.*

Surface relatively smooth, ribs more raised than in *D. punctatostriatus;* ribs becoming obsolete toward anterior end, narrower with wider interspaces posteriorly; interspaces (radial striae) punctate; punctations larger toward anterior end, replaced by fine concentric lineations on posterior slope. Traces of periostracum sometimes present at shell margin.

Hinge as in *D. punctatostriatus.*

More brightly colored externally than *D. punctatostriatus,* with a range of color—from dark tan through purple to red—often in radial bands; internally dark purple.

Distribution & Habitat: In the Gulf of California from Bahía de las Ánimas, Baja California North (28°50′ N; 113°20′ W) (LACM 67745), and Guaymas, Sonora (27°55′ N; 110°54′ W) (LACM 20147), Mexico, to Golfito, Costa Rica (8°37′ N; 83° 10′ W) (ANSP 198973); intertidal area to 3 m; sand.

Explanation of Figures *6* to *11*

Figures *6* to *9: Donax (Chion) obesulus* Reeve. Figure *6:* **lectotype** (herein) of *D. obesulus* Reeve, length 20.3 mm. Figure *7:* holotype of *D. peruvianus* Deshayes, length 32.0 mm. Figure *8:* **lectotype** (herein) of *D. radiatus* Valenciennes, length 30.0 mm. Figure *9:* holotype of *D. mancorensis* Olsson, length 25.3 mm

Figure *10: Donax (Chion) ecuadorianus* Olsson, holotype, length 18.6 mm

Figure *11: D. (Chion) obesus* Orbigny, holotype, length 11.3 mm

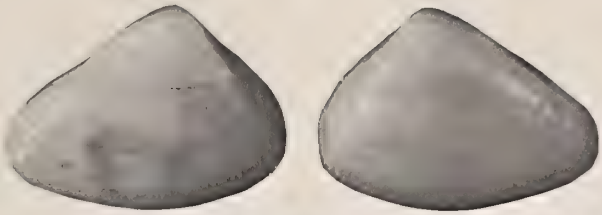

Figure *6*

Figure *7*

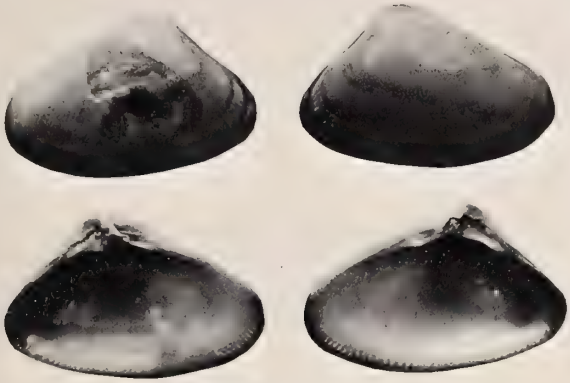

Figure *8*

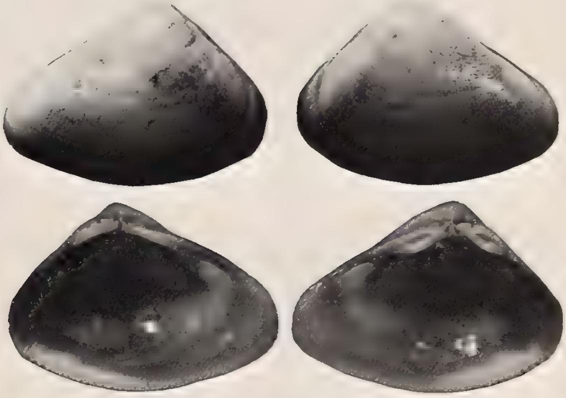

Figure *9*

Figure *10*

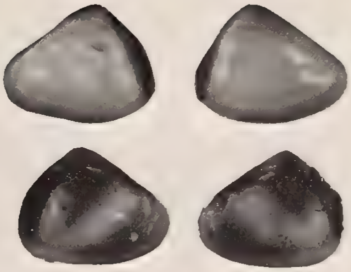

Figure *11*

Specimens from the southern end of the distribution are much smaller in size than those from central Mexico.

I have seen 90 lots.

Discussion: Of the various eastern Pacific species in the subgenus *Chion,* this one is closest to the Caribbean type species, *Donax (C.) denticulatus* Linnaeus, 1758, from which it may be separated by its finer ribs, less angulate posterior slope, more prominent beaks, and the lack of the oblique sculpture characteristic of the postero-dorsal slope of *D. (C.) denticulatus* (though some oblique lines are present in specimens of *D. caelatus* from Costa Rica).

Donax (Chion) caelatus ***rothi*** Coan, new subspecies

(Figures *4, 5*)

Type Material & Locality:

ANSP 353596, holotype, pair; length, 21.5mm; height, 13.1 mm; thickness 10.0mm (Figure *4*).

ANSP 353597, 6 paratypes (Figure *5*, a paratype).

[Punta] Malpelo, Tumbez Prov., Peru (about 3°30′ S; 80°31′ W); H. A. Pilsbry.

Description & Differential Diagnosis: Small for genus, to 22mm in length (USNM 517695; Ecuador); more ovate than *D. c. caelatus,* length 1.5 times height (sd, ±0.1); inflated, more so than *D. c. caelatus,* thickness 0.74 times height (sd, ±0.02); anterior end longer, slightly produced (less so than *D. c. caelatus);* posterior end rounded, less truncate than *D. c. caelatus;* ventral edge more rounded, without the flexure of the nominal subspecies; angle setting off posterior slope less evident.

Surface similar to that of the nominal subspecies, but sculpture more subdued, becoming almost obsolete toward central slope and near ventral margin. Periostracum as in nominal subspecies.

Hinge and color pattern as in the nominal subspecies.

Distribution & Habitat: Canoa, Manabi Prov., Ecuador (0°27′ S; 80°44′ W) (CAS 024805), to Punta Sal, Talara, Piura Prov., Peru (about 4°34′ S; 81°17′ W) (LACM 64544); intertidal area to 3m; no bottom types have been recorded. Presumably the subspecies occurs chiefly in the intertidal zone on open sandy beaches.

There is a single valve in the USNM supposedly from Salaverry, La Libertad Prov., Peru (USNM 792352), but it was encountered among a set of large, numbered valves of *Donax obesulus,* and I strongly suspect that this one valve has been mixed into the lot in recent years. Other than this questionable specimen, I have seen 16 lots.

Discussion: This subspecies was present among material referred by Olsson to *Donax mancorensis,* and it also accounts for some of the South American records of *D. punctatostriatus* (as Cauquoin, 1969: 582-583). It may be distinguished from punctate specimens of *D. obesulus,* with which it occurs throughout its distribution, by its radially deployed punctations and its fine concentric lineations between the radial ribs on the dorsal part of the posterior slope.

This subspecies is separated from the most southerly known occurrence of the nominate species by some 800 miles. It is named for Dr. Barry Roth of the California Academy of Sciences.

Referred Material:

CAS 024805—Canoa, Manabi Prov., Ecuador
CAS 024810—Manta, Manabi Prov., Ecuador
USNM 517695—between Manta and Manglaralto, Guayas Prov., Ecuador
CAS 024811—Manglaralto, Guayas Prov., Ecuador
MNHN—Santa Elena Peninsula, Guayas Prov., Ecuador
LACM 71-188—Punto Carnero, Guayas Prov., Ecuador
LACM 70-13—Playas, Guayas Prov., Ecuador
MCZ 233628—same locality
Coll. of Carol Skoglund of Phoenix, Arizona—same locality
ANSP 353596 & 353597—Punta Malpelo, Tumbez Prov., Peru —Type Lot
LACM 72-80—Caleta La Cruz, Tumbez Prov., Peru
ANSP 353534—same locality
ANSP 353435—same locality
ANSP 353431—Mancora, Piura Prov., Peru
CAS 024806—Punta Oreganos "Chica," Piura Prov., Peru
LACM 64544—Punta Sal, Talara, Piura Prov., Peru

Donax (Chion) obesulus Reeve, 1854

(Figures *6, 7, 8, 9*)

Donax obesulus Reeve, 1854, *ex* Deshayes MS
Reeve, 1854; plt. 5, fig. 30 [as *"obesula* Deshayes"]
Deshayes, 1855: 352 [as *"obesula"*]
Sowerby, 1866: 308; plt. 1 [= 280], fig. 15
Bertin, 1881: 101
Dall, 1909: 273
Smith, 1944: 63, fig. 825
Hertlein & Strong, 1949: 255
Keen, 1958: 186, 187; fig. 452
Olsson, 1961: 339 [as = *D. rostratus*]
Keen, 1971: 237, 238; fig. 594 [lower figure only]

Donax peruvianus Deshayes, 1855
Deshayes, 1855: 350-351 [as *"peruviana"*]
Römer, 1870: 55-56 [in part; the figures—plt. 9, figs. 18-20—seem to depict specimens of *D. marincovichi*]
Bertin, 1881: 104
Olsson, 1961: 343; 533 (plt. expl.); plt. 60, figs. 2-2c
Keen, 1971: 238, 239; fig. 597

Donax radiatus Valenciennes, 1827
  Valenciennes, 1827: 221-222; 224 (plt. expl.); plt. 50, figs. 3a-c, 4 [as *"radiata"*]
  Orbigny, 1845: 541
  Römer, 1870: 58-59 [as a variety of *D. punctatostriatus*]
  Bertin, 1881: 95-96; plt. 3, figs. 1a, b
  [*non D. radiatus* Gmelin, 1791: 3266—as *D. "radiata"*; an Asian taxon]
Donax aricanus Dall, 1909, replacement name for *D. radiatus* Valenciennes, *non* Gmelin
  Dall, 1909: 272 [as *D. "aricana"*]
Donax mancorensis Olsson, 1961
  Olsson, 1961: 340; 534 (plt. expl.); plt. 61, figs. 3-3b
  Keen, 1971: 235, 237; fig. 592
Donax punctatostriatus Hanley, *auctt.*, *non* Hanley, 1843

Type Material & Localities:

D. obesulus—BM(NH) 198218, **lectotype** herein, pair; length, 20.3 mm; height, 14.4 mm; thickness, 10.1 mm (Figure *6*). There are 3 probable **paralectotypes** in BM(NH) 198219.
Peru (Reeve, 1854). The sculpture is such that one may assume the specimen came from the northern coast of Peru, probably from the Gulf of Guayaquil, Tumbez Prov. (about 3°30′ S; 80°30′ W).

D. peruvianus—BM(NH) 1966.544, holotype, right valve; length, 32.0 mm; height, 20.0 mm; thickness, 6.8 mm (Figure *7*).
Peru (Deshayes, 1855); "graves [? Indian kitchen middens] in Peru; I. Fryer" (label).

D. radiatus Valenciennes (and *D. aricanus*)—MNHN, the larger of two pairs, **lectotype** herein; length, 30.0 mm; height, 18.5 mm; thickness, 14.6 mm (Figure *8*).
The second pair, a **paralectotype**, measures 29.2 mm in length, 18.4 mm in height, and 12.5 mm in thickness.
"Warm shores of the Pacific Coast of America." The specimens were probably obtained by Alexander von Humboldt and A. J. A. Bonpland in the area of Callao, Lima Prov., Peru, in November 1802 (12°3′ S; 77°10′ W) (concerning Humboldt's travels, see de Terra, 1955).

D. mancorensis—ANSP 218910, holotype, pair; length, 25.3 mm; height, 17.9 mm; thickness, 13.2 mm (Figure *9*).
Zorritos, Tumbez Prov., Peru (3°40′ S; 80°40′ W).

Description: Medium-sized for genus, to 38 mm in length (USNM 517694; Ecuador, between Manta and Manglaralto); elongate-rhomboidal, length 1.5 times height (sd, ±0.1); inflated, thickness 0.74 times height (sd, ±0.03); anterior end longer, produced; posterior end somewhat produced, rounded; posterior slope only slightly set off by an angle; beaks inflated; ligament short; ventral margin rounded, with only a slight flexure a little anterior to beaks.

Surface smooth, shiny; radial striae present but not very incised, fading out toward anterior slope, more crowded toward posterior slope; in most, with a few irregularly scattered punctations along radial striae on younger portion of shell in a radial zone near anterior end. (Occasional specimens lack punctations.) In specimens from the Gulf of Guayaquil area, the punctations are much more prevalent, forming a pattern that dips toward the ventral margin at anterior end, as in the type specimens of *D. obesulus* and *Donax mancorensis.* Periostracum evident only at shell margin.

Left valve with laterals close to cardinals, the anterior a little more distant; dorsal margin deflected above posterior lateral. Right valve with grooves for laterals of left valve, the submarginal ridges swollen into teeth.

White to tan externally, often with darker radial rays; internally flushed with purple, especially at umbones.

Distribution & Habitat: Canoa, Manabi Prov., Ecuador (0°27′ S; 80°7′ W) (CAS 024814), to La Rinconada, northwest end of Bahía Moreno, Antofagasta Prov., Chile (23°28′ S; 70°31′ W) (LACM 75-16). The only habitat recorded on labels is flat, sand beaches. I have seen 42 lots.

Discussion: It is unfortunate that the type specimen of *Donax obesulus* had not recently been studied, for it is virtually identical to the holotype of *D. mancorensis,* and both probably came from the Gulf of Guayaquil area—between Playas, Guayas Prov., Ecuador, and Talara, Piura Prov., Peru. It might be possible to restrict the name *D. obesulus* to populations in this area and to save the name *D. peruvianus* at the subspecific level, but two factors militate against this: first, material from still further north lacks the *D. obesulus*—pattern of punctations (as USNM 517694); secondly, some specimens from considerably further south have this punctate pattern (as USNM 368497, from Salaverry, La Libertad Prov., Peru). The punctate form may represent an ecological variant in calmer, warmer

Explanation of Figures *12* to *16*

Figures *12* to *16: Donax (Chion) culter* Hanley. Figure *12:* **lectotype** (herein) of *D. culter,* length 33.7 mm. Figure *13:* **lectotype** (herein) of *D. contusus* Reeve, length 33.4 mm. Figure *14:* **lectotype** (herein) of *D. conradi* Reeve, length 38.1 mm. Figure *15:* **lectotype** (herein) of *D. bitinctus* Reeve, length 27.8 mm. Figure *16:* two specimens from Petatlán, Guerrero, Mexico; CAS 024815, lengths 34.3 & 35.5 mm


Figure *12*

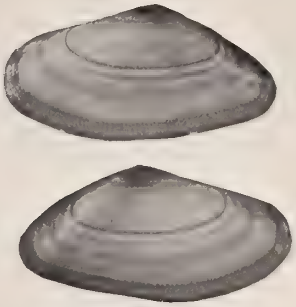
Figure *13*

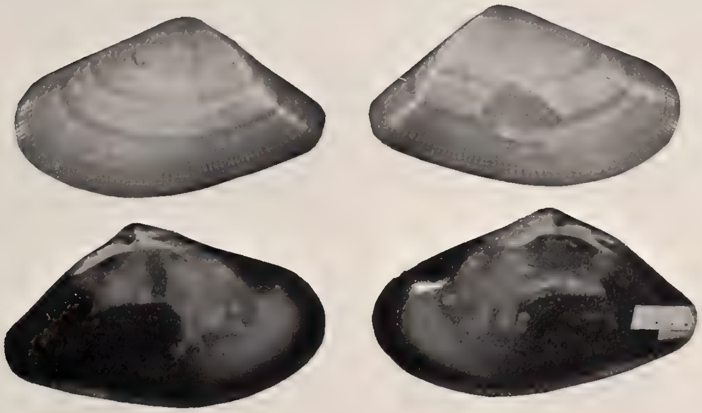
Figure *14*

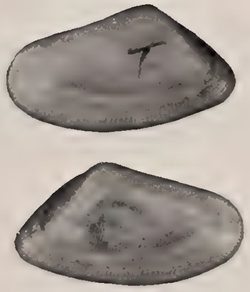
Figure *15*


Figure *16*

water. This sculptural pattern also suggests a phylogenetic relationship to *D. ecuadorianus,* which has the same ventrally dipping punctations (along with other features that make it unique).

The name *Donax obesulus* has been misapplied to *D. obesus* by Römer (1870) (see under the latter).

Donax (Chion) ecuadorianus Olsson, 1961

(Figure *10*)

Donax ecuadorianus Olsson, 1961
Olsson, 1961: 340-341; 534 (plt. expl.); plt. 61, figs. 2-2b
Keen, 1971: 235, 236-237; fig. 589

Type Material & Locality:

ANSP 218909, holotype, pair; length, 18.6mm; height, 13.0 mm; thickness, 9.0mm (Figure *10*).

Canoa, Bahía de Caráquez, Manabi Prov., Ecuador (0°27′N; 80°27′W).

Description: Medium-sized for genus, to 22mm in length (USNM 792347; Ecuador, between Manta and Manglaralto); rhomboidal-elongate, length 1.4 times height (sd, ±0.1); inflated, thickness 0.73 times height (sd, ±0.03); anterior end longer, produced, almost pointed; posterior slope set off by an angle, somewhat truncate ventrally; beaks produced; external ligament short; ventral edge flexed a little anterior to beaks.

Surface with heavy radial ribs that become lower toward anterior slope and closer together on posterior slope; concentric ribs also present, on posterior slope almost equal in strength to radial ribs, forming nodes on the latter; ventral to beaks concentric ribs appearing as lineations between radial ribs as well as roughening the latter; toward anterior end concentric ribs wider, forming broad bands that override radial rays and dip ventrally; pits present at intersections of radial and concentric sculpture on anterior slope.

Hinge as in *Donax punctatostriatus.*

White to tan externally, often with a bluish flush on beaks, sometimes with darker concentric bands; internally purple, but sometimes white.

Distribution & Habitat: Playa el Tamarindo, near Punta Ampala, Gulf of Fonseca, El Salvador (about 13°09′N; 87°52′W) (CAS 024445), to between Manta, Manabi Prov., and Manglaralto, Guayas Prov., Ecuador (about 1°30′S; 80°50′W) (USNM 792347); intertidal area to 1m; sand. I have seen 21 lots.

This species may occur further northwest in El Salvador. The specimens reported by Zilch (1954: 86) and Schuster-Dieterichs (1956: 31) from El Salvador as *"D. gouldii"* seem instead to be juveniles of this species. They came from Amate Campo (13°25′N; 89°10′W) (Senckenberg Mus. 254447) and La Pita (13°13′N; 88°50′W) (Senckenberg Mus. 254448). It would be best to await adult material to verify that the species is established at these stations.

Donax (Chion) obesus Orbigny, 1845

(Figure *11*)

Donax obesus Orbigny, 1845
Orbigny, 1845: 541; plt. 81, figs. 28-30
Reeve, 1854: plt. 7, fig. 49
Sowerby, 1866: 210; plt. 2 [= 281]; figs. 42, 43
Tryon, 1869: 109
Römer, 1870: 71-72; 120 (plt. expl.); plt. 12, figs. 11-13
Bertin, 1881: 96-97
Dall, 1909: 273
Hertlein & Strong, 1949: 254-255; 258 (plt. expl.); plt. 1, fig. 7
Keen, 1958: 186, 187; fig. 453
Olsson, 1961: 344-345; 534, 558 (plt. expls.); plt. 61, fig. 5; plt. 85, fig. 3
Keen, 1966c: 7
Keen, 1971: 237, 238; fig. 595
Donax obesulus Reeve, *auctt., non* Reeve, 1854
Römer, 1870: 72-73; 120 (plt. expl.); plt. 12, figs. 14-16

Type Material & Locality:

BM(NH) 1854.12.4.702, holotype, pair; length, 11.3mm; height, 9.2mm; thickness, 7.9mm (Figure *11*).

Paita, Piura Prov., Peru (5°5′S; 81°7′W); M. Fontaine.

Description: Small for genus, to 15.2mm in length (LACM 64547; Barranco, Costa Rica); ovate, length 1.3 times height (sd, ±0.05); inflated, thickness 0.72 times height (sd, ±0.03); anterior end longer; posterior end rounded, with only a hint of ventral truncation; posterior slope set off by a very rounded angle.

Surface with flat radial ribs on anterior end and central slope, with narrow, pitted, incised striae between them; radial ribs obsolete on ends of shell, narrower and denser on posterior slope. Periostracum not evident.

Hinge as in *Donax punctatostriatus.*

Externally white, tan, brown, or olive; internally bluish-purple.

Distribution & Habitat: ?Zihuatanejo, Guerrero, Mexico (17°38′N; 101°34′W) (AMNH 198975), but according to Dr. William K. Emerson (*in litt.,* 16 Oct. 1981), there is some chance of mixing in the AMNH's Beebe set of materials from the Templeton-Crocker expedition, so this record must be reconfirmed. Playa el Tamarindo, near Punta Ampala, Gulf of Fonseca, El Salvador (about 13° 9′N; 87°52′W) (CAS 024444), to Canoa, Manabi Prov., Ecuador (0°27′ S; 80°7′ W) (CAS 025753). Peña (1971) has reported this species from Puerto Pizarro, Tumbez Prov., Peru (3°30′ S; 80°25′ W), but I have not seen his material and this is a species that might easily be confused with *D. obesulus* or with *D. caelatus rothi.* It may occur as far south as the type locality of Paita, Piura Prov., Peru (5°5′ S; 81°7′ W), but there are no other records of this uncommon species from that far south. I have seen only 12 lots.

Donax (Chion) culter Hanley, 1845

(Figures *12, 13, 14, 15, 16*)

- *Donax culter* Hanley, 1845
  - Hanley, 1845a: 14
  - Reeve, 1854: plt. 4, fig. 21
  - Carpenter, 1857c: 47-49 [as = *D. conradi*]
  - Sowerby, 1866: 310; plt. 2 [= 281]; figs. 56, 57 [as "var." of *D. californicus, auctt.*]
  - Tryon, 1869: 112
  - Römer, 1870: 59-61; 119 (plt. expl.); plt. 10, figs. 11-16
  - Bertin, 1881: 92-93
  - Keen, 1958: 185; fig. 448
  - Olsson, 1961: 345-346; 532 (plt. expl.); plt. 59, figs. 5-5b
  - Keen, 1971: 235, 236; fig. 587
- *Donax contusus* Reeve, 1854
  - Reeve, 1854: plt. 4, fig. 24 [as *D. "contusa"*]
  - Carpenter, 1857c: 47-49 [as = *D. conradi*]
  - Sowerby, 1866: 210; plt. 2 [= 281]; figs. 53, 55
  - Tryon, 1869: 112
  - Römer, 1870: 59-61 [as = *D. culter*]
  - Bertin, 1881: 92
  - Tomlin, 1926: 52-53
  - Hertlein & Strong, 1949: 258 (plt. expl.); plt. 1, fig. 14
  - Keen, 1958: 184-185; fig. 447
  - Keen, 1971: 235, 236; fig. 586
- *Donax conradi* Reeve, 1854, *ex* Deshayes MS
  - Reeve, 1854: plt. 5, fig. 29 [as "Deshayes"]
  - Deshayes, 1855: 351
  - Carpenter, 1857c: 47-49
  - Sowerby, 1866: 310; plt. 2 [= 281], fig. 51
  - Römer, 1870: 59-61 [as = *D. culter*]
  - Bertin, 1881: 91-92
  - Tomlin, 1926: 52-53 [as = *D. contusus*]
  - Keen, 1958: 184 [as = *D. contusus*]
  - Olsson, 1961: 534 (plt. expl.); plt. 61, figs. 4-4b [not in text]
  - Keen, 1971: 236 [as = *D. contusus*]
- *Donax bitinctus* Reeve, 1855
  - Reeve, 1855: plt. 9, fig. 68 [as *D. "bitincta"*]
  - Tryon, 1869: 112 [as = *D. contusus*]
  - Römer, 1870: 38
  - Tomlin, 1926: 53 [as = *D. contusus*]
  - Keen, 1958: 184 [as = *D. contusus*]
  - Keen, 1971: 236 [as = *D. contusus*]
- *Donax californicus, auctt., non* Conrad, 1837
  - Reeve, 1854: plt. 6, fig. 40
  - Sowerby, 1866: 310; plt. 2 [= 281], fig. 54
  - [*non* Conrad, 1837: 254; plt. 19, fig. 21]

Type Material & Localities:

D. culter—BM(NH) 1966.547, **lectotype** herein, the specimen figured by Reeve, pair; length, 33.7 mm; height, 14.2 mm; thickness, 9.0 mm (Figure *12*).

There are two paralectotypes. Mazatlán, Sinaloa, Mexico (about 23°12′ N; 106°25′ W); H. Cuming.

D. contusus—BM(NH) 198216, **lectotype** herein, the specimen figured by Reeve, pair; length, 33.4 mm; height, 16.5 mm; thickness, 9.6 mm (Figure *13*).

There are no additional specimens in this BM(NH) lot. Mazatlán, Sinaloa, Mexico (about 23°12′ N; 106°25′ W).

D. conradi—BM(NH) 198217 **lectotype** herein, the specimen figured by Reeve, pair; length, 38.1 mm; height, 21.7 mm; thickness, 13.0 mm (Figure *14*).

There are two paralectotypes. Gulf of California, Mexico.

D. bitinctus—BM(NH) 1900.3.19.1, **lectotype** herein, the specimen figured by Reeve, pair; length, 27.8 mm; height, 15.4 mm; thickness, 9.4 mm (Figure *15*).

There are 2 paralectotypes. Locality unknown (Reeve, 1854).

Description: Medium-sized for genus, to 47 mm (CAS 024815; Bahía Petatlán, Guerrero, Mexico); elongate-ovate, length 2.0 times height (sd, ±0.2); flatter than other species of *Chion,* thickness only 0.59 times height (sd, ±0.03); anterior end longer, slightly produced; posterior end pointed, very slightly truncate ventrally; posterior end only a little set off by an angle; beaks not conspicuously inflated; ligament elongate; ventral edge only slightly flexed a little anterior to beaks, much less so than in *Donax punctatostriatus* or *D. caelatus.* Posterior end longer, broader in young specimens and in adults from the southern end of the species' distribution.

Surface relatively smooth, not unlike that in *Donax punctatostriatus,* with incised striae; striae closer together on posterior end, becoming obsolete on anterior end; striae with radial punctations, which are larger towards ends of shell. The deployment of the striae and their punctations differs among specimens to a greater degree than in either *D. punctatostriatus* or *D. caelatus,* with punctations missing on the central slope of some specimens and even the striae missing in this area on others.

Hinge as in other species of *Chion,* except that the posterior lateral of the left valve, the pocket for it in the right valve, and the tooth on the submarginal ridge of the right valve are more distant from cardinals. Additionally, the anterior laterals are closer to the cardinals than in other species, this feature especially pronounced in material from the southern end of the species' distribution.

White to tan externally, often with concentric bluish bands, a characteristic feature; internally purple.

Distribution & Habitat: Mexico from Isla San Ignacio, Sonora (25°25′ N; 108°55′ W) (LACM 109054; AMNH 180-442), and La Paz, Baja California Sur (24° 10′ N; 110° 19′ W) (USNM 34072), to Acapulco, Guerrero (16°51′ N; 99°56′ W) (many lots, including USNM 109348; LACM 64506; CAS 024809). Intertidal area to 2m; sand. I have seen 91 lots.

Ranson (1959: 74) reported *Donax conradi* from the Pleistocene north of Chimbote, Peru. I suspect that this record was based on *D. obesulus*. Records of *D. conradi* from California (Dall, 1916, 1921) are not confirmed by specimens in any collection examined.

Discussion: This is, beyond question, the most variable species of Eastern Pacific *Donax* in terms of proportions and especially outline. Of it, Carpenter (1857c: 47) said, "It is not without the most careful, laborious and often repeated examination of upwards of 1,000 specimens that I have felt compelled to depart from the views of the illustrious Deshayes and the very accurate Hanley, and group together the species above quoted [*D. conradi*, *D. contusus*, *D. californicus* of authors, and *D. culter*]....This creature loves liberty both in form and color....The lines of growth shew that the adult by no means thinks it necessary to preserve the form of early life." Unfortunately, Carpenter chose one of the later-proposed names for the species because he felt that its type specimens better expressed the adult form.

Specimens from the southern end of the distribution of this species tend to have more inflated, more truncate posterior ends than material from farther north. Northern material is not unlike the type specimens of *Donax culter*. Southern specimens, on the other hand, can be very truncate posteriorly (Figure *16*) and sometimes approach the shape of *D. (Amphichaena) kindermanni*, with which it occurs. It may be distinguished from this species by its more sculptured, punctate shells, its shorter posterior end, its somewhat more distant anterior lateral tooth, and its more prominent posterior lateral tooth, these hinge features most easily seen in right valves (see table under *D. kindermanni*). Some southern specimens, while having a shape characteristic of *D. culter* in those latitudes, have concentric sculpture between the radial ribs on the posterior slope that approaches the pattern of *D. (Chion) caelatus*. Future workers may want to give southern specimens a subspecific name, all of the synonyms evidently being based on northern specimens.

The clinal change in this species and the unusual southern material are both topics that are worth further investigation. It is not impossible that one explanation may lie in former or present hybridization among *Donax caelatus*, *D. culter*, and/or *D. kindermanni* in the Acapulco area.

Weisbord (1964) suggested that this species is similar to a new species he described from the Caribbean, *Donax higuerotensis* (pp. 366-368, 542; plt. 53, figs. 1-9). However, his new taxon proved to be a synonym of *D. vellicatus* Reeve, 1855 (Morrison, 1971: 564), which is not closely related to *D. culter*.

Group of *Donax assimilis*

This group of West American species is characterized by having large, high to quadrate shells, the right valve overlapping the left valve at the postero-ventral margin. The shells are thick to thin, and they lack a gape and surface punctations.

Left valve with two cardinals, the posterior often smaller; anterior and posterior laterals present. Right valve with two cardinals, the anterior the smaller; anterior and posterior laterals on sub-marginal ridges.

Donax assimilis Hanley, 1845

(Figures *17*, *18*, *19*)

Donax assimilis Hanley, 1845
Hanley, 1845b: 17
C. B. Adams, 1852a: 501 [1852b: 277]
Reeve, 1854: plt. 2, fig. 10
Carpenter, 1857b: 186, 236, 245, 279, 297, 304
Carpenter, 1857c: 44
Mörch, 1860: 192
Carpenter, 1864a: 366 [1872: 202]
Carpenter, 1864b: 537 [1872: 23]
Sowerby, 1866: 307-308; plt. 1 [= 280], fig. 21
Tryon, 1869: 107
Römer, 1869b-1870: 20-21; 119 (plt. expl.); plt. 4, figs. 13-17
Bertin, 1881: 85
Hertlein & Strong, 1949: 252
Keen, 1958: 184, 185; fig. 444
Olsson, 1961: 339 [as possibly = *D. dentifer*]
Keen, 1971: 236 [as = *D. dentifer*]
Donax panamensis Philippi, 1848
Philippi, 1848: 145
Reeve, 1855: plt. 9, fig. 63
Carpenter, 1857b: 295, 304
Tryon, 1869: 113
Keen, 1958: 184 [as = *D. assimilis*]
Olsson, 1961: 339-340; 532 (plt. expl.); plt. 59, figs. 3, 3a
Keen, 1971: 237, 238; fig. 596
Donax "cayennensis Lamarck," *auctt., non D. caianensis* Lamarck, 1818
Reeve, 1854: plt. 4, figs. 23a, b
Sowerby, 1866: 308; plt. 2 [= 281], figs. 46-48
Martinez y Saez, 1870: 17-18; plt. 4, figs. 6-8
[*non Donax caianensis* Lamarck, 1818: 550]
Donax curtus Sowerby, 1866
Sowerby, 1866: 308; plt 1 [= 280], fig. 20
Tryon, 1869: 108
Bertin, 1881: 85
Olsson, 1961: 338 [as = *D. rostratus*]
Keen, 1971: 237 [as = *D. obesulus*]
Donax reevei Bertin, 1881
Bertin, 1881: 85
Keen, 1958: 184 [as = *D. assimilis*]
Keen, 1971: 237 [as = *D. panamensis*]

Type Material & Localities:

D. assimilis—BM(NH) 198214, **lectotype** herein, the specimen figured by Reeve, pair; length, 41.2mm; height, 28.8mm; thickness, 17.9mm (Figure *17*).
There are 2 **paralectotypes.** [West coast of] Panama.

D. panamensis—BM(NH) 1952.10.30.93, **lectotype** herein, the specimen figured by Reeve, pair; length, 28.2mm; height, 19.1mm; thickness, 11.5mm (Figure *18*).
There were no additional syntypes in the BM(NH), or in either the Humboldt Museum (Kilias, *in litt.*, 27 Aug. 1980) or in the Museo Nacional de Historia Natural in Santiago, Chile (Bahamonde, *in litt.*, 16 April 1981). [West coast of] Panama; E. B. Philippi.

D. curtus—BM(NH) 1874.12.11.399, **lectotype** herein, the specimen figured by Sowerby; pair; length, 23.0mm; height, 17.4mm; thickness, 10.5mm (Figure *19*).
BM(NH) 1879.2.26.224, probable paralectotype.
ANSP 51567, 2 possible paralectotypes.
"Caraccas Bay" [Bahía de Caráquez], Manabi Prov., "W. Columbia" [Ecuador] (0°35′S; 80°25′W).

D. reevei—BM(NH) 198214, holotype, the lectotype of *D. assimilis* (see above) (Figure *17*).
[West coast of] Panama.

Description: Medium-sized for genus, to 44mm (AMNH 78389; Corinto, Nicaragua); ovate, length 1.5 times height (sd, ±0.1); moderately inflated, thickness, 0.61 times height (sd, ±0.03); anterior end longer, rounded; posterior end short, almost straight; posterior end set off by a rounded angle; beaks not especially inflated; ventral margin evenly arcuate.

Flat radial ribs present on central and anterior slopes, fading out at anterior end; ribs raised and more crowded on posterior slope; in some specimens with one or two larger radial ribs positioned about two-thirds of the way from the postero-dorsal margin to the angle setting off posterior slope, forming conspicuous interlocking "teeth" where they end at posterior margin (as in the lectotype of *D. assimilis*). Specimens with these larger ribs are not common, unlike in *D. dentifer* where they are nearly always present. Posterior slope also with concentric sculpture forming a network pattern that fades out anteriorly about under beaks. Periostracum not evident.

Left valve with a large anterior cardinal and a smaller posterior cardinal; an elongate anterior lateral parallels dorsal margin; posterior lateral shorter, closer to cardinals. Right valve with a large posterior cardinal and a very small anterior cardinal; anterior submarginal ridge with a tooth that is parallel to dorsal margin; tooth also present on posterior submarginal ridge.

External color purple, white, or pink; internally with a purple suffusion.

Distribution & Habitat: ?Zihuatanejo, Guerrero, Mexico (17°38′N; 101°34′W) (AMNH 198874) (see cautionary note under *Donax obesus*); Playa el Tamarindo, near Punta Ampala, Gulf of Fonseca, El Salvador (about 13°9′N; 87°52′W) (CAS 024448), to Punta Española, Isla de Puná, Gulf of Guayaquil, Guayas Prov., Ecuador (2°48′S; 79°56′W) (ANSP 53032). The only data recorded on labels is intertidal sand. I have seen 126 lots.

Discussions: The *Donax assimilis* reported by Parker (1964) from Mazatlán, Mexico, was instead a mixture of *D. punctatostriatus* and *D. culter* (MCZ 254104). The *D. panamensis* [= *D. assimilis*] reported by Dexter (1974) from La Punta, Costa Rica, was a mixture of *D. asper, D. dentifer,* and *D. ecuadorianus;* the *D. panamensis* from Sámara, Costa Rica, is *D. asper;* the *D. panamensis* from Playa Cocal, Costa Rica, is *D. caelatus;* the *D. panamensis* from Jacó and Playa Espadilla, Costa Rica, are *D. ecuadorianus* (all MCZ, no assigned numbers).

Donax dentifer Hanley, 1843

(Figures *20, 21*)

Donax dentifer Hanley, 1843
Hanley, 1843a-1844: 84; 9 (plt. expl.); plt. 14, fig. 20 [as *D. "dentifera"*]

Explanation of Figures *17* to *21*

Figures *17* to *19: Donax assimilis* Hanley. Figure *17:* **lectotype** (herein) of *D. assimilis* Hanley and holotype of *D. reevei* Bertin, length 41.2 mm. Figure *18:* **lectotype** (herein) of *D. panamensis* Philippi, length 28.2mm. Figure *19:* **lectotype** (herein) of *D. curtus* Sowerby, length 23.0mm

Figures *20* to *21: Donax dentifer* Hanley. Figure *20:* **lectotype** (herein) of *D. dentifer,* length 32.0mm. Figure *21:* **lectotype** (herein) of *D. paytensis* Orbigny, length 28.2mm

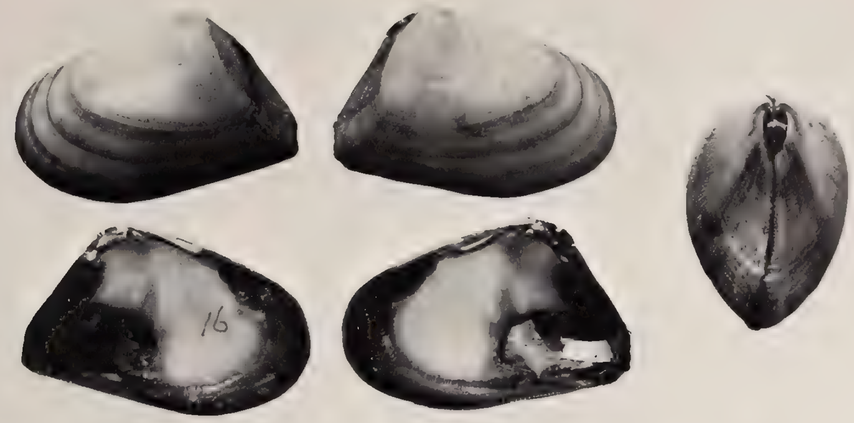

Figure *17*

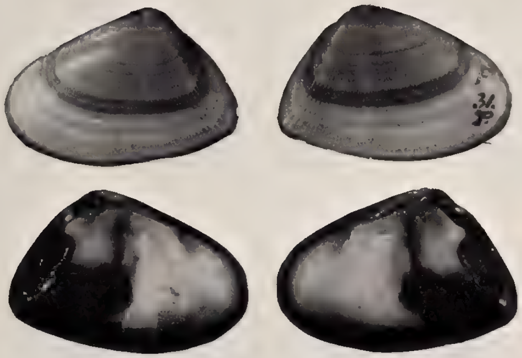

Figure *18*

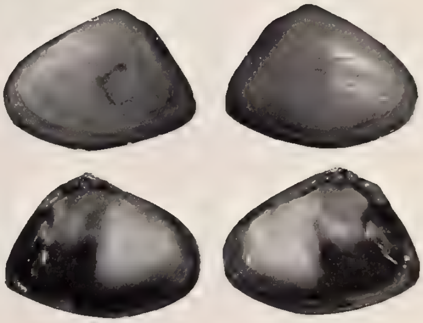

Figure *19*

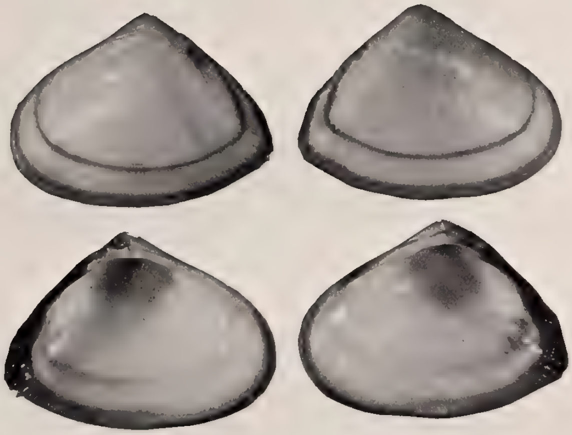

Figure *20*

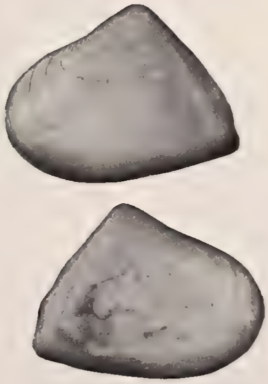

Figure *21*

Hanley, 1843b: 6 [as *D. "dentifera"*]
Reeve, 1854: plt. 1, figs. 2a, b [as *D. "dentifera"*]
Mörch, 1860: 192
Sowerby, 1866: 307; plt. 1 [= 280], fig. 23 [as *D. "dentiferus"*]
Tryon, 1869: 111 [as *D. "dentifera"*]
Römer, 1869b-1870: 12-13; 119 (plt. expl.); plt. 3, figs. 11-15
Bertin, 1881: 80
Keen, 1958: 185; fig. 449
Olsson, 1961: 344; 532, 558 (plt. expls.); plt. 59, figs. 2-2b [as *D. "dentiferus"*] [his plt. 85, fig. 4, is *D. assimilis*, a paralectotype from the type lot of *D. paytensis*]
Keen, 1971: 235, 236; fig. 588

Donax paytensis Orbigny, 1845
Orbigny, 1845: 541-542
Bertin, 1881: 103
Dall, 1909: 273
Olsson, 1961: 344 [as = *D. dentifer*]
Keen, 1966c: 7 [as = *D. dentifer*]
Keen, 1971: 236 [as = *D. dentifer*]

Type Material & Localities:

D. dentifer—BM(NH) 1912.6.18.28, **lectotype** herein, presumably the pair figured by Hanley; length, 32.0mm; height, 23.8mm; thickness, 15.2mm (Figure *20*).
"South America" (Hanley, 1843a).

D. paytensis—BM(NH) 1854.12.4.703, **lectotype** herein, the larger, higher specimen, a sealed pair; length, 28.2mm; height, 21.4mm; thickness, 13.4mm (Figure *21*).
There are 3 **paralectotypes,** one of which is a *D. assimilis* (length, 27.8mm) and was figured by Olsson (1961: plt. 85, fig. 4). A third specimen (16.7mm long) is a young *D. dentifer*, and a fourth (21.5mm), possibly added to the lot later, is a specimen of *D. obesulus* Reeve.
Paita, Piura Prov., Peru (5°5′S; 81°7′W); M. Fontaine. This locality may be in error, as it is farther south than any modern record.

Description: Medium-sized for genus, to 48mm (Skoglund Coll.; Playas, Ecuador); trigonal, length 1.3 times height (sd, ±0.1); valves moderately inflated, thickness 0.59 times height (sd, ±0.04); thin-shelled; anterior end longer, slightly produced, rounded; posterior end short, truncate ventrally; posterior end set off by a sharp angle; beaks inflated; ventral margin evenly curved.

Very fine, flat radial ribs present on central and anterior slopes, fading out at anterior end; ribs narrow toward posterior end, widely spaced at the sharp demarcation of central slope from the posterior end, close together on posterior slope; two-thirds of the way from posterior margin to demarcation of central slope one or two ribs much larger than others, projecting to form interlocking "teeth" at shell margin; concentric sculpture also present on posterior slope, forming a network pattern.

Left valve with a large anterior cardinal and a smaller posterior cardinal; anterior lateral close to cardinals, elongate, anteriorly directed; posterior lateral shorter, more distant. Right valve with a large posterior cardinal and a very small anterior cardinal; anterior submarginal ridge with an elongate lateral tooth; posterior submarginal ridge with a shorter tooth. Pallial sinus short, not reaching past beaks.

Externally bluish, often with darker circular bands; internally purplish.

Distribution & Habitat: "Coast of Guatemala" (CAS 024-454) (thus at least as far north and west as 13°46′N; 90° 10′W); Los Blancos, El Salvador (13°20′N; 89°00′W) (Senckenberg Mus. 254449, 254450); Playa el Tamarindo, near Punta Ampala, Gulf of Fonseca, El Salvador (about 13°9′N; 87°52′W) (CAS 024446), to Playas, Guayas Prov., Ecuador (2°39′S; 80°23′W) (CAS 025754); possibly as far south as Paita, Piura Prov., Peru (5°5′S; 81°7′W), the type locality of *Donax paytensis.* The only habitat information recorded on labels is intertidal sand. I have seen 49 lots.

Donax asper Hanley, 1845

(Figures *22, 23*)

Donax asper Hanley, 1845
Hanley, 1845b: 14-15
Reeve, 1854: plt. 2, fig. 12
Sowerby, 1866: 307; plt. 1 [= 280], fig. 24
Tryon, 1869: 111
Römer, 1869b-1870: 14-15; 119 (plt. expl.); plt. 3, figs. 7-10
Bertin, 1881: 80-81
Dall, 1909: 159, 273; 294 (plt. expl.); plt. 28, fig. 7
Smith, 1944: 63; fig. 818
Hertlein & Strong, 1949: 251-252
Hertlein & Strong, 1955: 202
Keen, 1958: 184, 185; fig. 443
Olsson, 1961: 343-344; 532 (plt. expl.); plt. 59, figs. 1-1d
Keen, 1971: 235, 236; fig. 583

Donax granifer Reeve, 1854, *ex* Deshayes MS
Reeve, 1854: plt. 7, fig. 43 [as *D. "granifera* Deshayes"]
Deshayes, 1855: 353
Sowerby, 1866: 307; plt. 1 [= 280], fig. 18 [as *D. "graniferus"*]
Römer, 1870: 68-69; 120 (plt. expl.); plt. 12, figs. 5-7
Bertin, 1881: 96 [as *D. "graniferus"*]

Donax rostratus C. B. Adams, *auctt., non* Adams, 1852
Olsson, 1961: 338-339; 534 (plt. expl.); plt. 61, figs. 1-1b

Type Material & Localities:

D. asper—BM(NH) 198212, **lectotype** herein, the specimen figured by Reeve, pair; length, 42.6mm; height, 32.5mm; thickness, 21.0mm (Figure *22*).
There are 2 **paralectotypes** in this lot, and 3 probable **paralectotypes** in BM(NH) 198213.
Tumbez, Tumbez Prov., Peru (3°32′S; 80°25′W).

D. granifer—BM(NH), **lectotype** herein, the figured syntype, pair; length, 18.5mm; height, 13.4mm; thickness, 9.3mm (Figure *23*).

There are two **paralectotypes.**
Loc. unknown (Reeve, 1854); Colombia (Deshayes, 1855).

Description: Medium-sized for genus, to 42 mm (CAS 024450; Tumaco, Colombia); rhomboidal, length 1.3 times height (sd, ±0.1); moderately inflated, thickness 0.60 times height (sd, ±0.03); valves heavier on an average than those of either *Donax assimilis* or *D. dentifer;* anterior end longer, somewhat pointed; posterior end short, often with a shallow indentation, giving it a rostrate appearance; posterior margin almost straight; posterior end set off by a sharper angle than in *D. assimilis;* posterior end somewhat flattened; beaks more inflated than in *D. assimilis;* ventral margin a little flexed below beaks and indented posterior to this.

Radial ribs flat on central and anterior slopes, becoming obsolete toward and on posterior slope, closer together where ventral margin is indented; concentric sculpture present on posterior end, producing a network pattern; the stronger sculpture on posterior slope tending to end more abruptly toward central slope than in *Donax assimilis.*

Left valve with cardinals of nearly equal size; anterior lateral short, closer to beaks and more ventrally directed than that in *Donax assimilis;* posterior lateral short, about equidistant. Right valve with a large posterior cardinal and a small anterior cardinal; anterior lateral on sub-marginal ridge, close to cardinals, ventrally directed; posterior lateral on a sub-marginal ridge, about equidistant.

Externally purple to tan; internally purple to white.

Distribution & Habitat: Playa el Tamarindo, near Punta Ampala, Gulf of Fonseca, El Salvador (about 13°9′N; 87°52′W) (CAS 024447 & 024449), to Caleta La Cruz, near Zorritos, Tumbez Prov., Peru (about 3°37′S; 80°34′W) (ANSP 236397, 234766, & 234862). The habitat information available on labels is scant. Occurrence seems to be in the intertidal area on sand beaches, though two labels have it in mangrove areas. I have seen 85 lots.

There is a lot in the ANSP (#51576) labeled as coming from Callao, Lima Prov., Peru (12°3′S; 77°10′W). This is not confirmed by other records, and I think it is probably incorrect. I have not located the specimens reported by Hertlein & Strong (1949: 252) from Bahía Tangola-Tangola, Oaxaca, Mexico. I suspect the record was based on a misidentification.

(Machaerodonax) Römer, 1870

[Type species: *Donax scalpellum* Gray, 1825; by SD of Dall, 1900]

Anterior end longer, deflected dorsally; posterior end short, truncate, pointed ventrally, with multiple folds; posterior slope sharply set off, generally by a carina.

Left valve with widely divergent cardinals of nearly equal size; posterior lateral below hinge margin. Right valve with a large, bifid posterior cardinal; anterior lateral fitting beneath that of left valve; posterior lateral socket with teeth both above and below slot for posterior lateral of left valve.

I am here redefining the concept of this subgenus. Rather than using *Machaerodonax* to encompass several species with elongate, somewhat gaping shells, which was Römer's basis for grouping the four species he included, I recognize an alternative set of three species with what I regard as more fundamental similarities. In addition to the type species, which occurs in the Gulf of Aden, I include the West American *Donax carinatus* and *D. transversus.*

Donax (Machaerodonax) carinatus Hanley, 1843

(Figures *24, 25, 26*)

Donax carinatus Hanley, 1843
  Hanley, 1843a-1844: 84; 9 (plt. expl.); plt. 14, fig. 28 [as *D. "carinata"*]
  Hanley, 1843b: 5-6 [as *D. "carinata"*]
  Reeve, 1854: plt. 2, fig. 4 [as *D. "carinata"*]
  Carpenter, 1857b: 208, 232, 245, 285, 304
  Carpenter, 1857c: 43
  Carpenter, 1864b: 537, 552, 668 [1872: 23, 38, 154]
  Sowerby, 1866: 305; plt. 1 [= 280], figs. 4, 5

Explanation of Figures *22* to *27*

Figures *22* to *23: D. asper* Hanley. Figure *22:* **lectotype** (herein) of *D. asper* Hanley, length 42.6 mm. Figure *23:* **lectotype** (herein) of *D. granifer* Reeve, length 18.5 mm

Figures *24* to *26: Donax (Machaerodonax) carinatus* Hanley. Figure *24:* holotype of *D. carinatus* Hanley, length 30.3 mm. Figure *25:* holotype of *D. rostratus* C. B. Adams, length 52.0 mm. Figure *26:* lectotype of *D. culminatus* Carpenter, length 23.8 mm

Figure *27: D. (Machaerodonax) transversus* Sowerby, a specimen from Estero El Tamarindo, El Salvador; CAS 028712, length 27.3 mm

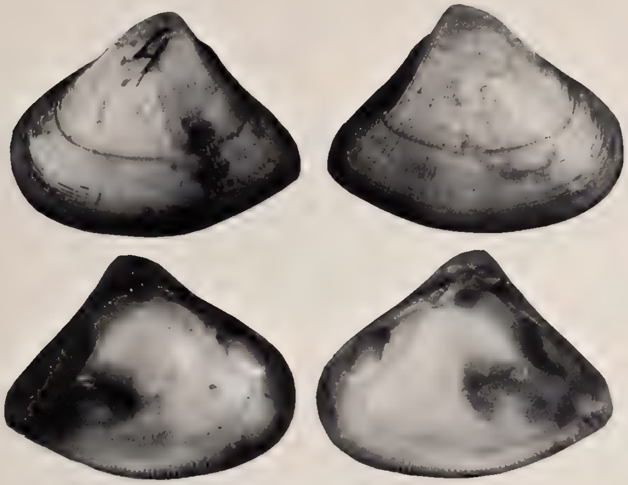

Figure 22

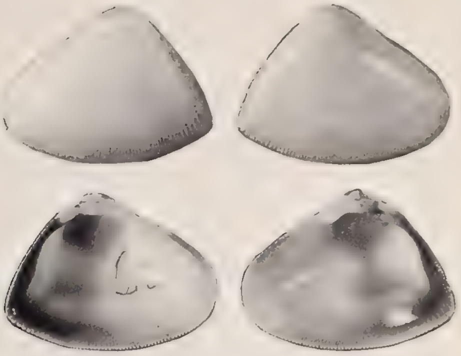

Figure 23

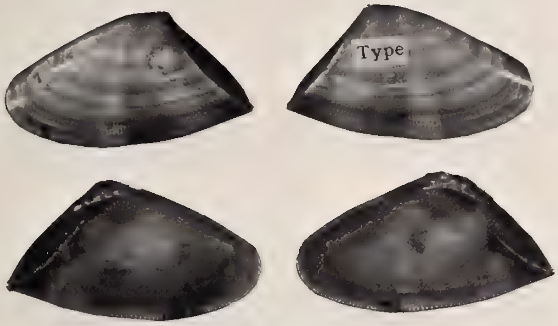

Figure 24

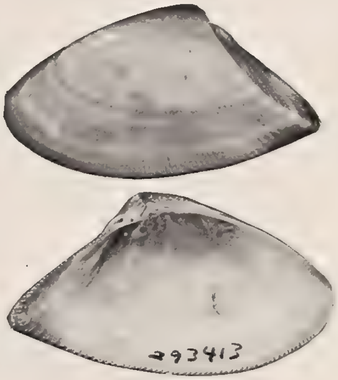

Figure 25

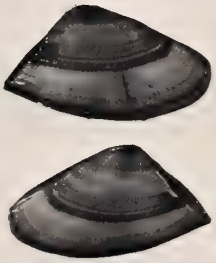

Figure 26

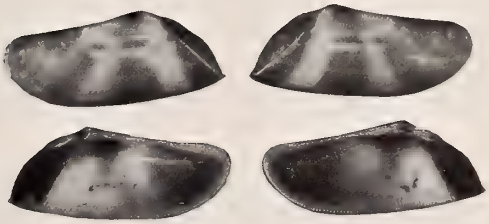

Figure 27

Tryon, 1869: 111
Römer, 1869b-1870: 10-11; 119 (plt. expl.); plt. 3, figs. 4-6
Bertin, 1881: 80
Smith, 1944: 63; fig. 820
Hertlein & Strong, 1949: 253; 258 (plt. expl.); plt. 1, fig. 9
Keen, 1958: 184, 185; fig. 446
Olsson, 1961: 342-343; 533 (plt. expl.); plt. 60, figs. 4-4b
Keen, 1971: 235, 236; fig. 585

Donax rostratus C. B. Adams, 1852
C. B. Adams: 1852a: 502-503, 545 [1852b: 278-279, 321]
Carpenter, 1857b: 229, 245, 279, 304, 364
Carpenter, 1857c: 548
Mörch, 1860: 193
Carpenter, 1864a: 366 [1872: 202]
Carpenter, 1864b: 537, 541, 552, 668 [1872: 23, 27, 38, 154]
Tryon, 1869: 111
Römer, 1869b-1870: 11-12; 119 (plt. expl.); plt. 3, figs. 1-3
Bertin, 1881: 81
Turner, 1956: 82

Donax culminatus Carpenter, 1857
Carpenter, 1857b: 229, 245 [*nomen nudum;* as = *D. rostratus*]
Carpenter, 1857c: 43-44, 548 [as = *D. rostratus* on p. 548]
Carpenter, 1864a: 366 [as = *D. carinatus*] [1872: 202]
Carpenter, 1864b: 552 [as = *D. carinatus*] [1872: 38]
Tryon, 1869: 111 [as = *D. carinatus*]
Keen, 1958: 184 [as = *D. carinatus*]
Palmer, 1963: 312
Keen, 1968: 399; 402 (plt. expl.); plt. 56, figs. 33a, b [as = *D. carinatus*]
Keen, 1971: 236 [as = *D. carinatus*]

Type Material & Localities:

D. carinatus—BM(NH) 1900.2.8.4, presumably the holotype, pair; length, 30.3 mm; height, 17.0 mm; thickness, 10.8 mm (Figure *24*).

Loc. unknown (Hanley, 1843a, 1843b).

D. rostratus—MCZ 293413, probable holotype, left valve; length, 52.0 mm; height, 27.9 mm; thickness, 10.0 mm (Figure *25*).

Turner (1956: 82) believed this specimen to be lost. Indeed, it was not labeled with the name *D. rostratus,* and its length in particular differs significantly from that given by Adams (length, 40.6 mm; height, 29.2 mm; thickness, 20.3 mm, evidently calculated to represent a pair of matched valves). However, I suspect that his measurements were incorrect or were miscopied, for they would depict a *Donax* with proportions that would not match any specimens of *D. carinatus,* to which Adams' description fits closely otherwise. The specimen was labeled "Panama ¡CBA!," and could not be any other species of *Donax* in Adams' catalogue of Panama mollusks; all the rest are accounted for. Moreover, a tracing in the margin of Carpenter's copy of Adams's book strongly indicates that this is the specimen Carpenter took to be the type specimen of *D. rostratus.*

Panama; C. B. Adams. Presumably from near Panama City, Panama (about 8°58′ N; 79°32′ W); between Nov. 27, 1850, and Jan. 2, 1851.

D. culminatus—BM(NH) Mazatlán Coll. 1857.6.4.139, lectotype (Keen, 1968), pair, the only specimen from Mazatlán (there are two paralectotypes in the lot from Central America); length, 23.8 mm; height, 12.5 mm; thickness, 8.6 mm (Figure *26*).

Mazatlán, Sinaloa, Mexico (23°12′ N; 106°25′ W); F. Reigen.

Description: Medium-sized for genus, to 52 mm (probable holotype of *Donax rostratus,* MCZ 293413; MCZ 293415, Nicaragua); rhomboidal-elongate, length 1.7 times height (sd, ±0.04); moderately inflated, thickness 0.60 times height (sd, ±0.01); anterior end longer, somewhat pointed and deflected dorsally; posterior end short, sharply pointed, somewhat truncate ventrally; postero-dorsal slope with multiple folds (less so than in *D. transversus*); posterior slope set off by a sharp carina in most specimens.

Most of surface smooth, with radial ribs evident only by the striae between them; posterior slope with fine, raised radial ribs, which are reticulated by concentric sculpture in most specimens.

Left valve with widely divergent cardinals of nearly equal size; anterior lateral close to beaks; posterior lateral more distant, on a submarginal ridge. Right valve with a large, bifid posterior cardinal and a thin anterior cardinal; anterior lateral close to beaks, fitting beneath that of left valve; posterior lateral socket with teeth both above and below slot for posterior lateral of left valve.

Externally tan with concentric and radial bands of darker color; purple within.

Distribution & Habitat: Altata, Sinaloa, Mexico (24°32′ N; 107°50′ W) (USNM 63671; CAS 024808), and Bahía Magdalena, Baja California Sur (about 24°38′ N; 112°9′ W) (AMNH 106015), Mexico, to Puerto Pizarro, Tumbez Prov., Peru (3°30′ S; 80°25′ W) (USNM 537987). Olsson (1961: 339) reports the species from Mancora, Tumbez Prov., Peru (4°6′ S; 81°4′ W); I have not seen his specimens, but there is no reason to doubt this record. There is a lot in the MCZ (#260064) labeled as coming from Estero de Tastiota, Sonora, Mexico (about 28°24′ N), much farther north than any other lot from this well-studied area. I suspect an error has crept into this material from Parker's 1964 study, for he reports the species (pp. 161, 167; plt. 2, fig. 19) from only one station (#160), that south of Mazatlán. There is a single lot labeled as coming from Pisco, Ica Prov., Peru (13°44′ S) in the AMNH (#149964), which would represent an extremely southern record. I would regard this lot, too, as questionable unless additional specimens are taken this far south. Intertidal area to 12 m, sand. I have seen 72 lots.

Discussion: Carpenter (1857c) reported *Donax carinatus* from Mazatlán, and he described a new species, *D. culminatus,* from there as well. But, in the errata to this book (p. 548), Carpenter concluded that this new species was the same as *Donax rostratus* described by C. B. Adams from Panama in 1852. Then, after Carpenter had had a chance to see Adams' unique holotype, he concluded that *Donax rostratus* was instead identical to what he had previously thought was *D. carinatus* Hanley, and that his *D. culminatus* was identical with Hanley's *D. carinatus* (Carpenter, 1864a: 366). In fact, Adams himself had compared *D. rostratus* with *D. carinatus* (misspelled as *D. "cardinatus"*).

The type of *Donax rostratus* and the specimens that Carpenter isolated in 1857—from Mazatlán and elsewhere—and associated with Adams' *D. rostratus* in 1864 are truly unique specimens of *D. carinatus.* (Carpenter's Mazatlán specimens are in the BM(NH), #1857.6.4.138.) They lack a sharp posterior keel, and the posterior slope lacks the concentric sculptural elements that roughen the radial sculpture of typical *D. carinatus,* having instead smooth, shiny radial ribs. In other respects, they are identical to *D. carinatus.* There are similar specimens from throughout the distribution of the species—Mazatlán (MCZ 87325), Nicaragua (MCZ 293415), and Ecuador (MCZ 233580), for example. I suspect that this set of characters is a common genetic variation.

The originally stated height of the type of *D. rostratus* (29.2 mm) would suggest a specimen much higher in proportion to the length that Adams gave than any specimens of *D. carinatus* I have seen. (And, as stated above, I think that this last measurement was in error and that the specimen in the MCZ is actually his unique holotype.) Olsson (1961: 338-339; 534; plt. 61, figs. 1-1b) was led astray by these measurements and said he was "fairly certain" of what Adams had from Panama, and he figured a high juvenile of *D. asper* from Ecuador to illustrate his concept, a species that does not in any other way fit Adams' description. (What was illustrated as *D. rostratus* by Keen (1958: 186, 187; fig. 456) is a specimen of the Caribbean *D. striatus* Linnaeus, 1767, that had been mislabeled as coming from "Panama.")

Donax (Machaerodonax) transversus Sowerby, 1825

(Figure *27*)

Donax transversus Sowerby, 1825
- Sowerby, 1825: iv [as *D. "transversa"*]
- Reeve, 1854: plt. 6, fig. 36 [as *D. "transversa"*]
- Carpenter, 1857b: 174, 245, 304
- Carpenter, 1857c: 44, 548
- Carpenter, 1864b: 537, 668 [1872: 23, 154]
- Sowerby, 1866: 306; plt. 1 [= 280], fig. 11
- Tryon, 1869: 114
- Römer, 1870: 79-80; 120 (plt. expl.); plt. 14, figs. 1-3
- Bertin, 1881: 107
- Hertlein & Strong, 1949: 256; 258 (plt. expl.); plt. 1, fig. 3
- Keen, 1958: 186, 187; fig. 457
- Olsson, 1961: 345; 532 (plt. expl.); plt. 59, figs. 4-4b
- Keen, 1971: 239, 241; fig. 599
- [not to be confused with *D. transversus* Deshayes, 1830—see discussion under *Donax (Paradonax)* below]

Donax scalpellum Gray, *auctt., non* Gray, 1825
- Hoffstetter, 1952: 42
- [*non* Gray, 1825: 136]

Type Material & Locality:

D. transversus—BM(NH) 1839.6.10.17, probable holotype, pair; length, 36.5 mm; height, 14.7 mm; thickness, 9.5 mm (located after manuscript submitted; not illustrated).

No locality was given by Sowerby (1825), or by Reeve (1854), who was the first person to illustrate the species, an illustration undeniably of the West American species. Carpenter (1857b, 1857c) was the first to attribute the species to the Panamic Province. The original board with the newly located type says "San Blas," Nayarit, Mexico (21°32′ N; 105° 19′ W).

Description: Medium-sized for genus, to 42 mm in length (CAS 024443; Acapulco, Mexico); elongate, length 2.3 times height (sd, ±0.2); not very inflated, thickness 0.56 times height (sd, ±0.05); anterior end much longer, produced dorsally, the postero-dorsal slope concave; posterior end short, very truncate, pointed ventrally, with multiple folds; posterior slope set off by a sharp carina.

Most of surface smooth, with radial ribs visible only as striae, but posterior slope with fine, raised radial ribs reticulated by concentric sculpture. Periostracum not evident.

Left valve with widely divergent cardinals of nearly equal size; anterior lateral close to beaks; posterior lateral more distant, on a ridge below dorsal margin. Right valve with a large, bifid posterior cardinal and a thin anterior cardinal; anterior lateral close to beaks, fitting beneath that of left valve; posterior lateral socket with teeth both above and below slot for posterior lateral of left valve.

Externally with tan or brown radial bands; internally purple, often with radial bands corresponding to the external bands.

Distribution & Habitat: Altata, Sinaloa, Mexico (24°32′ N; 107°50′ W) (USNM 63672), to Cabo Blanco, Piura Prov., Peru (4°17′ S; 81°16′ W) (CAS 024816). Olsson (1961: 345) cites the species from Paita, Piura Prov., Peru (5°5′ S; 81°7′ W); while I have not seen his specimens, I accept this record. The only habitat noted on labels is intertidal sand. I have seen 39 lots.

Discussion: *Donax scalpellum* Gray, 1825, was described without a type locality. Reeve (1854) attributed it to the "Gulf of California" and Sowerby (1866) to "California." These incorrect localities have echoed through the literature and the name evidently applied to specimens of *D.*

transversus, but the only published record unquestionably based on a specimen of *D. transversus* is that of Hoffstetter (1952). Gray's species, however, is native to the Gulf of Aden (see Hertlein & Strong, 1949: 256). (*Donax elongatus* Mawe, 1823: 39; 37 (plt. expl.); plt. 9, fig. 6, an earlier name for *D. scalpellum*, is a homonym of the West African *D. elongatus* Lamarck, 1818: 550.)

(Amphichaena) Philippi, 1847

[Type species: *A. kindermanni* Philippi, 1847b; by M]

Relatively thin-shelled, with radial striae; punctations lacking. Pallial sinus does not reach anteriorly past beaks. The valves gape at ends.

Left valve with two cardinals, the anterior larger; anterior lateral very close to cardinals (so close it has been mistaken for a third cardinal); posterior lateral scarcely evident. Right valve with two cardinals, the posterior larger; anterior lateral close to beaks, on a ridge below dorsal margin; posterior lateral scarcely evident.

There has been some speculation that this genus might belong in the Psammobiidae (Giebel, 1864: 146; Keen, in Cox, *et al.*, 1969: N631), based on its smooth, gaping shell. However, I agree with Olsson (1961) and Keen (1971) in assigning it to the Donacidae based on its hinge, internal crenulations, and virtual indistinguishability from some other donacids. Its soft parts seem very similar to other donacids (CAS 028716).

Donax (Amphichaena) kindermanni (Philippi, 1847)

(Figures *28, 29, 30*)

Amphichaena kindermanni Philippi, 1847
  Philippi, 1847b: 63-64; plt. 3, figs. 7
  Carpenter, 1857b: 297
  Giebel, 1864: 146 [as *Psammobia*]
  Palmer & Hertlein, 1936: 71-72; 80 (plt. expl.); plt. 18; plt. 19, figs. 5-10 [as *Amphichaena*]
  Keen, 1958: 188-190; fig. 463
  Olsson, 1961: 345-346 [as = *D. (Amphichaena) culter*]
  Keen, 1971: 239, 241; fig. 600 [as *Amphichaena*]
Donax petallinus Reeve, 1854, *ex* Deshayes MS
  Reeve, 1854: plt. 8, fig. 51 [as *D. "petallina* Deshayes"]
  Deshayes, 1855: 350 [as *D. "petalina"*]
  Sowerby, 1866: 315; plt. 3 [= 282], fig. 86
  Römer, 1870: 51-52; 119 (plt. expl.); plt. 9, figs. 7-10
  Dall, 1909: 273
Donax petalina, *auctt.*, a misspelling
Amphichaena gracilis Mörch, 1860
  Mörch, 1860: 192
  Keen, 1966b: 14; 12 (plt. expl.); figs. 15, 15a
  [*non Donax gracilis* Hanley, 1845]

Type Material & Localities:

Amphichaena kindermanni—Evidently lost, for it is in neither Berlin's Humboldt Museum (Kilias, *in litt.*, 8 Aug. 1980) nor in the Museo Nacional de Historia Natural in Santiago, Chile (Bahamonde, *in litt.*, 16 April 1981). There is no need of a neotype; the original illustration is unmistakable. Philippi's specimen measured 30 mm in length, 8.2 mm in height, and 8 mm in thickness.

The type specimen was said to have come from Mazatlán, Sinaloa, Mexico (23°12′N; 106°25′W), by way of a Mr. Kindermann of Valparaiso, Chile, but there is no material from as far north as Mazatlán in any of the collections I have examined. The farthest north I have seen specimens is Bahía Tenacatita, Jalisco, Mexico (see "Distribution" below). Given the early date of Philippi's material, a lack of precision would not be unexpected. A more likely station would have been Acapulco, Guerrero, Mexico.

Donax petallinus—BM(NH) 198221—**lectotype** herein, right valve, the specimen figured by Reeve; length, 13.9 mm; height, 6.3 mm; thickness, 1.8 mm (Figure *28*). **Paralectotypes**, one pair and two left valves. Keen (1966b: 15) suggested that three of the type specimens could be identified with *Donax culter.* I have examined all of this material, and it represents *D. kindermanni.*

Locality unknown (Reeve, 1854: Deshayes, 1855; Sowerby, 1866). It may have come from the Acapulco area (16°51′N; 99°56′W), where the species is common.

Amphichaena gracilis—Univ. Zool. Mus., Copenhagen, **lectotype** herein, the intact left valve; length, 13.4 mm; height, 5.4 mm; thickness, 1.7 mm (Figure *29*). **Paralectotypes**, 3 broken right valves, 3 broken left valves, 1 intact right valve.

Sonsonate [Prov.], El Salvador. The specimens may have come from the port of Acajutla (13°35′N; 89°50′W).

Description: Medium-sized for genus, to 48 mm in length (CAS 025751; Petatlán, Guerrero, Mexico); elongate, length 2.6 times height (sd, ±0.2); moderately inflated, thickness 0.59 times height (sd, ±0.03); approximately equilateral; anterior end produced; posterior end broadly truncate; beaks small; external ligament elongate; central slope indented ventral to beaks; surface smooth or with rounded, raised striae that are most prominent and more closely spaced on posterior slope, where they are sometimes lightly reticulated by irregular concentric lines; radial ribs becoming obsolete on anterior slope; rarely with only concentric lines evident on posterior slope. Periostracum present only as a marginal fringe. Pallial sinus broad.

Left valve with two cardinals, the anterior larger; anterior lateral very close to cardinals; posterior lateral distant, scarcely evident. Right valve with two cardinals, the posterior larger; with an anterior lateral close to beaks, on a submarginal ridge; posterior lateral scarcely evident.

Externally white, tan, and purple, with one or two light and dark radial bands and sometimes darker concentric bands.

The available type material being juvenile specimens, I have illustrated an adult in Figure *30*.

Distribution & Habitat: Bahía Tenacatita, Jalisco, Mexico (19°16′ N; 104°52′ W) (CAS 025752), to Costa del Sol, Dept. la Paz, El Salvador (13°26′ N; 89°9′ W) (CAS 028715); Playa el Tamarindo, near Punta Ampala, Gulf of Fonseca, El Salvador (about 13°9′ N; 87°52′ W) (Hernández, 1979: 205), specimens not seen in this study, but record accepted. There is one lot in the ANSP labeled as having come from the "Gulf of California" (ANSP 51578), but I doubt this record. There is one lot in the USNM (#133771) labeled as coming from Panama, but there are no other specimens from this far south in collections, and I suspect that this is an error. The only habitat noted on labels is intertidal sand. I have seen 39 lots.

One of the largest lots examined (CAS 025751, from Petatlán, Mexico) contained beach-worn specimens in fairly good condition (Figure *30*). It contains 47 right valves and 87 left valves. (A Chi-Square test shows that this would occur by chance only once in more than 1000 times; $\chi^2 = 11.94$). One wonders why such non-random sorting of valves takes place.

Discussion: Southern populations of *Donax (Chion) culter* approach the morphology of *D. (Amphichaena) kindermanni,* a fact first noted by Keen (1966b: 15), who suggested a number of criteria for separating the two. Unfortunately, both species are somewhat variable and change shape as they grow, so some of the criteria she gives won't work with all specimens. (Moreover, the subgeneric units are poorly defined, and it is not impossible that there is or has been some hybridization between the two.) The following table presents the characters I have found most reliable:

Donax petallinus, named from an unknown locality, was first attributed to the eastern Pacific by Bertin (1881: 94), who thought it came from Chile. Bales (1938) reported it from Acapulco, which may be close to the place from which Reeve's specimens actually came. I have seen no specimens of this species from South America, so what Bertin had—and what was later reported under this name by Gigoux (1935: 284) from Atacama, Chile—remains a mystery. The checklist of Carcelles & Williamson (1951: 344) also records this taxon from "Chile and Peru." The *D. petallinus* reported by Parker (1964) from the coast of Hermosillo, Mexico, are *D. punctatostriatus* (MCZ 260123).

	Donax (Amphichaena) kindermanni	*Donax (Chion) culter*
Shape		
juvenile	slightly longer posteriorly, narrowed anteriorly	longer, broad anteriorly
adult	about equilateral	longer anteriorly (almost equilateral in some)
Gape	valves gaping	very little gape
Sculpture	with radial striae, never punctations	with radial sculpture, punctations in nearly all
Hinge (left valve)	anterior lateral *very close* to cardinals; posterior lateral scarcely evident	anterior lateral near to but not *very* close to cardinals; posterior lateral evident
Beaks	small	prominent
Pallial sinus	short, not reaching to below beaks	long, reaching to below beaks
Interior ventral margin	smoother in center	denticulate throughout

Explanation of Figures *28* to *33*

Figures *28* to *30: Donax (Amphichaena) kindermanni* (Philippi). Figure *28:* **lectotype** (herein) of *D. petallinus* Reeve, length 13.9 mm. Figure *29:* **lectotype** (herein) of *A. gracilis* Mörch, length 13.4 mm. Figure *30:* a specimen from Laguna Potosi, Zihuatanejo, Guerrero, Mexico; CAS 028713, length 35.4 mm

Figure *31: D. (Paradonax) californicus* Conrad, lectotype of *D. navicula* Hanley, length 24.9 mm

Figure *32: D. (Paradonax) gracilis* Hanley, **lectotype** (herein), length 25.1 mm

Figure *33: D. (Paradonax) punaensis* Pilsbry & Olsson, holotype, length 24.7 mm

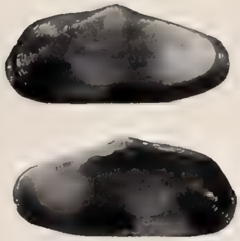

Figure 28

Figure 29

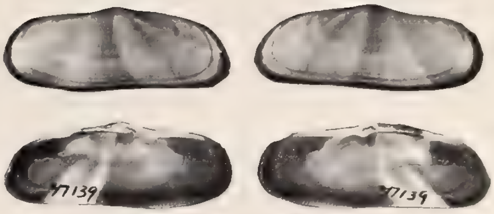

Figure 30

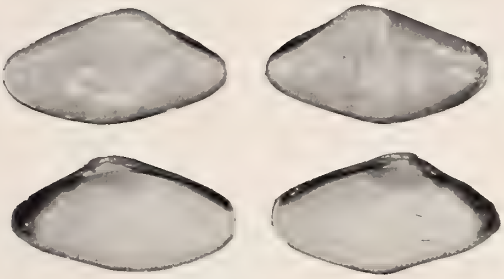

Figure 31

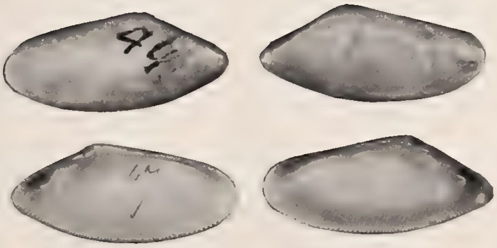

Figure 32

Figure 33

Keen (1966b) synonymized *Amphichaena gracilis* Mörch with *Donax culter*, but the latter does not occur as far south as *D. (A.) kindermanni*, and not at the type locality of *A. gracilis*. After careful study of Mörch's type specimens, I have little hesitation in placing *A. gracilis* in synonymy with *D. (A.) kindermanni*.

(Paradonax) Cossmann, *in* Cossmann & Peyrot, 1911

[Type species: *D. transversus* Deshayes, 1830; by OD]

Deshayes' *Donax transversus* is a homonym of the earlier, West American *D. transversus* Sowerby, 1825. A replacement name is probably unnecessary, because there are several possible synonyms in the literature, including *D. burdigalensis* DeFrance, 1819, and *D. (Paradonax) sallomacensis* Cossmann & Peyrot, 1911.

Medium-sized; relatively thin-shelled, elongate; smooth externally, with radial striae only; without punctations or a gape. Left valve with two cardinals, the anterior larger; posterior and anterior laterals present. Right valve with two cardinals, the posterior much larger, bifid; grooves present for laterals of left valve.

A possible ancestral form to one or both of the West American species of *Donax (Paradonax)* is *D. (P.) petersoni* Olsson, 1931 (pp. 66, 140; plt. 9, figs. 6, 7), from the Oligocene of Peru.

Donax (Paradonax) californicus Conrad, 1837

(Figure *31*)

Donax californicus Conrad, 1837
- Conrad, 1837: 254; plt. 19, fig. 21 [as *D. "californica"*]
- Dall, 1900: 968-969
- Arnold, 1903: 170; 388 (plt. expl.); plt. 8, fig. 9
- Strong, 1924: 83
- Oldroyd, 1925: 183
- Grant & Gale, 1931: 379-380
- Smith, 1944: 63; fig. 816
- Burch, 1945a: 20; 1945b: 17
- Hertlein & Strong, 1949: 252-253; 258 (plt. expl.); plt. 1, figs. 2, 5
- Keen, 1958: 185, 186; fig. 445
- Keen, 1966a: 170
- Keen, 1971: 235, 236; fig. 584
- Coan, 1973b: 134-135; figs. 4-6

Donax navicula Hanley, 1845
- Hanley, 1845a: 15
- C. B. Adams, 1852a: 502 [1852b: 278]
- Reeve, 1854: plt. 4, fig. 18
- Carpenter, 1857b: 186, 229, 246, 279, 304
- Carpenter, 1857c: 50, 548
- Mörch, 1860: 193
- Carpenter, 1864a: 366 [1872: 202]
- Carpenter, 1864b: 537, 541, 620, 640 [1872: 23, 27, 106, 126]
- Sowerby, 1866: 314; plt. 3 [= 282], fig. 80
- Römer, 1870: 56-57; 119 (plt. expl.); plt. 10, figs. 1-3
- Bertin, 1881: 97
- Hertlein & Strong, 1949: 254; 258 (plt. expl.); plt. 1, fig. 1
- Keen, 1958: 186, 187; fig. 451
- Olsson, 1961: 341; 533 (plt. expl.); plt. 60, figs. 3, 3a
- Keen, 1971: 237, 238; fig. 593
- Coan, 1973b: 134-135 [as *D. "naviculus"* and probably = *D. californicus*]

Type Material & Localities:

Donax californicus—Lost, but Conrad's description and 23mm-long figure are sufficient to identify the taxon (figured in Coan, 1973b: fig. 4). (The specimens in the BM(NH) Nuttall Coll. 1861.5.20.91 that were thought by Nuttall, Carpenter, and others to have been the type material of this species are really *Donax gouldii* Dall, 1921—Coan, 1973b: fig. 3). Near Santa Barbara, Santa Barbara Co., Calif. (about 34° 24′ N; 119°43′ W); sand; T. Nuttall; spring 1836 (Graustein, 1967: 313-315).

D. navicula—BM(NH) 1967.697, lectotype (Coan, 1973b), the specimen figured by Reeve, pair; length, 24.9mm; height, 13.0mm; thickness, 8.6mm (Figure *31*).

There are 2 paralectotypes.

Gulf of Nicoya, Costa Rica (about 9°59′ N; 84°50′ W); H. Cuming.

Description: Medium-sized for genus, to 33mm in length (LACM 67754; San Diego, Calif.); elongate, length 1.9 times height (sd, ±0.2); not very inflated, thickness 0.63 times height (sd, ±0.10); anterior end longer, somewhat pointed; posterior end pointed; posterior slope set off by a rounded angle; beaks only slightly inflated; external ligament short; ventral edge with a slight flexure directly under or a little anterior to beaks.

Surface smooth, with faint radial striae. Periostracum adherent, somewhat shiny.

Left valve with two cardinals, the anterior slightly larger; laterals about equidistant from cardinals, the anterior more elongate. Posterior cardinal of right valve much larger, bifid; grooves in right valve for laterals of left valve, only the posterior submarginal ridge much swollen into a tooth.

Tan to brown externally; internally flushed with purple, often with dark purple radial bands on anterior and posterior dorsal margins.

Distribution & Habitat: Evidently not now occurring as far north as Santa Barbara, the type locality. This is the most wide-ranging species among the eastern Pacific Donacidae: Mugu Lagoon, Ventura Co., Calif. (34°6′ N; 119°6′ W) (USNM 348175), to and throughout the Gulf of California, and south to Puerto Pizarro, Tumbez Prov., Peru (3°32′ S; 80°25′ W) (LACM 72-84). Intertidal area to 10m; fine sand in protected situations, including bays and estuaries. I have seen 280 lots.

Discussion: The differences that have been advanced to separate *Donax californicus* from *D. navicula* are, at best, clinal. Material in the Panamic Province tends to be more trapezoidal than specimens from California, but this feature is not consistent. The "concave posterior area" mentioned by HERTLEIN & STRONG (1949) as a hallmark of *D. navicula* is also present to a degree in Californian specimens of *D. californicus,* although it is more evident in Panamic material.

The name *Donax californicus* was used by REEVE (1854: plt. 6, fig. 40) and by SOWERBY (1866: 310; plt. 2, fig. 54) to apply to material now referable to *D. culter* Hanley, 1843. Moreover, due to the supposed type specimens in the BM(NH), *Donax gouldii* was for a while mistakenly called *D. californicus.* Finally, a few authors used the name *D. flexuosus* Gould, 1853, for this species. However, the type specimen of *D. flexuosus* has proven to be a mislabeled pair of the Caribbean *D. striatus* Linnaeus, 1767.

Donax (Paradonax) gracilis Hanley, 1845

(Figure *32*)

Donax gracilis Hanley, 1845
- HANLEY, 1845a: 15
- C. B. ADAMS, 1852a: 501-502 [1852b: 277-278]
- REEVE, 1854: plt. 6, fig. 38
- MÖRCH, 1860: 193
- CARPENTER, 1864a: 366 [1872: 202]
- SOWERBY, 1866: 314; plt. 3 [= 272], figs. 76-79
- RÖMER, 1870: 80-82; 120 (plt. expl.); plt. 14, figs. 4-8
- BERTIN, 1881: 97
- DALL, 1909: 273
- HERTLEIN & STRONG, 1949: 253-254; 258 (plt. expl.); plt. 1, figs. 4, 6
- KEEN, 1958: 185; fig. 450
- OLSSON, 1961: 341; 533 (plt. expl.); plt. 60, fig. 5
- KEEN, 1971: 235, 237; fig. 591

Type Material & Locality:

Donax gracilis—BM(NH) 1966.551, **lectotype** herein, the specimen figured by Reeve, pair; length, 25.1 mm; height, 10.7 mm; thickness, 6.4 mm (Figure *32*). There are 2 **paralectotypes** in this lot, and 3 in BM(NH) 198221 from another locality. Bay [Gulf] of Guayaquil, Ecuador (about 3°S; 81°W); H. Cuming.

Description: Medium-sized for genus, to 30.2 mm (Skoglund Coll.; Pasorja, Ecuador); elongate, longer than *Donax californicus,* length 2.3 times height (sd, ±0.1); not very inflated, thickness 0.57 times height (sd, ±0.04); anterior end longer, pointed; posterior end not set off, as in *D. californicus;* beaks not inflated, even less so than in *D. californicus;* external ligament more elongate than in *D. californicus;* ventral edge evenly curved, without any flexure. Surface smooth, radial striae not evident. Periostracum adherent, very shiny, more so than in *Donax californicus.*

Left valve with a large anterior cardinal and a smaller posterior cardinal; laterals equidistant from cardinals, the anterior more elongate. Right valve with a large, bifid posterior cardinal and a much smaller anterior cardinal; posterior submarginal ridge swollen into a tooth; but area for receipt of anterior lateral of left valve can scarcely be termed a socket.

Externally mottled with color, generally tan or brown, in rays, blotches, or bands; internally tan, sometimes with darker color along dorsal margin; thinner-shelled than *Donax californicus.*

Young specimens and mixed lots of the two species may be sorted on the basis of the elongate shape of *Donax gracilis* and its finer, more plentiful ribs, reflected along the inner ventral margin as bumps.

Distribution & Habitat: Bahía San Bartolomé, Baja California Sur (27°39′N; 114°51′W) (LACM 38-1), to and throughout the Gulf of California, to southwest of Playas, Guayas Prov., Ecuador (2°49′S; 80°31′W) (LACM 66-193); Negritos, Piura Prov., Peru (4°40′S; 81°19′W) (OLSSON, 1961) (specimens not seen but record accepted); intertidal area to 50 m, deeper than *Donax californicus,* more often occurring offshore than that species; both mud and sand substrates have been recorded. I have seen 147 lots.

Discussion: This species is a close relative of *Donax punaensis* PILSBRY & OLSSON, 1941 (pp. 72-73, 78; plt. 12, fig. 2), from the Pliocene of Isla Puna, Guayas Prov., Ecuador (holotype: ANSP 13713). The type of *D. punaensis* differs in being wider posteriorly than any specimens of *D. gracilis* I have seen (Figure *33*).

Donax (sensu lato)

The next two subtropical species probably do not belong in the same subgeneric unit. They are both smooth and lack punctations, but their hinges differ considerably.

Donax gouldii Dall, 1921

(Figure *34*)

Donax gouldii Dall, 1921
- DALL, 1921: 49 [not described in 1919, as stated]
- DALL, 1923: 2
- STRONG, 1924: 83-84
- OLDROYD, 1925: 183; plt. 49, figs. 8, 9
- GRANT & GALE, 1931: 380; 906 (plt. expl.); plt. 13, fig. 12
- BURCH, 1945a: 20-21, 24-26 (text figs.); 1945b: 17
- GREGG, 1945: 20-21 [in the preceding]
- COAN, 1973b: 131-134; figs. 1-3

Donax gouldi, auctt., spelling error
Donax obesus Philippi, 1851
Philippi, 1851 (July): 75
[*non* Orbigny, 1845; *non* Gould, 1851]
Donax obesus Gould, 1851
Gould, 1851 (Nov.): 90
Gould, 1853: 394-395; 408 (plt. expl.); plt. 15, fig. 9
Gould, 1862: 212
Johnson, 1964: 117
[*non* Orbigny, 1845; *non* Philippi, 1851]
Donax laevigatus Reeve, 1854, *ex* Deshayes MS
Reeve, 1854: plt. 5, fig. 31 [as *D. "laevigata* Deshayes"]
Deshayes, 1855: 352 [as *D. "laevigata"*]
Sowerby, 1866: 309; plt. 2 [= 281], figs. 30-32
Bertin, 1881: 91
Dall, 1900: 969
Arnold, 1903: 170-171; 388 (plt. expl.); plt. 13, fig. 8
[*non D. laevigatus* Gmelin, 1791: 3265, a west African *Iphigenia* —as *D. "laevigata"*]
Donax californicus Conrad, *auctt.*, *non* Conrad, 1837
Gould & Carpenter, 1857: 200
Carpenter, 1857a: 213
Carpenter, 1857b: 195-196, 227, 229, 232, 241, 246, 287, 296, 304, 349, 351, 352
Carpenter, 1857c: 47, 548
Carpenter, 1864b: 536, 540, 640, 665 [1872: 22, 26, 126, 151]
Römer, 1870: 41-43; plt. 4, figs. 5-8
Donax abruptus Carpenter, *ex* Gould MS
Carpenter, 1857b: 232 [as = *D. californicus, auctt.*]
Carpenter, 1864b: 542 [as = *D. obesus*] [1872: 28]

Type Material & Localities:

D. gouldii—USNM 664935, holotype, the specimen figured by Gould (1851), pair; length, 23.5 mm; height, 14.8 mm; thickness, 10.4 mm (Figure *34*).
San Diego, San Diego Co., Calif. (32°42′N; 117°14′W); T. P. Green.

D. obesus Philippi—Lost; neither in Berlin's Humboldt Museum (Kilias, *in litt.*, 27 Aug. 1980) nor in the Museo Nacional de Historia Natural in Santiago Chile (Bahamonde, *in litt.*, 16 April 1981). The original specimen was said to measure 20.7 mm in length, 13.1 mm in height, and 9.3 mm in thickness.
"California"; from a dealer.

D. obesus Gould—USNM 664935, lectotype (Coan, 1973b), same pair as for *D. gouldii;* USNM 664936, 5 paralectotype pairs.
Same locality as *D. gouldii.*

D. laevigatus—BM(NH) 1981.143, pair, the largest specimen, lectotype (Coan, 1973b); length, 22.6 mm; height, 14.35 mm; thickness, 10.05 mm (figured in Coan, 1973b: fig. 2). There are two paralectotypes, BM(NH) 1981144 (the figured syntype) and 1981145.
"North America"; H. Cuming.

Description: Medium-sized for genus, to 31.5 mm in length (Draper, 1980: 25; Pismo Beach, California; presumably in Stillman Berry Coll.); quadrate, length 1.5 times height (sd, ±0.1); inflated, thickness 0.72 times height (sd, ±0.05); anterior end much longer, only slightly produced; posterior slope set off by a rounded angle, truncate; beaks produced; external ligament short; ventral edge with a little flexure anterior to beaks.

Surface smooth, shiny, with very faint radial striae, which become obsolete on anterior slope; ribs more prominent on posterior slope. Periostracum tan, present as shreds at shell margin.

Left valve with cardinal teeth of approximately equal size; anterior lateral tooth more distant from cardinals and more elongate. Anterior cardinal of right valve smaller than the posterior; anterior submarginal ridge with a tooth, more distant from cardinals than tooth on posterior submarginal ridge.

White to tan externally, often banded, rayed, or blotched with brown, tan, blue, or other colors; internally white to purple, with a brown flush.

Distribution & Habitat: Sporadic northern records: Dillon Beach, Marin Co., California (38°15′N; 122°58′W) (Hedgpeth, *in* Marcus, 1961: 58) (specimen not in CAS, now home of the Dillon Beach Marine Station Coll.); Davenport, Santa Cruz Co., Calif. (37°1′N; 122°13′W) (McLean, 1975: 68; Univ. Calif. Santa Cruz Marine Station Coll.); Monterey, Monterey Co., Calif. (36°38′N; 121°56′W) (MCZ 118780; AMNH 32896; ANSP 225910). But, populations not permanently established north of Pismo Beach, San Luis Obispo Co., Calif. (35°9′N; 120°45′W) (SDNHM 20042; SBMNH 10666), from where it occurs more or less continuously to Arroyo Conejo, Baja Calif. Sur (24°5′N; 110°5′W) (LACM 71-17). Also Isla Socorro, Islas Revillagigedos, Mexico (18°42′N; 110°58′W) (USNM 153085), but probably not established there. Records and specimens from the mainland coast of Mexico are probably labeling errors (as ANSP 142637), or misidentifications of young *D. punctatostriatus.* Intertidal area to 5 m, in sand, mainly on open beaches but also at bay entrances (see also Coan, 1973b: 133; Fitch, 1959).

I studied 23 lots from the outer coast of Baja California in the course of the present study, one of them being from farther south than the species had previously been reported. In preparing my earlier paper on the northern species of *Donax,* I examined about 200 additional lots, chiefly from California.

Donax marincovichi Coan, spec. nov.

(Figures *35, 36*)

Donax radiatus Valenciennes, *auctt.*, in part, *non* Valenciennes, 1827
Donax peruvianus Deshayes, *auctt.*, in part, *non* Deshayes, 1855
Römer, 1870: plt. 9, figs. 8-10

Type Material & Locality:

Donax marincovichi—ANSP 313474, **holotype**, pair; length, 27.8 mm; height, 15.2 mm; thickness, 9.4 mm (Figure *35*). ANSP 353598, 18 **paratypes** (Figure *36*, a paratype).

"Taken by fishermen at surf line"; Pisco, Ica Prov., Peru (13°44′ S; 76°15′ W); Oct. 1966; Edgar Bauer.

Description: Medium-sized for genus, length to 32 mm (USNM 792354; Punta Parinas, Peru) (**holotype**, 27.8 mm); elongate, length 1.7 times height in type lot (sd, ±0.07), 1.6 times height in another (LACM 67753) (sd ±0.07); only moderately inflated, thickness 0.60 times height in type lot (sd, ±0.03), 0.65 in another (LACM 67753) (sd, ±0.04); anterior end longer; posterior end produced ventrally; posterior slope not set off; beaks not inflated; ligament short; ventral margin relatively straight posteriorly, with only a slight flexure well anterior to beaks.

Surface smooth; radial striae present, not very incised, fading out toward posterior end, more crowded toward posterior slope; punctations absent. Periostracum dark, often evident in a wide concentric band at shell margin.

Left valve with a large anterior cardinal and a smaller posterior cardinal; anterior and posterior laterals present, the dorsal margin not reflected above posterior lateral. Right valve with a large posterior cardinal and a very small, thin anterior cardinal. The anterior submarginal ridge elongate, swollen into a lateral tooth; the posterior submarginal ridge with a tooth, the dorsal margin not reflected above it.

Externally, shell white to tan, sometimes with radial rays, occasionally with concentric bluish bands.

Distribution: Salinas, Guayas Prov., Ecuador (2° 12′ S; 80° 58′ W) (LACM 71-191), to Playa Miller, Arica, Tarapaca Prov., Chile (18°28′ S; 70°20′ W) (AMNH 198971). The only data available on labels suggest that the species occurs on intertidal sandy beaches. There are 12 lots in collections I have examined.

Differential Diagnoses: This species has been confused with *Donax obesulus*, which occurs throughout its distribution. It is less inflated than *D. obesulus*, and the posterior end is longer. The beaks are not inflated, as are those of *D. obesulus*, and the postero-ventral margin is straighter. The surface of *D. marincovichi* is never punctate and is less shiny than that in *D. obesulus;* the periostracum is darker, and is present in a wider band than in *D. obesulus.* The hinges of the two species are similar, but the posterior laterals are more distant in *D. marincovichi.* The dorsal margin is not produced above the posterior laterals in the new species as it is in *D. obesulus.* The anterior cardinal of the right valve is thinner than that in *D. obesulus.*

Key features in distinguishing the two are given here:

D. marincovichi	*D. obesulus*
Never has punctations	Punctations present on most specimens
Less inflated, th/h between 0.57-0.69	More inflated, th/h between 0.71-0.77
Beaks low	Beaks inflated
Periostracum dark, adherent in a wide marginal band	Periostracum light, marginal traces only
Surface silky	Surface shiny
Smaller, only to 32 mm in length	Larger, to 38 mm
Posterior lateral more distant; dorsal margin not produced above it	Posterior lateral close to cardinals; dorsal margin produced above it
Anterior cardinal of right valve small, thin	Anterior cardinal of right valve thickened

Donax marincovichi is longer and less inflated than *D. gouldii.* The cardinal teeth of the left valve are more nearly equal in size in *D. gouldii,* whereas in the new species they are unequal, the anterior being larger. In *D. gouldii,* the posterior lateral is shorter and closer; in *D. marincovichi,* the anterior lateral is shorter and closer.

Donax marincovichi differs from *D. culter* in not having surface punctations and in having an anterior lateral that is more distant from the cardinal teeth.

Explanation of Figures *34* to *38*

Figure *34: Donax gouldii* Dall, holotype, and lectotype of *D. obesus* Gould, length 23.5 mm

Figures *35* to *36: D. marincovichi* Coan, new species. Figure *35:* holotype, length 27.8 mm. Figure *36:* a paratype, length 27.5 mm

Figures *37* to *38: Iphigenia altior* (Sowerby). Figure *37:* **lectotype** (herein) of *Capsa altior* Sowerby, length 84.0 mm. Figure *38:* holotype of *I. ambigua* Bertin, length 56.1 mm

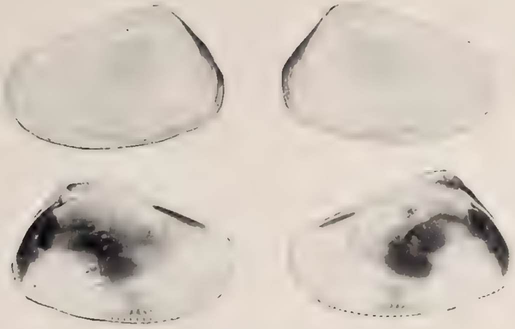

Figure *34*

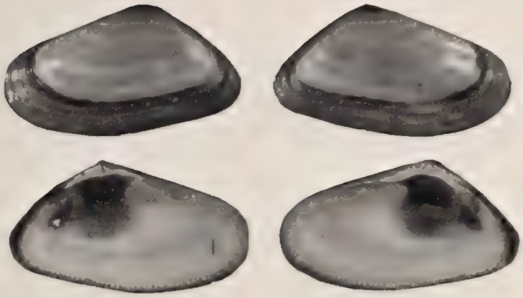

Figure *35*

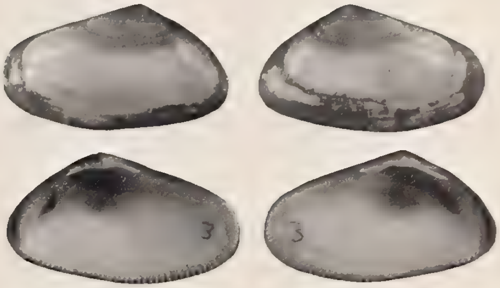

Figure *36*

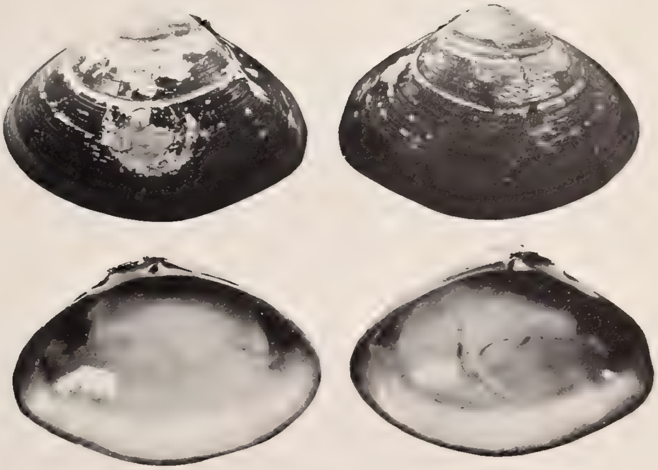

Figure *38*

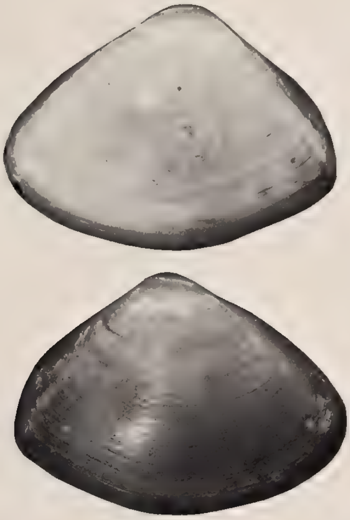

Figure *37*

Discussion: This species, which is named for Dr. Louie Marincovich of the United States Geological Survey, probably accounts for a good many records of *D. obesulus* (as *"D. radiatus"* or *"D. peruvianus"*). It appears to be what Römer (1870) illustrated as *D. peruvianus.*

Referred Material:

LACM 71-191	— Salinas, Guayas Prov., Ecuador
USNM 792354	— Punta Parinas, Piura Prov., Peru
ANSP 30834	— same locality (very worn; probably this species)
LACM 72-80	— 1 km south of Asia, Lima Prov., Peru
USNM 709963	— approximately the same station
ANSP 313474, 373598	— Pisco, Ica Prov., Peru—the type lot
LACM 67753	— same locality
AMNH 134595	— same locality
AMNH 149748	— same locality
AMNH 198972	— same locality
LACM 72-77	— Laguna Grande, Ica Prov., Peru
AMNH 198971	— Playa Miller, Arica, Tarapaca Prov., Chile

Iphigenia Schumacher, 1817

[**Type species:** *Donax laevigatus* Gmelin, 1791: by M]

Trigonal to ovate, with a conspicuous periostracum; smooth, without evident radial sculpture. Laterals weak, scarcely evident. Marine to brackish water.

The type species is from West Africa, and the genus also occurs in the western Atlantic. Recent papers on the biology of this genus are by Narchi (1972), who studied *I. brasiliensis* Lamarck, 1818, of the western Atlantic, and by Yoloye (1977) who examined an African species. In contrast to *Donax,* there are few species and only one in the eastern Pacific.

Iphigenia altior (Sowerby, 1833)

(Figures *37, 38*)

Capsa altior Sowerby, in Broderip & Sowerby, 1833
Sowerby, in Broderip & Sowerby, 1833: 196-197
Hanley, 1843a-1844: 86-87; 9 (plt. expl.); plt. 14, fig. 34
C. B. Adams, 1852a: 500-501 [1852b: 276-277]
Carpenter, 1857c: 42 [as *Iphigenia*]
Mörch, 1860: 193
Römer, 1869a: 152-154
Römer, 1870: 114-116; 120 (plt. expl.); plt. 21, figs. 1-4
Bertin, 1881: 119-120
Dall, 1909: 159-160, 274; 293 (plt. expl.); plt. 25, fig. 8
Smith, 1944: 63; fig. 822
Hertlein & Strong, 1949: 257
Hertlein & Strong, 1955: 202
Keen, 1958: 186, 187; fig. 458
Olsson, 1961: 346-347; 533 (plt. expl.); plt. 6, figs. 1, 1a
Keen, 1971: 239, 241; fig. 601
Iphigenia ambigua Bertin, 1881
Bertin, 1881: 120; plt. 4, figs. 4a-c
Hertlein & Strong, 1949: 257 [as = *I. altior*]
Hoffstetter, 1952: 42, 43; fig. 9
Iphigenia laevigata (Gmelin), *auctt., non Donax laevigata* Gmelin, 1791
Carpenter, 1857c: 42-43, 548
[*non* Gmelin, 1791: 3265]

Type Material & Localities:

C. altior—BM(NH) 198215, **lectotype** herein, the specimen measured by Sowerby, pair; length, 84.0 mm; height, 61.2 mm; thickness, 35.0 mm (Figure *37*). There is one **paralectotype** from this locality and another from Peru.
Gulf of Nicoya, Costa Rica (about 9°59′ N; 84°50′ W); 22 m; coarse gravel; H. Cuming.

I. ambigua—MNHN, holotype, pair; length, 56.1 mm; height, 40.2 mm; thickness, 25.5 mm (Figure *38*).
"Pacific Coast of Central America"; Marolles.

Description: Large for family, to 84 mm (**lectotype**); ovate, length 1.4 times height (sd ±0.1); moderately inflated, thickness 0.59 times height (sd ±0.03); anterior end a little longer, rounded; posterior end somewhat truncate; ventral margin evenly curved.

Concentric sculpture present only, consisting of fine, irregular ribs; tan to dark brown periostracum covering most of surface.

Left valve with a large anterior cardinal and a thin posterior cardinal; lateral teeth not evident. Right valve with a large, bifid posterior cardinal and a thin anterior cardinal; elongate anterior lateral present, a third of the way to anterior end; a much less conspicuous posterior lateral present, slightly closer to cardinals.

White to pale purple internally; externally white under periostracum.

Distribution & Habitat: Mazatlán, Sinaloa, Mexico (23° 12′ N; 106°25′ W) (USNM 715280), to Bayovar, Piura Prov., Peru (5°50′ S; 81°4′ W) (Olsson, 1961) (specimens not seen, but presumed correctly identified); intertidal area to 11 m (type of *C. altior* was reported from 22 m); mud. I have reviewed 60 lots.

Discussion: Olsson (1932) described *Iphigenia peruviana* (pp. 142, 242; plt. 13, fig. 5) from the Miocene of Peru. It is more elongate, and its ventral margin is more evenly curved than in *I. altior.* The western Atlantic *I. brasiliensis* Lamarck, 1818, is more elongate than *I. altior.*

Other Records

Several species have been described or reported from the eastern Pacific in error, the specimens involved actually being from other areas. This list also includes taxa that proved not to be donacids.

(1) *Donax affinis* **Deshayes**, 1855: 351, was described from the Red Sea. The type material has not been located in the British Museum (Natural History) (*in litt.*, S. Morris, 20 July 1981), and the species was not discussed by **Reeve** (1854-1855). **Tryon** (1869: 112) synonymized it with *D. contusus*, but no one else has done so, and there seems little reason to doubt the original locality.

(2) *Donax bellus* **Reeve**, 1854: plt. 16, fig. 41, was proposed for specimens reportedly from Acapulco. Instead, the specimens in the BM(NH) are really the Atlantic *Donax variabilis* Say, 1822. (A typographical error in **Tryon**, 1869: 112, made this taxon appear as *D. "vellus."*)

(3) **Menke** (1847: 118) reported *Donax compressus* Lamarck, 1818, from Mazatlán, Mexico, though with some question. His doubts were justified, for the species is Asian.

(4) *Donax flexuosus* **Gould**, 1853, was described from Santa Barbara, California, but this was in error. The type specimens (MCZ 169144 & 169145; USNM 611264) are, in reality, the Caribbean *Donax striatus* Linnaeus, 1767; a lectotype was designated and illustrated by **Johnson** (1964: 77; plt. 29, fig. 1).

Because of the use of the name *D. californicus* Conrad for the wrong Californian species, the name *Donax flexuosus* was used by some workers for the true *D. californicus.*

(5) **Reeve** (1854: plt. 5, fig. 27) described *Donax lamarckii* from an unknown locality, crediting the species to Deshayes, who never proposed it in print. **Römer** (1870: 63) synonymized the taxon with *Donax sulcatus* Philippi, 1847a, and suggested that it might be west American. **Carpenter** (1864b: 535) thought that it might be the same as *Donax flexuosus.* Most recent authors, however, have placed it in the synonymy of the Caribbean *Donax striatus* **Linnaeus**, 1767.

(6) *Donax lessonii* **Deshayes**, 1830 (p. 99), described from the Moluccas Islands, was synonymized by **Carpenter** (1857b: 246; 1857c: 59) and by **Dall** (1909: 284) with the Eastern Pacific *Tivela (Planitivela) planulata* (Broderip & Sowerby, 1830).

(7) *Donax nuculoides* **Reeve**, 1854 (plt. 8, fig. 59), proved to be the oldest name for a northwest American *Tellina*, now known as *T. (Cadella) nuculoides* (Reeve, 1854) (**Coan**, 1971).

(8) *Donax ovalinus* **Reeve**, 1854 (plt. 3, fig. 17) is a synonym of *Heterodonax pacificus* (Conrad, 1837) (**Coan**, 1973a).

(9) *Donax semistriatus* **Carpenter**, 1856: 230, described from Baja California, is a homonym of *D. semistriatus* Poli, 1795 (pp. 79-80, 257; ii; xiv (plt. expl.); plt. 19, fig. 17). It was renamed *D. carpenteri* by H. & A. **Adams**, 1856: 405. However, Carpenter's specimen was not west American and is, in fact, a specimen of the Mediterranean *D. semistriatus* Poli. The probable holotype is in BM(NH) 198223. It measures 19.8mm in length.

(10) *Donax stultorum* **Mawe**, 1823 (pp. 37, 40; plt. 9, fig. 7), is the original proposal of the common Californian *Tivela stultorum* (Mawe).

(11) *Donax sulcatus* **Philippi**, 1847a (p. 76), described from an unknown locality, was attributed to the west coast of Mexico by **Carpenter**, 1857b: 226, and to the west coast of Central America by **Römer**, 1870: 63. The original description suggests that this taxon is probably a synonym of the Caribbean *Donax striatus* Linnaeus, 1767.

(12) *Donax vellicatus* **Reeve**, 1855 (plt. 9, fig. 66), was proposed from an unknown locality. **Tomlin** (1926: 53) synonymized it with *Donax contusus*, itself here regarded a synonym of the eastern Pacific *Donax culter.* However, Reeve's species has been recognized as a valid Caribbean form (**Morrison**, 1971: 563-565; plt. 1 (p. 547), fig. V; plt. 2 (p. 549), fig. V).

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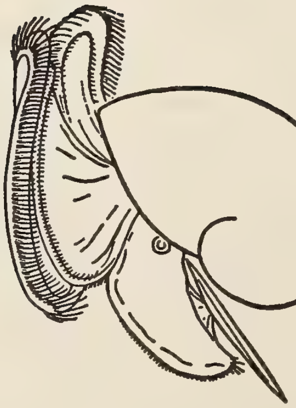

Reproductive Biology of *Colus stimpsoni*

(Prosobranchia : Buccinidae)

V. Nutritive Egg Formation[1]

BY

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(2 Plates; 4 Text figures)

INTRODUCTION

The overall reproductive strategy of an animal may be divided into various components, such as mode of fertilization, larval dispersal, and larval food supply. The emphasis placed upon a particular component of any reproductive strategy depends upon the relative significance of the different choices within that component. Within the element of food supply for the embryo, the most obvious and common method is that of yolk stored within the egg. The amount of yolk, in turn, may be coupled to modifications in the length of the developmental period or larval feeding structures. In addition to yolk, many invertebrate species provide additional sources of food for their developing young. The albumin surrounding and suspending the eggs within an egg capsule, for example, is often consumed by the larvae, providing additional nutriment. The strategy of providing supplemental food sources has reached a high level of specialization in many molluscan species in which the young emerge from the spawn mass as fully metamorphosed juveniles. In these species, of which the neogastropods are particularly well represented (Thorson, 1935, 1940, 1950; Fretter & Graham, 1962; Spight, 1976), hundreds or thousands of eggs are deposited within a single capsule but only a small percentage develop. The remaining undeveloped eggs are consumed by the larvae.

A variety of terms, such as "nurse egg" and "food egg," have been applied to those eggs which serve as additional nutritional sources (in this report the term "egg" implies any spawned female germ cell regardless of its developmental phase or whether or not it is fertilized). The term "nutritive egg" ("Nähreier" in the German literature and "oeufs nourriciers" in the French) is a more appropriate term for those eggs which are consumed by larvae and will be used throughout this report (see Davidson, 1976, and Raven, 1961, for surveys of accessory cell-oocyte arrangements and terminology).

The nutritive egg phenomenon is widespread within neogastropods. Approximately 75% of the Stenoglossans, 19% of the Taenioglossans and about 6% of the Rhipidoglossans are estimated to exhibit this phenomenon (Franc, cited in Dupouy, 1964). Early investigators of prosobranch nutritive egg determination and formation have presented two hypotheses to explain nutritive egg formation. One rests upon the existence of sperm dimorphism and atypical sperm (Ankel, 1924, 1930a; Portmann, 1931; Tuzet, 1930). This hypothesis suggests that nutritive eggs arise from eggs fertilized by atypical sperm (Portmann, 1926, 1927, 1930; Ankel, 1930b; O. Hyman, 1923, 1925). The alternative hypothesis suggests that nutritive eggs arise from dimorphic eggs, which are formed in a similar fashion to dimorphic sperm (Glaser, 1906, 1907; Burger & Thornton, 1935; Dupouy, 1964). Glaser (1906) further suggested that these atypical eggs were predetermined to form nutritive eggs. Staiger (1951) later proposed a third hypothesis, based somewhat on Glaser's *(op. cit.)* predetermination concept. This hypothesis postulated that nutritive egg determination is dependent upon a genetic system which may affect either the male or female gamete or the zygote and is of a multiple factor nature. All of these proposed mechanisms allow for a small percentage (1-2%) of nutritive eggs which may arise from pathological polyspermy or from non-fertilized eggs. Since atypical sperm are reported to be incapable of participating in egg penetration or amphimixis (Staiger, 1951; Thompson, 1973) and a semilethal genetic system may not be tenable because the

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[1] Contribution No. 112 from the Marine Science Institute, Northeastern University.

parental genome may not be transcribed during early embryogenesis (Davidson, 1976), the mechanism(s) involved in nutritive egg determination and formation remain obscure.

The buccinid *Colus stimpsoni* (Mörch, 1867) ranges from Maine to North Carolina along the Atlantic coast of North America. Females deposit about 4000 to 5500 eggs within a capsule, but only 1-4 larvae develop, with the remaining eggs becoming nutritive eggs (West, 1973). Male *C. stimpsoni* do not exhibit sperm dimorphism (West, 1978b), and oogenesis appears normal for all eggs, at least through germinal vesicle stage (West, 1981). The present study concerns egg maturation, early embryogenesis and nutritive egg formation to elucidate some factors involved in the nutritive egg phenomenon in *C. stimpsoni.*

MATERIALS AND METHODS

Materials and histological procedures used in this study were in accordance with those reported in the preceding papers of this series (West, 1978a, 1978b, 1979, 1981). Estimates of the number of eggs (including embryos) per capsule were made by opening recently deposited capsules and dispersing their contents in sea water in a 9 cm plastic petri plate which had 5 mm squares etched on the bottom. All eggs within 15 randomly selected grid squares were counted under a stereomicroscope and the average number of eggs per square calculated; the number of eggs per capsule was computed from this average. In one capsule all eggs were counted, since it contained only 200 eggs plus 3 embryos.

The number of young per capsule was determined from old capsules (4 months or older) in which all nutritive eggs had been consumed. Some old capsules (4 months or older) which were full of nutritive eggs but had no embryos or their fragments were scored as 0 embryos.

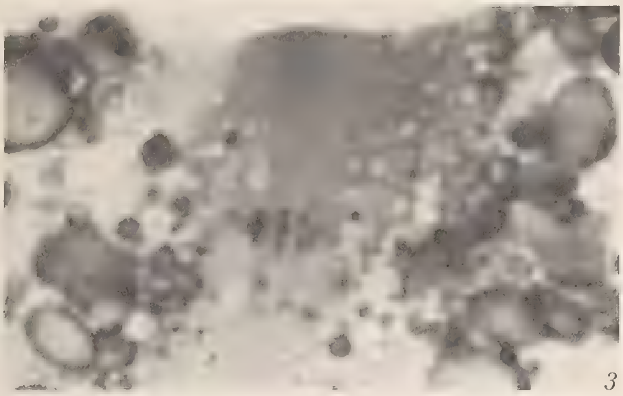
Capsules and the central regions containing eggs (egg chamber) were measured under a stereomicroscope with a millimeter ruler attached to the bottom of a petri plate and recorded to the nearest whole millimeter. For light microscopy, capsules at various times after deposition (20 min. to 5 months) were cut into halves or quarters with razor blades while immersed in fixative and processed by routine procedures (West, *opp. cit.*). For electron microscopy, eggs were removed from halved capsules by gentle pipetting while in primary fixative. Eggs were transferred into small vials and processed by routine procedures. Early cleavage stages were obtained from freshly deposited (30 min. to 6 hr.) capsules and individually processed for electron microscopy, using the same procedures as for nutritive eggs.

OBSERVATIONS

Spawning behavior, capsule morphology and oogenesis in *Colus stimpsoni* were considered in earlier papers (West, 1973, 1979, 1981) and will only be briefly reviewed here. In the laboratory, females deposit egg capsules throughout the year with increased activity from February to May. Capsules are deposited singly and attached to various hard substrata. They are circular to oval in surface view, measuring 10-16 mm in diameter ($\bar{X}$, 14.4 mm; SD, 1.9 mm), and hemispherical to subhemispherical (4-8 mm in height) in side view. Eggs are suspended in a viscous, albuminous fluid within the egg chamber. Egg chambers are also hemispherical (3-8 mm in height) in side view and circular, occasionally oval, in surface view, measuring 8-11 mm in diameter ($\bar{X}$, 9.6 mm; SD, 0.9 mm). Oocytes (180-190 μm in diameter) are ovulated in germinal vesicle stage. They are yolk laden and the deutoplasm consists of proteid and lipoid inclusions and large amounts of glycogen. Fertilization occurs in the posterior region of the pallial oviduct before pallial secretions are added to the egg mass.

Explanation of Figures *3* to *10*

Figure *3:* Metaphase I	× 900
Figure *4:* Metaphase I, polar view	× 500
Figure *5:* Mid Anaphase I. Note pair of dyads (arrow) preceding remaining dyads	× 500
Figure *6:* Late Anaphase I. The pair of dyads (arrow) reaches the poles before the others	× 500
Figure *7:* Telophase I	× 500
Figure *8:* Metaphase II	× 500
Figure *9:* Anaphase II	× 500
Figure *10:* First Zygote Prophase	× 500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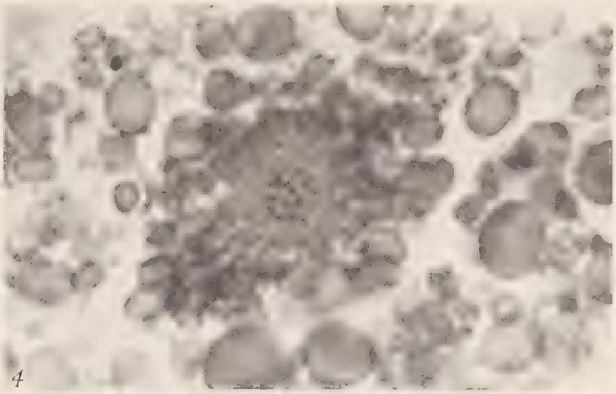
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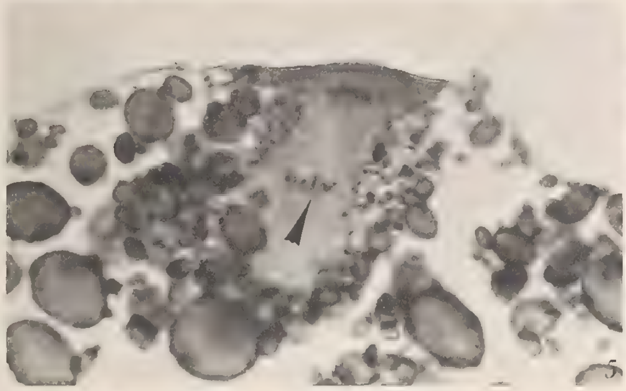
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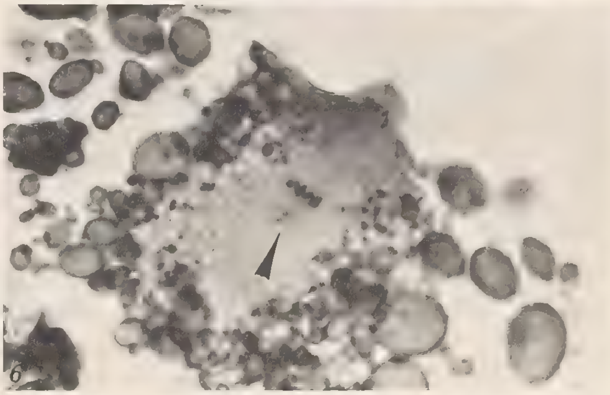
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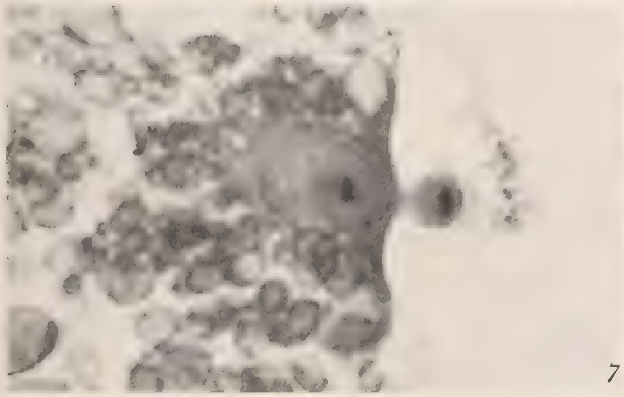
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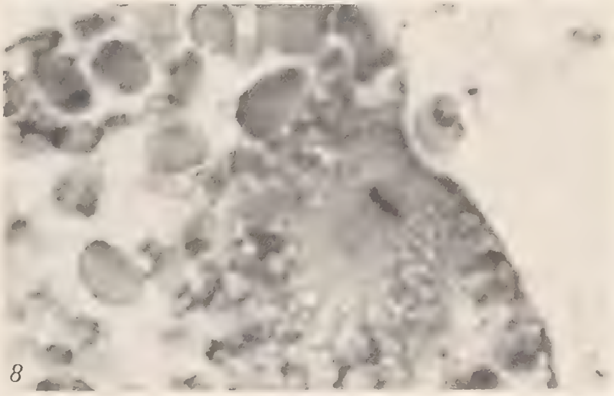
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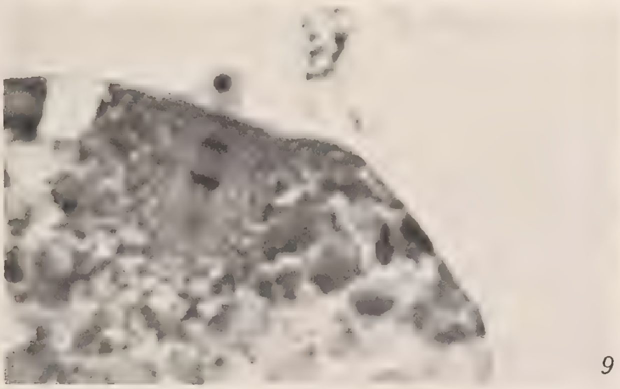
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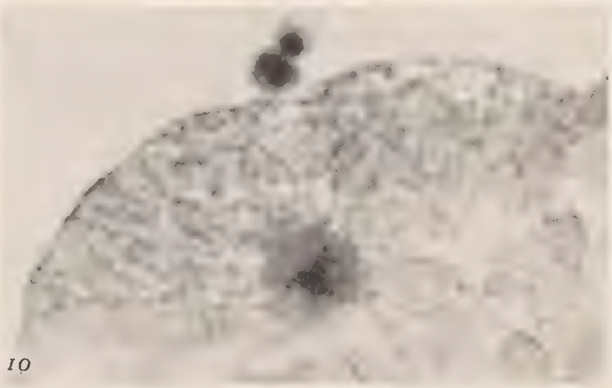
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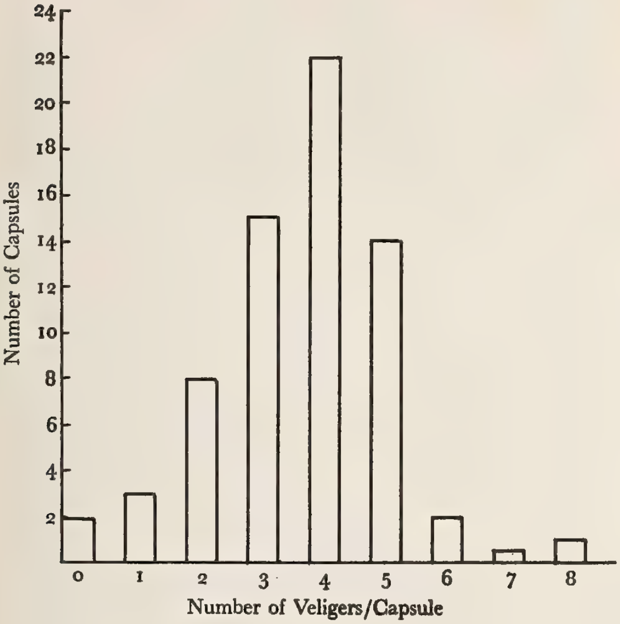


Figure 1

Frequency distribution of the number of juveniles per capsule. (X̄ = 3.6; SD, 1.4; range, 0-8; N, 67)

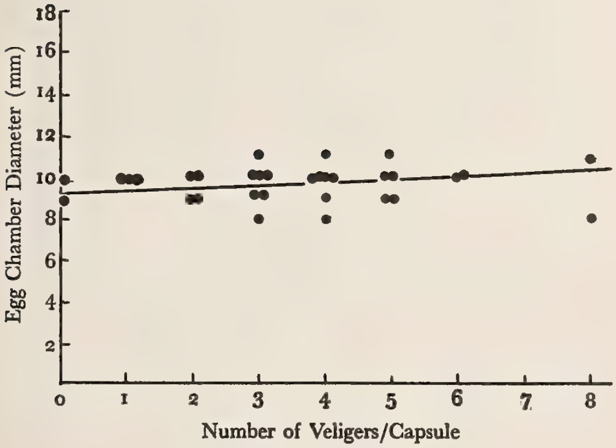


Figure 2

Relation of egg chamber diameter to the number of juveniles per chamber. (X̄, 4.3; SD_x, 1.7; Ȳ, 9.6; SD_y, 0.9; Y = 9.14 + 0.1X; r, .199; N, 20)

An average of 4668 eggs (SD, 579) are deposited within each capsule, with a range of 200-6800. Generally, however, capsules contain between 4000 and 5500 eggs. Veligers metamorphose as juveniles within the capsule and hatch 5-6 months after deposition. Generally, only 4 juveniles (X̄, 3.6; SD, 1.4; range 0-8) develop and hatch from each capsule. Figure 1 shows the frequency distribution of the number of juveniles per capsule counted in 67 capsules. On an average, 0.08% of deposited eggs are viable and hatch as juveniles. The number of embryos per capsule does not appear to correlate well with egg chamber size (r = 0.199) (Figure 2), nor with the number of eggs per capsule. One capsule containing the smallest number of eggs (200) had 3 embryos, while capsules with a larger number of eggs did not always contain the largest number of embryos.

EGG MATURATION AND KARYOKINESIS:

FERTILE EGGS

Fertilized oocytes within a common capsule undergo maturation divisions more or less synchronously. Oocyte maturation is initiated about ½ hour after spawning and metaphase I occurs within 45-60 minutes after capsule deposition. Metaphase I chromosomes (Figures *3* and *4*) are short, highly condensed, and the largest ones are distributed around the periphery of the metaphase plate with the smaller chromosomes more centrally arranged (Figure *4*). Counted only from sectioned material, there are 20-23 tetrads at Metaphase I. Meiosis I proceeds rapidly and essentially all oocytes within a capsule attain anaphase I about 1 hour after deposition. Chromosomal behavior during anaphase I is similar to that reported for other neogastropods. Two small dyads slightly precede the remaining dyads (Figure *5*) and reach the poles before the others (Figure *6*); but all dyads are clustered at the poles at telophase (Figure *7*). Advancement to metaphase II (Figure *8*) proceeds quickly with no visible intervening nuclear membrane. Monad behavior during anaphase II (Figure *9*) is similar to that of dyads. Second polar body formation occurs about 2-2½ hours after capsule deposition. Polar bodies are more or less equal in size (10-15 μm in diameter) and their relative positions to one another are variable. The second polar body may be directly beneath the first, or to one side of it. The male pronucleus forms at the onset of female pronuclear formation. The male pronucleus migrates toward the female pronucleus, and they come to lie in a relatively yolk-free area of cytoplasm in the animal pole region. Pronuclei are 20-30μm in diameter. Following juxtaposition and breakdown of pronuclear envelopes, the chromosomes condense (Figure *10*) and migrate to the metaphase plate (*Ascaris*-type fertilization). First zygote karyokinesis (Figure *11*) occurs about 3-3½ hours after capsule deposition and follows a normal spiralian pattern. Essentially all eggs within a capsule complete karyokinesis; however, a few of the eggs abort in various stages of meiosis or zygote karyokinesis. Some zygotes are apparently polyspermic as they present various abnormalities in chromosomal distribution during anaphase. Approximately 1-2% of the eggs within a capsule show these anomalies. Second karyokinesis occurs prior to first cytokinesis and about 98% of the eggs in a capsule have 4 nuclei per cell within 4-5 hours after deposition. Differences between embryos and nutritive eggs appear with first cytokinesis. Embryos undergo cytokinesis, whereas nutritive eggs do not. Embryogenesis appears to be an "all or none" phenomenon in which only those eggs that will give rise to embryos undergo both karyokinesis and cytokinesis.

NUTRITIVE EGGS

Nutritive eggs constitute the greatest percentage (99.9% or more) of the eggs within a capsule. They undergo a variable number of nuclear divisions, in synchrony with karyokinesis of embryos, before karyokinesis ceases. As a consequence, they contain a variable number of nuclei ranging from one to as many as 20 per cell. Nuclei are generally of equal size in those eggs with few (2-8) nuclei; however, in those with many nuclei, they are of unequal size.

Nuclei of nutritive eggs are generally situated near the oolemma in the animal pole region (Figure *12*) and are spherical to irregular in outline. Chromatin is finely granular in electron micrographs (Figure *13*), and the nuclear envelope is perforated by numerous pores. Each nucleus contains a single nucleolus (Figure *12*).

Nutritive egg cytoplasm is dominated by deutoplasmic inclusions (Figure *13*). Cytoplasmic fine structure of nutritive eggs is very similar to that of postvitellogenic eggs (*c.f.* West, 1981); however, there are a few differences. The mitochondrial matrix of nutritive eggs is more electron dense than in postvitellogenic oocytes. There is also a considerable decrease in the number of ooplasmic vesicles and an increase in the number of profiles of smooth endoplasmic reticulum in nutritive eggs. The cortex is thin and not well delineated.

Fertile Eggs: The earliest observable distinguishing characteristic between viable embryos and nutritive eggs is the two-cell stage. First cytokinesis is equal, holoblastic and occurs after the second nuclear division which results in each blastomere having 2 nuclei. The third karyokinesis occurs before second cytokinesis and each blastomere has 4 nuclei before the 4-cell stage. By the 8-cell stage, however, each blastomere contains one nucleus and karyokinesis is in tempo with cytokinesis.

In the 2-cell stage, blastomere nuclei are generally situated near the plasmalemma in the vicinity of the polar bodies. In later 2-cell stages, two nuclei are located medially, near the cell membrane separating the blastomeres, and the other two nuclei of each blastomere are situated more apically, subjacent to the cell membrane in the animal pole (Figure *14*).

Nuclei are polymorphic and each contains a single nucleolus (Figure *14*). The cytoplasmic fine structure of blastomeres is similar to that of nutritive eggs. The animal pole cytoplasm contains less yolk and lipid droplets than the vegetal pole, and cellular organelles are more abundant in this region. In addition, the animal pole cytoplasm, subjacent to the cell membrane in the polar body region, contains a number of electron dense particles (Figure *15*).

Explanation of Figures *11* to *15*

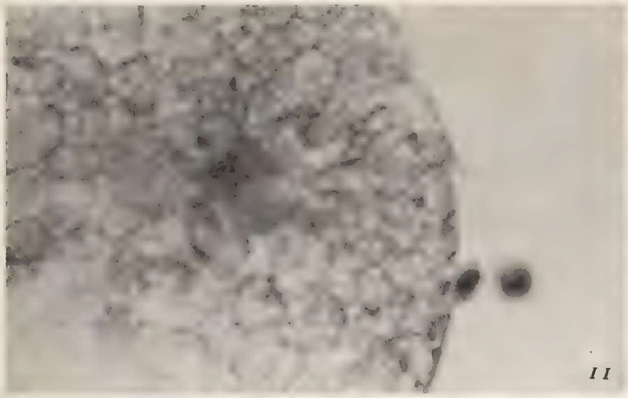
Figure *11:* First Zygote Anaphase × 500

Figure *12:* Early nutritive egg, animal pole region. Note the four nuclei with one nucleolus each × 700

Figure *13:* Section through animal pole region of nutritive egg. N–nucleus; L–lipoid yolk; P–proteid yolk × 20000

Figure *14:* Section through blastomere animal pole of 2 cell stage. Each blastomere at this stage contains four nuclei (N) each with one nucleolus × 3500

Figure *15:* Electron-dense particles (arrows) in animal pole region of 2-cell blastomeres × 21000



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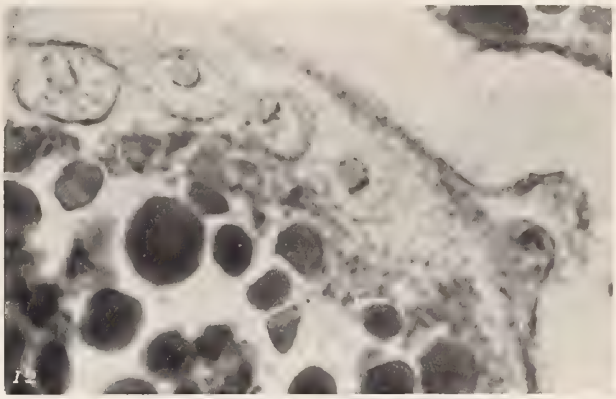

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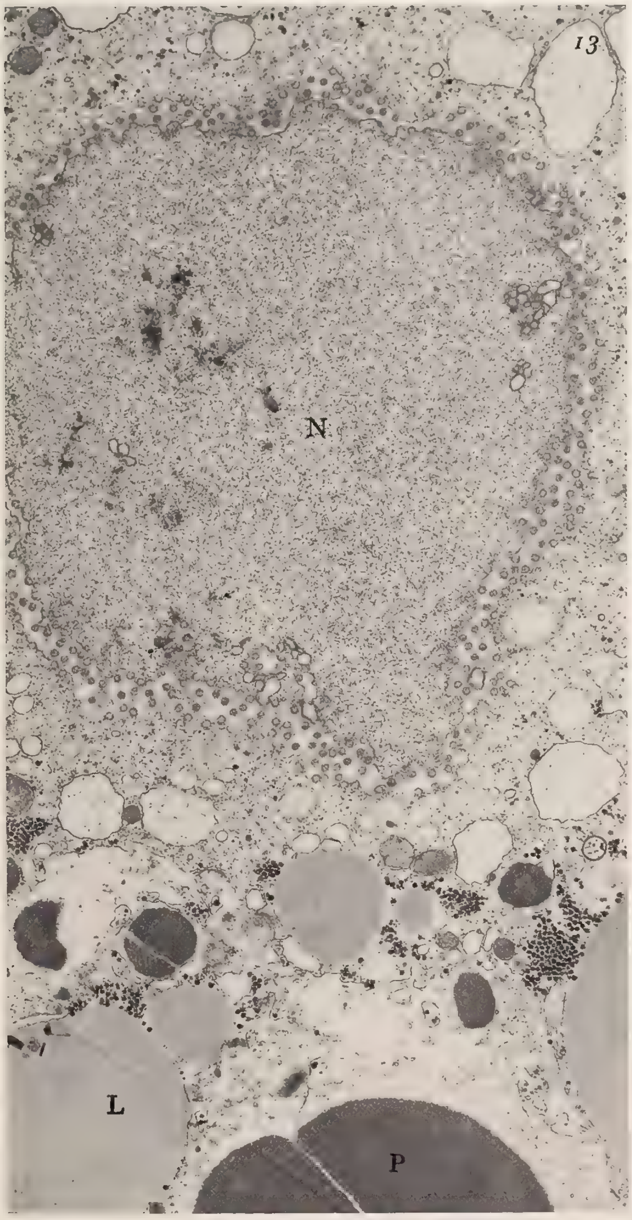

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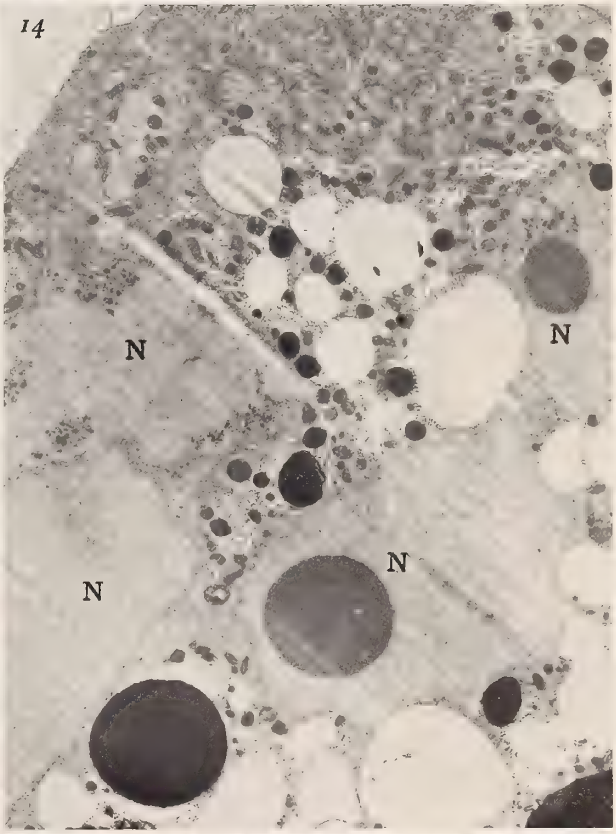

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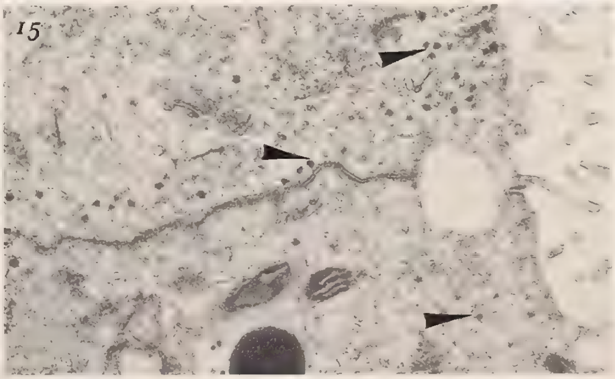

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These particles are about 40 nm in diameter, slightly larger than glycogen granules, and homogeneous in appearance. The composition and function of these particles is unknown.

Polar lobe formation is normal in embryonic sequence. However, the precise time after capsule deposition is unknown. Subsequent embryonic development is similar to that of other neogastropods.

The distribution of embryos within a capsule is variable. Early embryos may be adjacent to one another, or widely distributed within a capsule. Viable eggs cannot be distinguished from nutritive eggs until first cytokinesis.

DISCUSSION

Fertilization is a multistep phenomenon which is initiated with the interactions of egg and sperm and terminates in the association of paternally and maternally derived chromosomes (Wilson, 1925). Fertilization generally follows ovulation, and eggs may be inseminated before, during or after oocyte maturation. Essentially 4 classes of eggs have been distinguished (Wilson, 1925; Austin, 1965; Longo, 1973) based upon the stage of meiosis when sperm incorporation occurs: Class I eggs are inseminated in female pronuclear stage (*e.g.*, cnidaria and some echinoderms), Class II in second metaphase (*e.g.*, mammals), Class III in first metaphase (*e.g.*, some polychaetes), and Class IV eggs in germinal vesicle stage (*e.g.*, some molluscs). Further, Wilson *(op. cit.)* recognized that the association of maternally and paternally derived chromosomes occurs in either of two modes: pronuclei may fuse forming a single, membrane-limited zygote nucleus before first cleavage ("sea urchin"-type of fertilization), or both male and female pronuclei, following their juxtaposition, give rise to two closely associated groups of chromosomes which migrate to the first zygote metaphase plate without an intervening single zygote nucleus (*"Ascaris"*-type of fertilization).

Generally, the egg cell becomes arrested at certain phases of meiosis in the ovary. The egg cell cycle is then stimulated by hormonal action or through ovulation and then attains another arrestment stage. Sperm incorporation or activation then triggers the resumption of meiosis and allows cleavage to begin (Meyerhof & Masui, 1977, 1979; Ziegler & Morrill, 1977; Hara, *et al.*, 1980; Davidson, 1976). These blocks have been suggested to reside in cytoplasmic components, being designated as cytostatic factor(s) (Meyerhof & Masui, 1977), and under maternal genetic control (Von Borstel, 1957). In general, eggs attain a state of arrest in various specific stages of meiosis before ovulation. Ovulation may remove this block and the eggs attain another state of arrestment which is unblocked by insemination. Thus, in general, insemination is the final trigger which initiates the final stages of meiosis and allows cleavage under normal conditions.

Nutritive Egg Formation: The present cytological evidence suggests that in *Colus stimpsoni* the majority of nutritive eggs undergo the normal sequence of events from sperm incorporation to the completion of zygotic karyokinesis. However, these eggs fail to undergo cytokinesis. A small percentage of the nutritive eggs (about 2%) exhibit abnormalities generally encountered in embryology such as anarchic cleavage, abnormal female meiotic divisions, and eggs not inseminated. A few of these eggs also demonstrate failure of typical pronuclear migration.

The majority (about 97%) of the nutritive eggs follow the scheme diagrammed in Figure 16. The few (about 0.1%) anarchic embryos observed are probably the result of poly-

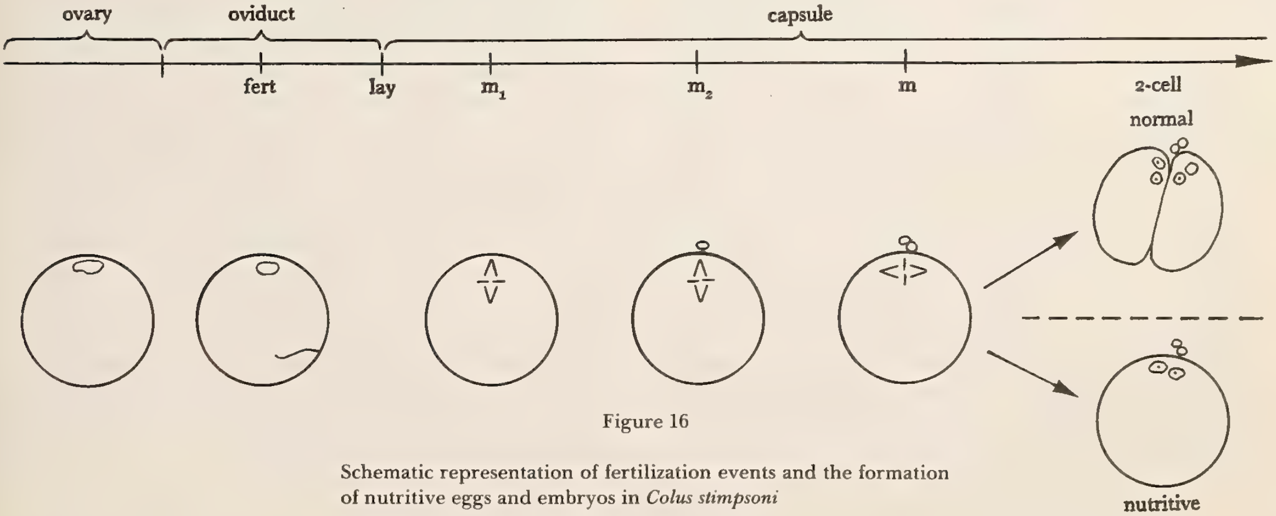

Figure 16

Schematic representation of fertilization events and the formation of nutritive eggs and embryos in *Colus stimpsoni* spermic zygotes in which the normal sequence of events occurs, but because of polyspermy, anarchic cleavage ensues. Those eggs (about 0.5%) which were observed to have more than 2 pronuclei are also a result of polyspermy but, presumably, would not complete cytokinesis. In the egg capsules investigated, a greater number of eggs with 3 or more pronuclei were observed than the number of anarchic embryos. This suggests that many of the polyspermic zygotes also fail to undergo cytokinesis. Staiger (1951) has shown that eggs incorporating 2 spermatozoa undergo normal development as one of the spermatozoa remains inactive in the ooplasm and the other fertilizes the egg (physiological polyspermy). Physiological polyspermy is usually not pathological and results in the suppression of supernumerary male pronuclear formation and only one male pronucleus forms. By contrast, pathological polyspermy inevitably leads to abnormal embryonic development. Physiological polyspermy has been reported in a few gastropods (Raven, 1958). Generally, however, gastropods exhibit pathological polyspermy (Staiger, 1951; Fretter & Graham, 1962).

Evidence from the present study indicates that the viable zygotes undergo more than one nuclear division before cytokinesis which results in each blastomere having more than one nucleus. The time lag between cytokinesis and karyokinesis is shortened at the 8-cell stage such that each blastomere contains only one nucleus. In egg capsules which contain early veligers, the majority of nutritive eggs have 4 nuclei which are equal in size and each nucleus has one nucleolus. However, in capsules which contain pediveligers (see West, 1973, for description of larval stages) the number of nuclei per egg increases and these nuclei are of different sizes which is probably the result of abnormal karyokinesis in these older eggs (about 3-4 months after capsule deposition). In *Colus stimpsoni* there is no significant morphological difference between nutritive eggs and the blastomeres of the 2-cell stage. Thus, nutritive eggs apparently fail to undergo cytokinesis.

In species of prosobranchs which exhibit the nutritive egg phenomenon, all the eggs within a capsule are deposited under identical conditions. In those species which have been studied, sperm incorporation occurs as the eggs pass down the oviduct and are deposited in a common egg capsule (Fretter & Graham, 1962; Staiger, 1950, 1951). However, a great majority (90% or more) of the eggs discontinue their development at various stages of embryogenesis. The stage at which this arrestment occurs is variable between species and, in some cases, within the same egg capsule. Figure 17 schematically represents the various stages of nutritive egg arrestment in prosobranchs which have been studied.

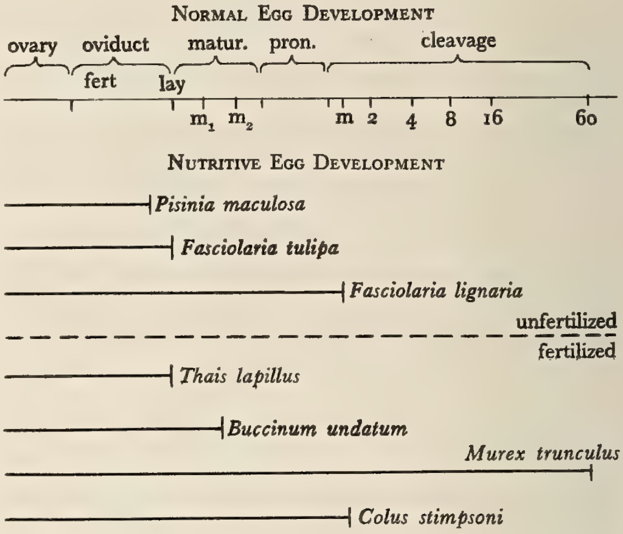

Figure 17

Schematic representations of nutritive egg development in various species of gastropods. (From Staiger, 1951; Fretter & Graham, 1962; Portmann, 1926, 1927, 1930; Dupouy, 1964)

According to Staiger (1951), nutritive eggs result from eggs in which sperm incorporation occurs as well as those in which it does not occur. Species in which the nutritive eggs usually do not have sperm incorporation, as in *Pisania maculosa* (family Buccinidae), *Fasciolaria tulipa* and *F. lignaria* (family Fasciolariidae), sperm incorporation may occur, but these eggs usually abort development in various stages of meiosis and even as late as metaphase of the first zygote mitosis (Staiger, 1950, 1951). In other species the nutritive eggs usually have sperm incorporation, as in *Buccinum undatum* (family Buccinidae), *Thais lapillus* and *Murex trunculus* (family Muricidae) (Portmann, 1926, 1927, 1930; O. Hyman, 1923; Staiger, 1951). In *Buccinum undatum,* the eggs do not undergo cleavage as has been recorded here for *Colus stimpsoni.* However, in *Thais lapillus* and *Murex trunculus* the nutritive eggs undergo abnormal cleavage.

In those species in which oogenesis has been studied, no definite atypical oocyte line has been demonstrated (Kostitzine, 1949; Raven, 1961). Dupouy (1964) has shown that chromosome elimination occurs during meiosis in *Theodoxus fluviatilis,* and he suggested that this behavior is similar to the atypical spermatozoa found in other gastropods. However, these eggs do not have sperm incorporation and undergo a "vegetative" maturation. Further, these eggs do not constitute the bulk of nutritive eggs in *T. fluviatilis.*

Portman (1926, 1927, 1930), O. Hyman (1923), Dupouy (1964) and Burger & Thornton (1935) have suggested that nutritive eggs are a result of otherwise normal eggs which are fertilized by atypical sperm. However, Staiger (1951) and Thompson (1973) suggested that atypical sperm do not participate in egg fertilization. Dupouy *(op. cit.)* also suggested that in those species which do not demonstrate sperm dimorphism, nutritive eggs are a result of certain undefined biochemical factors which are intrinsic in the egg and are obscured by internal fertilization. Staiger (1951) postulated that nutritive egg formation is dependent upon a genetic system which may affect either male or female gamete or the zygote. This system is of a multiple-factor nature and the various possible genetic combinations result in lethal zygotic combinations. This multiple-factor system would account for the different stages of arrest seen in egg capsules.

Generally, the sequence of events which follow sperm incorporation or the artificial activation of eggs does not necessarily require the participation of the paternal genome (Davidson, 1976). Once the sequence of meiotic divisions and first cleavage is initiated, evidence suggests that the sequence is completed even in the absence of the male pronucleus (Raven, 1958; Rappaport, 1973). Thus, there is no evidence for a self-sterility type genetic system which necessarily involves a paternally derived genome in the zygote. Generally it appears that the nutritive eggs in prosobranchs result from otherwise normal eggs which are inseminated by normal sperm but do not follow the normal sequence of events which occur following sperm incorporation and the ensuing cleavage. The mechanism which is responsible for the multiple series of events which become sequentially functional during fertilization and first cleavage is not properly activated or is defective at one or more points.

As previously stated, the sequence of events beginning with sperm incorporation, through meiotic division and formation of polar bodies, and terminating in first cleavage, is a multiple series of activities which become functional sequentially. Some eggs which are artificially activated proceed with maturation and then attain a state of arrest while eggs of other species reach other levels of maturation before arrest. In normally fertilized eggs which are chemically delayed, evidence suggests that the process of fertilization and maturation is due to a progressive change in the state of the cytoplasm (Raven, 1958). Longo & Anderson (1969a, 1969b) suggest that the differences in morphology of the first and second polar bodies and the transformation exhibited by the maternal chromatin during the meiotic events involve various cytoplasmic factors which influence the physiological integrity of the maternal chromatin. Evidence suggests that cytoplasmic factors are involved in the sequence of events in fertilization and cleavage (Marshland, 1958). Further, the proper sequence of events must occur and the proper stimulus must be present.

Nutritive eggs could possibly arise through cytokinetic inhibitory substances secreted by developing embryos. That is, the first eggs to undergo cytokinesis, and thus the viable embryos, secrete substances which inhibit surrounding eggs from undergoing cytokinesis. However, because of the random and varied distribution of embryos within a capsule and since some capsules contain only nutritive eggs, this notion is not tenable. Therefore, it is hypothesized, based on the present study and in view of other evidence, that the determinative factor(s) in the formation of nutritive eggs in *Colus stimpsoni,* rests on cytoplasmic factors contained within the egg. It is suggested that these factors are synthesized by the oocyte before ovulation and are under maternal genetic control. Following ovulation, the mechanism is activated and the proper events occur. However, in *C. stimpsoni* it is suggested that the factor for final cytokinesis is abnormal or absent. Thus, the eggs behave normally before they arrest prior to cytokinesis. In other species, eggs may be activated and the proper sequence initiated, but one of the factors, for example pronuclear formation, is defective and the development terminates without first zygote karyokinesis, such as in *Buccinum undatum.*

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Special thanks to Drs. N. W. Riser and M. P. Morse for their encouragement and suggestions during this study. Many thanks to Drs. E. Anderson, C. H. Ellis and H. Lambert for their many helpful comments. Much appreciation goes to Dr. K. J. Eckelbarger for reading the manuscript. Part of this study was submitted in partial fulfillment of the requirements for the Ph.D. Degree at Northeastern University. This study was supported in part by HEW Grant RR 01743.

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The Chiton Fauna of the Revillagigedo Archipelago, Mexico

BY

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(2 Plates; 10 Text figures)

THE REVILLAGIGEDO ARCHIPELAGO comprises the three islands of San Benedicto (19°18′N; 110°49′W), Socorro (18°45′N; 111°00′W) and Clarion (18°22′N; 114°45′W), and the nearby rocks of Partida and Alijos (Figures 1, 2, 3, 4). Volcanic in nature, the Revillagigedos stand isolated in the Pacific some 400km south of the tip of Baja California, 650km west of the Mexican mainland, 1000km north of Clipperton island, and over 5000km east of the Hawaiian islands. Scientific expeditions to the Revillagigedos have been relatively few and concerned mostly with the marine vertebrates, terrestrial biology and geology (JORDAN & MCGREGOR, 1899; SNODGRASS & HELLER, 1905; HANNA, 1926; RICKER, 1959; BRYAN, 1964; RICHARDS, 1966; CHAN, 1974). Thus, the marine invertebrate fauna of Revillagigedos, the mollusks in general, and the chitons in particular have remained poorly known. Information on the chiton fauna of the Revillagigedos has been limited to PILSBRY'S (1898: 51) brief report on 3 species of chitons collected by R. C. McGregor at Socorro. STRONG & HANNA'S (1930) list of 61 marine mollusks from Socorro and Clarion did not include a single chiton species.

This paper reports on data obtained in two collecting trips to the Revillagigedos aboard the R/V *Baja Explorador.* With a group of biologists led by Dan Gotshall, California Department of Fish and Game, intertidal exploration and SCUBA-diving at San Benedicto and Socorro (3-8 November 1979, collecting station numbers AJF 488-510) and Clarion (26-30 November 1981, AJF 640-648) produced a reasonably satisfactory first sampling of the chiton fauna of the Revillagigedos. The observations have since been supplemented with data and material available at the California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), National Oceanic and Atmospheric Administration (NOAA), Academy of Natural Sciences of Philadelphia (ANSP), United States National Museum of Natural History (USNM) British Museum (Natural History) (BMNH), and in the private collection of Antonio J. Ferreira (AJF station numbers on file at CAS).

Eight species of chitons are here recognized in the Revillagigedo Archipelago, two new to science:

Lepidochitona keepiana Berry, 1948
Ischnochiton muscarius (Reeve, 1847)
Ischnochiton rugulatus (Sowerby, 1832)
Stenoplax corrugata (Carpenter *in* Pilsbry, 1892)
Lepidozona ***clarionensis*** Ferreira, spec. nov.
Lepidozona ***rothi*** Ferreira, spec. nov.
Chaetopleura scabricula (Sowerby, 1832)
Chiton articulatus (Sowerby, 1832)

SYSTEMATIC TREATMENT

POLYPLACOPHORA Gray, 1821

Neoloricata Bergenhayn, 1955

Ischnochitonina Bergenhayn, 1930

LEPIDOCHITONIDAE Iredale, 1914

Lepidochitona Gray, 1821

Type-species: *Chiton marginatus* Pennant, 1777 [= *Chiton cinereus* Linnaeus, 1767], by M.

Lepidochitona keepiana Berry, 1948
(Figures 5, 6)

Lepidochitona keepiana BERRY, 1948: 13-15—MCLEAN, 1969: 61; fig. 34.3 (reprinted, 1978)—BURGHARDT & BURGHARDT, 1969: 19; plt. 2, figs. 24-25—ABBOTT, 1974: 397—FERREIRA, 1982: 107-108; figs. 28-33

[?] *Lepidochitona* sp., SMITH, 1963: 148

"Lepidochitona dentiens (Gould)" BERRY, 1922: 410, 415, 438-439; tbl. 1; plt. 1, figs. 7-9 (fossil) [not *Lepidochitona dentiens* (Gould, 1846), *fide* BERRY, 1948: 15]

"Ischnochiton (Trachydermon) dentiens (Gould)" PILSBRY, 1892: 73-74; plt. 8, figs. 61-65; 1894: 65; plt. 15, fig. 26 [not *Lepidochitona dentiens* (Gould, 1846), *fide* BERRY, 1948: 15]

Type Material and Type Locality:

Lepidochitona keepiana Berry, 1948: Holotype (S. S. Berry private colln., Redlands, California, Cat. no. 11992); para-

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Figure 1

Location of the Revillagigedo Archipelago, Mexico

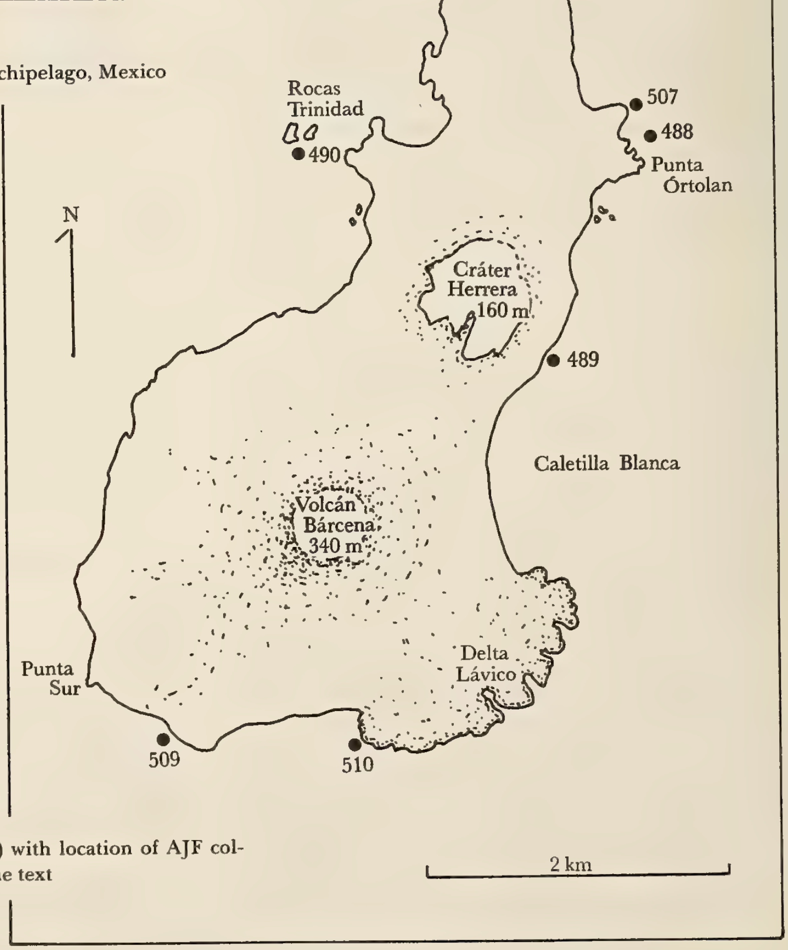

Figure 2

San Benedicto Island (19′N; 118°49′W) with location of AJF collecting station numbers mentioned in the text

Figure 3

Socorro Island (18°45′ N; 111°00′ W) with location of AJF collecting station numbers mentioned in the text

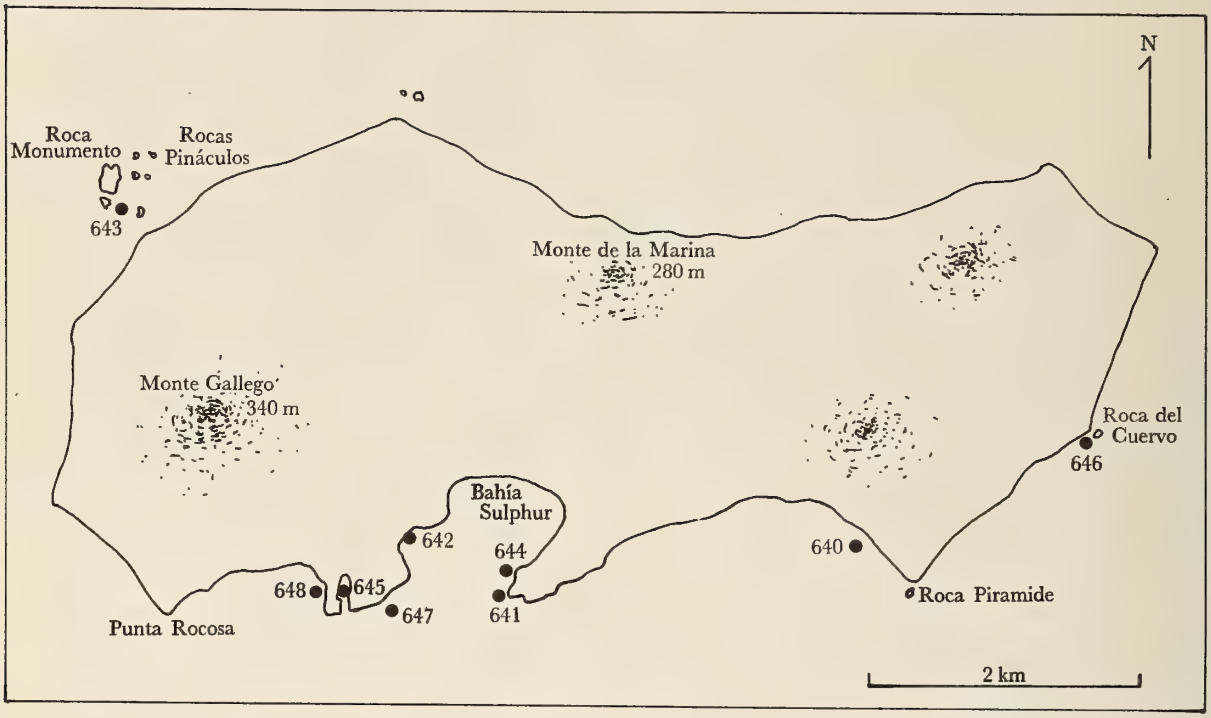

Figure 4

Clarion Island (18°22′ N; 114°44′ W) with location of AJF collecting station numbers mentioned in the text

types (S. S. Berry colln., Cat. no. 3978; SDNH T.S.18; USNM; BMNH; A. G. Smith colln. [now at CAS]; E. P. Chace colln.) *fide* Berry (1948); locality, Newport Bay, Orange County, California [33°37′ N; 117°56′ W]

Material Examined: SOCORRO: (ANSP 72499), 3 specimens, *leg.* R. C. McGregor [cited in Pilsbry, 1898: 51].

Description: Pilsbry (1898) reported the species at Socorro Island under the name of *dentiens* Gould, 1846, as "Rather small, black with indistinct dirty yellowish speckling and the usual sutural dots. Gills ambient, 15 on the right, 13 on the left side." (p. 51). The extant material (ANSP 72499) is accompanied by a museum label which reads, in part "T. dentiens Gld. / Socorro Island / R. C. McGregor ! off W. Mexico"; it consists of 3 specimens, dry, two intact but curled, one reduced only to the disarticulated valves. Large intact specimen, estimated length, 10 mm, width (including girdle), 7.2 mm. All specimens dark grayish green, with some vaguely defined lighter spots at posterior edge of valves i and ii. Carinate, slightly beaked valves with straight side slopes; curved outline. Tegmental surface shagreened, with very minute granules better defined in central areas where they tend to align themselves in longitudinal rows (Figure 5); sculptureless otherwise. Lateral areas hardly defined to obsolete, indicated only by slightly noticeable change in direction of tegmental granules. Mucro well defined, central to slightly anterior; postmucro concave. Disarticulated specimen's articulamentum light blue; valve i, 1.6 mm long, 4.3 mm wide; valve viii 4.0 mm wide. On valve viii, sinus 0.8 mm wide; rectangular sutural laminae, 1.7 mm wide; sinus/sutural laminae, 0.46. Insertion teeth sharp, relatively regular, directed outward on viii; slits, 11-1-10, followed by slit rays defined by a line of minute orifices; at anterior edge of articulamentum of intermediate valves another row of orifices arranged as a second, spurious slit-ray. Eaves moderately spongy. Holobranchial. Girdle's upper surface dark greenish gray with sandy appearance, covered with minute scales, averaging 70 μm long, 38 μm wide, with a marginal fringe of longitudinally striated spicules, 140 μm long, 25 μm thick; undersurface with imbricated, transparent, spiculoid scales about $50 \times 12\,\mu$m.

Although the specimens differ slightly from mainland specimens (see Ferreira, 1982), their identification as *Lepidochitona keepiana* is unequivocal.

Distribution: The known geographical range of *Lepidochitona keepiana* extends from Otters' Point, Monterey Bay, California (36°38′N; 121°55′W) to Rancho Socorro, Baja California, Mexico (30°20′N; 115°45′W). Berry's (1948) report of the species at San Ignatio Lagoon, Baja California, Mexico (26°42′N) has not been corroborated (Ferreira, 1982). Pilsbry's (1898) cited specimens (ANSP 72499) would place the species at Socorro Island, Revillagigedos, Mexico (18°45′N; 110°58′W).

Bathymetric range of mainland specimens, 0-10m.

Remarks: The presence of *Lepidochitona keepiana* at the Revillagigedos, if confirmed, constitutes an extraordinary eight degrees of southward range extension, and an adaptation to radically different thermal conditions. The verified geographical range of *L. keepiana* along the California to Baja California coast (Ferreira, 1982) corresponds to mean surface water temperatures between 12°C and 20°C. This fact makes the presence of *L. keepiana* at Socorro an apparent anomaly, since the habitual temperature range for *L. keepiana* falls outside the 21-28°C range of mean water surface temperatures at the Revillagigedos (Robinson, 1973; NOAA charts of monthly mean values of sea surface temperature) (Figure 6).

ISCHNOCHITONIDAE Dall, 1889

Ischnochiton Gray, 1847a

Type species: *Chiton textilis* Gray, 1828, by SD (Gray, 1847b). The re-definition of the genus proposed by Kaas (1979: 856) is here adopted, and the name *Simplischnochiton* Van Belle, 1974, suppressed as a synonym.

Ischnochiton muscarius (Reeve, 1847)

(Figures 6, *7, 8*)

Chiton muscarius Reeve, 1847: sp. & fig. 164; plt. 24

Ischnochiton muscarius (Reeve). Keen, 1958: 521, Amphineura, fig. 16 (with syn. *Lepidopleurus macandreae* Carpenter)

Radsiella muscaria (Reeve). Thorpe *in* Keen, 1971: 869, Polyplacophora, fig. 17 (with syn. *L. macandreae* Carpenter)

Lepidopleurus macandreae Carpenter, 1857c: 196-197, 500 (as *macandrei* on p. 196-197)—Brann, 1966: 45; plt. 20, fig. 255 —Keen, 1968: 433-434; plt. 59, fig. 93

Type Material and Type Locality:

Chiton muscarius Reeve, 1847: Types unascertained; locality not stated

Lepidopleurus macandreae Carpenter, 1857: Holotype, Carpenter collection Tablet 904 (BMNH); locality, Mazatlan, Sinaloa, Mexico (23°13′N; 106°25′W)

Material examined: SOCORRO: 13 specimens, Caleta Binmer, intertidal zone (AJF 497) (Figures *7, 8*).

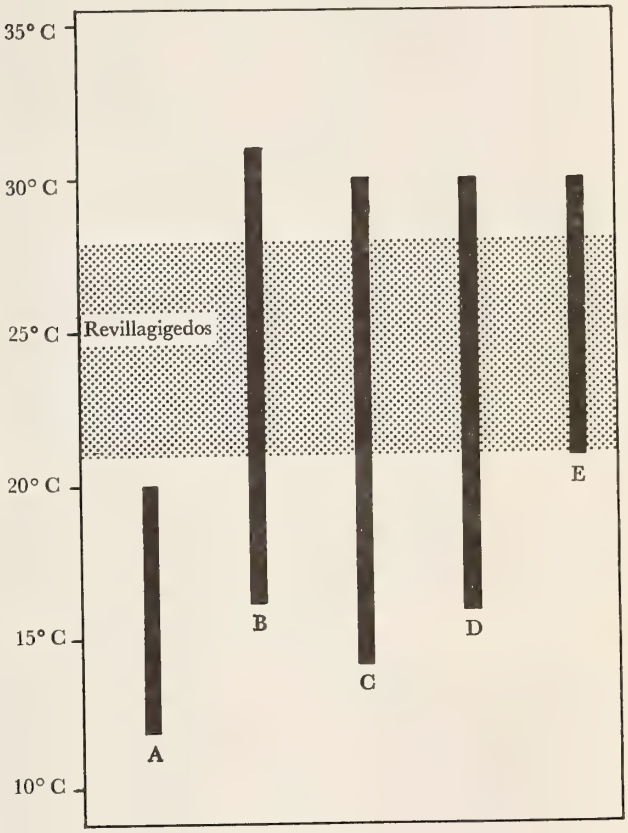

Figure 6

Range of mean water surface temperatures at the Revillagigedos versus range of water surface temperatures at the mainland for chiton species assumed common to both areas. Water temperature data from Robinson (1973) and NOAA charts. Chiton species: A = *Lepidochitona keepiana;* B = *Ischnochiton muscarius;* C = *Ischnochiton rugulatus;* D = *Chaetopleura scabricula;* E = *Chiton articulatus*

Description: The specimens, preserved dry and flat, are grayish-brown, speckled with tawny brown and cream; 10 to 19.5mm long; width/length average 0.56. Carinate; valves posterior edge straight, not beaked; mucro central to slightly anterior; postmucro straight to slightly concave. Tegmental surface microgranular; central areas sculptureless; lateral areas with microgranules V-shaped in the center, defining 5-8 tenuous radial riblets; anterior valve and postmucro area of posterior valve with sculpture similar to that of lateral areas defining some 40-50 radial riblets. Girdle's upper surface with imbricated, elongate, strongly convex scales, about 200μm long, very finely striated.

The specimens agree in every respect with specimens of *Ischnochiton muscarius* from the mainland.

Distribution: *Ischnochiton muscarius* ranges from Venado Id., Guaymas, Sonora, Mexico (27°58′ N; 111°07′ W) (LACM 73-6) to La Ventosa, Salina Cruz, Oaxaca, Mexico (16°10′ N; 95°12′ W) (AJF Colln., *leg.* Nancy J. & A. J. Ferreira, December 1971), in the intertidal and low subtidal zones, 0-7 m.

Remarks: Largest mainland specimen of *Ischnochiton muscarius* examined, 30.5 mm long (AJF 302, Puerto Angel, Oaxaca, Mexico).

Ischnochiton rugulatus (Sowerby, 1832)

(Figures 6, *9, 10, 11, 12, 13*)

Chiton rugulatus Sowerby (1st) *in* Broderip & Sowerby, 1832: 58 — Sowerby (1st & 2nd), 1840: 5; sp. no. 62, figs. 42, 143, 144 — Reeve, 1847: plt. 19, fig. 118

Chiton catenulatus Sowerby (1st) *in* Broderip & Sowerby, 1832: 104 — Sowerby (1st & 2nd), 1840: 5, sp. no. 61, fig. 145 — Reeve, 1847: plt. 20, fig. 130

Chiton petaloides Gould, 1846: 144; 1852: 328, plt. 28, fig. 435 [reprinted, 1862: 6] — Smith, 1977: 231-232

Radsiella petaloides (Gould). Thorpe *in* Keen, 1971: 869, Polyplacophora, fig. 19 (with syn. *I. mariposa* Dall and *S. histrio* Berry).

Ischnochiton (Rhodoplax) petaloides (Gould). Smith & Ferreira, 1977: 85; fig. 5

Ischnochiton mariposa Dall, 1919: 505-507 — Smith, 1977: 227-228

Stenoplax mariposa (Dall). Keen, 1958: 528, Amphineura, fig. 46 (with syn. *S. histrio* Berry)

Stenoplax histrio Berry, 1945: 493-495; figs. 10-18

Type Material and Type Locality:

Chiton rugulatus Sowerby, 1832: **Lectotype** (BMNH 198028) and **paralectotypes** (BMNH 198029; BMNH 198030; BMNH 198031) designated herein; locality, "ad oras Americae Centralis (Puerto Portrero and Inner Lobos Island)" here restricted to Isla Lobos de Tierra [= Inner Lobos Island], Peru (6°27′ S; 80°52′ W)

Chiton catenulatus Sowerby, 1832: **Lectotype** (BMNH 198032) and **paralectotypes** (BMNH 198033) designated herein; locality, "ad oras Peruviae (Inner Lobos Island)"

Chiton petaloides Gould, 1846: Holotype (USNM 12922); locality, "Sandwich Ids."

Ischnochiton mariposa Dall, 1919: Syntypes (USNM 58865); locality, "Gulf of California, W. J. Fisher"

Stenoplax histrio Berry, 1945: Holotype (CAS 029671 [formerly CAS 8040], and paratypes (S. S. Berry Collection Cat. No. 7116; "others to be deposited in the collections of the National Museum of Mexico, United States National Museum, and San Diego Museum of Natural History"); locality, "El Gallo, Mulege, Baja California," Gulf of California, Mexico

Material Examined: SOCORRO: 1 specimen, Caleta Binmer, 0-1 m (AJF 497); 5 specimens, Caleta Trueno, 0-1 m (AJF 501); 1 specimen, Islotes Rocosos, 13 m (AJF 506, *leg.* Gwen Cornfield)

Description: The 7 specimens of *Ischnochiton rugulatus* collected at Socorro vary in color from green to tan mottled but showing characteristic bright blue dots; 6.8 to 10 mm in length. Girdle scales oval, flattish, about 150 μm long, and some 30 very fine striations. No essential differences were found between specimens from Socorro (Figures *9, 10*) and specimens from the mainland or Hawaii.

Distribution: *Ischnochiton rugulatus* has a unique distribution. It is the only eastern Pacific chiton present in Hawaii (holotype of *Chiton petaloides,* Gould, 1846; AJF colln., Oahu Id., *leg.* Kay Gudnason, 1974, H. Bertsch, 1977, R. & Anty Schock, 1977; Bishop Museum, Maui Id., *leg.* C. H. Edmondson, 18-19 June 1931). On the Pacific side of Baja California, Mexico, it has been collected from as far north as Malarrimo Point (27°44′ N; 114°43′ W) (LACM-AHF 2022-51) to Cabo San Lucas, throughout the Gulf of California up to Puerto Peñasco, Sonora (31°20′ N; 113°33′ W) (AJF colln., *leg.* A. J. Ferreira, December 1971, H. Bertsch, December 1975), in many localities along the coast of Mexico (AJF colln.), Costa Rica (LACM 72-52), Nicaragua (AJF 133), Panama (LACM B-23), Ecuador (LACM 70-9), south to Isla Lobos de Afuera, Peru (6°57′ S; 80°42′ W) (LACM 74-6). The species is also present in the Galápagos Islands (CAS 019943; CAS 020073; CAS 020074; CAS 020075; CAS 020076; see Smith & Ferreira, 1977).

Explanation of Figures *5* and *7* to *13*

Figure *5: Lepidochitona keepiana* Berry, 1948. Specimen ca. 10 mm long (ANSP 72499). Tegmental surface of intermediate valves

Figure *7: Ischnochiton muscarius* (Reeve, 1847). Specimen 15 mm long (AJF 497, Socorro Id., Revillagigedos, Mexico)

Figure *8:* Same as in Fig. *7.* Close-up of intermediate valves

Figure *9: Ischnochiton rugulatus* (Sowerby, 1832). Specimen 10 mm long (AJF 501, Socorro Id., Revillagigedos, Mexico)

Figure *10:* Same as in Fig. *9.* Close-up of intermediate valves

Figure *11: Chiton rugulatus* Sowerby, 1832. **Lectotype** (BMNH 190828)

Figure *12:* Same as in Fig. *11.* Close-up of intermediate valves

Figure *13: Ischnochiton rugulatus* (Sowerby, 1832): *Chiton catenulatus* Sowerby, 1832. **Lectotype** (BMNH 190832)


Figure 5


Figure 7

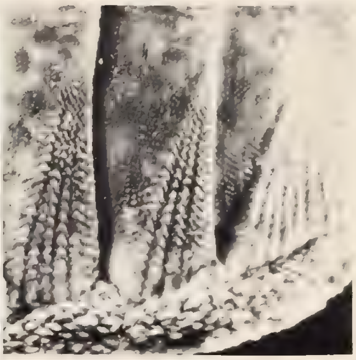
Figure 8


Figure 9


Figure 10

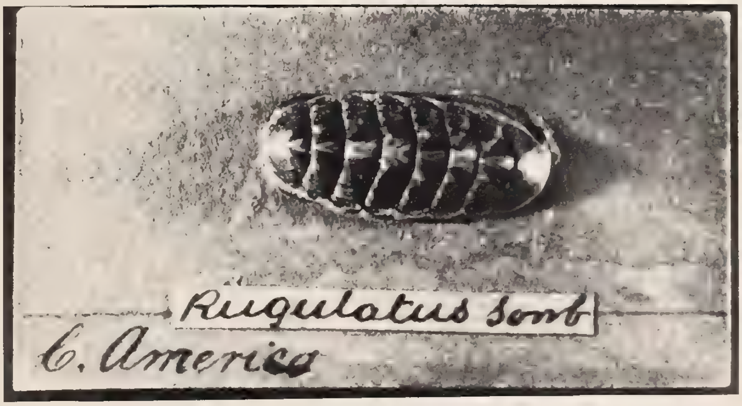

Figure 11


Figure 12


Figure 13

Bathymetric range, intertidal to shallow subtidal zones, 0 to 20m (AJF 128, off San Diego Id., Gulf of California, Mexico).

Remarks: The type material of *Chiton rugulatus* Sowerby, 1832, consists of 4 lots from the H. Cuming collection. The figured specimen (Sowerby, 1840, fig. 143; Reeve, 1847, plt. 19, fig. 118) is here designated **lectotype** (BMNH 198028). It is accompanied by a blue museum label which reads, in part "Chiton rugulatus Sowerby / Syntype / Central America." The specimen, dry, flat, well preserved, glued to a wooden board (Figures *11, 12*) is 19.5mm long and 8.5mm wide; dark green with creamy blotches and electric-blue dots parajugally on all valves; concentric rugosities or wrinkles on valve i, postmucro area of valve viii, and lateral areas of intermediate valves; the tegmental wrinkles tend to continue onto the pleural areas as vague riblets; jugum mostly smooth with occasional minute pits; valve viii inflated with central, prominent mucro; girdle scales small, striated. The specimens in the other three lots are here designated **paralectotypes**. They include a lot (BMNH 198019) of 4 dry specimens glued to a wooden tabloid, one partly disarticulated, 17mm, 15.5mm, and 10.5mm long; one specimen black with white jugal stripe, three others mottled, showing characteristic electric-blue dots. Accompanying label reads, in part, "Syntypes / Central America / Figured in Conch. Illust. fig. 42 = black & white spec.? and fig. 144 = spec. measuring 14mm ?" A second lot (BMNH 198030), contains a single specimen, also labelled "Syntype / Central America," 10.5mm long. A third lot (BMNH 198031), labelled, in part, "? Syntypes (labelled rugulatus var.) / Central America" consists of two specimens, 12.1mm and 11.2mm long, uniformly brown color. In every respect the specimens agree with Sowerby's (1832) description and illustration (1840), and with the current concept of *Ischnochiton petaloides* (Gould, 1846).

The type material of *Chiton catenulatus* Sowerby, 1832, consists of a lot of 4 specimens, dry flat, glued on a wooden board on which is written "Ischnochiton catenulatus / Inner Lobos I. Sow." A blue museum label reads, in part, "Syntypes / Inner Lobos I. / H. Cuming colln. / 4 specs." The specimens are all uniform light cream-brown color; they measure 18.4mm, 14.6mm, 15.3mm, and 16.0mm in length. In shape, tegmental sculpture, and girdle characteristics, they correspond in every respect to Sowerby's (1932; 1840) description and illustration of the species. The largest specimen is here designated **lectotype** (BMNH 198032) (Figure *13*); the others, **paralectotypes** (BMNH 198033).

The type specimens of *Stenoplax histrio* Berry, 1945, (CAS 029871), *Ischnochiton mariposa* Dall, 1919, (USNM 58865), and *Chiton petaloides* Gould, 1946, (USNM 12922), previously examined, have been reported elsewhere (Smith, 1977; Smith & Ferreira, 1977).

Stenoplax Dall, 1879

Type Species: *Ischnochiton limaciformis* Sowerby, 1832, by OD.

Stenoplax corrugata (Carpenter *in* Pilsbry, 1892)
(Figure *14*)

Ischnochiton corrugatus Carpenter *in* Pilsbry, 1892b, 14: 123-124—Dall, 1921: 192—Keep, 1904: 349—Oldroyd, 1927: 881—Palmer, 1945: 101

Ischnochiton (Stenoplax) corrugatus Carpenter *in* Pilsbry. Smith, 1947b: 18; 1947c: 7-8—Palmer, 1958: 271; plt. 29, figs. 5-8

Stenoplax corrugata (Carpenter *in* Pilsbry). Smith, 1963: 148—Burghardt & Burghardt, 1969: 35 (with syn. *S. biarcuata* (Dall, 1903))—Abbott, 1974: 396-397 (with syn. *Ischnochiton biarcuatus* Dall, 1903)

Ischnochiton biarcuatus Dall, 1903: 176—Lowe, 1904: 19

Ischnochiton (Stenoplax) biarcuatus Dall. Dall, 1921: 190—Oldroyd, 1927: 881—Smith, 1947a: 18; 1947b: 6

Stenoplax circumsenta Berry, 1956: 72—Ferreira, 1972: 55-56, figs. 1-2—Hanselman, 1973: 20-21; figs. 1-8—Poorman & Poorman, 1978: 373

Type Material and Type Locality:

Ischnochiton corrugatus Carpenter *in* Pilsbry, 1892: Holotype (Redpath Museum, No. 37); locality, "Catalina Is. 40fms." California [33°23′N; 118°24′W]

Ischnochiton biarcuatus Dall, 1903: Holotype (USNM 109308); locality, "Off Avalon [Santa Catalina Island, California], 50fms"

Stenoplax circumsenta Berry, 1956: Holotype (S. S. Berry colln., No. 13602) and paratype (S. S. Berry colln. 13627); locality, Isla Concha, Scammons Lagoon, Baja California, Mexico [27°50′N; 114°20′W]

Material Examined: CLARION: 1 specimen, off Sulphur Bay (18°19′05″N; 114°45′25″W), 57 fathoms [107m], January 5, 1934 (LACM-AHF 137-34)

Description: The single specimen (Figure *14*) dry, curled, estimated length (if extended flat) 6mm, width 2.5mm, is uniformly salmon red. Tegmentum mostly smooth, somewhat shiny. Lateral areas of intermediate valves moderately elevated, with 4-6 concentric corrugations better defined towards periphery. Anterior valve and postmucro area of posterior valve with similar sculpture. Central areas smooth. Posterior valve rather depressed; mucro central, postmucro slightly concave. Articulamentum white; sinus wide; slits 8-1-9. Girdle's upper surface, in same color as tegmentum, covered with minute, ca. 110 $\times 70\mu$m, translucent, imbricated scales with 6-8 strong ribs defining equally wide striations; marginal fringe of spicules, about $150 \times 25\mu$m, with longitudinal striations; undersurface juxtaposed, transparent, rectangular scales, ca. $70 \times 30\mu$m, featureless otherwise; girdle bridges (see Ferreira, 1983), empty. Radula 2.0mm long, comprising 45 rows of mature teeth; median teeth elongate, incurved sides, blade at anterior end; first lateral teeth wider, incurved outer edge with knob at anterior-outer corner; heads of major lateral tooth, bicuspid; outer marginal teeth, elongate, length/width = 1.5.

In every respect, the specimen exhibits the characteristics of a juvenile of *Stenoplax corrugata.*

Distribution: *Stenoplax corrugata,* as here understood, is found both, on the Pacific side of Baja California, and in the Gulf of California. In the Pacific it ranges from Santa Cruz Id., California (34°01′ N; 119°45′ W) (AJF colln., *leg.* December 1970, at 17m) to Magdalena Bay (24°40′ N; 112°00′ W) (LACM 71-14), having been collected, also, at San Pedro, Los Angeles Co. (LACM 75-111), Santa Barbara Id. (AJF 243), Santa Catalina Id. (AJF colln., *leg.* November 1971), Coronados Is. (AJF 96), Punta Banda (LACM 67-53), Todos Santos Bay (CAS 029670; AJF 91), Sacramento Reef (AJF 94), San Martin Id. (AJF 95), Guadalupe Id. (LACM-AHF 1919-49; CAS 029668; CAS 029669) and San Pablo Pt. (LACM 71-178). In the Gulf of California, it has been collected at Pichilingue, La Paz, Baja California (AJF colln., *leg.* July 1971), Espiritu Santo Id. (AJF colln., *leg.* October 1970), Partida Id. (AJF colln., *leg.* September 1971), Danzante Id. (AJF 124, *leg.* E. Janss, Ann Howell, & A. J. Ferreira, aboard M/V *Disappearance,* 25 November 1973), north end of Monserrate Id. (25°43′ N; 111°03′ W) (AJF 628, aboard R/V *Baja Explorador,* 27 October 1981), and Medio Id., off Guaymas, Sonora, Mexico (27°55′ N; 111° 58′ W) (Hanselman, 1973).

Bathymetric range, 3-103m.

Remarks: A specimen of *Ischnochiton corrugatus* (CAS 029-670 [formerly CASG 2854]), from Todos Santos Bay, Baja California, Mexico, collected by H. Hemphill [Loc. 4041 (H. H.)], considered by S. S. Berry, in a hand-written note, to have "practically the significance of a type," preserved dry, soft parts removed, uniform salmon color, 18mm long, agrees with the current interpretation of the species.

The conspecificity of *Stenoplax corrugata* and *S. circumsenta* had not been previously recognized. The two species were assumed to differ in the upward-pointing, sharply triangular, spinelet-like girdle scales, conspicuously present in *S. circumsenta,* absent in *S. corrugata.* Comparing the two species, Berry (1956: 72) stated, "In sculpture this species [*Stenoplax circumsenta*] somewhat approaches *S. corrugata* (Carpenter). It sharply differs from that species, however, as from every other known *Stenoplax,* in the curious acute spines of the girdle."

However, several observations have led to the conclusion of conspecificity:

1) The number and distribution of triangular spinelets in *Stenoplax circumsenta* is extremely variable from specimen to specimen, making for gradients between the appearance of the girdle of "typical" *S. corrugata* and *S. circumsenta.*

2) Specimens of *S. circumsenta* have been found at Santa Barbara Id., Channel Is., California, (AJF 243), practically at the type locality of *S. corrugata.*

3) Comparison of specimens referrable to either species on the basis of the girdle elements showed them in every other respect—shape, size, color, tegmental sculpture, articulamental features, and radula—identical.

4) Aside from the triangular spinelets, the other girdle scales of *S. circumsenta* are indistinguishable from those of *S. corrugata.*

5) Examination of a lot of 8 specimens of *S. circumsenta* from Magdalena Bay (LACM 71-14) revealed that the number and size of triangular spinelets in the girdle is, to some extent, a function of the size (age) of the specimen: the larger two specimens, 24 and 22mm long show abundant spinelets; smaller specimens, 16 to 12mm long, display only occasional ones; the smallest specimen, 11mm long, shows none.

From these observations it is clear that the appearance of the large, triangular spinelets in *Stenoplax "circumsenta"* is a secondary phenomenon, the outgrowing of the girdle scales of *S. corrugata.*

Lepidozona Pilsbry, 1892b

Type Species: *Chiton mertensii* Middendorff, 1847, by OD.

Lepidozona clarionensis Ferreira, spec. nov.

(Figures *15, 16,* 17, 18)

Diagnosis: Small chitons (up to 1.5cm long), high-arched, carinate; valves' posterior edges straight, not beaked, but serrate. Color variable with rose and cream tones predominating, often variegated. Radial granose ribs in anterior valve (15-20, often bifurcating), postmucro area of posterior valve (10-12, poorly defined), and lateral areas of intermediate valves (mostly 2, or bifurcating into 3-4). Central areas with longitudinal, mostly parallel, latticed ribs, extending onto jugum forming no wedge figure. Girdle scales oval, moderately convex, ribbed to form 12-15 well defined striae. Radula's major lateral teeth, bicuspid.

Description: **Holotype** (Figure *15*) fully extended, preserved in alcohol, 14.3mm long, 8.5mm wide, 2.0mm high. Width/length ratio, 0.59. Jugal angle about 105°. Carinate; posterior edge of valves straight, not beaked. Gills holobranchial, abanal, 22 plumes per side extending about 90% of foot length.

Tegmental surface microgranular, predominantly cream color with dark grayish brown blotches at periphery. Anterior valve with 15 granose radial ribs, tending to bifurcate at periphery; posterior edge serrate due to some 10 tubercles protruding at suture; tegmental surface 2.0mm long, 4.6mm wide, length/width ratio 0.43. Lateral areas of intermediate valves well defined, moderately elevated, with 2 (bifurcating to 4) similar radial ribs; posterior edge serrate due to protruding tubercles at sutures. Central areas with about 15 longitudinal riblets, neatly latticed, mostly parallel and extending onto jugum. Posterior valve somewhat depressed; mucro central; postmucro with some 12, poorly defined, granose radial ribs; postmucro slightly concave; tegmental surface 2.8mm long, 4.4mm wide, length/width ratio 0.64. Widths of valves i/viii, ratio 1.05.

Articulamentum white. Sutural laminae semi-oval; sinus well defined, relatively wide. On valve viii, width of sinus / width of sutural laminae = 1.0mm / 2.1mm = 0.5. Insertion teeth sharp, well defined; slits, 11-1-11, followed by slit rays. Eaves solid.

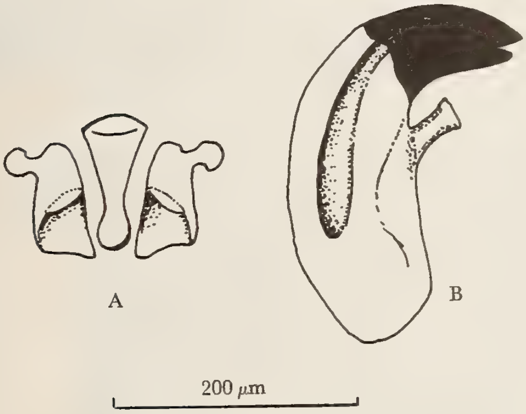

Figure 17

Lepidozona clarionensis Ferreira, spec. nov. **Holotype,** CAS 030662. Radula: A) Median and first lateral teeth, B) Major lateral tooth

Girdle cream with dark blotches; maximum width at valve iv, 1.4mm. Upper surface covered with oval, translucent, imbricated scales, largest 160μm long, with 12-15 ribs defining that many striae of about equal width. Girdle bridges (see FERREIRA, 1983), empty. Undersurface paved with imbricated, transparent, rectangular scales, about 80 × 15μm (Figure 18).

Radula 3.4mm long (24% of specimen's length), comprising some 35 rows of mature teeth. Median tooth about 100μm long, 85μm wide at anterior blade, narrowing posteriorly to 15μm but enlarging again to about 30μm at posterior end. First lateral teeth about 100μm long, 60 μm wide, rectangular, with conspicuous round knob, 20μm in diameter, at outer-anterior corner. Major lateral teeth about 270μm long, with bicuspid head, and large knob at inner edge (Figure 17). Spatulate teeth with simple, round spatula, 85μm wide. Outer-marginal teeth about 100μm long, 80μm wide, width/length ratio 1.2.

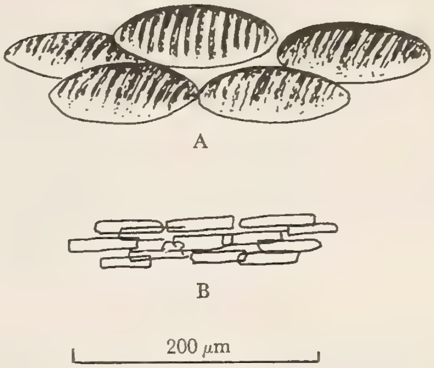

Figure 18

Lepidozona clarionensis Ferreira, spec. nov. **Holotype,** CAS 030662. Girdle: A) Scales of dorsal surface, B) Scales of ventral surface

Type Material: **Holotype** (disarticulated valves and girdle; mounted fragments of radula and girdle scales) (CAS 030662); the specimen is the largest of 4 specimens collected by J. Hewitt & A. J. Ferreira with SCUBA on the southeast side of Clarion, near Roca Piramide, at 15m, 26 November 1981 (AJF 640). All 25 other specimens of *Lepidozona clarionensis* collected at Clarion in the course of the same expedition of November 1981 are here designated **paratypes** (CAS 030663; LACM 1821; ANSP A9449; USNM 792398; AJF private colln.). They were collected by J. Hewitt & A. J. Ferreira as follows: 3 specimens (in addition to holotype), 6.5 to 14.3mm long, near Roca Partida, at 15m, 26 November 1981 (AJF 640); 4 specimens, 6.2 to 12.4mm long, east entrance of Sulphur Bay, at 10m, 26 November 1981 (AJF 641); 1 specimen, 11.5mm long, Monument Rock, on northwest corner of the island, at 17-20m, 27 November 1981 (AJF 643) (Figure *16*); 2 specimens, 11.3 and 15.3mm long, unnamed cove on south side of the island, at 17m, 27 November 1981 (AJF 645); 5 specimens, 10.0 to 14.7mm long, east end of the island, at 13m, 28 November 1981 (AJF 646); 6 specimens, 11.0 to 15.0mm long, west entrance of Sulphur Bay, at 20m, 28 November 1981 (AJF 647); 4 specimens, 10.0 to 13.7mm long, southwest side of the island, at 25m, 28 November 1981 (AJF 648).

Type Locality: Clarion Island, Revillagigedo Archipelago, Mexico (18°22′N; 114°44′W).

Other Material: CLARION: Sulphur Bay, 5 January 1934 (LACM-AHF 134-34), 3 specimens, 6.5 to 9.5mm long. SOCORRO: Braithwaite Bay, at 8-10m, 4 November 1979 (AJF 494), 3 specimens 8.0 to 12.5mm long; Punta Pinaculo, Caleta Grayson, at 10-17m, 5 November 1979 (AJF 496), 1 specimen, 14.1mm long; Cabo Henslow, at 25m, 6 November 1979 (AJF 498), 1 specimen, 13.0mm long; Islotes Rocosos, at 13m, 7 November, 1979 (AJF 506), 1 specimen, 17.0mm long.

Distribution: *Lepidozona clarionensis* seems to be endemic to the Revillagigedos Islands, having been collected only at Clarion and Socorro. Bathymetric range, 8-25m.

Remarks: Except in color, specimens of *Lepidozona clarionensis* do not show much intraspecific variation; Socorro specimens do not differ from Clarion specimens. Largest specimen, 17.0mm long, 10.0mm wide (AJF 506, Islas Rocosas, Socorro, *leg.* Gwen Cornfield at 13m). Body width/length ratio, mean = 0.59 (s.d. = 0.03; n = 32).

Lepidozona clarionensis is rather similar to *L. sinudentata* (Carpenter *in* Pilsbry, 1982) with which it was initially confused. Although there are subtle differences in tegmental sculpture between the two species, reliable differentiating characters were found only upon microscopic examination of the girdle scales (160μm long, with 12-16 striae in *L. clarionensis;* 200μm long, with 10 striae in *L. sinudentata*) and the radula (major lateral teeth head, bicuspid in *L. clarionensis;* unicuspid in *L. sinudentata*). Likely, the two species are phylogenetically close.

The species is here named *clarionensis* after Clarion Island, its type locality.

Lepidozona rothi Ferreira, spec. nov.

(Figure *19, 20,* 21, 22)

Diagnosis: Chitons small (up to 1.5cm long), high-arched, carinate. Valves' posterior edge straight, not beaked, not serrate. Anterior valve with 30-35 radial ribs cut into granules by some 10 concentric grooves; similar sculpture on lateral areas (4-6 radial ribs), and postmucro area (about 20 radial ribs, poorly defined). Central areas with longitudinal, latticed riblets extending onto jugum and forming wedge figure on jugal area of second valve. Girdle scales moderately convex, 200μm long, with obsolete striation, mammillate. Radula's major lateral teeth, unicuspid.

Description: **Holotype** (Figures *19, 20*) fully extended, preserved in alcohol, 12.5mm long, 8.0mm wide, 2.3mm high. Width/length ratio, 0.64. Jugal angle about 110°. Carinate; posterior edge of valves straight, not beaked or serrate. Gills holobranchial, abanal, 23 plumes per side, extending 100% of foot's length.

Tegmental surface microgranular, light cream color. Anterior valve with 35 radial ribs cut into some 10 granules by concentric grooves; posterior edge relatively smooth, not serrate; valve 2.2mm long, 5.5mm wide, length/width ratio 0.6. Lateral areas of intermediate valves well defined, moderately elevated, with 4-6 similar radial ribs, posterior edges relatively smooth. Central areas with about 24 longitudinal riblets, neatly latticed, parallel and extending onto jugum; on valve ii jugal riblets diverge forward forming wedge-like figure. Posterior valve 2.7mm long, 4.5mm wide, length/width ratio 0.6; mucro slightly anterior; postmucro area slightly concave, with some 20 granose, ill-defined radial ribs. Widths of valves i/viii, ratio 1.22.

Articulamentum white, dull. Sutural laminae semi-oval; sinus well defined, relatively wide. On valve viii, width of sinus / width of sutural lamina = 1.0mm / 2.1mm = 0.5. Insertion teeth well defined, thick, blunt; slits 10-1-10, without slit-rays. Eaves solid.

Girdle light cream color; maximum width at valve iv, 1.5mm. Upper surface covered with oval, imbricated scales, largest 200μm long, with some 12 obsolete striations, some bearing nipple-like protrusion 20-25μm high, 60-80 μm long, vaguely striated. Girdle bridges, empty. Undersurface paved with imbricated, transparent, rectangular scales, about 75 × μm (Figure 22).

Explanation of Figures *14* to *16, 19, 20, 23* to *25*

Figure *14: Stenoplax corrugata* (Carpenter *in* Pilsbry, 1892). Specimen 6mm long (? juvenile). Anterior, 2 intermediate, and posterior valves

Figure *15: Lepidozona clarionensis* Ferreira, spec. nov. **Holotype** (CAS 030662). Anterior, intermediate, and posterior valves

Figure *16: Lepidozona clarionensis* Ferreira, spec. nov. **Paratype**, 10mm long (AJF 643) (CAS 030663). Side view of lateral areas

Figure *19: Lepidozona rothi* Ferreira, spec. nov. **Holotype** (LACM 1818). First, second, fourth, and eight valves

Figure *20:* Same as in Fig. *19.* Close-up of lateral and pleural areas of fifth valve

Figure *23: Chaetopleura scabricula* (Sowerby, 1832). Specimen 20mm long (AJF 496, Socorro Id., Revillagigedos, Mexico). Close-up of anterior valves

Figure *24: Chiton articulatus* Sowerby, 1832. Specimen 65mm long (AJF 500, Socorro Id., Revillagigedos, Mexico)

Figure *25:* Same as in Fig. *24.* Close-up of intermediate valves


Figure *14*

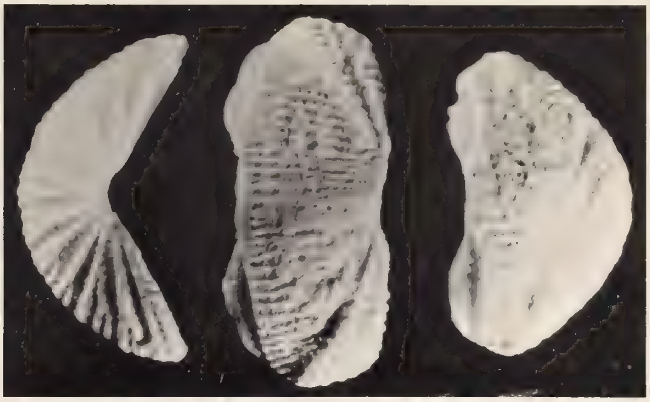
Figure *15*


Figure *16*

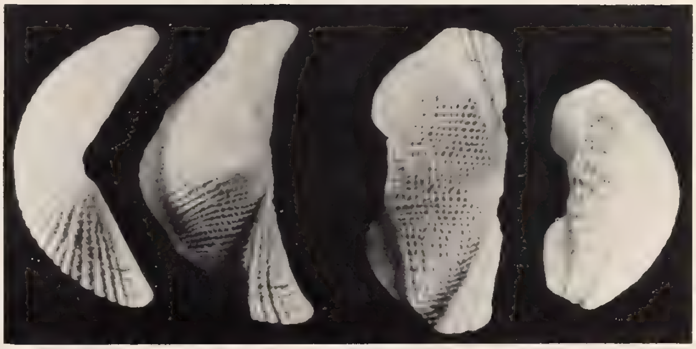
Figure *19*

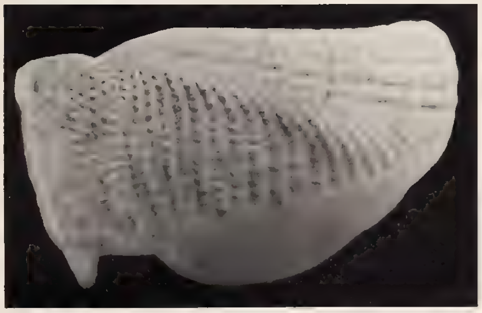
Figure *20*


Figure *23*


Figure *24*


Figure *25*

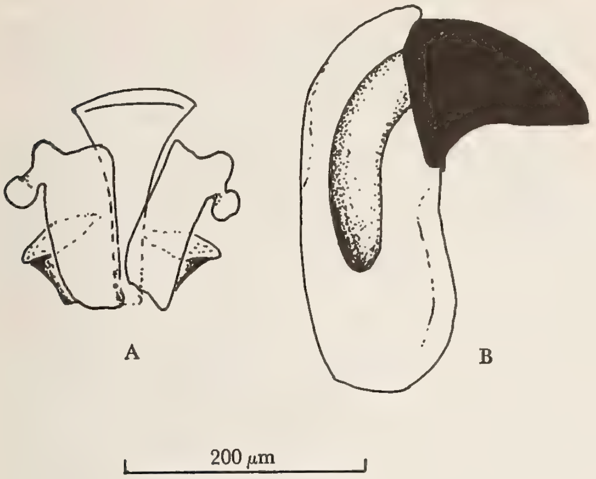

Figure 21

Lepidozona rothi Ferreira, spec. nov. **Holotype**, LACM 1818. Radula: A) Median and first lateral teeth, B) Major lateral tooth

Radula 5.0mm long (40% of specimen's length), comprising 26 rows of mature teeth. Median tooth 100μm wide at anterior blade narrow posteriorly to 50μm. First lateral teeth about 150μm long, 60μm wide, rectangular, with round knob, 22μm in diameter, at outer-anterior corner. Major lateral teeth 300μm long, with robust, unicuspid head, about 120μm long, 100μm of maximum width (Figure 21). Spatulate teeth with simple, round spatula, 80μm wide. Outer-marginal teeth 140μm long, 90μm wide, length/width ratio 1.6.

Type Material: **Holotype** (disarticulated valves and girdle; mounted fragments of radula and girdle scales) (LACM 1818). It was collected off Sulphur Bay, Clarion Island, Revillagigedos, Mexico, at 40-50 fathoms [82-91m] during an expedition of the Allan Hancock Foundation, 16 March 1939 (LACM-AHF 918b-39).

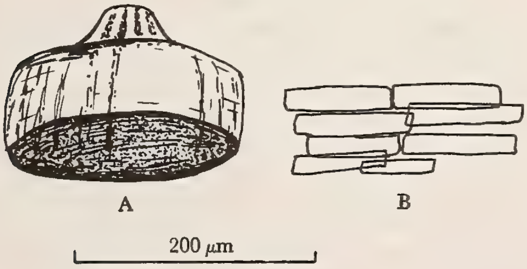

Figure 22

Lepidozona rothi Ferreira, spec. nov. **Holotype**, LACM 1818. Girdle: A) Scale of dorsal surface, B) Scales of ventral surface

Type Locality: Off Sulphur Bay, Clarion Island, Revillagigedos, Mexico (18°19'45"N; 114°44'35"W), at 82-91m.

Other Material: COCOS ISLAND, Costa Rica: Chatham Bay (5°33'50"N; 86°59'50"W), at 40-60 fathoms [70-110m], 14 January 1938 (LACM-AHF 780a-38), 4 specimens, about 10mm to 12mm long; off Nuez Island (5°34'00"N; 86°59'20"W), at 30-50 fathoms [55-90m], 14 January 1938 (LACM-AHF 779-38), 1 specimen, 11mm long.

Distribution: *Lepidozona rothi* is known only from Clarion Id., Mexico, and Cocos Id., Costa Rica, from 55-110m.

Remarks: In general appearance, *Lepidozona rothi* is similar to *L. clarionensis* and *L. sinudentata.* It differs from *L. clarionensis* mainly in its 1) relatively wider body, 2) more numerous radial ribs on end valves and lateral areas, 3) more numerous riblets on central areas, 4) larger and mammillated girdle scales, and 5) unicuspid radula's major lateral teeth. It differs from *L. sinudentata* in its 1) relatively wider body, 2) more numerous radial ribs on end valves, 3) more numerous riblets on central areas, 4) smaller and mammillated girdle scales.

The species is here named **rothi** after Dr. Barry Roth, Department of Invertebrate Zoology, California Academy of Sciences, who, ever patiently, has given much of his time and knowledge to guide and enrich my research efforts.

Chaetopleuridae Plate, 1899

Chaetopleura Shuttleworth, 1853

Type Species: *Chiton peruvianus* Lamarck, 1819, by SD (Dall, 1879).

Chaetopleura scabricula (Sowerby, 1832)
(Figures 6, *23*)

Chiton scabriculus Sowerby (1st) *in* Broderip & Sowerby, 1832: 28—Sowerby (1st and 2nd), 1840: 8, no. 100, fig. 21—Reeve, 1847, plt. 15, sp. & Fig. 81—Pilsbry, 1892a, 14: 33 (as syn. of *Chaetopleura lurida* (Sowerby, 1832))—Keen, 1958: 524 (as syn. of *C. lurida)*—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*).

Chaetopleura scabricula (Sowerby). Ferreira, 1983

"Chaetopleura lurida (Sowerby)" *ex auttore* treating Panamic species. Pilsbry, 1892a, 14: 33-35, plt. 12, figs. 53-54—Steinbeck & Ricketts, 1941: 552, plt. 12, figs. 53-54 [reprinted, 1971]—Keen, 1958: 524, Amphineura, fig. 35—

Thorpe *in* Keen, 1971: 877-878, Polyplacophora, fig. 41—Abbott, 1974: 401—Smith, 1977: 217, 243, 246. [not *Chiton luridus* Sowerby, 1832, a *nomen dubium*]

"*Chiton columbiensis* Sowerby, 1832." Pilsbry, 1892a, 14: 34-35, plt. 12, figs. 51-52 (as var. of *C. lurida*)—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*). [not *Chiton columbiensis* Sowerby, 1832, a *nomen dubium*]

"*Chiton catenulatus* Sowerby, 1832." Thorpe *in* Keen, 1971: 877 (as syn. of *lurida*). [not *Chiton catenulatus* Sowerby, 1832]

"*Chiton jaspideus* Gould, 1846." Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Abbott, 1974: 401 (as syn. of *C. lurida*). [not *Chiton jaspideus* Gould, 1846 (= *Chaetopleura hennahi* (Gray, 1828))]

Lepidopleurus bullatus Carpenter, 1857a: 252 *nomen nudum;* 1857b: 195-196—Brann, 1966: 45, fig. 254—Keen, 1968: 434, plt. 59, fig. 95—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 243 (as syn. of *C. lurida*)

Lepidopleurus bullatus calciferus Carpenter, 1857a: 252, *nomen nudum;* 1857b: 196—Brann, 1966: 45, fig. 245b—Keen, 1968: 434, plt. 59, fig. 96—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 243 (as syn. of *C. lurida*)

Chaetopleura bullata (Carpenter). Pilsbry, 1892a, 14: 31-32—Keen, 1958: 524, Amphineura, figs. 33, 33a

Chaetopleura bullata calcifera (Carpenter). Pilsbry, 1892a, 14: 32—Keen, 1958: 524, Amphineura, fig. 33, 33a

Ischnochiton parallelus Carpenter, 1864a: 314 (reprinted, 1872: 213); 1864b: 618 (reprinted, 1872: 104)—Keen, 1958: 524 (as syn. of *C. lurida*)—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 246 (as syn. of *C. lurida*)

Chaetopleura lurida var. *parallela* (Carpenter *in* Pilsbry, 1892a, 14: 34, plt. 12, fig. 50

Chaetopleura parallela (Carpenter). Dall, 1921: 193—Oldroyd, 1927: 889-890—Smith, 1947a: 18; 1947b: 4—Palmer, 1945: 100; 1958: 267—Abbott, 1974: 401 *("lurida ?")*

Ischnochiton prasinatus Carpenter, 1864a: 315 (reprinted, 1872: 213); 1864b: 618 (reprinted, 1872: 104)—Keen, 1958: 524 (as syn. of *C. lurida)*—Thorpe *in* Keen, 1971: 877 (as syn. of *C. lurida*)—Smith, 1977: 217, 246 (as syn. of *C. lurida*)

Chaetopleura lurida var. *prasinata* (Carpenter). Pilsbry, 1892a, 14: 34

Chaetopleura prasinata (Carpenter). Dall, 1921: 193—Oldroyd, 1927: 889—Burch, 1942: 7—Smith, 1947a: 18; 1947b: 4-5—Palmer, 1958: 267—Abbott, 1974: 407 *("lurida ?")*

Choetopleura [sic] *dacrydigera* Rochebrune, 1882: 193

Type Material and Type Locality:

Chiton scabriculus Sowerby, 1832: Lectotype (BMNH 1980113) and paralectotypes (BMNH 1980114); locality, Puerto Portrero, Costa Rica (10°28′N; 85°47′W) (Ferreira, 1983)

Material Examined: SAN BENEDICTO: Punta Ortolan, at 18m (AJF 508), 1 specimen, *leg.* G. Corsi. SOCORRO: (ANSP 72501), 1 specimen, 15.5mm long, *leg.* R. C. McGregor [cited in Pilsbry, 1898: 51]; S end, at 2-7m, 14 February 1971 (LACM 71-26), 1 specimen, 8mm long, *leg.* C. Swift aboard R/V *Searcher*; Punta Pinaculo, Caleta Grayson, at 9-15m, 5 November 1979 (AJF 496), 26 specimens, 8-28mm long; Caleta Binmer, at 0-1m, 5 November 1979 (AJF 497), 1 specimen, 15mm long; Cabo Middleton, E side of Academy Bay, at 8-25m, 7 November 1979 (AJF 503), 2 specimens, 10.5 and 16mm long; N side of Academy Bay, at 8m (AJF 504), 3 specimens, 15-18mm long.

Description: The examined 36 specimens of *Chaetopleura scabricula* from Socorro and San Benedicto, 8-28mm long, are mostly tan to brown, often with wide, darker, parajugal bands and zebra-like pattern of brown/cream lines on lateral areas. Body width/length, mean 0.62 (s.d. = 0.04; n = 15). Tegmentum pustulose; on end valves and lateral areas of intermediate valves, large pustules (up to 100μm in height and diameter) rise against smooth, almost shiny surface background; on central areas, much smaller pustules (about 20μm in height, 30μm in diameter) often coalesced into 15-20 riblets per side, and extending onto jugum; on valve ii, subdued jugal tract of longitudinal riblets diverges out forward outlining wedge-like figure (Figure *23*). Mucro slightly anterior; postmucro straight to concave. Articulamentum white. Insertion teeth sharp; slits, 9-1-9, followed by slit-rays. Sutural laminae subtriangular to subrectangular. Girdle's upper surface with chaffy scales, about 25 × 10μm, and abundant, large (up to 1.5mm long), simple, golden-brown hairs; bridges, outer ¼ with crowded, transparent, slender spicules, 100 × 15μm, but with no spicules or other elements in middle ½; undersurface covered with transparent, rectangular scales, about 35 × 20μm, with convex outer edge and concave inner edge. Radula with rectangular, wide median tooth, and tricuspid major lateral teeth.

Compared to mainland specimens of *Chaetopleura scabricula*, Revillagigedos specimens are indistinguishable in size, body proportions, girdle elements, articulamentum, and radula. They are, however, phenotypically distinct in their subdued tegmental sculpture. Most Revillagigedos specimens show only occasional pustules on end valves and lateral areas, a characteristic which, together with subdued riblets on central areas, confers upon them a rather smooth appearance sharply different from the scabrous one of mainland specimens. These differences in tegmental sculpture are particularly evident in larger (older) specimens.

Distribution: *Chaetopleura scabricula* ranges from Bahía de San Francisquito, Baja California, México (28°26′N; 112°53′W) (CAS 030249), the central part of the Gulf of California, to Gorgona Id., Colombia (2°58′N; 78°11′W) (LACM-AHF 405-35). Bathymetric range, 0-30m.

Remarks: Although, in time, histological, biochemical, electrophoretic, or other studies may prove otherwise, morphological observations alone indicate that the Revillagigedos population of *Chaetopleura* is conspecific with the mainland populations of *Chaetopleura scabricula* (Sowerby, 1832). The phenotypical distinctions noted above do not seem sufficient to separate the two populations taxonomically at the species level. Unquestionably, some workers would regard the Revillagigedos population of *Chaetopleura* as distinct enough to receive subspecies status.

Indeed, the tegmental differences, though relatively minor, are constant enough to meet the "75-percent rule" required of subspecies (Mayr, 1969: 190); and the question of geographical separation is reasonably satisfied by the remoteness of the islands. But since no perceptible advantage seems to accrue from the coining of a new name, it is preferred here to speak of the Revillagigedos' *Chaetopleura* simply as a geographical variation or race of *Chaetopleura scabricula* and, while avoiding evolutionary connotations, save a "new name" for a better occasion.

Chitonidae Rafinesque, 1815

Chiton Linnaeus, 1758

Type Species: *Chiton tuberculatus* Linnaeus, 1758, by SD (Dall, 1879).

Chiton articulatus Sowerby, 1832
(Figures 6, *24*, *25*, 26)

Chiton articulatus Sowerby (1st) *in* Broderip & Sowerby, 1832: 59—Keen, 1958: 517, Amphineura, fig. 2—Thorpe *in* Keen, 1971: 864, Polyplacophora, fig. 3

Chiton laevigatus Sowerby (1st) *in* Broderip & Sowerby, 1832: 59 [not Fleming, 1815]—Pilsbry, 1893, 14: 159-160, plt. 34, figs. 68-71 (with *C. articulatus* as syn.)

Lophyrus striatosquamosus Carpenter, 1857a: 252, *nomen nudum;* 1857b: 192-193—Brann, 1966: 43, fig. 692—Keen, 1968: 433, plt. 59, fig. 91—Smith, 1977: 254 (as syn. of *C. articulatus*)

Chiton striatosquamosus (Carpenter). Pilsbry, 1893, 14: 168—Keen, 1968: 518, Amphineura, fig. 4

Type Material and Type Locality:

Chiton articulatus Sowerby, 1832: Types unascertained; locality, "Sinu Californiensi. (St. Blas)" [= San Blas, Nayarit, Mexico, 21°31′N; 105°16′W]

Chiton laevigatus Sowerby, 1832: Types unascertained; locality, "Sinu Californiensi...Guaymas" [Sonora, Mexico, 27° 56′N; 110°54′W]

Lophyrus striatosquamosus: Holotype, Reigen Mazatlan Collection, Tablet No. 897 (BMNH); locality, "Mazatlan" [Sinaloa, Mexico, 23°13′N; 106°25′W]

Material Examined: SAN BENEDICTO: S and E side of island, intertidal, 8 November 1979 (AJF 507, 509 & 510), 20 specimens, 63-83 mm long, *leg.* Gwen Cornfield & M. Campbell. SOCORRO: (ANSP 72500), 1 specimen disarticulated, *leg.* R. C. McGregor [cited in Pilsbry, 1898: 51]; (CASG-SU 42710), 5 specimens, largest ca. 80 mm long; Caleta Binmer intertidal, 5 November 1979 (AJF 497), 50 specimens, 46-68 mm long; Cabo Henslow, intertidal (AJF 500), 10 specimens, 63-107 mm long. CLARION: Sulphur Bay, intertidal, 27 November 1981 (AJF 644), 6 specimens, 59-80 mm long, *leg.* M. Campbell.

Description: The examined 92 specimens of *Chiton articulatus* from Revillagigedos agree in every respect with the current understanding of the species (Figures *24*, *25*). They vary in color from slate gray to tan, sometimes with some discrete creamy markings. Largest specimen, preserved in alcohol, 107 mm long (AJF 500). Width/length ratio, mean 0.65 (s.d. = 0.03; n = 20). Subcarinate; posterior edge of valves, straight; not beaked. Gills holobranchial, abanal, 55-70 plumes per side. Tegmentum smooth, shiny (if not eroded), sculptureless except in a single specimen which shows wavy surface with undulations on end valves and lateral areas of intermediate valves. Lateral areas moderately elevated. Mucro anterior, almost touching posterior edge of valve vii. Valve i, length/width ratio, 0.37; valve viii, length/width ratio, 0.46. Ratio of width of valves i/viii, 0.96. Articulamentum blue with darker blotch near anterior edge of valves, and, in some specimens, light red discolorations flanking darker area. Sutural laminae subrectangular; sinusal lamina strongly pectinated. Sinus well defined and narrow; on valve viii, width of sinus / width of sutural lamina, ratio 0.27. Insertion plates strongly

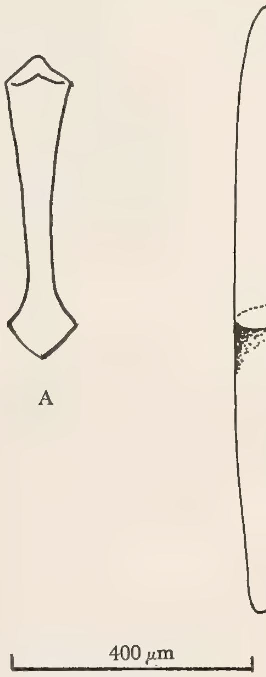

Figure 26

Chiton articulatus Sowerby, 1832. Specimen 72 mm long (AJF 507, San Benedicto Id., Revillagigedos, Mexico). Radula: A) Median tooth, B) First lateral tooth pectinated on outside; slits, 15-1-17, with no slit-rays. Eaves spongy. Girdle's upper surface covered with smooth, solid, opaque, somewhat keeled, round to quadrangular, large (up to 1.3mm long) scales, imbricated, in quincunx; bridges, empty; undersurface with transparent, rectangular scales, about 75 × 25 μm, vaguely striated. Radula (of specimen 72mm long) 30mm in length (41% of specimen's), comprising 130 rows of mature teeth; median tooth elongate, 500 μm long, 110 μm wide at anterior blade narrows to 50 μm at posterior ⅕ where it suddenly enlarges to 140 μm; first lateral teeth very elongate, knife-shaped, about 1000 μm long, 150 μm wide at anterior ⅔ ("blade" of the knife), 60 μm wide at posterior ⅓ ("handle" of the knife) (Figure 26); second lateral teeth, 1000 μm long, with discoid head about 250 μm wide; spatula of spatulate teeth, simple, ovoid, about 300 μm wide; outermarginal teeth, 170 μm long, 350 μm wide, length/width ratio, 0.5.

Distribution: *Chiton articulatus* ranges from Mazatlan, Sinaloa, Mexico (23°13′N; 106°25′W) (AJF 428 & 429) to Puerto Angel, Oaxaca, Mexico (15°40′N; 9°29′W) (AJF colln., *leg.* Nancy J. & A. J. Ferreira, 5 December 1971; AJF 302), at 0-1m, often exposed at low-tide.

Remarks: *Chiton articulatus* is the only chiton species present in all three islands of San Benedicto, Socorro and Clarion. On the Revillagigedos, the large number and size of its specimens attest to the absence of man on the islands; by contrast, on the mainland of Mexico, specimens of *C. articulatus,* sought after by local people as tasty morsels, are rare on accessible shores, relicts of wiped out populations (AJF personal observations).

Table 1

Meristic distinctions between specimens
of the Caribbean *Chiton marmoratus*
and the eastern Pacific *Chiton articulatus.*

	Chiton marmoratus	*Chiton articulatus*
Maximum length	57mm	108mm
Width/length ratio	0.54	0.57
Girdle's width/specimen's length ratio	0.09	0.08
Girdle scales: height/length ratio	0.62	0.89
Slits on end valves: i	11-16	13-18
viii	13-19	16-22
Radula:		
number of rows mature teeth	65-80	105-130
first lateral tooth shape	"rectangular"	"knife-like"
anterior blade	present	absent
length first lateral tooth/ length median tooth ratio	1	2

In size, shape, color, tegmental sculpture, girdle elements, articulamentum, and habitat, *Chiton articulatus* Sowerby, 1832, is remarkably similar to *C. marmoratus* Gmelin, 1791, from the Caribbean. Since the two species have never been formally contrasted in the literature, the omission is here remedied (Table 1). Comparison of specimens of the Caribbean *C. marmoratus* and the eastern Pacific *C. articulatus,* reveals decisive differences in girdle scales and radula confirming the generally accepted view that the two species, although similar, are biologically distinct.

DISCUSSION

The Revillagigedo Islands, located along the Clarion fracture zone, are an expression of late Cenozoic and Recent volcanoes. Clarion appears to be the oldest island in the Archipelago; Roca Partida the second oldest; Socorro and Benedicto, the youngest, but "older than late Pleistocene" (Richards, 1966: 405). In historical times, active volcanism has been confined to Socorro (reported eruptions in 1848, 1896, and 1951) and San Benedicto (eruption of Volcán Bárcena in 1952).

Of the eight species of chitons in the Revillagigedo Archipelago, only one, *Chiton articulatus,* is present at all three islands of San Benedicto, Socorro and Clarion. *Chaetopleura scabricula,* was collected at San Benedicto and Socorro; *Lepidozona clarionensis,* at Socorro and Clarion. *Lepidochitona keepiana, Ischnochiton muscarius,* and *I. rugulatus* are known only at Socorro; *Lepidozona rothi* and *Stenoplax corrugata* only at Clarion (Table 2).

To a great extent, the particular distribution of these chiton species in the Revillagigedos seems to be a function of the geography of the respective islands. Although all three islands, San Benedicto, Socorro and Clarion, offer excellent conditions for *Chiton articulatus,* only Socorro possesses a few bights and shallow-water coves where *Ischnochiton rugulatus, I. muscarius,* and *Lepidochitona keepiana* could prosper. There are no protected shores at San Benedicto and Clarion; even at Sulphur Bay, under the pounding action of the Pacific waves only *C. articulatus* thrives in the intertidal zone. The other chiton species at these islands, *Chaetopleura scabricula* at San Benedicto, *Lepidozona clarionensis* at Clarion, as well as *Lepidozona rothi* and *Stenoplax rugulatus* were found deeper in the water, on the underside of bottom rocks, where the wave action is no longer of significance.

The mean water surface temperature at the Revillagigedos parallels that at the mainland, being about 2°C cooler for the same latitude throughout the year (see Robinson, 1973). Except for *Lepidochitona keepiana,* a colder

Table 2

Chiton species of the Revillagigedos present (*) at the islands of San Benedicto, Socorro and Clarion.

	San Benedicto	Socorro	Clarion
Lepidochitona keepiana Berry, 1948		*	
Ischnochiton muscarius (Reeve, 1847)		*	
Ischnochiton rugulatus (Sowerby, 1832)		*	
Stenoplax corrugata (Carpenter in Pilsbry, 1892)			*
Lepidozona clarionensis Ferreira, spec. nov.		*	*
Lepidozona rothi Ferreira, spec. nov.			*
Chaetopleura scabricula (Sowerby, 1832)	*	*	
Chiton articulatus (Sowerby, 1832)	*	*	*

water species questionably present at Socorro, the chiton fauna of the archipelago and mainland Mexico are consistent. *Lepidozona rothi*, a relatively deep water species, has been collected at both Clarion and Cocos Island. Only one chiton species, *Lepidozona clarionensis*, is endemic to the Revillagigedos, an endemism rate of 12.5% which justifies considering the archipelago as part of the Panamanian Province (Briggs, 1974).

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Ecological and Phylogenetic Implications of the Unusual Radula of *Laevinesta atlantica*

(Mollusca : Gastropoda)

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(1 Plate)

INTRODUCTION

Although *Laevinesta atlantica* (Farfante, 1947) has been classified since the time of its original description as a fissurellid limpet, the radular pattern is too different from all known fissurellacean radulae to warrant this allocation. Scanning electron microscopic examination clarifies radular characters that were ambiguous in the line drawing of Pilsbry & McGinty (1952) and shows that several details in the drawing are incorrect. Although *L. atlantica* was originally described under the genus *Nesta* H. Adams, 1870, the type species, *N. candida*, differs significantly in shell characters and is probably a fissurellid. The unusual radular morphology of *L. atlantica* suggests not only a separate phylogenetic history, but also an unusual feeding ecology.

MATERIAL

The single specimen of *Laevinesta atlantica* that constitutes the basis for this report was collected at a depth of 58.5 m in 1980 on Transect III, Sta. No. 17 (25°45′15″ N; 83°19′15″ W), as part of the Bureau of Land Management 3-year survey of the Charlotte Harbor to the Dry Tortugas area of the Atlantic Continental Shelf. The animal had been damaged in handling, and the fragile internal shell broken. The shell pieces and a permanent light microscopic mount of a segment of the radula are deposited at the United States National Museum under USNM 792397.

RADULAR MORPHOLOGY

The radula of *Laevinesta atlantica* is illustrated in Figures *1, 3, 5, 6*. The most striking feature of the radula is its division into a central field of small, but very well-developed and robustly cusped teeth, flanked by broad fields of heavy, elongate plates that stand topographically high above the central field. A single plate in the lateral field is slightly more than seven times the width of one of the small teeth in the central field (Figure *5*). The rachidian is slightly asymmetric, but this kind of asymmetry has developed many times within gastropod radulae (Hickman, 1981) and does not, in this instance, provide any reliable clues as to phylogeny. The four lateral teeth on either side of the rachidian are similar in size and morphology to the central tooth, each with a robust central cusp and one or two smaller prong-like cusps on either side. When the radula is bent to simulate its configuration during feeding (Morris & Hickman, 1981), the cusps on the rachidian and lateral teeth are erected into a tangle of anteriorly- and laterally-projecting cusps. (Figure *3*).

In the normal rhipidoglossan radula, including that of fissurellacean limpets, the central field of rachidian and lateral teeth is flanked by fields of marginal teeth that are usually much finer and are used in food gathering rather than in food preparation. In *Laevinesta atlantica*, the most robust teeth in the radula are in the area that is analogous with the marginal tooth fields. In each half row, there is an elongate-quadrate heavy tooth that has a heavy, but relatively blunt, cusp that is inclined at a 50° angle to the longitudinal axis of the radula. There is a small secondary cusp along the inner margin of the main cusp. The outer end of this heavy quadrate tooth rests against and interacts with a facet on the surface of a small articulatory plate that in turn articulates with another elongate, but uncusped, plate that is nearly as long as the elongate-quadrate cusped element. There is a problem defining a single row of teeth in this portion of the radula. If a row is defined by one sequence of articulations, then it includes the sequence of teeth that are illustrated in Figure *1* by the letter A. If it is defined by an alternative set of articulations, it includes the sequence of teeth lettered B. A row could also be considered to include the two major elongate teeth that share a common axis perpendicular to the longitudinal axis of the radula, although these two teeth are not directly articulated; and the articulatory plates would necessarily be considered to fall between rows rather than within rows. The problem of how to define a row is not unique to this radula and is discussed in detail elsewhere (Hickman, in press).

At the outer end of the second major element there is another small, quadrate plate; and adjacent to this are two marginal teeth that are comparable in form to true rhipidoglossan marginals. These teeth are not attached in any way to the outer plate as illustrated by Pilsbry & McGinty (1952: 2, fig. 1) nor are they moveable upon a basal plate as indicated in the text. They are, instead, attached to the outermost margin of the radular membrane. Pilsbry and McGinty were also in error in illustrating only one marginal tooth per row: there are two. As illustrated in Figures *1* and *6*, the marginal teeth in collapsed configuration completely cover both the column of small outer plates and the column of outermost heavy elongate-quadrate elements.

PHYLOGENETIC AND ECOLOGIC IMPLICATIONS

Is this a fissurellid radula? Pilsbry & McGinty (1952) stated that the teeth in the central field of *Laevinesta* resemble the teeth in the central field of the emarginuline genus *Clypidina*. The rachidian and inner lateral teeth of the type species, *Clypidina notata* (Linnaeus, 1767) are illustrated for comparison in Figure *7*, and the width of the radula is illustrated in Figure *2* to show the typical fissurellid pattern. Although the rachidian and laterals are multicusped, the cusps are bent over and more flattened in cross-section than prong-like. Likewise, the shafts and bases in *Clypidina* are of typical fissurellid form, which is never so robust as in *Laevinesta*. The heavy lateral fields of plates in the radula of *Laevinesta* have no analog in the fissurellid radula, although they possibly could be derived by fusion of marginal teeth.

The problem is that we are dealing with a radula that is so highly derived and modified from typical rhipidoglossan form that there are no clues as to what it might have been derived from. The radula is convergent on some of the equally bizarre radulae of several families of deep-sea limpets (*e.g.* the Addisoniidae and Bathysciadiidae), in which robust fields of plates replace normal teeth. The radula of *Bathysciadium* is illustrated in Figure *4*. It is an even more highly modified radula in that the radular membrane supports no central field of teeth; but the lateral fields of plates in this radula are analogous to the plates in *Laevinesta* and share the characteristic of being topographically highly elevated above the central field. The significance of evolutionary convergence on this grade of radular morphology is not clear; but all the groups that share it occur on unusual substrata. The deep-sea species with plate fields occur on such substrata as wood, skate egg cases, and concentrations of undegraded squid beaks. *Laevinesta* is associated with sponges, although the nature of the association is not known.

Laevinesta is not closely related to *Nesta* H. Adams, 1870, even though *L. atlantica* was originally described by Farfante (1947) under *Nesta*. *Nesta candida* H. Adams, 1870, the type species, is unfortunately known from a single specimen that was not well illustrated. The illustration and accompanying description do, however, indicate typical

Explanation of Figures *1* to *7*

Figure *1:* Radula of *Laevinesta atlantica* (Farfante, 1947). Width of radula showing central field of small teeth flanked by lateral fields of heavy elongate plates. The pairs of connecting arrows, A and B, represent alternative sets of articulations of plates that can be construed as rows Bar = 100μm

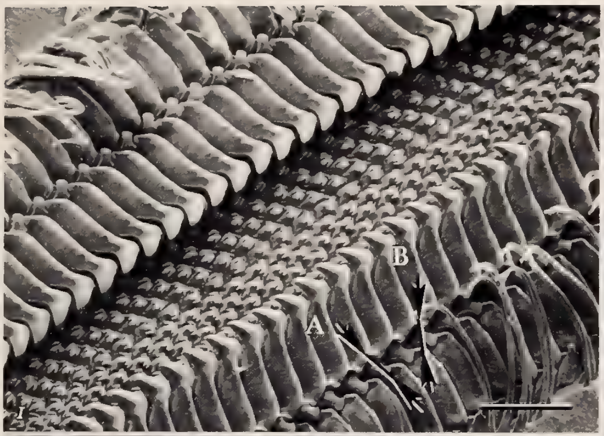
Figure *2:* Radula of *Clypidina notata* (Linnaeus, 1767) specimen from Ceylon (courtesy of J. Christiaens) illustrating the typical emarginuline (putatively primitive) condition of the fissurellid radula Bar = 400μm

Figure *3:* Erected teeth of central field of *Laevinesta atlantica* radula in a simulation of protracted functional configuration Bar = 10μm

Figure *4:* Radula of *Bathysciadium pacificum* Dall, 1908, with toothless central field flanked by lateral fields of interlocking plates. (Los Angeles County Museum of Natural History Loc. LACM 66-152) Bar = 100μm

Figures *5* and *6:* Enlargement of fundamental tooth units from right half of radula of *Laevinesta atlantica*. The right margin of Figure *5* overlaps slightly with the left margin of Figure *6* Bars = 20μm

Figure *7:* Rachidian and inner lateral teeth of the radula of *Clypidina notata* Bar = 100μm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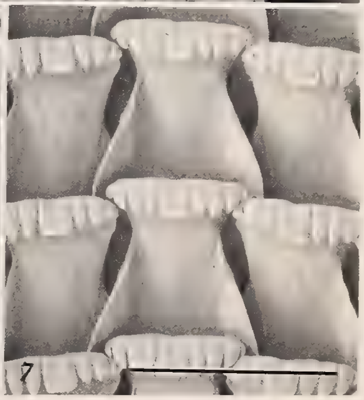
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fissurellid surface ornamentation and a crenulate margin, making it structurally dissimilar to the extremely thin, fragile, and unornamented shell of *L. atlantica.* Retention of external shell sculpture is a remarkable characteristic of fissurellid shells that are partially enclosed by mantle tissue, a phenomenon that is recognized and discussed by McLean (in press). There are further indications that the shell of *L. atlantica* has a unique microstructure, unlike anything occurring in the Fissurellidae (Lindberg, pers. comm. 1982). Although the animal does have some anatomical features in common with the Fissurellidae (PILSBRY & McGINTY, 1952; McLean, pers. comm., 1982), the lack of concordance with the Fissurellidae in both shell and radular characters demands careful consideration.

The affinities of *Laevinesta* are thus cast in doubt. The tendency to enclose the shell in mantle tissue is common in fissurellids, but modifications of the relationship between the animal and the shell do not involve evolutionary change in the basic form of the radula (or shell microstructure). The fundamental characters of the fissurellid radula (particularly the form of the asymmetry, the heavy paired outer lateral or inner marginal food-preparing teeth and their alternating or zipper-like folding together when the radula is retracted, and the poorly developed central tooth field) are recognizable even in the least typical fissurellids (HICKMAN, 1981). Even in the deep-water *Zeidora* A. Adams, 1860, in which the form of the radular asymmetry is reversed from that of other fissurellids (HICKMAN, 1981), the radula is clearly of fissurellacean derivation even if it does represent a separate line of evolution.

Molluscan systematists face two problems in interpreting any bizarre morphological structure. The first is the recognition of elements that might indicate that the structure is bizarre because it is primitive, an evolutionary holdover that is no longer otherwise represented in the living world. The second is recognition of elements that might indicate that it is derived and modified from something familiar. The radula of *Laevinesta* does provide a few clues. It is not a primitive or generalized form of radula. It is barely recognizable as rhipidoglossan. It is, however, so highly derived and modified that it is not possible to say where within the Rhipidoglossa it originated. Although it is possible to construct scenarios for deriving it from a number of fundamental rhipidoglossan plans, all such attempts involve considerable imagination and are to be avoided. Fortunately, it is very rare that we encounter a radula that is so bizarre and so highly modified as to elude classificatory attempts.

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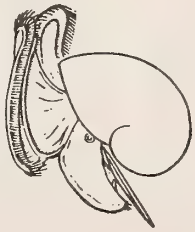

Functional Microstructure of the Lithodesma of *Mytilimeria nuttalli*

(Bivalvia : Anomalodesmata)[1]

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INTRODUCTION

THE LITHODESMA, a calcareous ossicle aragonitic at least in Lyonsiidae, is an intricate, functional part of the hinge system of many Anomalodesmacean bivalve molluscs. Microstructure of the lithodesma of *Laternula* has been examined by S. Morris (unpublished data) and described by J. Taylor (Pers. Comm.) as consisting of crystallites similar to spherulites. Aside from this, no ultrastructural research on this ossicle has been published. Since the lithodesma is a fundamental structural feature with potential significance as an important taxonomic tool, we report here the unique and complex microstructure and growth patterns of this ossicle in the lyonsiid *Mytilimeria nuttalli* Conrad.

METHODS AND MATERIALS

Specimens of *Mytilimeria nuttalli*, endosymbionts of compound ascidians along the western coast of North America (YONGE, 1952), were obtained from Venice, California. After removal from their host tunicates, clams were stored in 70% ethanol. Soft parts were later removed from the valves and the hinge region carefully fractured from the rest of the shell. Samples of the hinge region were treated in a 5% sodium hypochlorite solution for 15 to 60 minutes to remove organic materials, including the ligament and aragonitic fibers associated with the resilium. The lithodesma was easily freed from the hinge area after treatment. Specimens treated with organic solvent were washed in distilled water prior to dehydration in absolute ethanol for five days and further drying in a 70°C oven for an additional five days. Some lithodesma were fractured for cross-sectional examinations; others were left entire. All specimens were mounted on aluminum stubs using silver paint, coated with a thin layer of carbon and gold, and examined on a Philips 501 or AMR 1000 scanning electron microscope at accelerating voltages of 15 or 30kv.

RESULTS AND DISCUSSION

The lithodesma of *Mytilmeria nuttalli* is a small semirectangular, dorsoventrally flexed structure that has slightly concave anterior and posterior ends and tapers slightly posteriorly (Figure *1*A). It is approximately ⅛th of the length of the shell and is situated just posterior to the usually recurved umbones of the valves. A dark brown primary ligament ensheaths the ossicle anteriorly and laterally and forms a thin veneer over the lithodesmal dorsum. A narrow extension of the mantle covers and secretes this veneer (YONGE, 1976). The ventral surface and posterior edge of the lithodesma is void of ligament and is in direct contact with mantle epithelium. The lithodesma thus grows in size only ventrally and posteriorly.

The mantle epithelium abutting the posterior-dorsal region of the lithodesma deposits only a thin dorsal calcareous layer. This surface of the lithodesma is replete with growth lines that cross from side to side over the central part (Figure *1*B). These lines curve sharply at either side of the ossicle toward the anterior margin (Figure *1*B). Fine growth lines range in width from 20-40μm. Major growth

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[1] University of Delaware College of Marine Studies Contribution No. 160.

bands are as wide as 220μm. Major bands located at the posterior lithodesmal margin (Figure *1*C) show an arborescent growth pattern typical of bands that dominate the central region of the dorsum (Figure *1*B). Prisms in these regions are broad and irregular. While at low magnifications they appear to grow individually in longitudinal dendritic fashion (Figure *1*, B and C), at high magnifications prisms show an arborescent pattern leaving wide gaps between basal regions (Figure *1*D). Large prisms are probably deposited during periods of rapid growth. Remnants of dense organic material, either conchiolinal or ligamental, remain adhering to prisms treated only briefly with sodium hypochlorite (Figure *1*D). Small prisms, approximately 1.0μm in diameter and ⅛th the size of large prisms, form lines of discontinuity along the lithodesmal dorsum. These are fine growth lines composed of tightly packed prisms uniformly and obliquely arranged with respect to the lithodesmal surface (Figure *1*E). Wide bands of arborescently grouped, broad, irregular prisms with variable directional growth thus alternate with narrow zones of small, densely packed prisms with a high degree of directionality. These minor growth bands are most dense laterally (Figure *1*B). Minor bands or lines are probably deposited during periods of slow growth. Individual longitudinal branches of arborescent growth may run for long distances along the dorsal length of the lithodesmal surface and pass through several growth zones (Figure *1*B). Rapid central arborescent growth may thus override deposition of minor bands of small prisms. The latter appears in cross-section as a layering of tall prisms over small prisms (Figure *1*F).

The microstructure of the dorsal surface of the lithodesma is reminiscent of that of nymphal prisms of the oyster *Crassostrea virginica* (Carriker & Palmer, 1979). Nymphal prisms constitute the ligostracum situated between foliated calcite and organic ligament and are characterized by a granular, highly irregular surface. As does the oyster ligostracum, the lithodesma abuts ligament. Both nymphal ligostracum and dorsal lithodesma have irregular surfaces with pits and wide gaps between prism ends. Carriker & Palmer (1979) suggest that ligostracum in *C. virginica* functions in binding organic to calcareous layers. This appears to be the case for the lyonsiid lithodesma as well.

The prismatic nature of the lithodesma dorsum is evident in cross-sectional fractures (Figure *1*, F and G). Well defined prisms, aligned normal to the lithodesmal surface, vary in height from more than 50μm in the central region to less than 1.0μm laterally. This variation in height is a reflection of the divergence of the large central prisms of major growth bands and the smaller prisms of laterally recurved minor growth lines. The internal structure of the lithodesma submerged beneath the outer dorsal prismatic layers is also prismatic but consists primarily of very small, compact prisms less than 1.0μm in both diameter and length (Figure *1*, G and H).

The ventral lithodesmal surface is composed of a layer of regular, relatively tall prisms ranging from 10 to 15μm in height and running normal to the ventral, convex surface (Figure *1*H). This surface, in contrast to the dorsal surface, can grow considerably in thickness. Growth in this region is evidenced by subsurface deposits of taller prisms (Figure *1*H). The ventral lithodesmal surface is relatively smooth with only gentle circular swellings (Figure *1*I), a surface very similar to that of myostracum (Carriker *et al.*, 1981; Prezant, 1981). Myostracum is deposited only in regions of shell that serve or have served for muscle attachment as for the adductor muscle and mantle pallial line. The ventral surface of the lithodesma is in contact with an extension of the mantle; firm muscular connection between these two structures has yet to be ascertained.

The compact organization of the lithodesma, composed internally of densely packed small prisms and surrounded by a resilient ligament reinforced with supporting aragonitic fibers, lends strength and fracture resistance to the structure. Fractures from excessive strain, for example, can dissipate through the numerous, minute pathways between microprisms. Strains of this sort can occur during periods of rapid or extended adduction. Similar microstructural adaptations for fracture dissipation are found in the shells of bivalves with homogeneous or crossed-lamellar structures (Taylor & Layman, 1972; Prezant, 1981). Rapidly growing ascidian tissue surrounding the bivalve may also place some constraint on valve abduction.

All families of the Pandoracea, subclass Anomalodesmata, include at least some taxa that possess a lithodesma. These groups include the Lyonsiidae, Pandoriidae, Myochamidae, and Cleidothaeridae (Yonge & Morton, 1980). Lithodesmas are also found in the Verticordiidae, Cuspidaridae, Thraciidae, Periplomatidae, and Laternulidae, other major taxa of the Anomalodesmata. In all Pandoracea the lithodesma is situated posterior to the umbones; in the Thraciidae, Periplomatidae, and Laternulidae it is located anterior to the umbones (Yonge & Morton, 1980). The interfamilial variations between lithodesma of these groups are thought to be of systematic and functional significance (Yonge & Morton, 1980).

The ligament in the Pandoracea is depressed (*i.e.*, sunk) between the umbones and is thus necessarily broad to interconnect the two shell valves. If this ligament were a single organic unit, an artifactual bend inward would probably occur upon adduction of the valves resulting in ineffective abduction because of compromised compressive forces (Yonge, 1976; Yonge & Morton, 1980). The lithodesma structurally and behaviorally divides the organic ligament into two successfully compressive units insuring adequate abductive thrust. An external secondary ligament, composed of fused periostracum, serves to align the valves. In the three families with an anteriorly located lithodesma, the primary ligament is not sunk and the lithodesma merely serves to align the valves (YONGE & MORTON, 1980).

The abductive role of the lithodesma of *Mytilimeria nuttalli* is supported by the internal, microprismatic structure that readily absorbs possible stress in valvular movement; a firm connection between ligamental resilium and the rugose lithodesmal dorsum; and close contact between mantle and ventral lithodesmal surface permitting increase in size with growth of the animal.

Potentially different functions of the lithodesma in various families of the Anomalodesmata reflected by different morphological locations may be confirmed by future interfamilial studies of the microstructure of this calcareous plate.

ACKNOWLEDGMENTS

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Explanation of Figure *1*

Scanning electron micrographs of lithodesma of *Mytilimeria nuttalli*. Direction of growth is to the top (posterior) in all micrographs but those showing cross-sections

(A) Entire lithodesma showing (d) minor growth lines and (m) major growth bands along dorsal surface Horizontal Field Width = 2.2mm

(B) Curvature of growth lines along dorsal, lateral border, (d) minor growth lines, (m) major growth bands Horizontal Field Width = 0.75mm

(C) Dorsal, posterior growth band showing arborescent growth patterns Horizontal Field Width = 190μm

(D) Detailed view of dorsal prisms of arborescent growth, (r) organic residue Horizontal Field Width = 48μm

(E) Small prisms of dorsum composing minor growth lines or lines of discontinuity Horizontal Field Width = 25μm

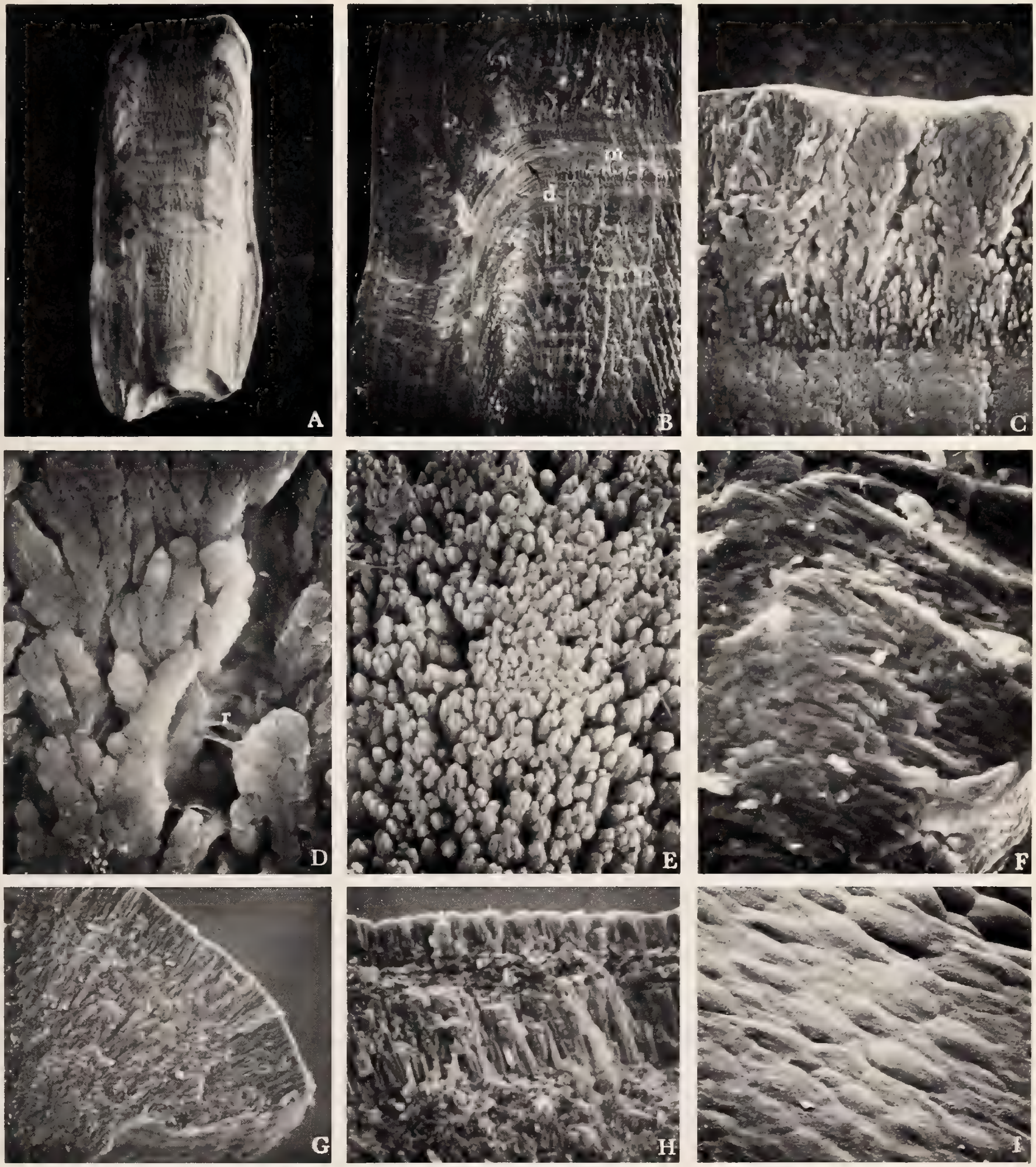
(F) Tall prisms in central region of dorsal surface, cross-sectional fracture Horizontal Field Width = 98μm

(G) Cross-sectional fracture through middle of lithodesma, ventral surface at top of micrograph Horizontal Field Width = 75μm

(H) Prisms of ventral surface of lithodesma, fine internal prismatic structure is evident Horizontal Field Width = 22μm

(I) Ventral myostracal-like surface Horizontal Field Width = 465μm

[PREZANT & CARRIKER] Figure 1



Sex Ratios in Oysters, Emphasizing *Crassostrea virginica* from Chesapeake Bay, Maryland

BY

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(1 Text figure)

INTRODUCTION

Settlement of spat of young eastern oysters, *Crassostrea virginica* (Gmelin, 1791), on Chesapeake Bay (Maryland) oyster beds has been at historical low levels in recent years (Krantz & Meritt, 1977). Because disrupted oyster reproduction might have been implicated in this recruitment decline, we initiated a study of oyster gametogenesis and spawning in 1977-78 (Kennedy & Krantz, submitted for publication). State resource managers thought that, in addition to possible disrupted gametogenesis and asynchronous spawning, unbalanced sex ratios (in favor of females) might be contributing to the general pattern of poor settlement. The rationale was that, because oysters are predominantly male in their early years of life (Coe, 1943; Andrews, 1979), the limited recruitment of young oysters might lead to a preponderance of older, female oysters on oyster grounds. There was concern that not enough males would be available to stimulate spawning or to fertilize adequate numbers of eggs.

I report here the results of a study of sex ratios of eastern oyster populations from central Chesapeake Bay, comparing information collected during the 1977-78 survey with historical material collected in the 1960's. Sex ratios were generally balanced in both time periods, with a tendency to a greater proportion of males in 1977-78. I also include information on the results of a preliminary experiment to determine the effects of an absence of the opposite sex on sex ratios of samples of eastern oysters held in the field in isolated groups for about a year. This experiment was performed because a survey of literature revealed that environmental factors, including proximity of other oysters, may exert an influence on lability of sexes of various oyster species. The same literature survey leads me to suggest in conclusion that an increased preponderance of males in an oyster population may indicate the presence of an environmental stressor.

MATERIALS AND METHODS

Recent Histological Material: Preparation of histological material collected from 18 oyster beds in Maryland's Chesapeake Bay has been described in Kennedy & Krantz (submitted for publication). Briefly, from March to December 1977, monthly samples of 50 oysters were collected from each of 15 oyster bars (Figure 1). From March to September

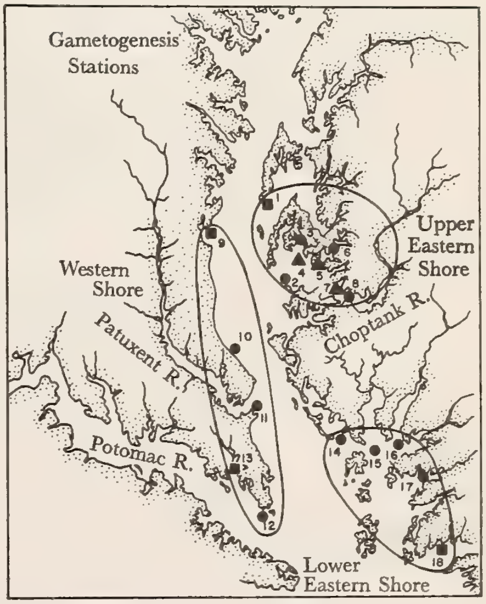

Figure 1

Location of the 18 oyster bars sampled in central Chesapeake Bay in 1977-78. ● sampled in both years; ■ sampled in 1977 only; ▲ sampled in 1978 only

1978, monthly samples of 25 oysters were collected from each of 14 oyster bars (Figure 1), 11 of which had been sampled in 1977. The 18 oyster bars sampled in 1977-78 are named and described in Kennedy & Krantz (submitted for publication). From June to September 1978, oysters were collected weekly from Deep Neck Bar (No. 3 on Figure 1) and Double Mills Bar (No. 6) to follow gametogenic activity on these beds more closely. The former bar generally receives higher numbers of spat per unit area than does the latter (KENNEDY, 1980).

In 1977 and 1978, usually 25 oysters in each sample were measured (hinge to opposite margin, to the nearest half cm) and prepared histologically to provide microscope slides bearing individual sections of gonad, *i. e.*, one slide per oyster (Kennedy & Krantz, submitted for publication). The extra (usually 25) oysters in each 1977 sample were not measured but were treated histologically as a group to provide two or three microscope slides bearing portions of germinal tissue taken from each member of the group. These grouped sections provided additional sample numbers for sex determinations. Oysters in the weekly samples from Deep Neck and Double Mills bars in summer 1978 were not measured, but were processed individually to produce one microscope slide per oyster.

Examination of the resulting slides revealed that spring and fall samples often contained animals whose sex could not be determined due to their immature or spent condition. Thus, only those oysters collected in June, July and August were used in determinations of sex because sex is ascertained readily and accurately at this time. All of the gonad material present on each slide was scrutinized. Oyster bars (Figure 1) were grouped for comparative purposes as follows: Upper Eastern Shore (Nos. 1-8); Western Shore (9-13); Lower Eastern Shore (14-18).

Historical Histological Material: Slides of oyster tissue collected in the 1960's from a variety of oyster beds in central Chesapeake Bay (FARLEY, 1975; Kennedy & Krantz, submitted for publication) were examined to determine sex. The resulting data enable a comparison of sex ratios to be made between 1977-78 and this earlier period (when spat settlement was generally higher than in 1977-78).

Experimental Manipulation of Sex Ratios: The results of both the sex ratio determinations and a literature review (below) led me to devise an experiment to determine any changes in sex that might occur in unisexual populations held over winter in the Choptank River. On August 14, 1980, oysters that had been collected from Deep Neck bar were spawned in the laboratory. The sex of each spawning individual was determined by examining the spawn. The shell of each oyster was marked with red (♀) or blue (♂) waterproof ink. Three trays were filled with oysters: 66 males in one; 34 males and 34 females in a second (control); and 92 females (the higher number due to a counting error) in a third. The trays were placed in the Choptank River on a water intake pipe which kept them off the bottom. Each tray was about 7 m away from its neighbor. The area had been dredged in 1977 and no wild oysters were seen in the vicinity of the trays. On July 6, 1981, the trays were retrieved. Each oyster was processed histologically and sexed as described earlier.

Presentation of Results: All sex ratios, including those from the literature, are presented as the proportion of functional females per functional male. Tests of significance of the various results were made using contingency tables coupled with X^2 tests (SOKAL & ROHLF, 1969). This allows for tests of independence to be made, *i. e.*, between years, or locations, or experimental treatments, facilitating comparisons among sex ratios derived under different conditions.

RESULTS

Information on temperature and salinity at time of collection and of size ranges and gametogenic patterns of oysters collected are presented in Kennedy & Krantz (submitted for publication).

Incidence of hermaphrodites was low in the populations sampled, as determined by examination of the histological material. In 1977-78, 15 of 3182 oysters were hermaphrodites (0.47%). In the period from 1961 to 1968, 9 of 2613 oysters (0.34%) were hermaphrodites.

Sex Ratio and Size: For the three major regions surveyed, the samples of individually treated oysters collected in June to August of various years were grouped according to five arbitrary size classes and sex ratios were determined (Table 1). Sex ratios within each size class at each of the three geographical regions in 1977-78 (Table 1A) or for all three regions combined (Table 1B) were independent of year ($P > 0.05$), *i. e.*, there were no statistical differences in sex ratios from 1977 to 1978.

In 1977-78, for oysters measuring from 4 to 7.5 cm in length, there were usually as many as or more males than females, with the sex ratios from different locations or years not being significantly different ($P > 0.05$) from a balanced (1:1) ratio (Table 1A, B). There was a tendency for the proportion of females to increase with increasing oyster size (note however that the largest oyster collected in our survey was a 21 cm male taken from Double Mills bar in 1978). Most sex ratios in the larger size classes were significantly different ($P < 0.05$) from a balanced ratio (Table 1A, B). However, this was not true for oysters larger

Table 1

Size and sex ratios for (A) oysters in three areas of central Chesapeake Bay, June-August, 1977 and 1978; (B) for these areas combined; and (C) for all locations and years during the 1960's and 1970's combined. Values are proportions of females per male, with numbers of oysters in parentheses. Underlined sex ratios are not significantly different (P > 0.05) from a balanced (1:1) ratio.

	Location	Year	Size range (cm)					Sizes combined
			0-3.5	4-7.5	8-11.5	12-15.5	16-19.5	
A.	Choptank River							
	(Oyster bars 2, 3, 6, 8)	1977	—	1.2 (24)	1.4 (176)	1.4 (92)	1 ♂	1.4 (293)
		1978	—	0.8 (25)	1.3 (163)	1.1 (89)	2.5 (7)	1.2 (284)
	Lower Eastern Shore							
	(Oyster bars 14-17)	1977	—	0.7 (34)	2.3 (201)	3.1 (49)	—	2.1 (284)
		1978	—	0.5 (17)	1.7 (199)	2.2 (65)	—	1.7 (281)
	Western Shore							
	(Oyster bars 10-12)	1977	—	1.0 (6)	1.2 (135)	2.5 (73)	2 ♀	1.5 (216)
		1978	—	1.0 (12)	1.7 (158)	1.7 (49)	—	1.7 (219)
B.	Combined	1977	—	0.9 (64)	1.6 (512)	2.0 (214)	2.0 (3)	1.6 (793)
		1978	—	0.7 (54)	1.6 (520)	1.5 (203)	2.5 (7)	1.5 (784)
C.	All locations, all years	—	0.5 (3)	0.8 (555)	1.7 (2662)	2.0 (783)	4.8 (35)	1.6 (4038)

Table 2

Sex ratios (June-August combined) on oyster bars in central Chesapeake Bay. Values are proportion of females per male. Numbers in parentheses are numbers of oysters. Underlined sex ratios are not significantly different (P > 0.05) from a balanced (1:1) ratio. Oyster bar numbers refer to Fig. 1.

Oyster bar	1961	1962	1963	1965	1966	1967	1968	1977	1978
Upper Eastern Shore									
1. Hollicutt Noose	—	—	—	1.3 (50)	2.0 (15)	1.8 (22)	—	1.0 (153)	—
2. Cook Point	—	—	—	—	2.1 (22)	1.8 (22)	1.4 (50)	0.9 (147)	1.6 (74)
4. Royston	—	—	—	—	—	—	—	—	1.6 (72)
5. Fox Hole	—	—	—	—	—	—	—	—	2.0 (70)
7. Howells Point	—	—	—	—	—	—	—	—	1.8 (74)
8. Green Marsh	—	—	—	—	—	—	—	2.0 (145)	1.1 (74)
Broad Creek	0.9 (130)	—	—	2.4 (48)	2.8 (15)	2.0 (15)	—	—	—
3. Deep Neck	—	—	—	—	—	—	—	0.9 (144)	1.3 (255)
6. Double Mills	—	—	—	—	—	—	—	1.0 (144)	1.1 (234)
Lower Eastern Shore									
Crab Point	1.0 (139)	—	—	1.6 (44)	1.7 (48)	—	—	—	—
14. Norman	—	—	—	—	—	—	—	1.7 (140)	1.7 (70)
Lambstone	—	—	—	0.7 (62)	1.3 (49)	2.0 (18)	—	—	—
15. Sharkfin Shoal	—	—	—	—	—	—	—	1.3 (140)	1.4 (72)
16. Middleground	—	—	—	—	1.3 (14)	4.0 (15)	—	3.1 (143)	2.4 (72)
17. Georges	—	—	—	1.3 (208)	1.9 (46)	2.7 (48)	4.3 (48)	1.2 (139)	1.4 (67)
18. Marumsco	1.4 (132)	2.1 (220)	2.3 (144)	—	—	—	—	1.0 (148)	—
Western Shore									
9. Herring Bay	—	—	—	1.8 (48)	2.1 (50)	3.0 (16)	—	1.1 (152)	—
Governors Run	—	—	—	2.0 (65)	2.0 (15)	1.0 (16)	—	—	—
10. Flag Pond	—	—	—	—	—	—	—	1.5 (143)	1.1 (74)
11. Hog Island	—	—	—	—	—	—	—	1.5 (145)	3.1 (74)
Cedar Point Hollow	—	—	—	2.2 (67)	2.1 (49)	2.0 (15)	6.5 (15)	—	—
12. Cornfield Harbor	—	—	—	0.8 (46)	1.3 (44)	—	—	1.6 (143)	1.4 (71)
13. Chicken Cock	—	—	—	—	1.4 (49)	1.2 (24)	0.9 (15)	1.3 (147)	—

than 16 cm, probably because numbers were low (Table 1A, B).

When sex ratios for the five size classes were determined using data on 4038 oysters from all locations and all years, including the 1960's and 1977-78 (Table 1C), the increase in predominance of females with larger size is shown clearly. In this case, only the ratio for the smallest size class (0-3.5 cm) was not significantly different from a balanced ratio ($P > 0.05$).

Sex Ratio, Location, and Year of Collecting: To obtain additional numbers of oysters for sex ratio studies, oysters treated histologically in groups (rather than as individuals) in June to August 1977, plus oysters collected weekly from Deep Neck and Double Mills bars in 1978, were combined with the data discussed in the previous section on sex ratio and size. These combined data for 4874 oysters appear in Table 2. Also included in this table are data obtained by examining historical histological slides of 810 oysters from five new locations (un-numbered in Table 2): Broad Creek oysters were from the same water body as Deep Neck oysters (No. 3); Crab Point bar is contiguous with Norman (No. 14); Lambstone bar is contiguous with Sharkfin Shoal (No. 15); Governors Run is about 10 km north of Flag Pond (No. 10); Cedar Point Hollow is about 1 km south of Hog Island (No. 11).

Females outnumbered males in 58 of the 69 samples examined (Table 2). However, most samples (65%) were not significantly different ($P > 0.05$) from a balanced sex ratio. It is not possible to compare these ratios with each other as they are presented in Table 2 because of size variations of oysters represented. In order to compare between sampling periods, it was necessary to determine a common size range first because of the influence of size on sex (Table 1). The grand mean and standard deviation for all the oysters represented in Table 2 were 9.6 ± 1.09 cm. Arbitrarily I selected a size range (7 to 12 cm) that would encompass the mean and two standard deviations. I re-examined the data on sex for all oysters ($n = 2832$) in this size range for the 1960's combined and for 1977-78 combined. The resultant sex ratios are presented in Table 3. In the 1960's, sex ratios were not significantly different ($P > 0.05$) from a balanced ratio in 5 of the 13 locations, compared with 7 of 13 locations in 1977-78. For each location, the two time periods were compared. For 9 of the 13 locations, the differences in sex ratios with time were not significant statistically ($P > 0.05$). In three of the four instances where the time periods differed significantly, the ratio of females per male declined from the 1960's to 1977-78.

Table 3

Sex ratios (June-August) for 7-12 cm oysters from central Chesapeake Bay for two time periods, and X^2 value and significance level of difference in sex ratios between the two periods as determined by contingency tables. Sex ratio values are proportions of females per male. Underlined ratios are not significantly different ($P > 0.05$) from a balanced (1:1) ratio. Numbers in parentheses are numbers of oysters. Number of oyster bar refers to location on Figure 1. + = increase; − = decrease; ns = not significant.

Location	1960's	1977-78	X^2	Significance level	Change in ratio with time
Upper Eastern Shore					
1. Hollicutt Noose	1.2 (74)	0.7 (52)	2.10	ns	−
2. Cook Point	1.6 (94)	1.3 (124)	0.44	ns	−
3. Broad Creek/Deep Neck	2.2 (138)	1.4 (128)	3.49	ns	−
Lower Eastern Shore					
14. Crab Point/Norman	1.8 (153)	2.0 (120)	0.12	ns	+
15. Lambstone/Sharkfin	1.0 (123)	1.6 (136)	3.92	< 0.05	+
16. Middleground	2.1 (28)	2.8 (103)	0.39	ns	+
17. Georges	2.8 (138)	1.1 (89)	11.78	< 0.05	−
18. Marumsco	2.4 (405)	1.4 (70)	3.86	< 0.05	−
Western Shore					
9. Herring Bay	2.0 (80)	0.6 (31)	6.98	< 0.005	−
10. Gov. Run/Flag Pond	1.7 (83)	1.3 (112)	0.81	ns	−
11. Cedar Pt. Hollow/Hog Island	2.2 (136)	2.0 (120)	0.18	ns	−
12. Cornfield Harbor	0.9 (75)	1.4 (120)	1.68	ns	+
13. Chicken Cock	1.2 (80)	1.9 (20)	0.65	ns	+

Experimental Manipulation of Sex Ratios: Mortalities in the trays holding the unisexual and mixed populations were low when the trays were retrieved in July 1981 (1.5% in the "all-male" population, 0% in the "all-female" population, and a 4.4% in the mixed population). One hermaphrodite was noted in the "all-male" group and three members of the "all-male" and "mixed" groups were infested with the trematode, *Bucephalus cuculus:* these four animals were left out of the analysis.

The sample that had been 100% male in 1980 now contained 20 females (31.2% change), whereas the group that had been all female now included 29 males (33.0% change). The control group held 34 females and 30 males, a ratio (1.1:1) not significantly different ($P > 0.05$) from a balanced ratio. It was also not significantly different from the 1:1 ratio at the start of the experiment ($P > 0.05$), whereas the changes in sex ratio in the two formerly unisexual populations were highly significant ($P < 0.001$).

Unfortunately, the marking ink on the control oysters was affected by the long immersion period of the experiment. We were not able to be confident in our identification of oysters that were initially male because oyster shell contains blue tones that could be confused with the faded 1980 markings. However, we did identify 10 oysters that had been females in 1980 whose red marks still were clear. Of those ten, eight remained female while two were now male (20% change). The proportions of sexes in this small sample were independent of the year of assessment, *i.e.*, they were not significantly different from 1980 to 1981.

DISCUSSION

Occurrence of Hermaphrodites: The low incidence of hermaphrodites in our study (< 1%) is similar to that noted in populations of *Crassostrea virginica* in Canada (NEEDLER, 1932a), eastern U.S.A. (COE, 1934), Louisiana (BURKENROAD, 1931), and California (BERG, 1969), and in other species of oysters elsewhere (DINAMANI, 1974; ASIF, 1979; NASCIMENTO *et al.*, 1980).

Sex Ratios in Chesapeake Bay: The pattern of an increase in predominance of females as size increases is a common one (COE, 1943; NASCIMENTO *et al.*, 1980). Data on oysters (in a more restricted size group) from Virginia are presented in ANDREWS (1979) and are similar to my findings.

Sex ratios from samples collected throughout central Chesapeake Bay over a number of years favored females (Table 2). However, most ratios were not as unbalanced as had been expected, given the limited recruitment of young (male) oysters over the preceding decade. A comparison of some different areas is instructive. For example, Deep Neck bar is in an area of historically good spat settlement whereas Double Mills bar is a poor settlement area (KENNEDY, 1980), yet their corresponding sex ratios were virtually identical (Table 2). Green Marsh bar lies near a sewage outfall and commercial harvests since 1964 have been almost totally restricted, whereas on nearby clean Howells Point bar, harvests have been average or above since 1964 (H. King, Maryland Department of Natural Resources, personal communication); nevertheless, the corresponding sex ratios did not exceed two females per male (Table 2) and the 1978 ratios for the two bars were not significantly different from each other ($P > 0.05$). Thus, harvesting pressure or the lack of it had not affected proportions of the two sexes. On the other hand, harvesting on Middleground bar has been much above average since 1964 (H. King, personal communication), yet on this bar were found the highest ratios of females to males of nearly all samples (Table 2). Spat settlement on Middleground from 1939 has been average for the region in which it is located (MERITT, 1977).

It appears, then, that oysters in central Chesapeake Bay have been able to maintain a general balance between females and males in spite of harvesting pressure or the lack of it, or of varying levels of recruitment success. Our experimental study showed that unisexual groups of both sexes demonstrated over 30% change to the opposite sex. This is a greater change than that (20%) of the females in the mixed control population (bearing in mind the limited sample size of oysters that were clearly identifiable as initially female in the mixed population). However, both rates of change are sufficient to allow for sexual equilibrium in a few years, assuming no mortality or recruitment to or loss from the population.

It is not clear what balanced sex ratios imply for the survival and reproduction of oyster populations. As noted earlier, 1:1 ratios were approximated for 65% of the samples examined here (Table 2). When size of oysters was allowed for, 46% of the sex ratios for combined samples collected in the 1960's and in 1977-78 were not significantly different from a 1:1 ratio (Table 3). However, there is no information on optimal proportions of female to male oysters, unlike the situation in animal husbandry where one male mammal or bird may provide adequate fertilization of numerous females. In hatchery production of oysters, the presence of excess sperm can lead to polyspermy (GALTSOFF, 1964) so presumably an excess of males above a certain abundance is not advantageous in nature.

Sex Ratios Elsewhere: The finding of generally balanced sex ratios under a variety of harvesting or spat settlement conditions led me to a review of the literature. Results of earlier investigations of sex change between breeding seasons for mixed populations of oysters of known sex composition are as follows (n = sample size):

	Percentage which changed to opposite sex		
Year	Males (n)	Females (n)	Reference
—	58 (138)	23 (234)	Amemiya[1], 1929
—	21 (24)	42 (12)	Needler, 1932b
—	8 (125)	13 (61)	Galtsoff, 1937
—	26 (27)	25 (16)	Burkenroad, 1937
1933	19 (31)	62 (26)	Needler, 1942 (same group followed from 1932 to 1936)
1934	7 (41)	25 (16)	
1935	19 (42)	53 (15)	
1936	31 (42)	47 (15)	
—	12 (312)	17 (176)	Galtsoff, 1964
Average for *C. virginica*	17.9%	35.5%	

[1] *Crassostrea gigas* (all others are *C. virginica*).

There is great variability in the percentages recorded. In a number of cases, variations are probably attributable to different age or size groups that may have been combined in a sample. However, it is clear that sexual composition of a population is not static.

Factors Influencing Sex Ratio: Given the demonstrated lability of sex ratio in *Crassostrea virginica* (and other oysters), what might influence such lability? Three major categories of environmental influences on sex ratios in eastern oysters have been proposed. Burkenroad (1931) felt that proximity of members of one sex might influence the sex of an individual. This suggests some kind of ectocrine or hormonal control. Coe (1943) postulated that temperature and nutritive conditions might influence sex change, with an oyster's physiological state in each breeding season affecting sexual phase. Others have suggested that environmental stressors (including limited food or nutrient supply) affect sex ratios. I will review Burkenroad's proximity hypothesis first, and follow with consideration of effects of environmental factors. The review includes information on species other than the eastern oyster. To increase insight into their significance, I have tested the various results statistically, as this had rarely been done in the original reports.

Proximity of Other Oysters: Burkenroad (1931) examined gonad smears of 744 mature oysters from Louisiana after their position relative to other oysters was recorded. The The sex ratio was 373♀ : 371♂ or 1:1. He noted an increasing proportion of females with increasing size. However, when individuals ($\geq$ 40mm) were grouped according to position in life, he found the following: Group A—single oysters (*i. e.*, not attached to another oyster) had a sex ratio of 3.9:1 (n = 165); Group B—oysters growing attached with their valve margins > 40mm apart had a ratio of 1.7:1 (n = 73); Group C—oysters growing attached with their valve margins < 40mm apart had a ratio of 1:1 (n = 167). Group A results are significantly different from Group B ($P < 0.01$) and Group C ($P < 0.001$). Results for Group B and Group C are (just barely) significantly different ($P < 0.05$). Burkenroad (1931) concluded that the likelihood of a large oyster being male decreased rapidly with increasing distance from associates. Small oysters, no matter what their position relative to others, were almost always male.

Smith (1949) determined sex of *Crassostrea virginica* growing either as single individuals or together in clusters in South Carolina. The ratio for single oysters was 1.1:1 (n = 134) compared with a ratio of 0.6:1 (n = 147) for clustered oysters. These ratios are significantly different ($P < 0.05$). Thus, increasing maleness was again associated with presence of other oysters.

Menzel (1951) examined sex of 8 to 15 month-old eastern oysters (40-90mm) living on shell and 8 to 20 month-old oysters (50-75mm) attached to older oysters (> 2 yr old) in Louisiana. The ratio of the former group was 1.2:1 (n = 345) compared with 0.3:1 (n = 100) for the second group. This difference is highly significant ($P < 0.001$). Again, an increase in the proportion of males was associated with the presence of living oysters.

My preliminary study of isolated unisexual groups revealed that about one-third of males and females changed sexual phase under test conditions compared with an estimated 20% of females in the control, mixed group. Since the mixed group had a slight increase in the proportion of females (1.1:1) after a year, then less than 20% of the males had changed sex. If these percentages are truly representative of changes in the mixed group, then presence of oysters of the opposite sex was associated with a smaller change in sexual phase than in the unisexual groups, with a slight tendency towards the female phase occurring.

All of these findings would suggest that some chemical material from the associated oysters may be influencing reproductive physiology of neighbors. This would be a useful area for further investigation as it may have application in aquaculture depending upon the proportion of sexes that is optimal for brood production.

Environmental conditions: There is evidence that factors other than proximity of other oysters may be involved in determination of sexual phase. AMEMIYA (1929) found *Crassostrea gigas* (Thunberg, 1793) taken from a good fattening ground in Japan to have a higher proportion of females (1st winter oysters—1.1:1; 2nd winter oysters—1.4:1) than did oysters from a poor fattening region (1st winter oysters —0.9:1; 2nd winter oysters—0.6:1). The ratios for the younger oysters are not significantly different ($P > 0.05$) but the difference for older oysters is highly significant ($P < 0.001$) between growing areas. AMEMIYA (1929) proposed that abundant food supply allowed for development of a preponderance of females or that limited food supply resulted in a greater proportion of males.

AMEMIYA (1935) removed one-third of all gill lamellae from three groups of Japanese *Crassostrea gigas* in late autumn and held treated and untreated oysters together in submerged cages for seven months. For all three replicates, the proportions of females were lower in the treated versus untreated samples (2.5:1 vs. 3.1:1, 1.3:1 vs. 1.7:1, 0.8:1 vs. 1.1:1, respectively). However, the differences within each group are not statistically significant ($P > 0.05$). AMEMIYA (1935) postulated that the loss of portions of the gills led to limited feeding, deficient nutrition, and increasing tendencies to maleness as a result.

EGAMI (1953) repeated AMEMIYA's (1935) experiments on *Crassostrea gigas;* he also excised portions of mantle as a second treatment. He performed these operations in October on one sample of oysters and later in January on another. The following summer, there were no significant differences in sex ratios for the two January treatments and the control group and no clear tendency for one sex to change proportionately as a result of any treatment. However, for the earlier October samples, the excision of portions of gill tissue had resulted in significantly more males than in the group with parts of the mantle excised ($P < 0.05$) or in the controls ($P < 0.05$). There was no significant difference between data for the control group and the mantle-excised group ($P > 0.05$).

AWATI & RAI (1931) found that Indian *Saccostrea (= Ostrea) cucullata* (Von Born, 1778) containing pea crabs had a sexual composition of 10% females, 83% males and 7% hermaphrodites, compared with 56% females, 41% males and 3% hermaphrodites in crab-free oysters. The pea crab may have been interfering with food intake or metabolism by its presence in the gill region.

RAO (1956) noted that the environmental conditions of high temperature and salinity led to a greater proportion of male *Crassostrea (= Ostrea) madrasensis* Preston in India, whereas low temperatures and salinity were associated with increased proportions of females. He provided no explanation for this.

NEEDLER (1932a) and COE (1934) found that, in the first winter after settlement, larger *Crassostrea virginica* on the east coast of North America were more likely to be female. COE (1934) noted that the proportion of females from populations held in experimental floats at West Sayville, Long Island, was greater than on natural bars in that area, and 8 to 10 times as great as on beds in New Haven Harbor where the growing season was shorter. The proportion of females in first year populations that he had surveyed increased towards the southern United States (COE, 1943) where growing seasons are longer.

BAHR & HILLMAN (1967) divided 40 *Crassostrea virginica* from Chesapeake Bay into groups. Two groups were fed and one of the two also had shell edges of each oyster filed weekly. The other two groups were starved, with one group also having shell edges filed. Eight months later the sex of each oyster was determined. For unfiled oysters, starvation led to a decrease (statistically insignificant) in proportion of females (1:1) compared with fed oysters (2.3:1). In damaged (filed) oysters, sex ratios were similar for fed (0.3:1) and starved (0.1:1) animals. The group of starved, undamaged oysters had proportionately more females (1:1) than did the starved, filed oysters (0.1:1) although the difference was not significant ($P > 0.05$), probably because of the small samples involved. Fed, shell-damaged oysters had significantly ($P < 0.05$) fewer females (0.3:1) than the fed undamaged oysters (2.3:1). Thus, in general, shell damage or lack of food, or both, were associated with increasing proportions of males, although sample sizes were small.

DAVIS & HILLMAN (1971) held two groups of *Crassostrea virginica* in trays in Duxbury Bay, Massachusetts and filed the shells of one group weekly from August to October and May to June. Sex was determined in June. The (male-dominated) sex ratio for filed oysters (0.4:1) was significantly different ($P < 0.01$) from that of undamaged oysters (1.2:1).

In Canada, KENNEDY & BATTLE (1964) found a higher proportion of male *Crassostrea virginica* from Malpeque Bay, Prince Edward Island, in contrast with NEEDLER's (1932a) findings in the same area. They postulated that increased silt deposition and prolific growth of eelgrass (with resultant inhibition of oyster growth) in the study area might have affected sex ratios by making the environment less favorable than it had been 30 years earlier.

Finally, there is one contrary report concerning environmental influence on oyster sex ratios. ROUGHLEY (1933) examined populations of *Saccostrea (= Ostrea) commercialis*

Iredale & Roughley, 1933) from four regions in Australia, including good fattening and poor growth areas. He found almost identical proportions of males and females in each region.

In summary, except for ROUGHLEY's (1933) report, these earlier surveys and experiments provide provocative evidence that environmental factors such as presence of other oysters, quantity or quality of food, and stress-producing situations (gill or shell damage) influence the sexual phase of oysters. The mechanisms responsible are not yet clear. With regard to situations involving food supply or body damage, energy allocation by oysters may play a role. DAVIS & HILLMAN (1971) attributed the differences in sex ratios between shell-damaged and control oysters to diversion of energy in the damaged group from gametogenesis to shell repair, thus leading to production of sperm rather than energy-demanding eggs. In fact, it is not clear if equal quantities (volume, weight) of male or female gametes require different amounts of energy for their production. If oogenesis is actually a more energy-intensive activity than spermatogenesis, then perhaps starvation or energy diversion to shell repair would result in appearance of the male phase due to lowered energy availability.

Possible Implications: If energy diversion does influence sexual phase, would the presence of some wide-scale environmental stressor be reflected in a modification of sex ratios in a region, such as KENNEDY & BATTLE (1964) suggested for Malpeque Bay? The 1930-31 sex ratio in Malpeque Bay oysters (1-10 yr) was 0.6:1 (n = 947), exactly the same as the 1961-62 ratio (n = 459). The sex ratios of the 1-3 year olds were also similar: in 1930-31 the ratio was 0.5:1 (n = 737); in 1961-62 it was 0.6:1 (n = 273). However, 4-10 yr old oysters (the general spawning population) differed from one time period to the other: in 1930-31 the ratio was 1.5:1 (n = 210); in 1961-62 it was 0.6:1 (n = 186). This difference is highly significant statistically ($P < 0.001$) and, as noted earlier, was attributed by KENNEDY & BATTLE (1964) to increased siltation in the 1961-62 period.

In the only other study that I have encountered that might be relevant, Butler (1949, personal communication) examined gonads of *Crassostrea virginica* collected from a low salinity (LS) (Tolchester Beach) and a high salinity (HS) (Eastern Bay) region of Chesapeake Bay. The LS area had been subject to freshwater flooding in 1945 and early 1946, with salinities of 0%. over the bars compared with 10-15%. before the flooding. Many oysters had died and the survivors were in poor condition. Butler found sex ratios of 3+ year old oysters in summer 1946 to be:

LS 74 ♀, 48 ♂, 2 hermaphrodites, 61 undifferentiated
HS 155 ♀, 65 ♂, 1 hermaphrodite

Although there were proportionately half as many females again in the HS area (2.4:1) compared with the LS area (1.5:1), the differences are not statistically significant ($P > 0.05$). Nevertheless, the increased proportion of males in the region having poorly conditioned oysters living under low salinity stress is intriguing in that it follows the general pattern reported in the literature reviewed above.

With regard to my findings (Table 3), it is difficult to suggest a clear, single explanation for the changes in sex ratios (declining proportions of females on most oyster bars) noted between the 1960's and 1977-78 (a period of lower recruitment of young, mostly male, oysters) for central Chesapeake Bay. The 1977-78 period was one of much lower salinity compared with the 1960's when rainfall and runoff were diminished. This may have affected the bars further up the Bay (Nos. 1, 2, 3, 9; to a lesser extent 10, 11) but should not have influenced the lower Bay bars. Thus, lower salinity may have resulted in the increased proportion of males on these upper six bars. On the other hand, oyster disease had affected oysters on the lower Maryland grounds in the early 1960's (FARLEY, 1975) with the epizootic having subsided by the late 1960's. One could speculate that the increased proportion of females on bars 12, 13, 14, 15 and 16 in 1977-78 might reflect this recovery from disease conditions. However, bars 17 and 18 had decreased proportions of females in the latter period, contradicting this speculation.

Retrospective analysis of a complex system, such as Chesapeake Bay, is difficult. Thus, the reasons for the changes in proportions noted in Table 3 and the significance of these changes remain to be elucidated, as does the general topic of influence of various environmental factors on sexual change in oysters. We can conclude, however, that the declining recruitment of young oysters in Maryland's Chesapeake Bay, which was the initial stimulus for the study, was not caused by undue imbalance in the ratio of functional female oysters to functional males.

SUMMARY

In summer 1977 and 1978, samples of eastern oysters, *Crassostrea virginica*, were collected from grounds in central Chesapeake Bay. Tissue sections were examined to determine sex of each oyster. The proportion of females per male increased directly with size. Females outnumbered males in 58 of the 69 samples examined. However, 65% of these samples were not significantly different ($P > 0.05$) from a balanced (1:1) ratio. Thus, in spite of reduced recruitment of young (mostly male) oysters before and during the survey, most oyster bars had remained in sexual

balance. Harvesting pressure or the lack of such pressure also appeared not to have affected this balance. Comparison with sex ratios in oyster samples collected in the 1960's in central Chesapeake Bay revealed that, for 9 of 13 locations, the differences in sex ratios from the 1960's to 1977-78 were not statistically significant ($P > 0.05$), although the proportion of males had increased in the latter period. A review of oyster literature (including species other than *C. virginica*) revealed that presence of oysters of the opposite sex, or of stress conditions (*e.g.*, poor food quality, shell or gill damage) may influence sexual composition of an oyster population. In a preliminary experiment, unisexual groups of oysters held isolated from other oysters had about 30% of their members change to the opposite sex within a year. In a mixed-sex control group, at least 20% of the females became male within a year. Based on the literature review, I suggest that an increased proportion of males in an area may indicate the presence of an environmental stressor.

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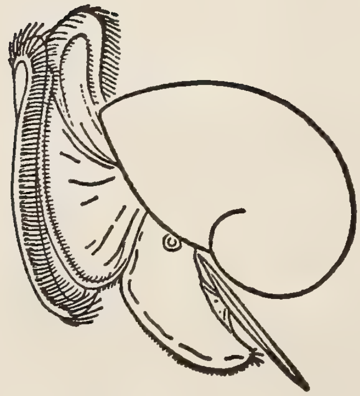

Depth Distribution and Settlement Times of the Molluscan Wood Borers *Bankia setacea* (Tryon, 1863) and *Xylophaga washingtona* Bartsch, 1921, in Monterey Bay

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(2 Plates; 1 Text figure)

INTRODUCTION

The major molluscan wood borer in shallow water along the Pacific coast of the United States is the shipworm *Bankia setacea*. In deeper water *Bankia* is replaced by the pholad *Xylophaga washingtona*. *Bankia* occurs commonly in wooden pilings and sea walls and in log rafts floating in sea water prior to being removed to sawmills. *Bankia* is also recovered occasionally in samples of wood dredged from deeper water, but in most cases these animals appear to have penetrated the wood before it settled to the bottom. *Xylophaga*, on the other hand, has been reported only from deep water, usually below 150m.

The study being reported on here was initiated in an attempt to learn as much as possible about the bathymetric distribution of *Bankia* and *Xylophaga* in Monterey Bay, and to determine if the two kinds of borers had a distributional overlap. It was also hoped to determine season or seasons and intensity of settlement of each, rates of growth and wood destruction, and wood substrate preference.

In previous studies, aspects of the biology of *Bankia setacea* in the shallow water of Monterey Bay was investigated (Haderlie & Mellor, 1973). *Bankia* was found down to depths of 70m but no *Xylophaga* was encountered. *Xylophaga washingtona* was first reported from the Pacific coast when Bartsch in 1921 described the species from wood dredged from 150-200m depth at ALBATROSS station 4523 off Point Pinos in Monterey Bay (Turner, 1955).

In order to gain more precise data on bathymetric distribution of wood borers, several investigators have employed experimental arrays of wooden panels or blocks placed on or near the bottom at various depths. Tipper (1968) exposed wooden panels off the coast of Oregon in water depths from 50 to 1000m. *Xylophaga washingtona* penetrated his panels at the 200, 500 and 1000m depth sites, but not in shallower water. *Bankia setacea* was found only at the 200m site, which is the greatest depth so far recorded for this shipworm.

In southern California, Muraoka (1966) exposed wooden panels down to depths of 2266 m off Port Hueneme and the panels were penetrated by *Xylophaga washingtona* and *X. duplicata* Knudson, 1961.

Starting in March 1979 and continuing for 2½ years, wooden panels were systematically placed on and near the bottom of Monterey Bay at eight sites ranging in depth from 20 to 1000m and recovered at intervals for examination. This short report discusses the results of these exposures.

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AREA OF STUDY

Earlier studies on wood borers in the open water of Monterey Bay were conducted at sites in the south end of the Bay off Fort Ord (Haderlie, 1971, 1972). During these investigations the panels were placed on taut vertical mooring lines and none of the panels were in contact with the sea-sediment interface. *Bankia* settled on all panels from shallow to deeper water, and from the surface to near the bottom, but the most intense settlement occurred on panels near the bottom in 70m of water at the deepest site studied. No *Xylophaga* settled on any of the panels, yet a few specimens were seen in burrows in form lumber that had been left accidentally on one concrete anchor at

70m depth. It was then realized that *Xylophaga* had been missed because the larvae move or are moved by currents along the bottom and not up in the water column as in the case of *Bankia.*

In this present investigation, therefore, the earlier work was repeated but with some panels in contact with the bottom sediment. Four sites along the southern edge of the Fort Ord Firing Range were selected (Figure 1): Site 1 had water 20m deep, Site 2, 35m, Site 3, 50m, and Site 4, 70m. The bottom was firm sand or sandy mud at all localities. In addition to these positions off Fort Ord, five additional sites northwest of Point Pinos were utilized: Site 5 (121°57.8′W; 36°40.7′N, water depth 100m), Site 6 (121°58.4′W; 36°44.5′ N, depth 200m), Site 7 (122°1.8′W, 36°40.81′N, depth 500m), Site 8 (122°3.0′W; 36°39.7′N, depth 670m), and Site 9 (122°3.08′W; 36°41.09′N, depth 1000m). All arrays were planted on flat firm substrate.

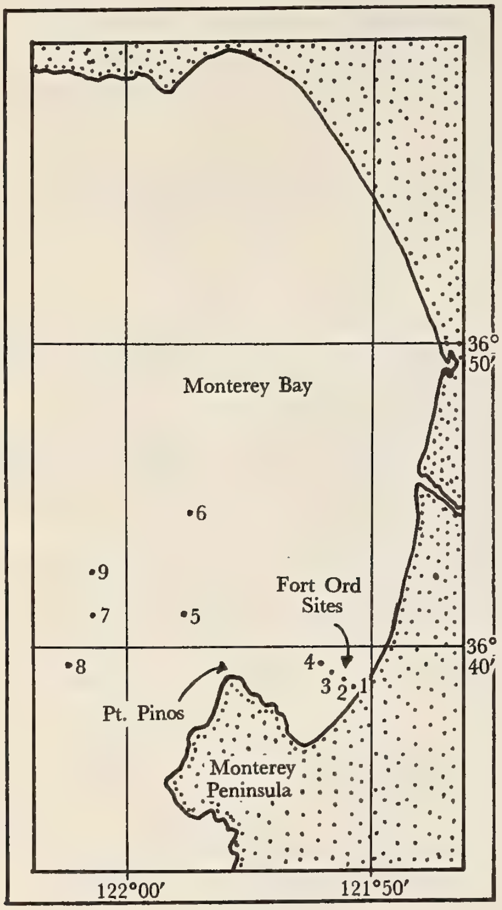

Figure 1

Map of Monterey Bay showing exposure sites

MATERIALS AND METHODS

At the first four sites off Fort Ord the panels were placed on arrays such as illustrated in Figure 2. A flat, square concrete clump weighing 250kg had panels arrayed around it on stainless steel bars. Some panels were placed so that their ends would be in contact with the sediment, others were placed one half meter above the concrete clump, and still others one and two meters above the anchor on the mooring line. A 2cm diameter polypropylene line or steel cable ran from the anchor to a large spar buoy on the surface.

This first series of arrays was deployed in March 1979 and, although a few arrays were lost in storms, some remained in place until September 1980. Each array carried panels of Douglas fir, white oak, and redwood, and each was recovered at 3 month intervals for examination and panel recovery. Some panels remained on the array for only 3 months, then were removed and replaced by new panels of the same kind of wood. Other panels remained on the array for 6 months, 9 months, or 1 year, or until the panels were destroyed by borers. Three arrays were planted at each depth, thus short term panels used to determine settling times were recovered monthly at each site.

In the deeper water off Point Pinos similar bottom arrays were employed, but timed or acoustic release mechanisms

Explanation of Figures *2* and *3*

Figure *2:* Concrete anchor clump with some wooden panels deployed to make contact with the sediment and others placed ½m above the bottom

Figure *3:* Douglas fir panel 30cm long exposed at Site 4 (70m depth) for 2 months showing numerous small entrance holes of *Xylophaga washingtona*

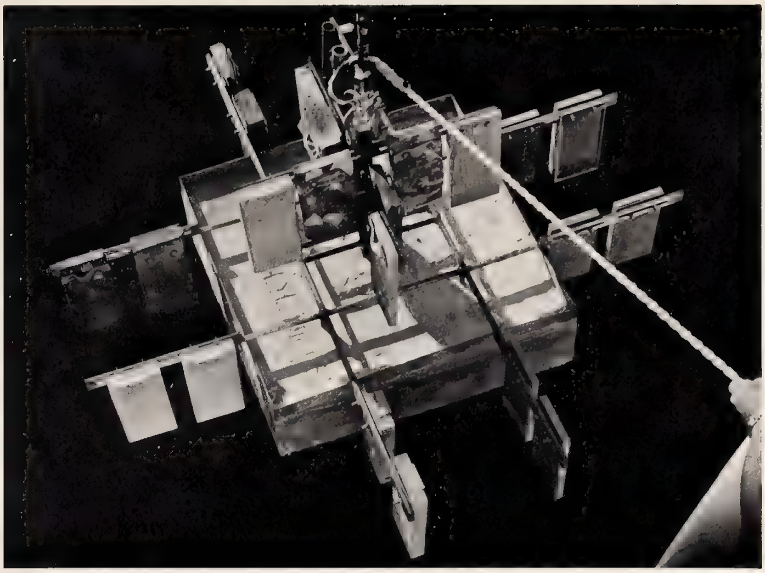

Figure *2*: Concrete anchor clump with some wooden panels deployed to make contact with the sediment, and others placed ½ m above the bottom

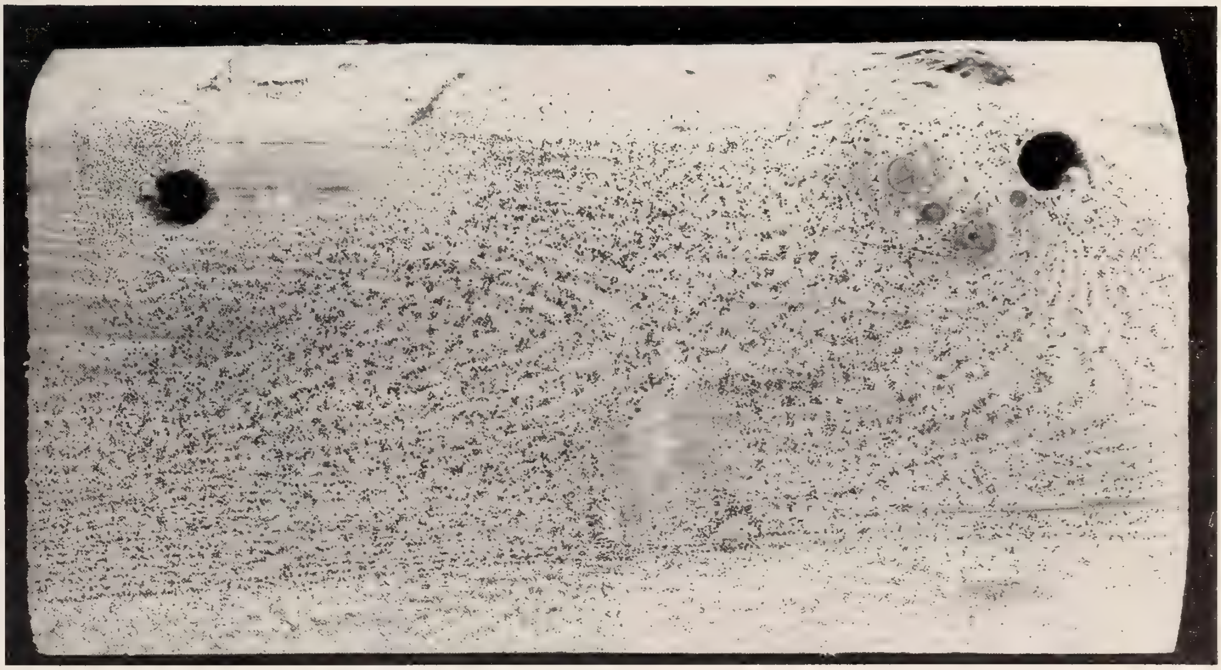

Figure *3*: Douglas Fir Panel, 30 cm long, exposed at Site 4 (70 m depth) for 2 months showing numerous small entrance holes of *Xylophaga washingtona*

were used to bring subsurface buoys to the surface at set times for recovery. The plan was to recover each of these arrays at 3 month intervals and to replace the entire array of panels each time. However, many of the release mechanisms failed and the arrays had to be recovered by grappling. Many of these were not recovered until 6 months after deployment and others at the deeper sites were never recovered. The data from all these deeper arrays, therefore, are incomplete but will be reviewed briefly.

RESULTS

The major results of this study can be summarized as follows: *Bankia setacea* and *Xylophaga washingtona* have a distributional overlap in Monterey Bay at depths of 35-70m. In shallower depths only *Bankia* was detected and in deeper water only *Xylophaga*. In water 70m or less deep *Bankia* larvae settled on panels throughout the water column. *Xylophaga* settled in numbers only on panels in contact with the bottom sediment at depths of 35m or more. Fir, oak, and redwood panels were all attacked, none of the woods being more resistant than the others. *Bankia* settled from October through July, whereas *Xylophaga* settled during all months of the year. Most wooden panels deployed near the bottom were destroyed by one or the other or both of these borers in less than nine months.

At depths of 35m, 50m, and 70m both *Bankia* and *Xylophaga* infested the panels. At 35m depth *Bankia* was the dominant borer in wood touching the substrate and in panels in the water above the array. The intensity of settlement and damage to wooden panels decreased with distance above the bottom. Only a few *Xylophaga* were ever detected at the 35m depth and always in panels in contact with the substrate. Settlement of *Xylophaga* occurred throughout the year.

At 50m depth, panels placed in contact with the bottom were heavily penetrated by *Bankia* in January and February, but by *Xylophaga* during all other months. Few panels at this depth survived beyond 4 months exposure.

At 70m depth *Xylophaga* dominated all the panels touching bottom, with only light infestations with *Bankia*. Small *Xylophaga* juveniles with bright golden shell valves were found on all the bottom panels at all months of exposure. The small clams crawled actively over the panels before penetrating the wood. They could also be seen exploring the concrete anchor and attempting to penetrate. Wooden panels in contact with the substrate at 70m depth often had tiny entrance holes in numbers up to 50/cm² of surface area (Figure *3*) and most of the panels were totally disintegrating after four months exposure (Figure *4*). The maximum diameter of *Xylophaga* shell valves after four months was 5mm. Panels placed above the bottom on the array at 70m depth collected very few *Xylophaga*, but numerous *Bankia* (especially in the winter months) and all these panels were destroyed by the shipworms after six months of exposure.

At the deeper sites at 100, 200, and 500m the data are less complete due to loss of many arrays, yet the panels recovered showed consistency at all depths. *Xylophaga* was the only wood borer found in any of the panels, these settled throughout the year, and only wood in contact with the substrate was heavily attacked. Rates of infestation were about the same at all the deeper sites as that reported above at 70m. Most wooden panels and large blocks of fir up to 10cm thick were crumbling and disintegrating after four to six months of exposure (Figure *5*). The maximum diameter of the shell valves of *Xylophaga* in these panels was 7mm.

Arrays planted at Sites 8 and 9 in 670 and 1000m of water were all lost.

Xylophaga washingtona should prove to be a useful pholad for life history studies in the laboratory, for these animals appear to be very hardy and temperature tolerant. At the 70m site in Monterey Bay the water temperature averages about 10°C and is somewhat colder at the deeper sites. Yet, *Xylophaga* in panels recovered from all depths continued to thrive for weeks when the panels were placed in sea water aquaria at 15°C. One set of panels recovered from 200m depth was left out of water on the deck of the ship for 24 hours, yet when placed in sea water the animals extended their siphons and began to circulate water. One is left to wonder why these borers do not therefore live in wood in shallow, warmer water.

During studies being reported on here, stone slabs were also placed on all the arrays near the bottom in an attempt to learn something about the depth distribution of stone boring pholads. Yet, in the 30 months of the investigation, no stone borers settled on any of the samples of stone exposed.

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Explanation of Figures *4* and *5*

Figure *4:* Douglas fir panel 30cm long exposed at Site 4 (70m depth) for 4 months. Panel disintegrating due to massive wood destruction by *Xylophaga washingtona*

Figure *5:* Douglas fir block (original size 10 × 10 × 20cm) exposed at Site 6 (200m depth) for 4 months. Block disintegrating due to attack by *Xylophaga*

Figure *4*: Douglas Fir panel, 30 cm long, exposed at Site 4 (70 m depth) for 4 months. Panel disintegrating due to massive wood destruction by *Xylophaga washingtona*

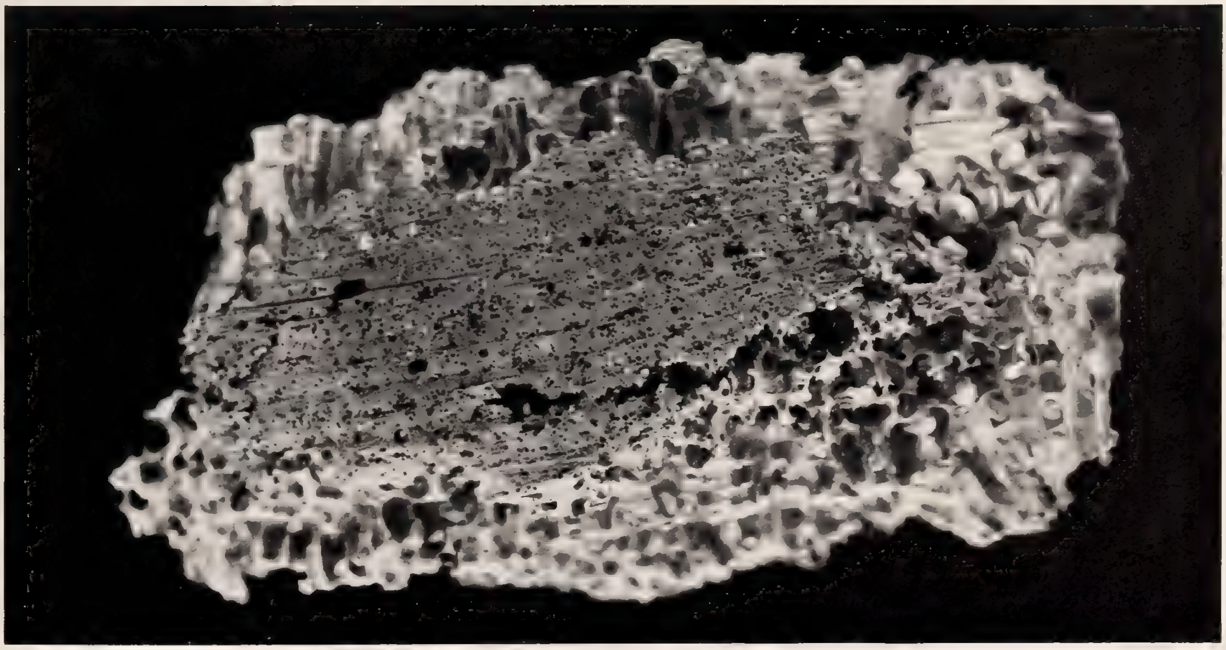

Figure *5*: Douglas Fir block (original size 10 × 10 × 20 cm) exposed at Site 6 (200 m depth) for 4 months. Block disintegrating due to attack by *Xylophaga*

Reproduction and Gonadal Changes in *Laevicardium laevigatum*

(Mollusca : Bivalvia : Cardiidae)

# of Golfo Triste, Venezuela

BY

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(2 Plates; 1 Text figure)

INTRODUCTION

Laevicardium laevigatum IS THE MOST COMMON and abundant of the Cardiidae on the Golfo Triste shelf between 18 and 60 m depth and coexists with three abundant Pectinidae, *Pecten papyraceus, P. laurenti* and *P. lineolaris.*

This research is part of a program conducted to determine the reproductive behaviour of the potentially commercial bivalves of Golfo Triste.

Sexuality and maturation cycles of Heterodonta are generally poorly known, and this is especially true for South American species. As far as we know, no previous report on the reproductive aspects of *Laevicardium laevigatum* had been published.

MATERIAL AND METHODS

From March 1978 to December 1979 monthly samples of *Laevicardium laevigatum* were obtained aboard fishing vessels during trawling operations. The samples were taken at depths between 18 and 35 m in the southeastern region of Golfo Triste, Venezuela. Fifty specimens, including representatives from all different size classes present, were processed from each monthly sample. Each specimen was fixed in Bouin's solution and the dissected foot was processed with usual histological techniques and paraffin sections 5-7 microns thick were stained with hematoxylin and eosine.

RESULTS

Gonadal development: Male gonads are first developed. They start to differentiate in the base of the powerful foot around the gastric mass (Figure *1*a). This differentiation takes place when the shell measures between 25 and 30 mm in length. The male follicles produce gametes before the ovarian structures are differentiated (Figure *1*b; Figure *2*d). The ovarian follicles appear in individuals whose shell length is between 35 and 40 mm; they originate from peripheral points of the testicular follicles (Figures *1*c-d). Both testicular and ovarian follicles grow and active gametogenesis takes place. Testicular follicles contain radially aligned spermatids and spermatozoids and the ovarian structures have oocytes in advanced stages of maturation (Figures *1*e-f).

When the first partial spawning occurs, the immature cells not evacuated undergo maturation (Figure *1*g). At the end of the reproductive season, the follicles are filled with large empty spaces and the foot is less swollen. After the final spawning of the season, two possible processes can take place. In the first there is an almost total reabsorption of the follicles (75% of the cases), in the second there is a proliferation of new immature elements simultaneously with necrotic disintegration of old elements (Figure *1*h; Figure *2*e). In the former case, testicular and ovarian regeneration is simultaneous and not asynchronous as in the first maturation. The ovarian acini are formed throughout the entire space and not at peripheral points of the testicular acini (Figure *1*i; Figures *2*a-b).

A condition of male and female cells both occurring in the same follicle was found only in 0.3% of the analyzed specimens (Figure *2*f). No cases of sexual reversal were registered and no cases of dioecious animals were recorded in sizes over 40 mm.

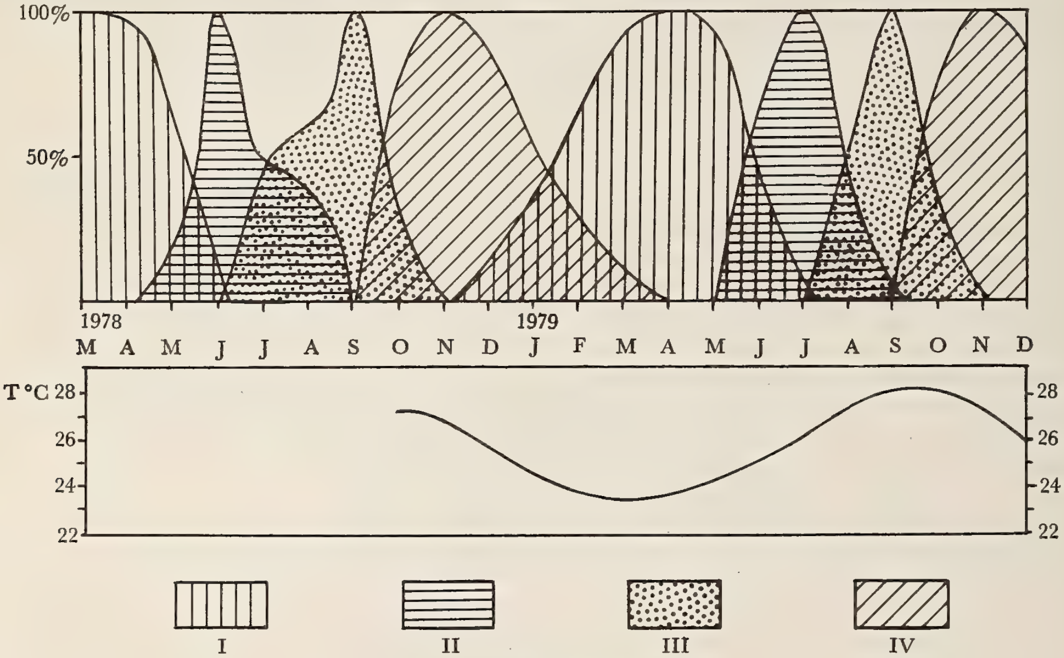
A modification of the distribution of the follicles resulting from trematode parasitism was observed in 0.5% of the specimens (Figure *2*c). In these cases the gonadal tissues were assembled in areas separated by the spaces occupied by cysts.

Reproductive Cycle: Four major phases in the reproductive cycle of *Laevicardium laevigatum* can be recognized:

I. Appearance and growth of follicles and initiation of gametogenesis.
II. Maturation of the gametes and repletion of the follicles which occupy completely the space.
III. Partial or total evacuation of the gametes.
IV. Total reabsorption of the gonad or alternatively necrosis of the nonevacuated gametes and proliferation of new cellular elements.

Phase I is the longest, usually beginning around December and continuing until June. This period coincides with the lowest bottom water temperatures registered (up to 23° C) (Figure 3). From May to August the temperatures are higher, from 24 to 26° C, and during these months the repletion stage occurs. Phase III, where the gametes are expelled from the gonad, takes place between July or August to October or November, when water temperatures are approximately 27° C.

The period of gonadic reabsorption and/or proliferation of new elements and necrosis of gametes coincides with the beginning of the decrease of temperature in October and lasts until February-March, when temperatures are between 23-24° C.



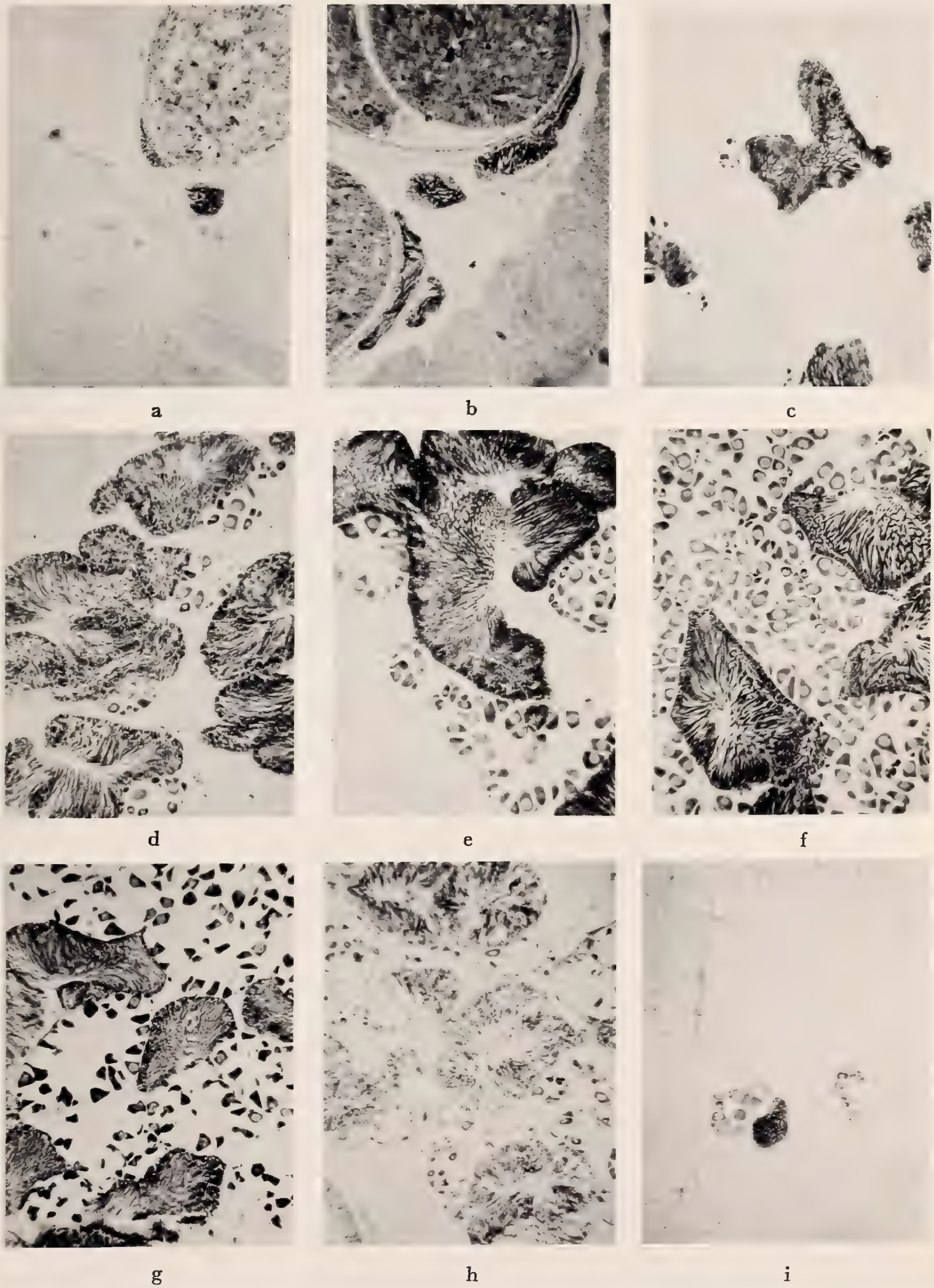
Explanation of Figure 3

Reproductive cycle of *Laevicardium laevigatum*
Frequency of gonadal phases in monthly samples
I. Growth of follicles and maturation of gametes
II. Ripening phase
III. Post-spawned phases (partial and complete spawnings)
IV. Main regressive phase; connective tissue fills up the area

Explanation of Figure *1*

Transverse sections of the foot base, showing different stages in the development of the gonad in *Laevicardium laevigatum* × 52

a. Start of the gonadal development in young *Laevicardium*. Male follicles appear first
b. Follicles growing in number and proliferation of sexual elements.
c. Female follicles appear anew
d. and e. Proliferation of female follicles and gametes
f. Fully ripe gonad in an adult *Laevicardium*
g. Partially spawned gonad
h. View of a gonad after its spawning season
i. Recuperation of the gonad after a regressive phase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DISCUSSION

The abundance of *Laevicardium laevigatum* in the trawl fishery area of Golfo Triste indicates that it may be a commercially exploitable species. Therefore, heavy harvesting efforts should be prevented during the spawning season, from August to October. This is important to reduce the risk that the population is exterminated, as has occurred with some scallop species that are harvested by trawling (Olivier, *et al.*, 1970).

The relationship between the sexual maturation cycle and the temperature has been reported for many bivalve species from temperate and cold waters. In the South American region it has been reported by Lozada (1968) and Penchaszadeh *et al.* (1974) in *Aulacomya ater;* Penchaszadeh (1971) in *Mytilus platensis;* Fiocchi (1974) in *Ameghinomya antiqua,* and Trancart (1978) in *Mytilus cf. chilensis,* among others. In tropical waters, where the temperature differences are much lower, reproduction generally takes place throughout the whole year, but with some peaks of maximal activity during a few months (*i. e., Donax denticulatus,* Wade, 1968: *Pecten papyraceus,* Salaya & Penchaszadeh, 1980; *Perna perna,* Velez (1971). *Laevicardium laevigatum* from Golfo Triste could be regarded as an unusual case in tropical species where the spawning could be related to higher temperatures.

Coe (1943) in his review on sexual differentiation stated that Pelecypods have generally separate sexes. Among studied South American Heterodonta, the dioecious condition is the most common (*i. e., Chama congregata,* LaBarbera & Chanley, 1971; *Donax denticulatus,* Wade, *op. cit.; Ameghinomya antiqua* Fiocchi, *op. cit.; Euromalea exhalbida,* Penchaszadeh, pers. com.; *Donax hanleyanus,* Penchaszadeh & Olivier, 1975). *Laevicardium laevigatum* is a protandric functional hermaphrodite and the structure of having intermingled testicular and ovarian follicles is very peculiar and notably different from that of other coexisting hermaphroditic species, such as *Pecten papyraceus, P. laurenti* and *P. lineolaris,* which have well-differentiated male and female glandular areas (Salaya & Penchaszadeh, *op. cit.* and Penchaszadeh and Salaya, in preparation).

Among the majority of the hermaphroditic bivalve species studied thus far, the condition of having intermingled male and female follicles is anomalous. The low percentage of individuals with both male and female gametes present in a follicle is similar to the unusual cases reported by Dinamani (1974) and Mason (1958) for *Crassostrea glomerata* and *Pecten maximus,* respectively.

SUMMARY

Laevicardium laevigatum is part of the benthic community of Golfo Triste at depths between 18 and 40m, where it forms banks together with the scallops *Pecten papyraceus, P. laurenti* and *P. lineolaris.* Gonads obtained from monthly samples for two years were studied histologically. The gonadic development is described and it is a typical case of protandric hermaphroditism; in specimens with shells between 25 and 36mm in length, the gland is a functional testicle, but in sizes over 40mm it is a mixed gonad where ovarian and testicular follicles are found intermingled. No dioecious cases were found in the largest sizes. Spawning activity is greater in July and August, when the water temperature is higher (approximately 27° C).

ACKNOWLEDGMENTS

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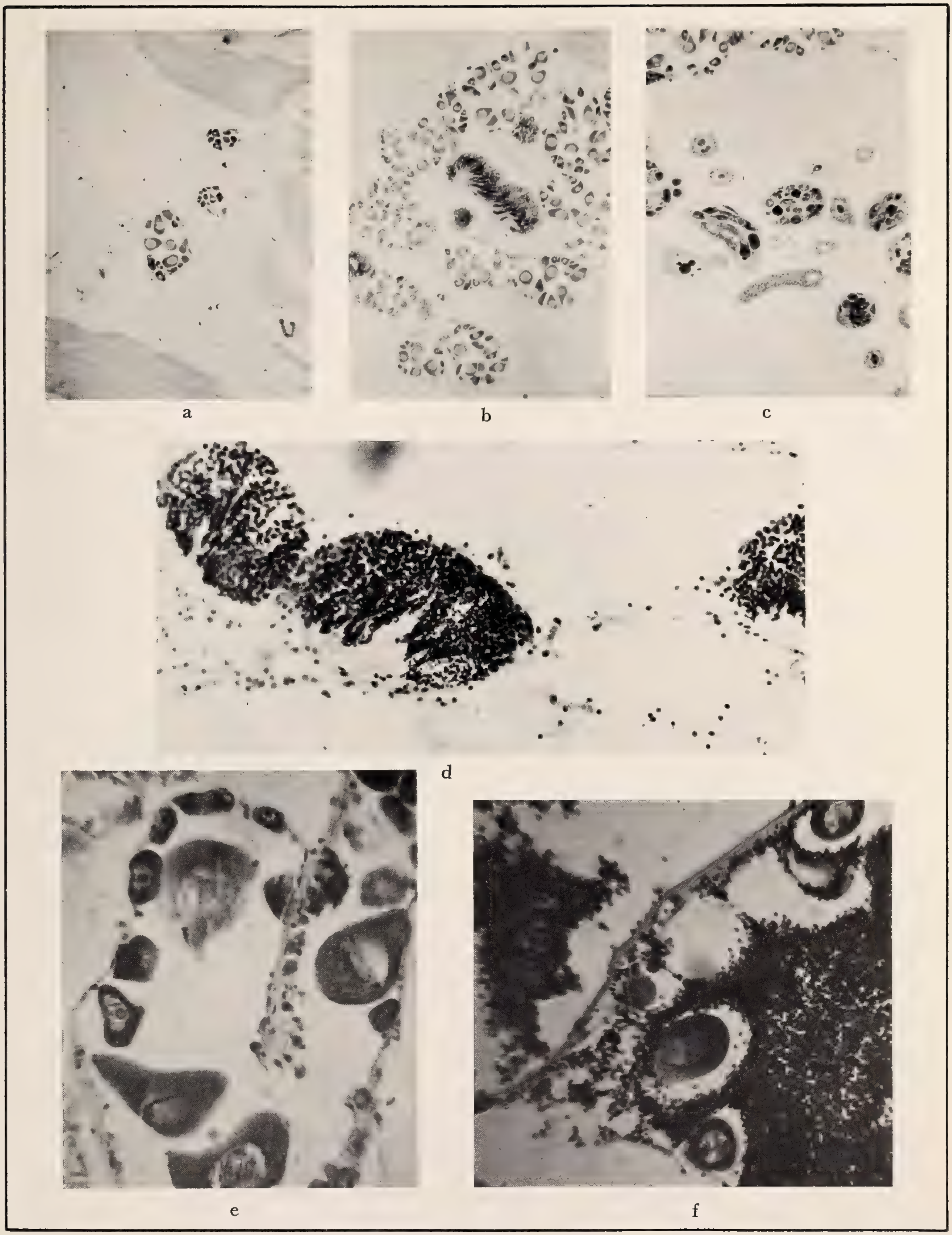
Explanation of Figure *2*

Transverse sections of the foot base, showing different stages in the development of the gonad in *Laevicardium laevigatum*

a. and b. Recuperation of the gonad after a resting phase × 52
c. Modification of the follicle distribution patterns from parasitism by Trematodes × 52
d. Detail of growing male follicles in young *Laevicardium* × 280
e. Detail of a female follicle showing young growing gametes and relict ovocytes in disintegration × 280
f. Detail of a follicle with both male and female gametes × 280



a
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Western Gull Predation on Owl Limpets: Different Methods at Different Localities

BY

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(1 Text figure)

THE OWL LIMPET, *Lottia gigantea* Sowerby, 1834, is a large (100+ mm) territorial acmaeid that occurs in waveswept middle intertidal areas from Central California to San Bartolomé Bay, Baja California, Mexico. During periods of wave splash and at night, limpets patrol their territories and feed. At high and low tides, when they are either completely submerged or completely exposed, the limpets return to and remain in one of several homesites within their territory (see STIMSON, 1970). When undisturbed, *L. gigantea* adheres weakly to the substrate, holding its shell edge slightly above the rock and exposing its muscular foot; lateral force will easily dislodge it. If disturbed, the limpet pulls its shell firmly against the substrate; depending on size, a force of 2 to 22 kg is required to remove it (WELLS, 1917).

Despite their size and strength, *Lottia gigantea* are preyed upon by large shorebirds (*e.g.*, Black Oystercatchers,

Figure 1

Dorsal views of *Lottia gigantea.* (a) Isla de Guadalupe specimen collected from clifftop; (b) Southeast Farallon Island specimen collected from marine terrace; (c) Southeast Farallon Island specimen found *in situ* near East Landing Bars = 25 mm

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Haematopus bachmani) and by gulls. We present here evidence that Western Gulls *(Larus occidentalis)* use different methods for detaching these limpets on two offshore islands: Isla de Guadalupe, Baja California, Mexico (29° 00′ N; 118°20′ W), and Southeast Farallon Island, San Francisco County, California (37°42′ N; 123°00′ W).

Predation on *Lottia gigantea* at Guadalupe is indicated by numerous empty shells wedged between intertidal rocks and strewn among clifftop boulders approximately 60 m above sea level. All shells in these sites are entire and undamaged by marginal chipping or dorsal fracturing (Figure 1a), indicating a predation method that does not affect the shell. Several days after the initial discovery, one of us (EWC) observed an adult Western Gull feeding on limpets. The gull alighted near its prey and, twisting its head and bill sharply, flipped the previously undisturbed limpet from the rock. The bird then carried the limpet a few meters away and plucked out the meat, leaving the empty shell whole. On another foray, the gull inadvertently struck a limpet without detaching it and flew off without a second attempt. Although we only once observed actual predation by the Western Gull, we saw no Black Oystercatchers or other sea- or shorebird species on the island that could account for the empty shells (see also Howell & Cade, 1954). Predation by feral cats or goats is unlikely.

At Southeast Farallon, large numbers of *Lottia gigantea* shells scattered over the marine terrace about 15 m above sea level again reveal the existence of a predator. Unlike the shells on Guadalupe, those from Southeast Farallon are not whole; typically their margins are chipped and large parts of the dorsal area broken away (Figure 1b). The dorsal fractures occur in the same weak shell area exploited by shore crabs that prey on smaller species of acmaeids (Chapin, 1968). Although no observations of gulls feeding on *L. gigantea* have yet been made on Southeast Farallon, a specimen of *L. gigantea* with chipped shell margins and broken dorsal region was found still adhering to a horizontal rock by W. G. Wright (Figure 1c). A predator had apparently been "caught in the act" and frightened off before it could consume its prey.

On Southeast Farallon Black Oystercatchers also feed on *Lottia gigantea* (Morrell *et al.*, 1979), but do not damage shells. Oystercatchers tend to leave whole empty shells; fewer than 20 of 400 shells recovered from oystercatcher nest sites showed damage to their margins, and none had dorsal fractures. The chipped and broken shells we found were scattered across the marine terrace, a major Western Gull rookery (Ainley & Lewis, 1974).

It appears then, that two different populations of Western Gulls use different methods for preying on *Lottia gigantea*. *Larus occidentalis wymani* on Isla de Guadalupe uses a method similar to the "stab" of oystercatchers (Hartwick, 1976), surprising its prey and quickly detaching it without breaking the shell. In contrast, *Larus occidentalis occidentalis* on Southeast Farallon forgoes the use of stealth and merely batters its still-attached prey until sufficient shell damage allows removal. Observation on other islands in the California Current (especially the California Islands) or along adjacent mainland can provide insight on the occurrence and ontogeny of these behaviors.

ACKNOWLEDGMENTS

We thank B. Le Boeuf and Scripps Institute of Oceanography for the opportunity of visiting Isla de Guadalupe. We also thank the personnel of the Point Reyes Bird Observatory Farallon Island Field Station (especially T. J. Lewis, S. H. Morrell, and H. R. Huber) for their assistance and friendship, and for samples of shells from oystercatcher nest sites. W. G. Wright brought to our attention the specimen illustrated in Figure 1c and furnished us with information on *Lottia gigantea*. We are grateful to J. S. Pearse, C. S. Hickman, D. G. Ainley, and R. LeValley for their helpful comments on the manuscript, and to S. Walker for her generous preparation of the illustrations. DRL's work on Southeast Farallon Island was conducted under the auspices of the Farallon Research Group, Oceanic Society, San Francisco, California.

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Geographic Variation of Banding and Color Morphs in *Monadenia fidelis* (Gray, 1834)[1]

(Gastropoda : Pulmonata)

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

Variation in color of helicid snails has been known to be genetically based for many years (Pilsbry, 1939). Although this information stimulated the present research on *Monadenia fidelis* (Gray, 1834), it also posed limitations. Although the color morphs and banding patterns are inherited, the factors involved in their selection are unknown or are poorly understood. Little research has been conducted on the polymorphic variation of *Monadenia*. However, such variation in related snails, especially *Cepaea nemoralis* (Linnaeus), is well documented (Bantcock & Price, 1965; Cain *et al.*, 1968). In *Cepaea*, banding and basic color morphs have been shown to be not only inheritable but also linked to both geographic and environmental conditions (Brussard, 1975; Clarke *et al.*, 1978). These findings shifted the emphasis of the present research from simple description of the variations to an attempt to identify some of the geographic and environmental factors that affect the natural selection of banding and color morphs in *Monadenia fidelis*. The incidence of variation in these features is high (Roth, 1981a; Talmadge, 1960; Chace & Chace, 1933). In fact, there appears to be a higher rate of polymorphic variation in this snail and other species of the genus than in most other large North American pulmonates, where the normal rate of polymorphic variation is less than 10 per cent (Clarke *et al.*, 1978). This makes *Monadenia* a rather unusual American helicid. Why is the rate of variation so high? What are the factors that control the variation?

Color and banding variation in this species appears to be closely linked to geographic and environmental conditions (Roth, 1981a). Roth's investigation of two coastal colonies of *Monadenia fidelis* in northern California and southern Oregon demonstrated that polymorphic variation occurs regularly over fairly short geographic distances and within individual populations (also noted by Chace & Chace, 1933). The geographic distance required for polymorphic variation apparently is usually extremely short, perhaps no more than one or two kilometers (Roth, 1981a; 1981b; Talmadge, 1960). Roth (1981a) only studied the variations between and within two very similar (in terms of geographical zonation, altitude, climate, and the distance between them) colonies of *Monadenia*, and he did not discuss the geographic and environmental factors that possibly affected the shell variations from the standpoint of selection. Since these factors have been strongly correlated with the selection of color morphs and banding (Ford, 1940; Comfort, 1951; Purchon, 1968; Brussard, 1975; Selander & Kaufman, 1975), the isolation and analysis of the factors is important to an understanding of geographic variation in these and similar snails.

The key to this problem is probably species adaptation to local environments and to extremely low vagility. Some aspects of this were presented by Roth's (1981b) study of the distribution, anatomy, and geographic variation of *Monadenia troglodytes* (Hanna and Smith), and Talmadge's (1961) taxonomic revision of *Monadenia fidelis baxteriana* Talmadge. Both investigators noted the extreme localized adaptation that occurred in these two snails, and Roth suggested that a new subgenus was needed for *M. troglodytes*. The low vagility of *Monadenia fidelis*, combined with its large range—Sitka, Alaska to the Bay counties of mid-northern California (Pilsbry, 1939)—has engendered a considerable amount of phenotypic variation that allows the species to exist over such a large, geographically and environmentally diverse area, factors that tend to stimulate subspeciation.

Previous researchers have analyzed the variations in one or two local populations rather than addressing the problem from a broader and more diversified section of the range. Their approach did not focus on the wider aspects of geographic polymorphic variation. When a species is distributed over a large geographic range, and there is

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[1] Supported by Eastern Kentucky University Faculty Grant.

Figure 1

Map showing distribution of *Monadenia fidelis* collecting stations in Washington and Oregon little or no interaction (gene exchange) between the populations, larger departures from the norm are observed as the species' populations adapt to localized environments, and the geographic variations of *Monadenia fidelis* exemplify this principle.

Thus, this paper attempts to delineate the polymorphic variations that occur in the species, and attempts to isolate the geographic and environmental factors that dictate the banding and color morph variations.

Table 1

Collecting stations in Oregon and Washington for *Monadenia fidelis.* The station numbers are correlated with those shown in Figure 1.

Station	Locality
	OREGON
1.	Siskiyou National Forest, Coastal Range, S 13, R 8 W, T 33 S, 457 m elevation; 9 June 1981. 3 specimens.
2.	Burned-over clear cut, 11.3 km E Loeb State Park, S 23, R 12 W, T 39 S, 33.5 m elevation; 10 June 1981. 5 specimens.
3.	Redwood Grove 0.3 km W Loeb State Park, 30.4 m elevation; 12 June 1981. 4 specimens.
4.	Humbug Mountain, S 25, R 15 W, T 35 S, 0-182 m elevation; 12 June 1981. 5 specimens.
5.	Humbug Mountain, 183-366 m elevation; 12 June 1981. 1 specimen.
6.	Near Middle Fork of Coquille River, SR 42, 16 km E Myrtle Point, 365.8 m elevation; 13 June 1981. 10 specimens.
7.	Bear Creek Recreation Area, SR 42, 44 km E Myrtle Point, at crest of Coastal Range, 520 m elevation; 13 June 1981. 1 specimen.
8.	Douglas fir-hemlock woodlot, 25 km E Florence, SR 126, 458 m elevation; 16 June 1981. 1 specimen.
9.	Latourell Falls State Park, 41 km E Portland, in Columbia River Gorge; 26 June 1981. 1 specimen.
10.	Starvation Creek State Park, 82 km E Portland; 27 June 1981. 2 specimens.
11.	Scrub oak-lava (extremely arid), 150 m below Mayer Point State Park, R 12 E, old U.S. 30; 28 June 1981. 2 specimens.
12.	Willamette National Forest in Lane Co., Salt Creek Forest Road; 11 July 1981. 2 specimens.
13.	Willamette National Forest, Forest Road 21 between Indigo Springs and Sacondoga Flats in Lane Co.; 12 July 1981. 2 specimens.
14.	Willamette National Forest, R 1 W, T 19 S, in Lane Co.; 12 July 1981. 1 specimen.
15.	Susan Creek State Park, 43.5 km E Roseburg, SR 138, in Lane Co.; 13 July 1981. 5 specimens.
16.	Eagle Rock Campground, SR 138 in Douglas Co.; 14 July 1981. 5 specimens.
17.	Rogue River National Forest, 11 km above Prospect, SR 62; 17 July 1981. 3 specimens.
18.	Umpqua National Forest, SR 227, S 12, R 2 W, T 32 S; 17 July 1981. 1 specimen.
	WASHINGTON
19.	Shelton Quadrangle, near New Kamilche, S 20, R 3 W, T 18 N, 23.4 m elevation; 29 June 1969. 1 specimen.
20.	Quilcene Quadrangle, North Point Lookout, S 27, R 2 W, T 27 N, 875 m elevation; 26 July 1969. 1 specimen.
21.	Deer Park, Blue Mountains, Olympic National Park, 1500 m elevation; 6 July 1969. 2 specimens.
22.	Cox Valley, S 14, R 5 W, T 29 N, 475 m elevation; 13 July 1969. 1 specimen.
23.	Blue Mountain Road, S 14, R 5 W, T 29 N, 457 m elevation; 24 June 1969. 3 specimens.
24.	Elwa River Campground, Olympic National Park, S 4, R 5 W, T 29 N, 610 m elevation; 23 June 1969. 2 specimens.
25.	Mount Storm King, S 4, R 5 W, T 29 N, 1220 m elevation; 21 June 1969. 2 specimens.
26.	Kloochmann Quadrangle, near Big Creek, S 3, R 9 W, T 23 N, 121 m elevation; 4 July 1969. 4 specimens.
27.	West Fork Shelter, West Fork Humptulips River, 244 m elevation; 2 July 1969. 2 specimens.
28.	Miller Creek Crossing, Forest Road N 90, Gifford Pinchot National Forest; 9 July 1973. 1 specimen.
29.	Larabee State Park, 7.25 km S Bellingham, 0-15 m elevation; 9 June 1970. 1 specimen.
30.	Rockport State Park, 4.8 km E Rockport, SR 20; 31 May 1973. 3 specimens.

MATERIALS AND METHODS

Although the number of specimens collected at each station is relatively small, the samples do reflect the types of variations encountered throughout Oregon and Washington. The number of stations and number of specimens collected (Table 1; Figure 1) were insufficient for statistical analysis but were large enough to permit a relatively accurate assessment of the geographic and environmental factors that tend to influence selection of the polymorphic color patterns.

Several major geographic factors were considered, including north-to-south, west-to-east, lowland-to-highland, and wet-to-dry gradients. The west-to-east gradient appears to be the most important factor, due to the Coastal and Cascade ranges that heavily affect the environment and limit the snail's distribution. These two mountain ranges provide four very diversified environments: the coastal plain, the Central Valley, the western shoulder and the eastern shoulder of the Cascade Mountain Range. The eastern shoulder of the Cascades was particularly interesting because of the extensive rain shadow cast by the mountains. This arid environment has induced many adaptations in *Monadenia* that allow it to survive (see below). Both the adaptations and the polymorphic variations that go hand-in-hand with them are poorly understood. These four zones are centers for significant banding and color morph variations. Some of the factors that make these areas important include latitude and longitude changes, altitudinal changes, ground cover and forest variations, edaphic conditions, and annual rainfall variation. These, and other factors, influence how *Monadenia* adapts, and therefore also influence the polymorphic variations.

Monadenia fidelis requires large amounts of moisture, as do most helicid snails, in its habitats. One of the best examples of this occurs on the Olympic Peninsula of Washington. The peninsula, from which several collections were derived (Figure 1), in certain areas maintains some of the largest populations of the species anywhere in its range (Branson, 1977; Branson, Sisk & McCoy, 1966). This peninsula is very important because it is small and has a diversified environment and, because of an attenuated connection with the mainland and the imposition of various marine barriers, doubtless imposes reduced gene flow and the possibility of significant variation.

In dealing with geographic variation in *Monadenia fidelis*, Roth (1981a) proposed a method for scoring the three main banding variations noted during the course of his research. During the present investigation, we looked for a correlation between the band variations and the apical and basal color morphology. These relationships were not studied by Roth (1981a, 1981b, 1979), nor by any previous investigators. The methods used to determine banding and color morph variations, however, were those proposed by Roth (1981a). It was necessary to make slight modifications because of that system's lack of a method for scoring the variations of the apex and basal patch and possible relationships between them, since many more of these variations were encountered than allowed for by Roth's system. The shells were placed at a 90° angle with reference to a flat surface and were scored in diffuse daylight. Other standard methods were those of Pilsbry (1939).

The bands observed were those on the shoulder, just to the left of the aperture. The basal patch and apex were scored on the basis of predominant color, subsurface pigment, streak color, and surface tints (green, red, terra cotta). All of the data were checked simultaneously for correlations that would be indicative of various types of relationships, *i. e.*, bands to apex, bands to basal patch, basal patch to apex, bands to both apex and basal patch, and so forth.

OBSERVATIONS

The polymorphic variations of *Monadenia fidelis* are correlatable with four geographic zones that are, in turn, associated with the Coastal and Cascade ranges. These four zonal boundaries are delineated thusly: coastal region (coast to the upper western shoulder of the Coastal Range); central valley (crest of the Coastal Range to the western base of the Cascade Range); western shoulder (western shoulder of the Cascades to their crest); and eastern shoulder (upper eastern shoulder of the Cascades). The polymorphic variations of *Monadenia* follow these geographic and environmental zones very closely, producing a distinct west-to-east variance gradient.

The populations in the western-most zone, *i. e.*, the coastal region, display one of the two most distinctive basal patches, a pronounced green or olive-green tint that covers the entire basal patch (stations 1 to 7, 19 to 27) (Figure *2*). On the Olympic Peninsula, the green tint is less pronounced but it is present. Southward, this green tint becomes progressively more pronounced until it is almost the predominant basal patch color in southern Oregon. On all specimens, the major basal patch color is brownish-black, including those with the green tint. On the latter specimens, the lower bands are usually reddish-straw and the upper ones are black in color. If the red is not present in the lower band then it is the normal straw color. The degree of color intensity in the lower band is paralleled by a similar intensity in the upper band. The apex of these shells is usually dark-straw in color, although it may be somewhat lighter. The apex is streaked with red and brownish-black—*i.e.*, the predominant color of the bands) and green. These streaks usually cut through or lead into the bands and into the basal patch. In approximately one

Explanation of Figures *2* to *7*

Figure *5: Monadenia fidelis* from the central valley, Oregon (Station 18)

Figure *6: Monadenia fidelis* from the northern portion of the central valley, Oregon (Station 10)

Figure *7: Monadenia fidelis* from the Columbia River gorge, Oregon (Station 9)

Figure *2: Monadenia fidelis* from the coastal region, 0.4km east of Loeb State Park (Station 2), Oregon

Figure *3: Monadenia fidelis* from the east slope of the Cascades, Gifford Pinchot National Forest, Washington (Station 28)

Figure *4: Monadenia fidelis* from the east slope of the Cascades, Lane County, Oregon (Station 15)

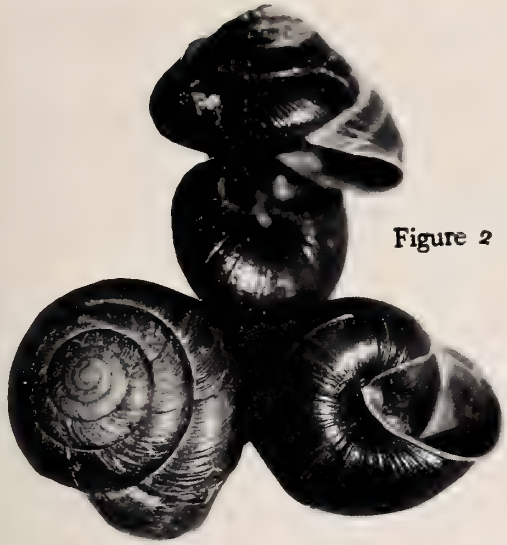
Figure 2


Figure 3

16.5 mm

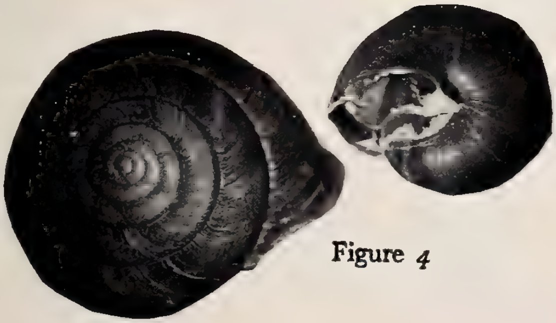
Figure 4


Figure 5


Figure 6


Figure 7

of 50 shells, the green basal tint, the streaks, and the red and black bands are lacking, but they are present in the majority. None of these green color variations were observed east of the crest of the Coastal Range, although shells with the extremely dark basal patch and the reddish-straw bands were observed in specimens taken from the western shoulder of the Cascade Range (stations 12, 13, 14, 16, 28, 30).

Populations in the central valley (stations 17, 18, 29) do not show extreme variations, but there is divergence from those of the coastal region. The basal patch is light-brown to brown, the bands are white to light-straw, and the apex is straw-colored with light-brown and light-straw streaks. There were few obvious west-to-east or north-to-south variations. However, samples collected at the western and eastern extremities of this zone did demonstrate increased variation, *i. e.*, intergradation with populations to the east and west. Specimens from these transition zones (the eastern shoulder of the Cascade Range and the western base and lowermost shoulder of the Cascade Range (stations 1 to 8 and 14 to 27)) show some of the variations characteristic of the adjacent zones (Figures *5*, *6*). The basal patch and apex is darker than in the main parts of the central valley, but the most significant variations of the adjacent zones, *i. e.*, the green tint and the reddish-straw bands, are lacking. In general, the population of the central valley is smaller than those of the coastal and western Cascade slopes.

The next zone eastward is the western shoulder of the Cascade Mountains (stations 12-18 and 30). Polymorphic variations in this region are few until the altitude begins to increase rapidly, *i. e.*, at the point where the annual rainfall is drastically increased. In the upper altitudes the color variations are considerably different from those observed elsewhere. The apex is dark-straw to light-brown with dark brown, rust-, and straw-colored streaks, whereas the basal patch is dark brown to brownish-black with brown, straw and rust-straw streaks. The lower bands are light-straw to rusty red, and the upper ones are brownish-black. The populations are fairly dense due to the amount of moisture and they display variations that are very similar to those seen in coastal populations, except for the green coloration, doubtless a reflection of similarity between the two areas.

The final geographic region inhabited by *Monadenia fidelis* is the upper eastern shoulder of the Cascade Range (stations 11 and 28; Figures *3*, *4*). Small populations occur east of the Cascade crest only in widely separated environments. These populations occur mostly in natural gaps such as the Columbia River gorge where the species range extends well beyond the eastern slope of the mountains (Figure *7*). Several other river gaps and passes have made colonization possible in other localities. The climate of this zone differs radically from the other zones previously discussed. The land is very arid and supports little plant cover. *Monadenia* lives in a few restricted regions where moisture is funneled past the Cascades.

Polymorphic variations in this region are considerably different from those west of the Cascades. The whole shell is tinted by terra cotta rather than the straw-brown of the other zones. Whereas shells west of the Cascades are reddish with straw, those east of the mountains have terra cotta to rusty tints suffused with light-brown. This tint appears in the basal patch as the predominant color with streaks of brown. The bands are poorly developed and defined. The lower band is usually terra cotta with some straw, whereas the upper one is terra cotta with some brownish pigment. The apex of the shell is usually straw-colored with considerable concentrations of the terra cotta pigment.

The upper and lower bands, located between the apex of the shell and the basal patch, of helicid snails are apparently controlled genetically as far as variation is concerned (Emberton, 1963). The upper band is practically always the same color as the predominant color of the basal patch, although often somewhat darker, and the lower band is similar to the apex in coloration. In *Monadenia*, the lower band is usually the same color as the apical streaks that are lighter than the predominant apical color. This is true unless a reddish-straw or terra cotta pigment is present, in which case the lower band assumes that tint. If no streaks are present, the lower band takes on the predominant apical coloration.

DISCUSSION

The basic patterns of polymorphic variation in *Monadenia* are subdivisible into two interrelated factors, those that influence the selection of banding and basic color morphs, and those that influence adaptation. The key to identifying these factors is the notation of the geographic positions at which the different variations occurred. The next step is to plot the geographic range of the observed variations and to correlate them with prevailing environmental factors. This identification process disclosed three major environmental factors; moisture, vegetation, and edaphic conditions, all three strongly interrelated. West of the Cascades, the basic variations involved the intensity of brown and the presence or absence of the green tint. Both of these could be easily correlatable with the three environmental factors, as were several other shell variations. The same is true for the variations observed in the other zones.

The overall patterns between geographic and environmental factors and their influence upon the selection of banding and coloration is probably very basic. Geographic factors and environmental factors are directly or indirectly involved in all forms of evolution, and therefore in the results of adaptation and polymorphic variation.

The Coastal and Cascade ranges are the most important physical factors that determine the range of *Monadenia fidelis* since they are potent barriers to dispersal, and they also greatly influence the regional environments. These two mountain ranges divide the range of *Monadenia* into four zones, each having differing climates, altitudes, and botanical zones, all of which influence the polymorphic variations of the snail.

The major basal patch variation west of the Cascades is the green tint that is associated with the moisture-rich strip west of the Coastal Range. The amount of annual rainfall west of the Cascades does not vary much, remaining high even during the crucial summer months, whereas east of the Cascade crest summer rainfall is essentially lacking. This is, of course, of great importance, since the abundant rainfall in the west supports lush plant growth and controls various edaphic factors. It is here that *Monadenia* populations are higher than elsewhere in Washington and Oregon.

It is probable that *Monadenia fidelis* is mostly restricted to the humid region west of the Cascade crest. If this observation is correct, then the populations located farther inland are probably more or less isolated from the main gene pool. In fact, some of these populations may actually be large but only narrowly connected with populations elsewhere, a fact that could explain the great deal of polymorphism in the species. The physical and environmental patterns within each of the four zones discussed previously, in conjunction with the genetic discontinuity, seem to determine the patterns of color and banding variation that is so distinctively obvious along the west-to-east gradient. Such linear variation patterns are probably the result of the semi-barriers that divide the species' range into the zones. This pattern, and the associated gene-flow retardation, is the most important aspect of the variation, for it provides a working model to explain polymorphic variation in terms of distribution and geographical-environmental factors simultaneously. If geographic factors are considered primary ones, then the environmental ones are of secondary importance. However, in these four zones the environmental factors and gradients doubtless interact with the population genetics of *Monadenia* to establish color and banding variation patterns because of the tendencies of these snails to adapt to highly localized conditions.

In order to understand widespread variation in color and banding, it is not only necessary to study a small number of populations in a single geographic region in order to determine intrapopulation variation, but research must also be conducted throughout a large section of the geographic and environmental range to determine overall patterns of variation. The Olympic Peninsula in Washington and the Columbia River gorge between Oregon and Washington are some exceptions. For example, the patterns of variation in samples collected on the Olympic Peninsula are complex. East of the Coastal Range on the peninsula the variations are like those of the transition zone between the coastal zone and the central valley previously discussed. However, west of the Coastals, the variations were like those seen in the coastal zone. It appears that a lower rate of gene exchange occurs between populations on the Olympic Peninsula and the mainland than elsewhere, as reflected in the lower rate of polymorphic variation observed there by comparison with data collected from similar zones on the mainland.

Observations from the Columbia River gorge tend to support this idea as well, with the moisture and altitudinal-change gradients being the most important factors involved. The transitional zones of the gorge demonstrated the importance of these gradients in the selection of banding and color variation. Along the Columbia River, these zones are well-known for their rapid and sharp demarcations of environmental features that would normally cover hundreds of kilometers elsewhere. The reduced scale of the area makes analysis of environmental change as related to the west-to-east gradient rather easy. These zones are best known to botanists. The botanical changes through the gorge reflect changes in available moisture, and those changes are likewise reflected in the observed color and banding adaptations in *Monadenia.*

SUMMARY

Analysis of specimens of *Monadenia fidelis* collected at 30 geographically and environmentally differing sites in Oregon and Washington demonstrated significant variation in shell color and banding patterns. Much of the geographical variation was associated with an east-to-west gradient, probably because of differences in moisture, plant cover, and the presence of significant barriers to dispersal and gene flow in the form of the Cascade and Coastal mountain ranges. These two mountain ranges divide the snail's range into four geographic and environmental zones with concomitant morphological variation. North-to-south variation was much less obvious, since there are few barriers to dispersal along that gradient and only moderate variation in the amount of annual rainfall. Zone by zone variation is discussed, including some exceptions found along the Columbia River gorge and several other major drainages.

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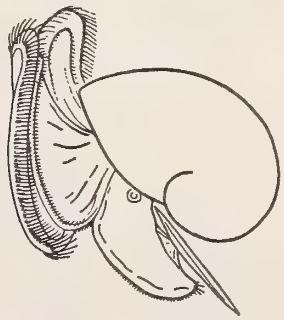

Distribution of Two Nudibranch Species on a Subtidal Reef on the Western Shore of Oahu, Hawaii

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(7 Text figures)

INTRODUCTION

Factors influencing the distribution of organisms have been central to many ecological studies (Connell, 1961a, 1961b; Paine, 1966, 1974; Dayton, 1971; and others). While most studies have dealt with sessile or relatively large, easy to count organisms, a few have been performed on nudibranchs (Miller, 1961, 1962, 1969; Potts, 1970; Nybakken, 1978; Todd, 1978). Most of these studies have been done in the intertidal zone, partially due to the difficulty of finding and sampling subtidal areas where nudibranch populations are sufficiently large. Moreover, little ecological work has been done on tropical nudibranchs.

Because most nudibranchs are highly food-specific animals (Thompson, 1964; Bloom, 1976), it is possible that prey distribution might be a primary factor influencing nudibranch distribution. Franz (1975) states that "the coevolution of predator-prey interaction among nudibranchs is a prime factor in affecting the distribution of these animals." Miller (1961, 1969) also suggests this, but points out that other factors must operate because nudibranchs may not be present where their food is abundant.

This study was undertaken to examine the nudibranch population on the cliff-like face of a shallow subtidal lava peninsula (Figure 1) on the western shore of Oahu, Hawaii (21°32′50″ N; 158°13′32″ W). Scuba dives made at this site prior to this study revealed the presence of a number of *Chromolaichma youngbleuthi* (Kay & Young, 1969) irregularly distributed along the different portions of the algae and sponge covered cliff. As the study progressed, it became apparent that another nudibranch species was common. The opportunity existed to 1) investigate the population fluctuations of two tropical nudibranch species, and 2) determine diet specificity in the two species, and as a consequence of this, the role played by food distribution in the distribution of nudibranchs.

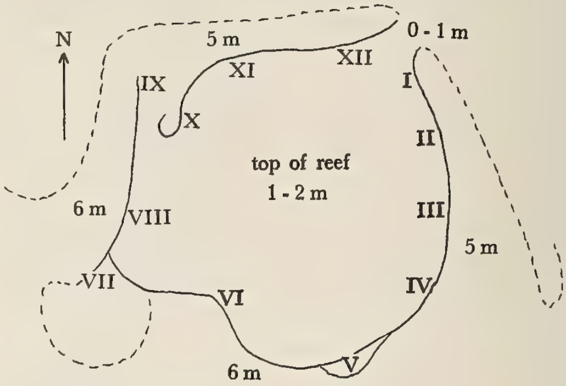

Figure 1

Diagram of the study reef (solid line), showing the locations of the fixed quadrats (Roman numerals), water depths, and extensions of the cliff beyond the study area (dashed line)

METHODS

The sampling area consists of a cliff varying in height from about 2 m (along a very short section) to 6 m. The portion of the cliff studied is approximately 200 m long and is in the shape of an irregular, nearly complete circle (Figure 1). The depth beneath the water surface to the top of the cliff varies from zero meters in some areas (around permanent quadrats I, XI, and XII) to 3 or 4 m in others (quadrat VII). Much of the cliff face is honeycombed with holes, ledges, and caves, many of which have a high percent cover of various sponges. Other common bottom alga cover includes the encrusting calcareous alga *Porolithon,* various other algal species, and live coral. Bryozoans, colonial tunicates, barnacles, and bivalve mollusks are present but less common.

Swells arriving from northwest to southwest create a gradient of exposure along the different sections of the cliff. The areas in which quadrats I, II, XI, and XII are located receive the greatest water agitation, primarily in the form of surge as the wave force is channeled along the cliffs, but also in swirling currents at the ends of the deep coves. The surge can be violent. Surf greater than one or two meters creates surge that makes sampling, as well as getting in and out of the water, difficult or impossible. Surf at this site is generally greater in the winter and early spring, and lower in the summer and fall, although occasionally southern swell causes high surf conditions during the summer. Out of necessity, more frequent sampling took place during calm periods.

For one year beginning November 5, 1977, the nudibranchs in the site were sampled approximately once every two weeks (as regularly as weather conditions would allow). All nudibranchs were counted in square meter quadrats, although the irregularities in the cliff face made this difficult. Each trip, 12 fixed and 15 or 25 random quadrats were sampled. The fixed quadrats were chosen approximately equidistant around the site, and were in ledges or caves with at least 50% cover of sponges. The fixed quadrats were marked by nails pounded into the substrate. The random quadrats were chosen each time, using random numbers between zero and 300, measured as swimming strokes along the reef. Repeated swimming of the site, plus the establishment of landmarks every 20 or so strokes, permitted the distance travelled with each stroke to be kept relatively constant from one trip to the next. Another random number between one and six determined the depth, measured as a fraction of cliff height rather than as an actual depth due to the irregular contours of the bottom.

Within each quadrat, the cliff topography was noted, as well as the approximate total percent cover of sponge. All nudibranchs and egg masses were counted and measured with a millimeter ruler. Nudibranchs were measured in a resting state, because the length of individuals increases dramatically when the animal is moving. Moving animals were touched lightly, causing them to contract, then relax, at which time they were measured. In addition, the substrate upon which each nudibranch occurred was noted, as well as whether or not the individual was active. Actively crawling nudibranchs were assumed not to be feeding.

Relative sponge composition on different parts of the cliff was determined by a point intersection method. Different substrates under centimeter marks on a randomly placed meter-long string were summed and used to derive proportions of different sponges in the different areas.

These data were used to determine seasonal changes in abundances and individual sizes and the spatial arrangement of nudibranchs and sponges within the site. Statistical tests were performed on a Hewlett-Packard HP-27 hand calculator and with the BMDP statistical package on the IBM 370 at the University of Hawaii.

Since distribution and abundance may depend on recruitment, eggs of *Chromolaichma youngbleuthi* were counted and measured to determine potential numbers of larvae produced and probable dispersal method. Nudibranch egg size correlates well with larval type; the smallest eggs are usually planktotrophic, the largest direct developers, and those in between, lecithotrophic (THOMPSON, 1967).

The effect of water agitation on *Chromolaichma youngbleuthi* was tested by placing marked individuals in areas that appeared to differ only in the degree of water agitation, and comparing the recapture of different groups. *Chromolaichma youngbleuthi* can be stained dark blue by several hours immersion in a weak methylene blue bath, and the dye was found to remain in the animal at least six weeks. Adverse effects of the methylene blue were tested by comparing the survival of marked and unmarked nudibranchs in aquaria, and by examining differences in predation upon marked and unmarked animals.

Experiments were also undertaken to determine the effect of grazing by *Chromolaichma youngbleuthi* on the prey sponge. Changes in the size of sponge colonies were monitored in colonies 1) from which all nudibranchs had been removed; 2) with unaltered numbers of nudibranchs; and 3) upon which nudibranchs had artificially been crowded together. The prey sponge is basically an irregularly shaped, massive species, usually growing in colonies less than 20 cm in diameter. Relative growth was determined by changes in the distance of the sponge perimeter from markers (nails) permanently affixed to the rock, and by changes in the distance from the highest point of the colony to a line between the tops of the markers.

RESULTS

Over one year, 300 permanent quadrats and 555 random quadrats were sampled. A total of 1749 nudibranchs were counted, 77.6% of which were *Chromolaichma youngbleuthi*, 15.3% chromodorid 1 ("locust" in BERTSCH & JOHNSON, 1981), and the remaining 7.1% spread over 18 additional species.

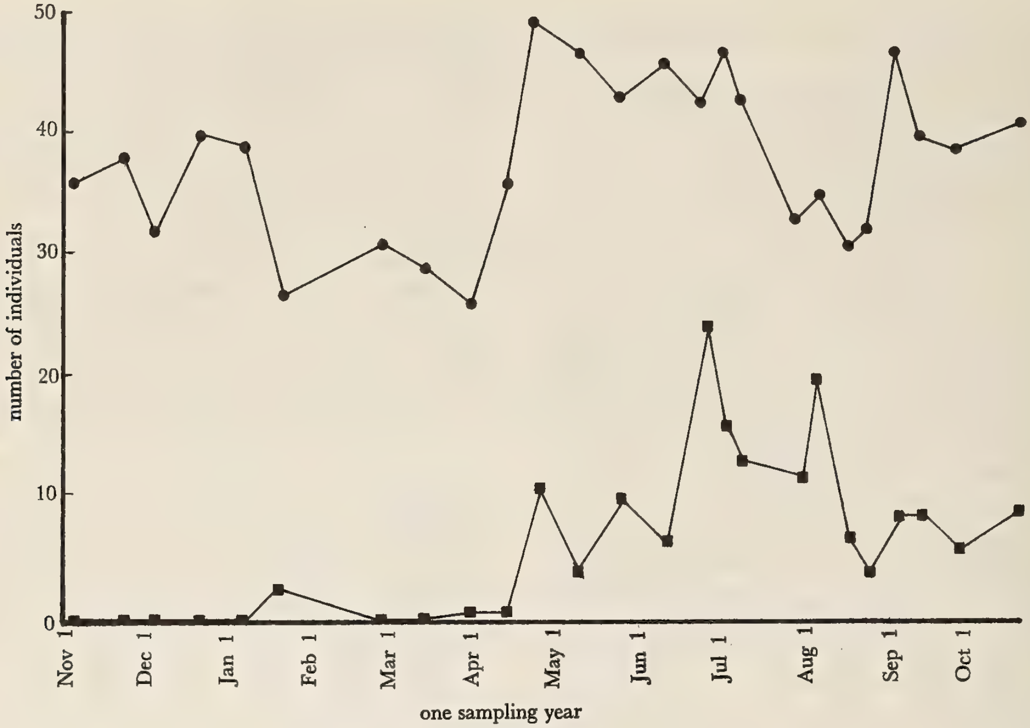

Figure 2

Changes in the numbers of *Chromolaichma youngbleuthi* (dots) and chromodorid 1 (squares) in the 12 fixed quadrats per sample through one sampling year

Considering only the 12 permanent quadrats sampled each trip, numbers of *Chromolaichma youngbleuthi* remained high throughout the year with a possible increase in April (Figure 2). Numbers of chromodorid 1 in the permanent quadrats remained low until mid April, when they dramatically increased. An annual cycle for chromodorid 1 is not indicated, however, because of data collected outside the permanent quadrats and outside the study period: 1) on the first sampling day on November 5, 34 chromodorid 1 individuals were found in a single random quadrat, even though none were found in the permanent quadrats, and 2) follow-up examinations of the reef beyond the end of the sampling year showed that relatively high numbers of chromodorid 1 remained.

Figure 3 summarizes the lengths of *Chromolaichma youngbleuthi* observed in the permanent quadrats throughout the sampling year. The data are broken into ten periods of 35 days each. Despite the increase in range in the latter half of the year, the mean length and the standard deviation remained relatively constant. Figure 4 shows the same data for chromodorid 1, with the addition of the nudibranchs in the random quadrats to increase sample sizes.

Chromolaichma youngbleuthi egg masses are generally present throughout the year (Figure 5). These egg masses average 7.74mm in diameter, and spawn coils this size contain approximately 6000 to 8000 ova. Eggs are 75 to 80μm in diameter, well within the range for planktotrophic larvae (Thompson, 1967). Chromodorid 1 egg masses were observed in the quadrats only twice, on November 5, 1977 and on August 24, 1978. Both times the eggs were with a cluster of twenty or more chromodorid 1 individuals. Eggs of this species were observed outside the quadrats on numerous occasions throughout the year, whenever aggregations of the nudibranchs were encountered.

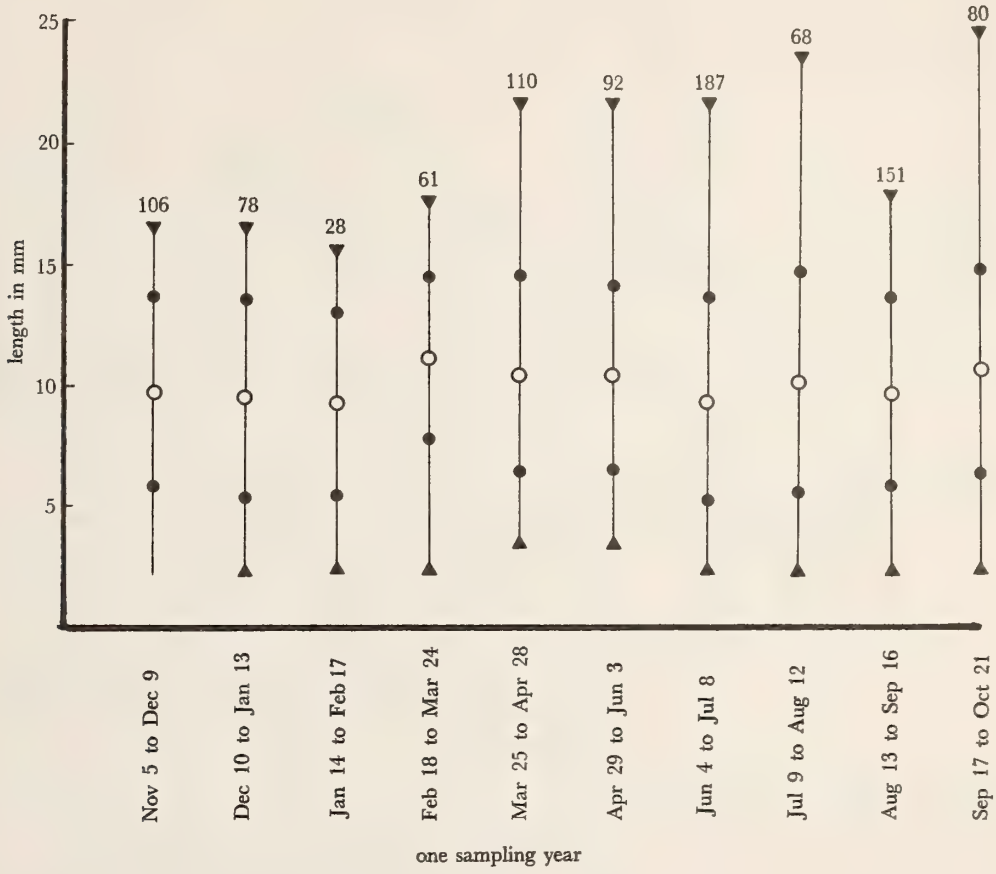

Figure 3

Lengths of *Chromolaichma youngbleuthi* in the fixed quadrats through 1 sampling year. The open circle is the mean length of nudibranchs observed over a particular period, and the triangles delimit the range of lengths measured. The black dots show 1 standard deviation to each side of the mean, and the sample sizes are listed at the top of each bar

Figure 6 clearly shows that *Chromolaichma youngbleuthi*, chromodorid 1, and sponges are not randomly distributed through the study site; all are more common near the extreme ends of the site near fixed quadrats I, II, XI, and XII. The distribution of *C. youngbleuthi* throughout the entire site can be fit to the negative binomial (see Bliss & Fisher, 1953), and is clearly clumped. Patchiness statistics (Lloyd, 1967) range from 1.38 to 23.64 on the different sampling days, with no pattern to the variation. In addition, a χ^2 test done on the numbers of *C. youngbleuthi* per quadrat gives a χ^2 value of 4359 185.9 ($\chi^2_{10,.001} = 29.59$), a very significant deviation from the Poisson distribution. Likewise, the χ^2 of chromodorid 1 distribution is astronomical due to the clumps of 23 and 34 individuals in two of the quadrats ($\chi^2 = 4.74 \times 10^{60}$, $\chi^2_{33,.001} = 60.88$).

Randomness of sponge distribution was checked by dividing the site into ten equal sections and comparing percent cover of sponges with a one way ANOVA. The variances in percent cover of sponge in different parts of the site are not equal (Levene's test: $p < 0.001$) and the tests assuming unequal variances indicated that sponges were distributed non-randomly (Welch test: $p < 0.001$/Brown-Forsythe test: $p < 0.001$). The statistics and Figure 6 show a direct correlation between the percent sponge cover and the number of nudibranchs.

Sponge composition as well as its presence is important

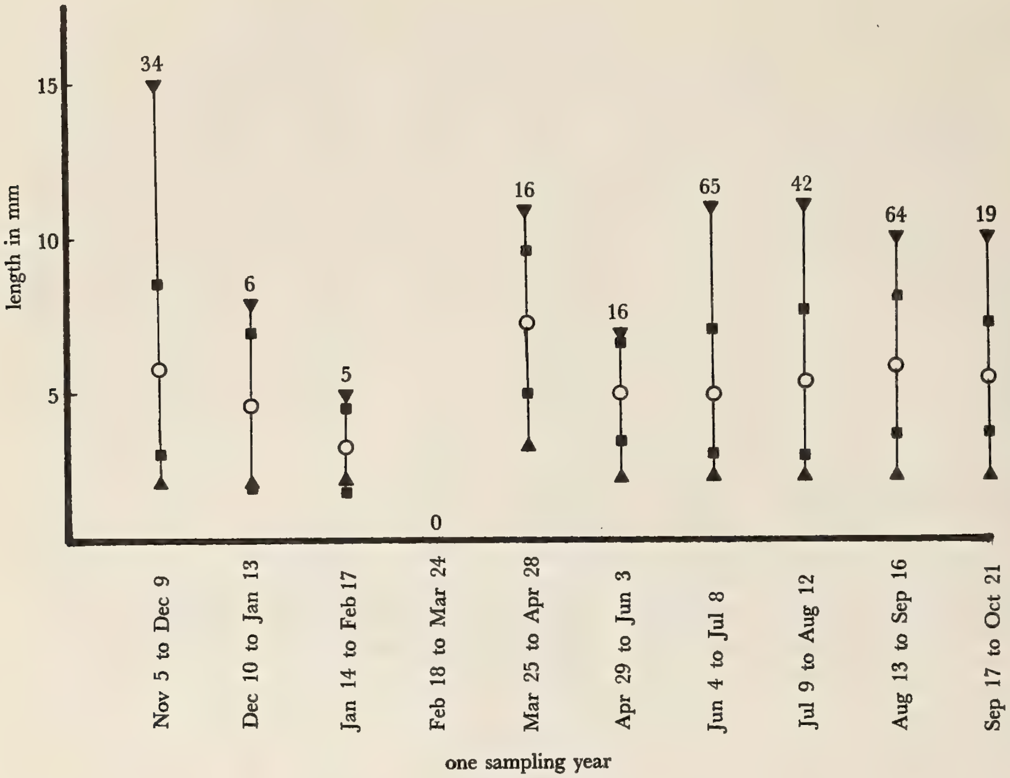

Figure 4

Lengths of chromodorid 1 in the fixed quadrats through 1 sampling year. The open circle is the mean length of nudibranchs observed over a particular period, and the open squares delimit the range of lengths measured. The black dots show 1 standard deviation to each side of the mean, and the sample sizes are listed at the top of each bar

in determining where nudibranchs are found (Table 1). Each of the two most common nudibranchs has a restricted diet consisting of only one sponge species. *Chromolaichma youngbleuthi* eats a *Dysidea* sp. and chromodorid 1 feeds upon a *Luffariella* sp. Both of these sponges are among the most common in the site, and both are distributed in the same way as their nudibranch predators (Figure 7).

Despite the fact that most *Chromolaichma youngbleuthi* are found on *Dysidea,* only about half of the egg masses are deposited on the sponge (Table 1). Virtually all the egg masses not deposited on *Dysidea* are laid on the *Porolithon* or on bare reef rock. The difference between the number observed and the number expected on the sponge based on the nudibranch substrates is highly significant ($\chi^2 = 332.28$, $\chi^2_{1,.005} = 7.88$). Presumably, it is not advantageous to begin a planktonic larval existence from the surface of an efficient filter feeding organism.

Table 2 summarizes the results of placing ten marked *Chromolaichma youngbleuthi* individuals on *Dysidea* colonies in three different areas. Two of these were the calmer and rougher areas where *C. youngbleuthi* is typically found, while the third was a very rough area where the nudibranchs were never observed. Under normal conditions, *C. youngbleuthi* individuals tend to move about very little (some *Dysidea* colonies were observed to have the same nudibranchs for periods of at least four months). Yet, individuals placed on the *Dysidea* colony in the very rough area vanished immediately. (A single marked nudibranch

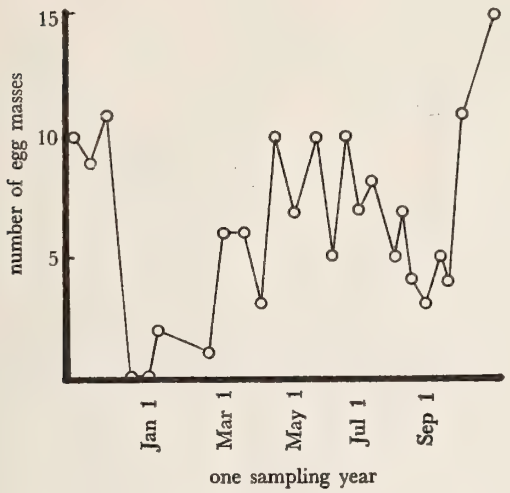

Figure 5

Number of *Chromolaichma youngbleuthi* egg masses observed in the 12 fixed quadrats through 1 sampling year

was discovered about 100 m from the study site the day following the transplant; probably, it was washed off the sponge by a surge and carried far from the reef). Marked nudibranchs placed on *Dysidea* colonies in areas where the nudibranchs are typically found only gradually declined to half the original number after nearly a month, at which time a three-week period of rough weather prevented observation. When observations could again be made, no marked *C. youngbleuthi* could be found.

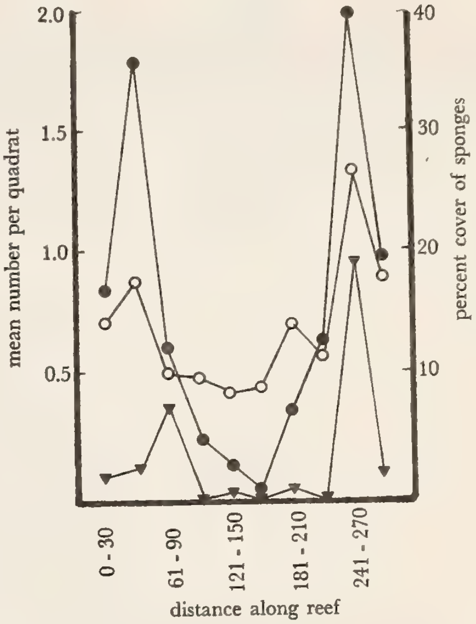

Figure 6

Mean number of nudibranchs per m² in a total of 555 random square meter quadrats, and percent cover of all sponges distributed through the study site. Dots refer to *Chromolaichma youngbleuthi*, triangles to chromodorid 1, and open circles to percent cover of sponges

The low densities in which *Chromolaichma youngbleuthi* are usually found have no measurable effect on the prey sponge (Table 3). Rarely are more than three or four *C. youngbleuthi* observed on a single sponge colony. Artificial crowding of five to ten times this number onto a sponge

Table 1

Percentages of the two most common nudibranchs observed on their respective prey sponges. For each species, the percentage of nudibranchs that were in the process of crawling is also recorded. It is assumed that actively crawling individuals are not feeding. In addition, percentages of *Chromolaichma youngbleuthi* egg masses on and off the sponge *Dysidea* are given.

Nudibranch species and egg masses	Quantity (Total number) examined	Percent on prey sponge		Percent not on prey sponge	
		total	crawling	total	crawling
C. youngbleuthi	1358	89.3	0.25	10.7	44.2
C. youngbleuthi egg masses	203	49.5		50.5	
chromodorid 1	267	57.3	0.00	42.7	66.7

Table 2

Number of marked *Chromolaichma youngbleuthi* transplanted to calm, rough, and very rough areas that were recorded on later observation. Intially, 10 marked individuals were placed at each site. "Calm" refers to the calmest areas in which *C. youngbleuthi* occur in the field, while "very rough" is an area of crashing surf where the nudibranchs are never found. High cover of *Dysidea* was present in all 3 areas.

Number of days later	Calm	Rough	Very rough
0	10	10	10
1	10	9	0
6	7	6	0
16	6	6	0
20	3	6	0
27	4	5	0

Table 3

Changes in the dimensions (length + width + height, in mm) of colonies of *Dysidea* subject to different levels of nudibranch predation. Sponge colonies chosen were all 35 to 45cm in summed dimensions. Repeated checking kept sponge A free of *Chromolaichma youngbleuthi*, sponge B with 3 to 4 nudibranchs, C with about 20 individuals, and D with about 40. The number 0 means no measurable change in dimension.

	Colonies of *Dysidea* sp.			
Weeks	A	B	C	D
1	0	0	0	−6
3	0	0	−1	−35
12	0	0	−1[1]	−39[1]
50	2	1		
101	6	5		

[1] After the third week, weather conditions prevented observation for over 2 months. At the next possible observation, sponge C was occupied by only 2 *C. youngbleuthi* and sponge D by only 5 of the nudibranchs.

colony was required before a noticeable portion of the colony was eaten. This test was prematurely interrupted by a period of rough weather, during which most of the nudibranchs disappeared from the crowded sponges. However, growth of sponges A and B was followed for the next year, and checked again the following year. Sponge A was never observed with nudibranchs, and sponge B had one to five individuals every time it was checked, yet there was no major difference in growth over two years.

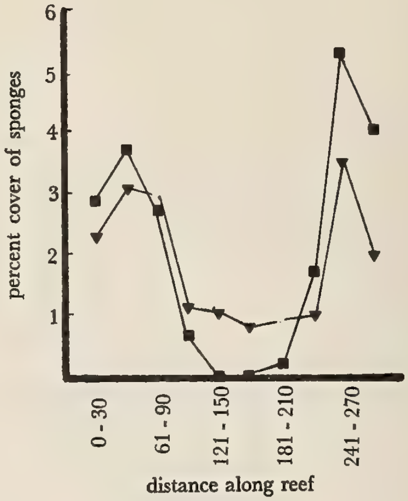

Figure 7

Percent cover of *Dysidea* sp. (squares) and *Luffariella* sp. (triangles) throughout the site, based on a point intersection method

DISCUSSION

The relatively constant numbers over time and individual mean sizes, and the presence of eggs year round all show the *Chromolaichma youngbleuthi* population to be permanent and continually reproducing. Year round egg laying has been reported in one other Hawaiian dorid nudibranch (Kay & Young, 1969) and is present in numerous other Hawaiian species as well (pers. obs.). The presence of a permanent population is also suggested for chromodorid 1, although there is more variability in the figures, probably due to the extremely patchy distribution of this species. Year round, stable nudibranch populations appear to agree with data of Nybakken (1978) on an assemblage of intertidal nudibranchs in California, but contrast with studies by Potts (1970) on *Onchidoris fusca* (Müller, 1776) and by Todd (1978) on *O. muricata* (Müller, 1776) on the coast of England. In the latter two cases, the population was strongly cyclic due to seasonal reproduction and the mass die-off of adult nudibranchs after breeding. These cycles could be caused by wider temperature fluctuations, making conditions for reproduction optimal only at certain times, or by fluctuations of the prey populations; the barnacle prey of *O. fusca* shows similar population cycles (Potts, 1970). Neither is the case in Hawaii. The sponge prey is present year round and the maximum seasonal surface water temperature fluctuation is only about 4°C (Blumenstock & Price, 1967).

Winter wind and sea conditions in Hawaii usually end between March and May (Blumenstock & Price, 1967). The termination of the winter northwest swell, larger than the southerly summer swell, could be responsible for the rather small increase observed in the numbers of nudibranchs in April. In addition, occasional southwest storms usually occur once or twice each winter (Blumenstock & Price, 1967), which can create extremely rough conditions in the study site. Table 2 gives evidence that such extremely rough conditions may adversely affect nudibranch numbers. Nybakken (1978) also noted a correlation between weather and nudibranch numbers.

The conclusions about the non-random distribution of *Chromolaichma youngbleuthi* are based in part on patchiness statistics. According to Lloyd (1967), patchiness statistics should be calculated only with data from a "relatively continuous, apparently uniform, habitat." The variations in this nudibranch study site may create a habitat that is not sufficiently uniform, and thereby invalidate the use of these statistics. Todd (1978) used these analyses to study nudibranch distribution in a not entirely continuous (and perhaps not totally uniform) boulder field, and feels that Lloyd may have been too restrictive in his conditions for which patchiness could be calculated. Results of the present study tend to support Todd's conclusion.

Table 2, plus many hours of personal observations, strongly indicate that *Dysidea* sp. is the sole prey of *Chromolaichma youngbleuthi* and *Luffariella* sp., the sole prey of chromodorid 1. Differences in the proportions of the two nudibranch species on their respective sponges may be due to different feeding strategies. Observations of *C. youngbleuthi* on the same sponge colonies for long periods of time with no apparent change in the sponge, plus the data in Table 3 both indicate that the average densities of *C. youngbleuthi* found in the field have little or no effect on sponge growth. Therefore, they probably only rarely have to move around in search of food. Chromodorid 1, on the other hand, occasionally aggregates in large numbers that completely devour sponge colonies (Bertsch & Johnson, 1981: 107). Several such aggregations were encountered during sampling. If this happens often, the nudibranchs probably have to wander occasionally in search of new *Luffariella* colonies.

Swennen (1959) pointed out that the relationship between nudibranchs and their prey often approached parasitism. Nudibranch species observed during this study clearly exhibit the distinction between what might be called ectoparasitic and predatory modes of nudibranch existence. Fourteen nudibranch species were observed at one time or another to be feeding, each one on a different species. Of these 14, one *(Chromolaichma youngbleuthi)* was of the ectoparasitic type; its grazing activity did not destroy the sponge colony. Nine nudibranch species (including Chromodorid 1) were considered predators, because they generally ate all or a large portion of their prey sponge colonies. Chromodorid 1 was the only species that fed in aggregations of more than two or three individuals. The remaining four species were not observed frequently enough to determine their feeding mode.

To determine the ultimate factors that control the distribution of *Chromolaichma youngbleuthi,* it is necessary to find out what controls the distribution of *Dysidea.* There are 3 interrelated possibilities. First, *Dysidea* may require a certain, relatively high degree of water agitation. As noted in the site description, the cove areas where the sponge is most abundant are the roughest parts of the study area. The water agitation presumably helps oxygenate the water, prevents settlement of silt, and brings in a continuous supply of food, all of which may be important for the survival and growth of this sponge species.

Second, light may also limit sponge distribution. Jokiel (1980) has found that the ultraviolet radiation in sunlight is detrimental to the growth of some species of sponges. There appear to be lower light levels in the coves (roughly confirmed with a photographic light meter), probably caused by the steep cliff walls shading the opposite wall of the cove, and the frequent occurrence of light-reflecting foam, caused by waves breaking on the shallow cliff tops.

A third possible reason why *Dysidea* is found primarily in the surgy cove areas is related to the hypothesis of Connell (1972), that physical factors can interfere with predator activity and permit continued prey existence. Water agitation may interfere with grazing by *Chromolaichma youngbleuthi,* preventing overexploitation of the sponge. In very calm areas, such as those in the middle of the study reef, nudibranchs may completely devour sponge colonies. This could not be adequately tested, because attempts to transplant *Dysidea* colonies to very calm areas failed. Whether nudibranchs were present or not, the transplanted sponge did not survive, indicating that it is not grazing that limits *Dysidea* distribution in calm areas. The sponge, however, grows firmly attached to the substrate, and transplanting requires that it be cut off. This handling may have reduced the transplanted colonies' ability to survive. This hypothesis also cannot explain why chromodorid 1 individuals are primarily in the coves, while at least some *Luffariella* is present throughout the site.

ACKNOWLEDGMENTS

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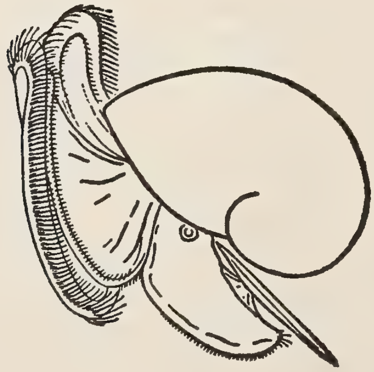

Redescription of *Platydoris macfarlandi* Hanna, 1951 A Rare Deepwater Doridacean Nudibranch

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(1 Plate; 6 Text figures)

INTRODUCTION

The cryptobranch dorid nudibranch *Platydoris macfarlandi* Hanna, 1951 has gone undocumented since its original description. To date, the only known specimens were three individuals dredged in 129-184m of water off Pismo Beach, San Luis Obispo County, California in 1950. Hanna's description, termed in his own words as a poor substitute for the very thorough manner of Dr. Frank Mace MacFarland, included only data on color and the external meristics of the specimens. Subsequently, McDonald (1977) described the radula of one of the paratypes. On October 7, 1981, Drs. Rimmon C. Fay and James A. Vallee collected two specimens of a cryptobranch dorid loosely matching the description of *P. macfarlandi* given by the above two authors. We present the details of this collection and a description of the specimens to broaden the understanding of this little-known species.

Collection Data: Both specimens were collected during a single trawl in 55-113m (30-61 fathoms) of water in Redondo Canyon, offshore of Redondo Beach, Los Angeles County, California (Lat. 33°50′20″ N; Long. 118°25′20″ W). The specimens were removed from a large piece of yellow sponge, *Subarites ficus* (Johnston, 1842) (*fide* Hartman, 1958). The animals were photographed alive on arrival at the laboratory (Figure *1*), then frozen and preserved. The specimens and color transparencies have been deposited in the collection of the California Academy of Sciences (CASIZ), San Francisco, California (CASIZ No. 029322). Color transparencies are also on file at the Santa Barbara Museum of Natural History, Santa Barbara (SBMNH Nos. 008SL and 009SL) and the Los Angeles County Museum, Los Angeles, California.

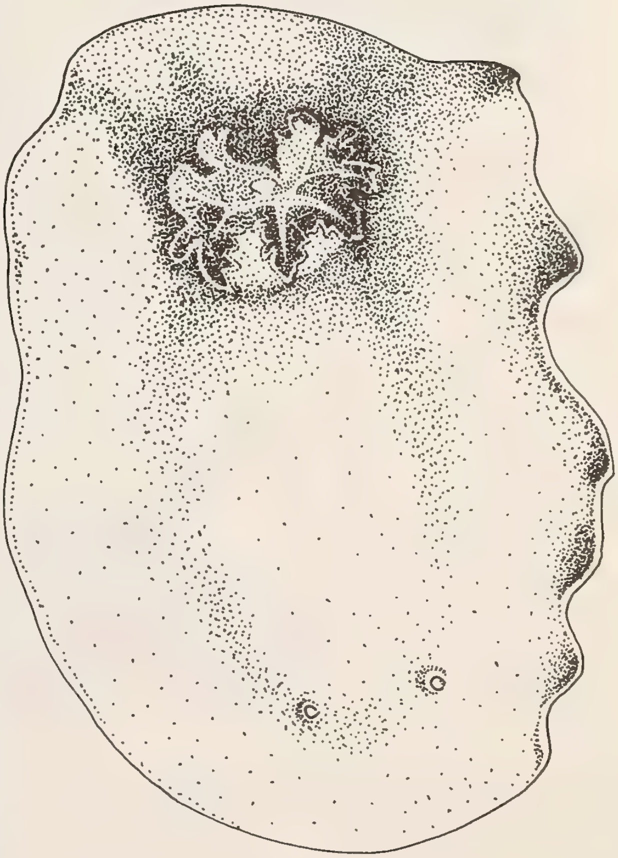

Figure 2

Dorsal view of *Platydoris macfarlandi* drawn from color transparency; 70mm

Description of Specimens: The preserved animals measured 52 by 27 mm and 70 by 48 mm, respectively. The body, as previously described, was firm, greatly flattened and broadly oval (Figure 2). The notal margins were flexible, undulating and outstanding, being held, in life, off the substrate. The surface of the notum appeared velvety smooth until examined closely. It was actually covered with minute, closely set villiform papillae (Figure 3a). The notal spicules were smooth rods of varying thickness, 30-40 widths in length (Figure 3b). They ranged from straight to slightly curved and did not protrude from the surface of the notum or papillae. Below the surface they formed a loose random lattice.

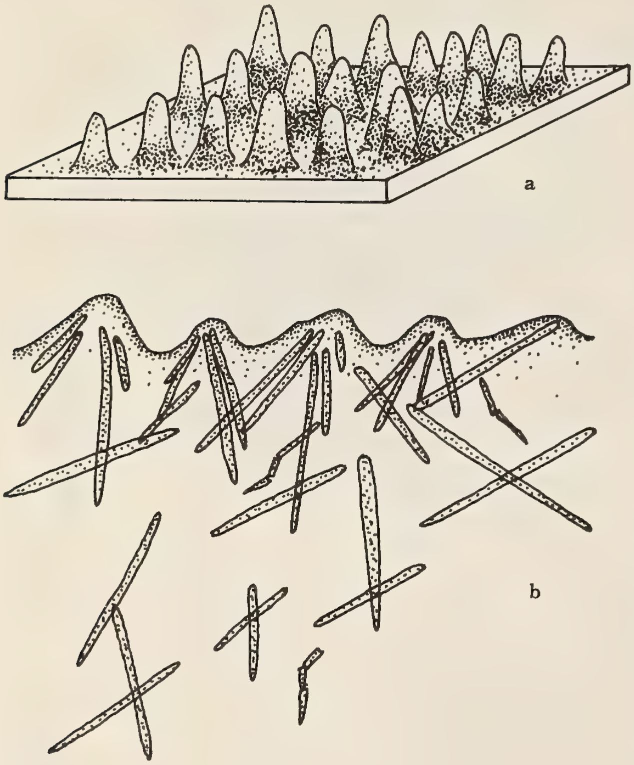

Figure 3

Notal surface of *Platydoris macfarlandi.* a) plain view, b) cross section

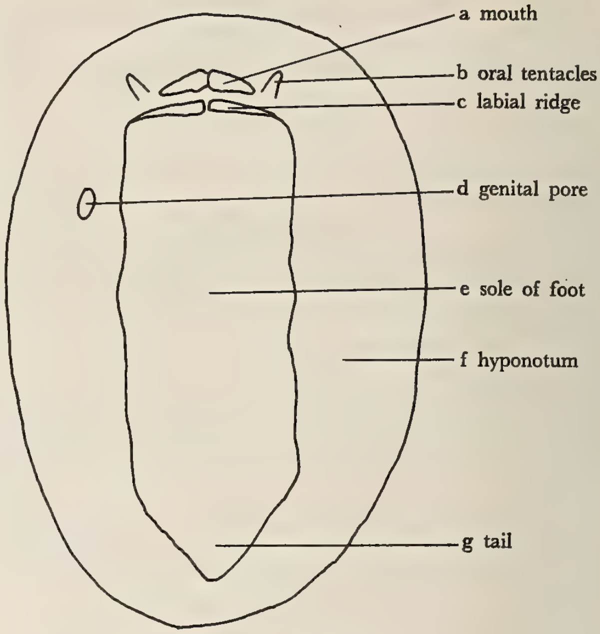

Figure 4

Ventral view of body of *Platydoris macfarlandi.* a) mouth, b) oral tentacles, c) labial ridge, d) genital pore, e) sole of foot, f) hyponotum, g) tail

The anterior margin of the foot was truncate and bilabiate with a deep cleft (Figure 4). The foot margins were parallel and the foot was about ½ the width of the body. The oral tentacles arose independently on each side of the head (Figure 4b). In the preserved specimens the foot width was about 40 percent of the length.

The body color described by Hanna was a "deep dark red above when alive, fading to a dull vinaceous grey in alcohol; light grey, almost white below." Our specimens differed slightly from this description, being a uniform pink above with a thin white to very light pink line along the margin of the notum. The body cavity produced a slightly darker area dorsomedially. The hypnotum and foot were white to very light pink. The rhinophores were entirely white. The basal portion of the branchial plume was pink, while distally the gills were tipped with white.

Explanation of Figure *1*

Figure *1:* Photograph of a living *Platydoris macfarlandi,* Redondo Canyon, Los Angeles County, California; 70 mm (Photograph by Jim Vallee)

Figure *1*: Photograph of a living *Platydoris macfarlandi,* Redondo Canyon, Los Angeles County, California; 70 mm (photograph by Jim Vallee)

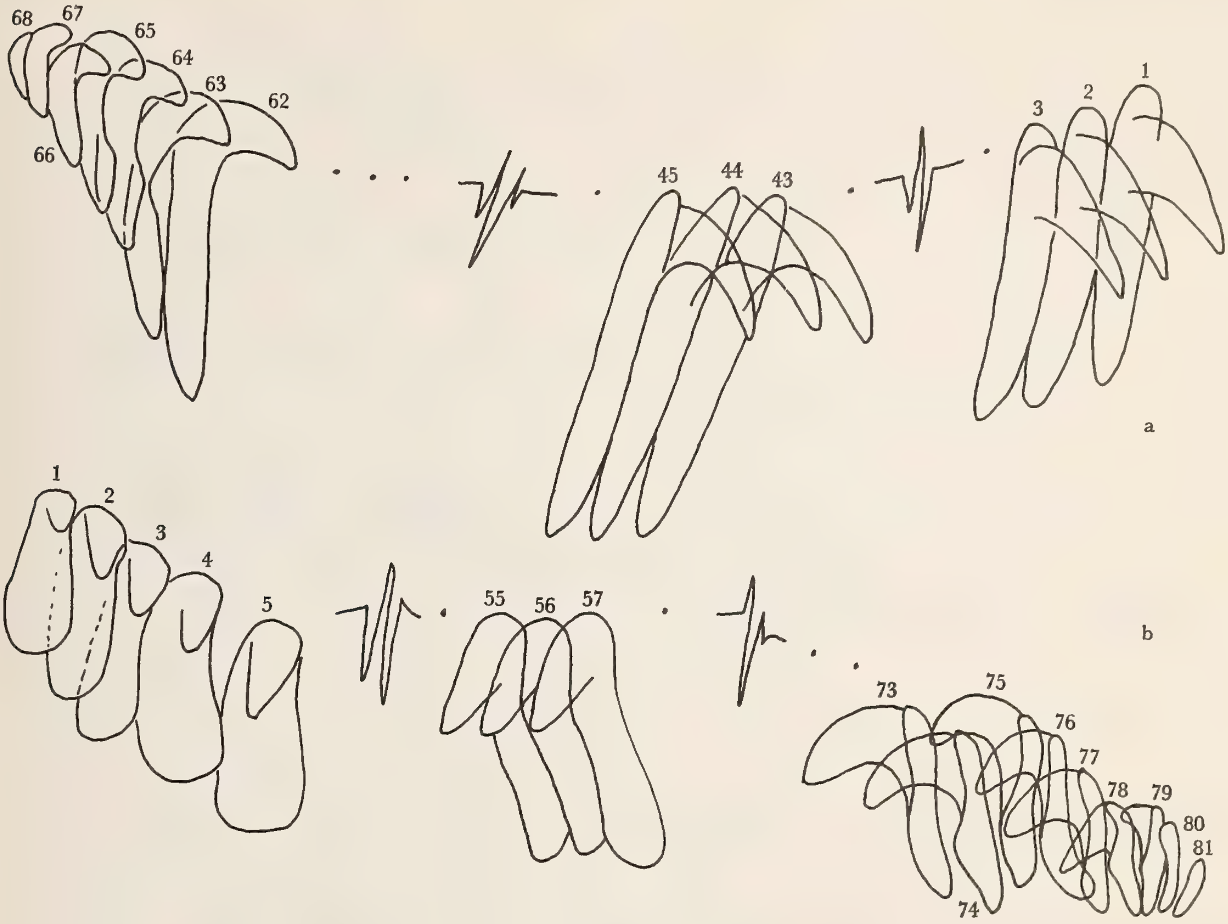

Figure 5

Radula of *Platydoris macfarlandi.* a) left lateral series, 18th row, 52 mm specimen, b) right lateral series, 32nd row, 70 mm specimen

The branchial plume was completely retractile into a raised branchial pit. The seven bi- and tripinnate branchiae were upstanding and spread less than half the distance to the edge of the notum. The anal papilla was situated centrally within the branchiae.

The rhinophores were short, never exposing the shaft, and were retractable into sheaths level with the notum. The clavus was perfoliate with 21 diagonal lamellae. The lamellae had a shallow furrow anteriorly and terminated in a smooth knob.

Hanna did not include the radula in the original description. As part of a master's thesis, McDonald (1977) described and figured the radula of "one of the paratypes." The radular formula of this specimen was 46 × 69-76·0·69-76. The formulae for the specimens collected here were 48 × 66-68·0·66-68 (52 mm specimen) and 59 × 79-81·0·79-81 (70 mm specimen). McDonald (1977) described the lateral teeth as hamate. We would concur and add that they increased in size to the mid-point of the row, and then decreased to the margin (Figure 5). Also, mid-lateral teeth were set on a high base (Figure 6) while the outermost laterals gradually became nearly rectangular in shape, losing their hamate appearance.

Both specimens examined here had distinct labial armature. Typically doridiform in shape, the cuticle was nearly smooth with what appeared as striae. Bergh (1877) excluded such jaws or a labial cuticle from his description of *Platydoris.* Eliot (1910), while discussing *Platydoris,* re-

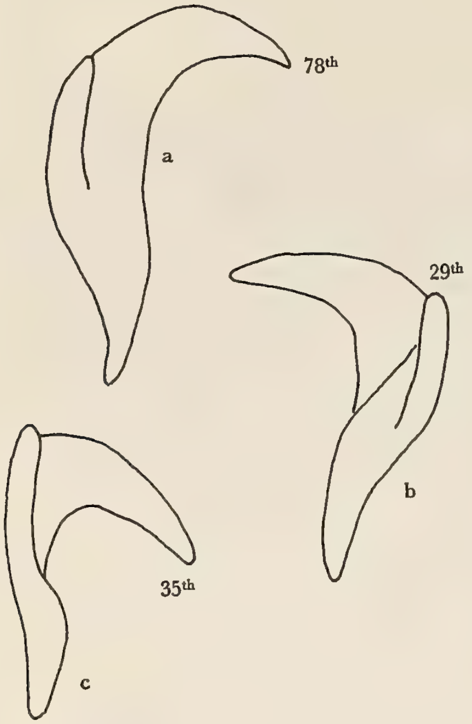

Figure 6

Radular teeth of *Platydoris macfarlandi;* 70mm specimen. a) 78th tooth, 17th row, b) 29th tooth, 2nd row, c) 35th tooth, 59th row

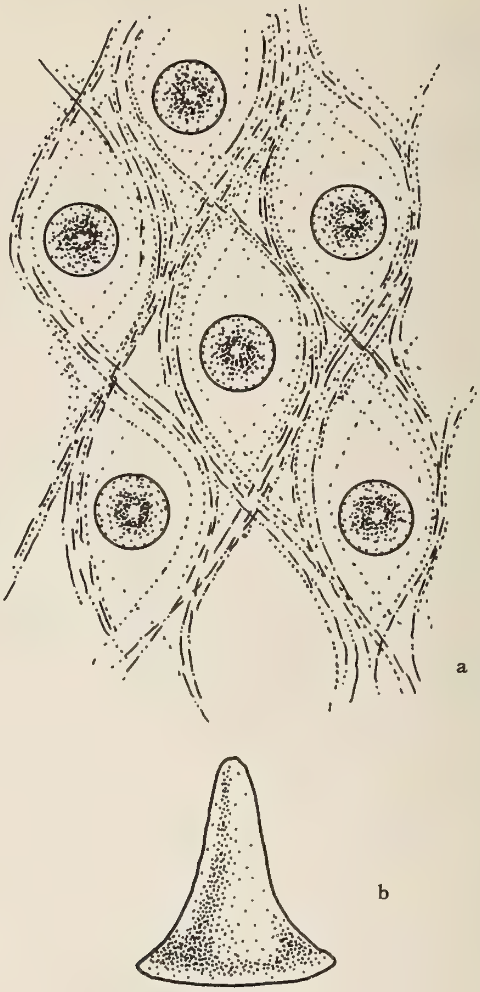

Figure 7

Genital armature of *Platydoris macfarlandi.* a) arrangement of spines in ejaculatory duct, b) spine

ferred to the jaws as being "an anomalous character," stating also that there has been some discrepancy in accounts of the labial armature in the genus. A cursory review of the species presently assigned to *Platydoris* indicates that labial armature is found in about half the described species.

The genital opening was located on the right side of the body, just below the hyponotum and posterior to the rhinophores (Figure 4d). The orifice was shared by the ejaculatory duct, vagina and oviduct. The vagina was lined with a thick convoluted cuticle. The ejaculatory duct was lined with the large spines characteristic of the genus. The spines were evenly distributed in a rhomboidal arrangement (Figure 7a). Each spine was shaped like a sloped cone on a broad base (Figure 7b). These spines, referred to by Hanna as "the spicular lining" of the "cloaca," and the cuticular-lined vagina are the primary discriminants of the genus.

Redondo Canyon, the collection site of our specimens, is a major topographical feature of the Santa Monica Bay. Water quality in this area is very good, probably attributable to heavy currents of very cold upwelled water prevalent in the area. In general, the substrate changes from sandy in shallow depths to very rocky in deeper, more steeply sloping areas. The trawl samples reported here were made on the periphery of the major drop-off where sand and cobble are still present. Examination of the trawl records for this area suggests an extremely diverse fish and invertebrate fauna (personal communication, Pacific Biomarine Laboratories). The only other opisthobranch species collected on October 7th during these trawls were a large (90mm) *Archidoris montereyensis* (Cooper, 1862), a *Tritonia diomedea* Bergh, 1894 and a *Pleurobranchaea californica* MacFarland, 1966.

DISCUSSION

The first documented collection of *Platydoris macfarlandi* since its description in 1951 has provided new range, depth, substrate and descriptive information.

Hanna (1951) did not include the size of his type specimens. At our request, Mr. Dustin Chivers, CASIZ, measured the type series and reports the following: Holotype (CASIZ 020581) 40.0 by 31.4mm; Paratypes (2) (CASIZ 020582) 29.5 by 19.0mm and 25.7 by 18.5mm.

Realizing that we have radulae from only three specimens, it is still interesting to note that with the increase in body size, there was a concurrent increase in radular formula counts. This relationship has been previously reported by Bertsch (1976) and Bloom & Bloom (1977) for other dorid species.

Many eudoridaceans closely match their sponge prey species in color and some even in texture (Thompson, 1976; Yonge & Thompson, 1976; Goddard, 1981; Behrens & Henderson, 1981); while examples exist also of species which do not (Thompson, 1972; Goddard, 1981). Our collection suggests that *Platydoris macfarlandi* lives on at least one sponge species of a color differing greatly from itself. Whether or not these colors are perceptibly different at a depth of 55-113m, thereby providing an ecological advantage to the nudibranch through protective resemblance, can only be speculated upon; however, we would certainly expect a reduction of the visual color red in the nudibranch at that depth. Similarly, the references cited above may have overlooked the phenomenon of color attenuation which occurs with increasing seawater depths (Strickland, 1958). Yonge & Thompson (1976: 134) report, in their discussion of crypsis, that opisthobranchs live predominantly in situations of low light in order to benefit directly from this phenomenon. Based upon data presented in Strickland (1958) all red light would be lost by a depth of between 5-15m, and at the depth which our specimens were trawled, only green light exists.

ACKNOWLEDGMENTS

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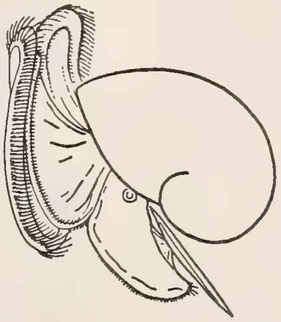

Diet Analysis for Three Subtidal Coexisting Chitons from the Northwestern Atlantic

(Mollusca : Polyplacophora)

BY

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(2 Text figures)

INTRODUCTION

THE SUBTIDAL COMMUNITY of northern New England has a complex faunal makeup consisting of boreal and several arctic species. Although the mollusc assemblage is diverse, only three species of chiton, *Tonicella rubra* (Linnaeus, 1767), *Tonicella marmorea* (Fabricius, 1780) and *Ischnochiton albus* (Linnaeus, 1767), are commonly found in the shallow subtidal zone. These three circumboreal chitons coexist on the same rock substrates in densities which may exceed 1000/m^2 (LANGER, 1973; 1978) and are the dominant subtidal epifaunal molluscs in selected habitats in northern New England (Langer, unpub. observation). The present study was designed to investigate the feeding habits of *T. rubra, T. marmorea* and *I. albus.* Elements examined in this study include analysis of diet composition, influence of season on diet and intraspecific and interspecific diet comparisons using data collected at two widely-separated sites.

MATERIALS AND METHODS

Quadrat samples were obtained monthly for a two-year period at rocky, subtidal sites in Deep Cove, Eastport, Maine and Cape Neddick, York, Maine using SCUBA. These sites, which represent northern and southern Maine, were chosen for this study based on latitudinal separation and accessibility throughout the year. Eight stations were established at Deep Cove ranging from mean low water to a depth of 10.5 m and stratified random samples were collected from an area having dimensions of $\frac{1}{16}$ m^2. Because of habitat differences and lower chiton densities (LANGER, 1978), simple random sampling encompassing an area of $\frac{1}{4}$ m^2 was conducted at Cape Neddick.

The dietary components of the chiton species were determined by examining wet-mount slide preparations of the stomach and intestinal contents from 2518 individuals. Prior to analysis, the gut contents were preserved in 10% buffered formalin to stop further digestion. The presence of carbonate compounds in the gut was determined using dilute hydrochloric acid. Fecal pellet examinations and field observations were used to supplement the feeding analysis. Identification of sponges was based on field observations and on spicules found in gut contents. Prey were assessed in the form of percent volumes of floral and faunal prey, and sediments in gut contents according to the methods of BARNAWELL (1960). The data for each species identified in the individual chiton groups from the two sites were pooled and normalized as a percentage of the total gut contents. The percentages were adjusted for sample size variability and evaluated intraspecifically and interspecifically using the arcsin transformation for testing the equality of percentages (SOKAL & ROHLF, 1969). Significance was designated at the level of $p \leq 0.05$.

RESULTS

Diet Composition: Table 1 lists the prey species found in the digestive tracts of *Tonicella rubra, T. marmorea* and *Ischnochiton albus* from Deep Cove and Cape Neddick. The majority of protozoan prey were foraminferans. Excluding diatoms, the algae ingested at both sites were principally filamentous in structure. Sources of carbonate compounds in chiton guts were foraminiferan tests, calcareous sponge spicules, serpulid tubes, ectoproct zooecia and calcareous algae *(Lithothamnium, Lithophyllum* and *Clathromorphum).* There was no evidence that calcareous algae were a major food source *per se,* since their presence in the gut can be attributed to the rasping of the epibenthic film from the surface of calcareous algal-covered substrates.

The total volume of prey ingested annually by each chiton species included three fractions: flora, fauna and sediments (Figure 1). The sediment fraction consisted principally of inorganic matter, whereas the floral and

Table 1

Tonicella rubra, Tonicella marmorea and *Ischnochiton albus.* Specific Prey in Chiton Diets for Deep Cove and Cape Neddick, Maine.

Protozoa	
Folliculina sp.	1-5[1]
Zoothamnium sp.	1-5
Tintinnid spp.[2]	1-5
Suctorian spp.[2]	1-5
Foraminiferan spp.[2]	1-5
Porifera	1-5
Calcispongiae	
Clathrina coriacea	
Leucosolenia botryoides	
Demospongiae	
Halichondria panicea	
Haliclona sp.	
Halisarca sp.	
Microciona prolifera	
Pellina sitiens	
Cnidaria	
Hydrozoa	
Sertularella sp.	2
Thuiaria sp.	4
Campanularid spp.[2]	1-5
Anthozoa	
Gersemia rubiformes	2
Mollusca	
Bivalvia	1-5
Hiatella arctica	
Mytilidae[2]	
Gastropoda	2
Arthropoda	
Ostracoda	
Loxoconcha sp.	5
sp.[2]	1-5
Harpacticoid Copepoda	2, 5
Amphipoda	5
Larval Arthropod[2]	1-5
Arthropod Appendages[2]	1-5
Rotifera	
Lepadella sp.	1
spp.[2]	1-5
Annelida	
Polychaete Setae[2]	1-4
Kinorhyncha	
Echinoderes sp.	1
sp.[2]	2
Nematoda	1-5
Ectoprocta	3, 5
Trochophore Larva[2]	1
Rhodophyta	
Callithamnion sp.	5
Erythrotrichia carnea	5
Rhododermis elegans	1, 2
Filamentous spp.[2]	1-5
Phaeophyta	
Ectocarpus sp.	4, 5
Filamentous spp.[2]	1-5
Chlorophyta	
Ulva lactuca	4
Filamentous spp.[2]	1-5
Chrysophyta	1-5
Achnanthes longipes	
Biddulphia aurita	
Coscinociscus sp.	
Fragillaria sp.	
Grammatophora marina	
Gyrosigma sp.	
Isthmia sp.	
Licmophora abbreviata	
Navicula sp.	
Nitzschia longissima	
N. seriata	
N. reversa	
Rhabdonema adriaticum	
Rhizosolenia hebetata	
R. setigera	
Schroderella delicatula	
Striatella unipunctata	
Surirella sp.	
Thalassionema nitzschoides	
Thalassiosira gravida	
T. nana	
Thalassiothrix longissima	

[1] 1. *T. rubra* (Deep Cove): 937-sample size
2. *T. marmorea* (Deep Cove): 595
3. *I. albus* (Deep Cove): 269
4. *T. rubra* (Cape Neddick): 494
5. *T. marmorea* (Cape Neddick): 223

[2] Unidentified species

faunal fractions represented the respective prey species (Table 1). The chitons were not considered detritophores because of the large inorganic nature of the sediments ingested.

Tonicella rubra: Chrysophyta, Porifera and Protozoa were the major annual dietary components of *Tonicella rubra* from Deep Cove (Table 2). The consumption of these phyla, as well as the other diverse prey phyla, varied seasonally (Table 3). This resulted in statistically significant variations in the volume of faunal and floral prey ingested (Figure 2). The volume of fauna found in chiton guts rose between summer and fall and declined from winter through spring (Figure 2). The omnivorous *T. rubra* displayed an overall herbivorous habit. Furthermore, the diet of *T. rubra* did not vary with depth.

Despite distinctive differences in community composition, the dietary components of *Tonicella rubra* from Cape Neddick were similar to those seen at Deep Cove (Tables 2 & 4). The only notable differences between the two sites were the greater frequency of protozoans (Table 2) (foraminiferans) in the diet of *T. rubra* at Cape Neddick, and a threefold increase in the volume of fauna ingested (Figure 1). *Tonicella rubra* maintained a herbivorous habit except during fall when a decline in the algal volume ingested concomitant with a rise in fauna consumed resulted in a seasonal shift to a carnivorous habit (Figure 2).

Tonicella marmorea: The major prey phyla of *Tonicella marmorea* at Deep Cove were Chrysophyta, Porifera and Protozoa (Table 2). Although percent volumes of flora and fauna ingested indicated a herbivorous habit for this grazing omnivore (Figure 1), overall seasonal variations in diet occurred (Table 3). The volume of algae consumed remained high except in winter, and the faunal complement showed a statistically significant twofold increase during fall (Figure 2). Further analysis revealed that the diet of *T. marmorea* also did not vary with depth.

The diet of *Tonicella marmorea* at Cape Neddick was similar in composition (Table 2) and seasonal adjustments to those described for Deep Cove (Table 4). However, a significant difference from Deep Cove was the ingestion of a larger volume of fauna than flora indicating an overall carnivorous habit (Figure 1). Seasonal analysis of chiton diet revealed that this shift to a carnivorous habit occurred in fall. *Tonicella marmorea* maintained a herbivorous habit during the other seasons (Figure 2).

Ischnochiton albus: The diet of *Ischnochiton albus* from Deep Cove consisted of four major prey phyla, Chrysophyta, Porifera, Protozoa and Arthropoda (Table 2). The remaining eight phyla occurred infrequently (< 4%). Although *I. albus* displayed an overall omnivorous diet consuming

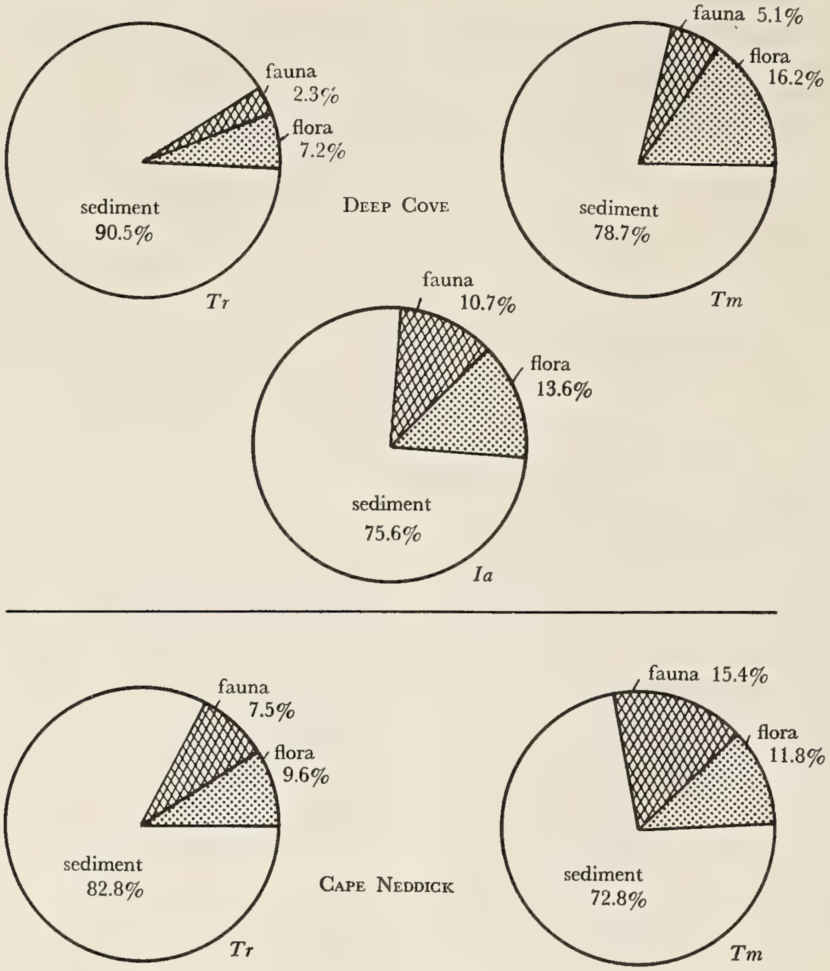

Figure 1

approximately equal volumes of flora and fauna (Figure 1), seasonal shifts in prey occurrence and volume consumed were observed (Figure 2 & Table 3). A herbivorous diet occurred during spring and summer which was replaced by a predominantly carnivorous diet during fall and winter (Figure 2). The fluctuations in diet composition were also unrelated to depth. *Ischnochiton albus* did not occur in the shallow subtidal area at Cape Neddick.

Intraspecific Diet Comparison: A comparison of the diet of *Tonicella rubra* from Cape Neddick and Deep Cove revealed significant qualitative and quantitative differences. Annually, both the algal volume consumed and the percent volume of fauna ingested were significantly higher at Cape Neddick (Figure 1). Also noted was a threefold increase in the frequency of occurrence of dietary protozoans at Cape Neddick (Table 2).

Tonicella marmorea consumed three times more faunal volume annually at Cape Neddick, whereas at Deep Cove the volume of flora ingested by *T. marmorea* was significantly higher (Figure 1). Quantitatively, this faunal difference ranged from 1.3-fold in winter to threefold in summer (Table 5). The algal volume consumed showed no seasonal differences during spring and summer between the two sites. However, in fall a doubling of the percent volume of algae ingested occurred at Deep Cove. A similar

Table 2

Tonicella rubra, Tonicella marmorea and *Ischnochiton albus.*
Annual Frequency of Occurrence of Prey Phyla in Chiton Gut Contents at Deep Cove and Cape Neddick, Maine.

	Deep Cove			Cape Neddick	
Prey Phyla	*T. rubra* %	*T. marmorea* %	*I. albus* %	*T. rubra* %	*T. marmorea* %
Porifera	38.6 +[1]	55.3 +	33.7 +	33.0	36.2
Protozoa	14.8 +	24.7 +	28.8 +	43.9 +	68.2
Arthropoda	1.7 +	4.1 +	15.9 +	3.0 +	10.2
Nematoda	1.7 +	4.3 +	2.7	2.6 +	6.7
Mollusca	0.4	0.7	0.8 +	3.4	6.7
Rotifera	0.1 +	0.5 +	1.9 +	0.9 +	6.2
Cnidaria	0.3	0.4	0.4	0.6	1.4
Kinorhyncha	0.1	0.2	0.0	0.0	0.0
Annelida	0.2	0.2	0.0	0.2	0.0
Ectoprocta	0.0	0.0	0.4 +	0.0	0.5
Chrysophyta	79.5 +	85.5	86.7 +	69.1	75.2
Phaeophyta	2.5 +	4.0 +	2.8	5.6 +	13.8
Chlorophyta	1.5 +	2.4 +	3.8 +	3.4	5.7
Rhodophyta	2.8	2.0	1.1 +	2.4	3.8
Unidentified algae	0.1 +	0.3	0.4 +	3.2	4.8

[1] Data composite of prey species at Deep Cove and Cape Neddick expressed as percentages of each species based on sample size. The percentages are compared interspecifically, + : $P \leq 0.05$.

shift to a higher percent volume of ingested algae was seen at Cape Neddick in winter (Table 5). The only annual variations in frequency of occurrence of prey phyla in the diet of *T. marmorea* between the sites occurred for Porifera and Protozoa. Porifera were 1.7 times more abundant in the diet at Deep Cove, whereas the occurrence of protozoans in the diet increased at Cape Neddick by 1.7-fold (Table 2).

Interspecific Diet Comparison: A comparison of the diets of *Tonicella rubra, T. marmorea* and *Ischnochiton albus* indicated that these chitons utilize the same major prey phyla. However, it was evident from Table 2 that the proportions of each phylum ingested by the three species were different. Similarly, the diets of the *Tonicella* species at Cape Neddick differed in the quantity of major prey consumed (Table 2). Significant seasonal differences in the faunal volumes of the chiton diets occurred at both sites (Table 5). At Cape Neddick the volume of algae ingested by *T. marmorea* was significantly higher during spring and fall than the volume ingested by *T. rubra.* No difference in the faunal volume was seen in winter. At Deep Cove, the amount of fauna consumed by *I. albus* was greater than that of *T. marmorea* and *T. rubra.*

DISCUSSION

Analysis of Diet Composition: The diet composition of many chitons, particularly those found intertidally, has been summarized as herbivorous by MacGinitie & MacGinitie (1949), Fischer-Piette & Franc (1960) and Hyman (1967). Subsequent authors (Barnes, 1972; Robb, 1975; Boyle, 1977) verified these reports and identified the algal contents as belonging to five major phyla, Chrysophyta, Chlorophyta, Cyanophyta, Phaeophyta and Rhodophyta.

Carnivorous habits have been reported predominantly among subtidal chitons. Protozoan prey were reported by Yakovleva (1952), Christiansen (1954) and Kues (1974). Plate (1901) and others (von Siegfried, 1954; Barnawell, 1960; McLean, 1962; Kues, 1974; Robb, 1975) confirmed chiton predation on sponges. Chiton prey also include arthropods (Barnawell, 1960; McLean, 1962; Boolootian, 1964), molluscs (Mestayer, 1920; Barnawell, 1960; Boolootian, 1964), annelids (Barnawell, 1960; McLean, 1962), hydroids (Barnawell, 1960) and bryozoans (Giese *et al.*, 1959).

The present study characterizes the diets of *Tonicella rubra, T. marmorea* and *Ischnochiton albus* as omnivorous.

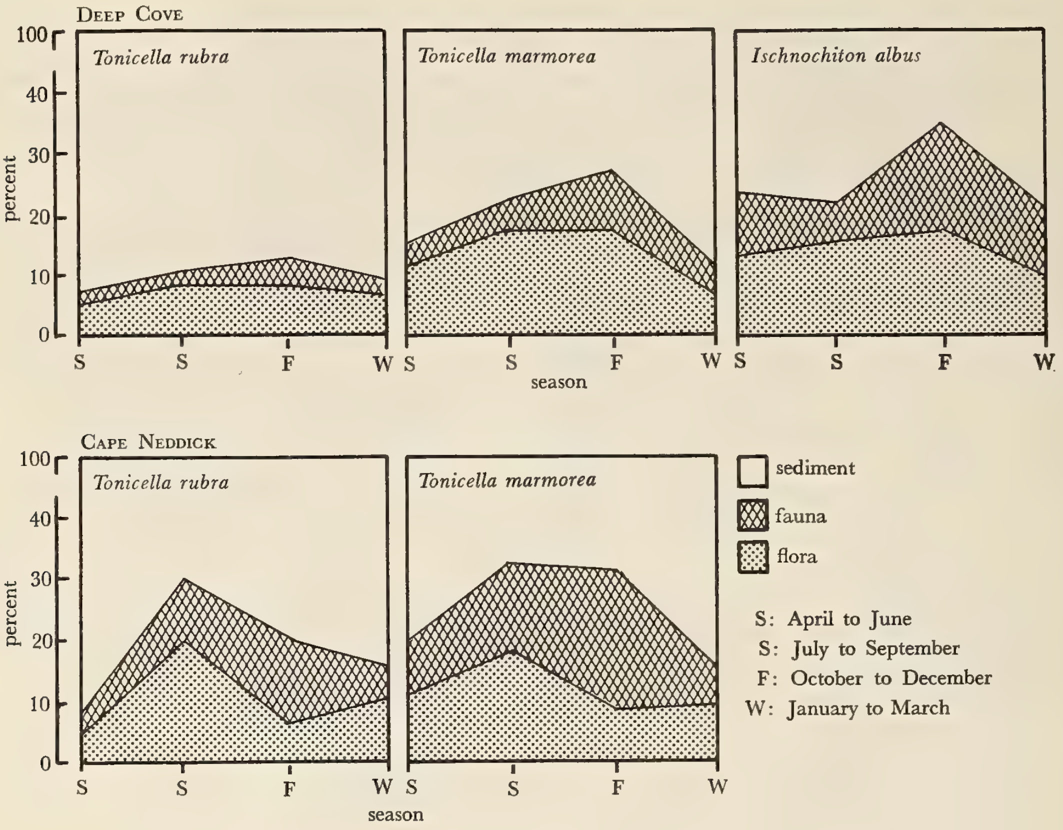

Figure 2

The principal prey species consumed were Chrysophyta, Porifera and Protozoa. The available feeding biology literature for these chitons consists of a report of foraminifera in the gut contents of *I. albus* by **Yakovleva** (1952) and an observation by **Milligan** (1916) of *T. rubra* feeding on "minute brownish vegetable growth which existed on shells and stones...". If this growth is interpreted as diatom film, then the observations of both Milligan and Yakovleva support the present results. Furthermore, this is the first report of the phyla Rotifera and Kinorhyncha as chiton prey.

Although a large proportion (> 75%) of the chiton gut contents consisted of sediment, this sediment is not considered to be an integral part of the diet. Strong currents and wave action produce turbid conditions which frequently leave subtidal rocks covered with fine sediment. Since these chitons are scraping omnivores, this feeding behavior probably results in ingestion of the sediment. Substantial quantities of sand and other sediment have been reported in gut contents of other chiton species (**Barnawell**, 1960; **McLean**, 1961; **Boolootian**, 1964; **Kues**, 1974). Kues found even larger quantities of sediment in a deep water chiton than the data reported for *Tonicella rubra.*

The data presented in this study also indicated a notable absence of calcareous algae as a dietary component of *Tonicella rubra, T. marmorea* and *Ischnochiton albus* and a predominance of diatoms and epifauna. The absence of calcareous algae in the diet is the result of the chiton populations occurring in many areas which are devoid of calcareous algae (**Langer**, 1978). However, chiton predation on calcareous algae has been observed for other chiton species. **Lowenstam** (1962) reported chitons feeding on calcareous algae and suggested that the hard goethite caps on radular denticles allowed chitons to scrape deeply into substrate without suffering excessive wear. **Barnes** (1972) similarly reported that a northeastern Pacific chiton, *Toni-*

Table 3

Tonicella rubra, Tonicella marmorea, and *Ischnochiton albus.*
Seasonal Variation in Frequency of Occurrence
of Prey Phyla in Diet at Deep Cove, Maine.

Prey phyla	Spring %	Summer %	Fall %	Winter %
Tonicella rubra				
Porifera	23.8 +[1]	25.2 +	50.3	47.0 +
Protozoa	6.7 +	10.2 +	19.1 +	13.2 +
Arthropoda	1.1 +	1.5	1.7 +	2.6 +
Nematoda	0.0 +	1.0 +	2.4	2.1 +
Mollusca	0.0 +	1.0	0.7	0.4 +
Rotifera	0.0	0.0 +	0.4 +	0.0
Cnidaria	1.1 +	0.0 +	0.4 +	0.0
Kinorhyncha	0.0	0.0 +	0.4 +	0.0
Annelida	0.0	0.0 +	0.4 +	0.0
Chrysophyta	77.2	77.7	77.8 +	83.3 +
Phaeophyta	1.7 +	3.9 +	1.7 +	3.0 +
Chlorophyta	2.8 +	1.9 +	0.4 +	1.7 +
Rhodophyta	0.6 +	4.9 +	3.8 +	1.7 +
Unidentified algae	0.0	0.0 +	0.4 +	0.0
Tonicella marmorea				
Porifera	40.3 +	57.1 +	72.0 +	54.9 +
Protozoa	15.1 +	29.3 +	32.6 +	23.2 +
Arthropoda	6.3 +	4.1 +	1.5 +	4.2 +
Nematoda	0.6 +	10.2 +	1.5 +	4.9 +
Mollusca	0.6 +	2.0 +	0.0 +	0.7
Rotifera	0.0	0.0 +	1.5	0.7 +
Cnidaria	0.6	0.7 +	1.5 +	0.0 +
Kinorhyncha	0.6 +	0.0	0.0	0.0 +
Annelida	0.0	0.0 +	0.8 +	0.0
Chrysophyta	80.5 +	94.6 +	90.9 +	54.9 +
Phaeophyta	3.8 +	6.8	3.0 +	2.1 +
Chlorophyta	2.5 +	1.4 +	2.3	2.1
Rhodophyta	1.2 +	0.7 +	5.3 +	2.1 +
Unidentified algae	0.0	0.0 +	1.5 +	0.0
Ischnochiton albus				
Porifera	17.6 +	24.1 +	68.0 +	38.5 +
Protozoa	17.6 +	60.3 +	23.1 +	18.0
Arthropoda	23.1	24.1 +	4.0 +	21.5 +
Nematoda	0.0 +	5.2 +	10.0 +	1.5 +
Mollusca	0.0	0.0 +	4.0 +	0.0
Rotifera	0.0	0.0 +	4.0 +	1.5 +
Cnidaria	0.0	0.0 +	2.0	1.5 +
Ectoprocta	0.0	0.0 +	2.0 +	0.0
Chrysophyta	89.0 +	96.6 +	92.0 +	83.1 +
Phaeophyta	0.0 +	1.7 +	4.0 +	0.0
Chlorophyta	5.5 +	1.7 +	4.0	3.0
Rhodophyta	0.0 +	1.7	2.0	1.5 +
Unidentified algae	0.0 +	1.7 +	0.0	0.0

[1] Prey assessment based on monthly samples and expressed as percentage of species based on sample size. The seasonal percentages are compared intraspecifically, + : $P \leq 0.05$.

Table 4

Tonicella rubra and *Tonicella marmorea.*
Seasonal Variation in Frequency of Occurrence
of Prey Phyla in Diet at Cape Neddick, Maine.

Prey phyla	Spring %	Summer %	Fall %	Winter %
Tonicella rubra				
Porifera	25.4 +[1]	13.1 +	38.5 +	48.3 +
Protozoa	24.5 +	52.4 +	55.5 +	43.2 +
Nematoda	0.8 +	0.0 +	4.7	3.4 +
Arthropoda	1.6 +	7.2 +	2.1	2.6
Mollusca	0.0 +	2.4 +	8.1 +	1.7 +
Rotifera	0.0	0.0 +	2.0 +	0.9 +
Cnidaria	0.0	0.0 +	0.7 +	1.7 +
Annelida	0.0 +	1.2 +	0.0	0.0
Chrysophyta	61.0 +	79.8 +	60.1 +	81.0 +
Phaeophyta	4.2	3.6 +	8.8 +	4.3
Chlorophyta	5.1	7.1 +	2.0	0.7 +
Rhodophyta	0.0 +	3.6	4.7 +	0.9
Unidentified algae	0.0 +	11.9 +	3.4 +	0.0
Tonicella marmorea				
Porifera	24.5	25.5 +	48.4 +	33.0 +
Protozoa	55.1 +	68.1 +	77.4 +	52.4
Nematoda	10.2 +	2.1 +	8.6 +	0.0 +
Arthropoda	16.3 +	8.5 +	5.4 +	0.0 +
Mollusca	0.0 +	6.4	11.8 +	0.0
Rotifera	0.0	0.0 +	12.9 +	4.8 +
Cnidaria	4.1	2.1 +	0.0	0.0 +
Ectoprocta	0.0	0.0 +	1.1 +	0.0
Chrysophyta	75.5	76.6	73.1 +	81.0
Phaeophyta	2.0 +	12.8 +	20.9 +	14.3 +
Chlorophyta	10.2	8.5 +	3.2 +	0.0 +
Rhodophyta	2.0 +	6.4 +	4.3 +	0.0 +
Unidentified algae	0.0 +	17.0 +	2.2 +	0.0

[1] Prey availability based on monthly samples and expressed as percentage of species based on sample size. The seasonal percentages are compared intraspecifically, + : $P \leq 0.05$.

cella lineata, feeds primarily on calcareous algae and to a lesser extent on epiphytes. Simpson (1976) also indicated a preference for coralline algae by the chitons, *Plaxiphora aurata* and *Hemiarthrum setilosum.*

Seasonality: Although the overall dietary pattern of these chitons is omnivorous, seasonal shifts to a carnivorous diet occurred at Cape Neddick for *Tonicella rubra* and *T. marmorea* during fall. Unpublished data suggest that this shift resulted from a combination of a low diatom population and a peak in the abundance of epifaunal biomass. Similar seasonal shifts to a carnivorous diet, attributed to a low abundance of algae during winter and spring, have been

Table 5

Tonicella rubra, Tonicella marmorea, and *Ischnochiton albus.* Percent Volumes of Flora and Fauna in Chiton Diets by Season.

Chiton species	Spring %	Summer %	Fall %	Winter %
Deep Cove				
Flora				
T. rubra	5.3 +[1] +[2]	8.3 +	8.3 + +	6.3
T. marmorea	11.7 +	17.4	17.3 +	6.8 + +
I. albus	13.2 +	15.8 +	17.3 + +	9.6 + +
Fauna				
T. rubra	1.5 +	1.6 + +	3.8 + +	1.9 +
T. marmorea	3.3 +	4.5 + +	9.0 +	4.1 +
I. albus	10.0 + +	5.7 + +	17.3 + +	11.0 +
Cape Neddick				
Flora				
T. rubra	4.7 + +	19.9 +	6.6 + +	10.9 +
T. marmorea	11.4 +	18.6 +	9.1	9.8
Fauna				
T. rubra	1.8 + +	9.9 + +	13.5 + +	4.3 +
T. marmorea	8.1 +	13.8 +	22.4 +	5.4

[1] Intraspecific comparison of volumes consumed between seasons, + : $P \leq 0.05$.

[2] Interspecific comparison of volumes consumed during the same season, + : $P \leq 0.05$.

described for *Mopalia* (Barnawell, 1960). Less dramatic seasonal shifts were observed at Deep Cove where the strong tidal currents and upwelling provide a renewal of nutrients and an abundance of diatoms.

Intraspecific and Interspecific Diet Analysis: The observed intraspecific diet differences at both Cape Neddick and Deep Cove may be explained on the basis of prey abundance or availability at each site. Several investigators (Giese *et al.,* 1959; Boolootian, 1964; Nishi, 1975; Robb, 1975) have suggested that the observed intraspecific diet differences for *Mopalia* and other chitons are a reflection of prey availability at the given locale.

Interspecific differences in diet were also evident at both sites. Although *Tonicella rubra, T. marmorea* and *Ischnochiton albus* coexist in the same habitat and feed on similar prey, the quantity of specific prey for each chiton species differed significantly (Table 5). Similar dietary consumption patterns for several coexisting species of *Mopalia* have been reported by Barnawell (1960) and attributed to the habitat of the animal. Likewise, the differences observed in the frequency of occurrence and percent volumes of prey in the diets of the three chitons in this study may be suggestive of separate feeding niches in the local environment similar to those of *Mopalia.*

SUMMARY

In the benthic marine environment of northeastern New England, three species of chitons, *Tonicella rubra, T. marmorea* and *Ischnochiton albus,* are numerically prominent on subtidal substrates. The present study analyzed the dietary components of these coexisting chitons at two widely-separated sites having dissimilar community compositions. The trophic level of these roving scrapers, whose diet includes fourteen faunal and floral phyla, is omnivorous. The major prey phyla are Chrysophyta, Porifera and Protozoa for the *Tonicella* species with the addition of Arthropoda for *I. albus.* The amounts and types of prey consumed showed shifts to herbivorous or carnivorous habits depending on seasonal changes in prey abundance. Interspecific and intraspecific diet analysis revealed that the prey phyla consumed showed quantitative differences among the chiton species. Furthermore, these differences do not appear to be the result of habitat variability.

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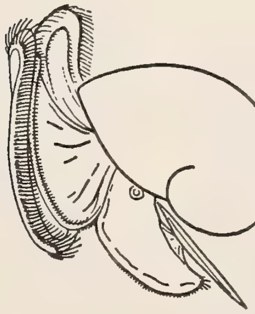

Littorina Trail Following: Sexual Preference, Loss of Polarized Information, and Trail Alterations

BY

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(5 Text figures)

INTRODUCTION

INTRASPECIFIC TRAIL-FOLLOWING has been observed in many species of *Littorina* (HALL, 1974; GILLY, 1978). Trail following reliably occurs in the direction of the trail-laying snail. The functional significance of this behavior has not been established, but it may be important in the locating of mating partners and in cluster formation. The underlying mechanisms of trail following are unclear. One proposed model is that a sparingly water-soluble pheromone may be secreted by organs in the foot (GILLY & SWENSON, 1978). Diffusion from slime trail to water leads to a chemical gradient from which trail polarity may be detected. Another possibility, not necessarily excluded from this hypothesis, is that the trail-laying snail also lays down an asymmetric "footprint" that can be tactically sensed by the following snail to provide trail polarity information.

In the experiments reported here, with *Littorina planaxis*, sexual preference in trail following, the loss of information in aging trails, and several different trail alterations are reported to characterize further the nature of directional information in the littorine trail.

MATERIALS AND METHODS

Due to the difficulty of trail visualization in the field, all trail following studies were performed in the laboratory. Snails were collected daily at Hopkins Marine Station, Pacific Grove, California. The snails were stored in finger bowls and used within two days.

Studies were performed upon 35 cm × 50 cm glass plates under low level indirect lighting at 20°C. Trail following was studied by placing 2-3 trail-laying snails upon the glass plate. As the trail was laid, encountering snails were placed one centimeter from the trails edge, along each side, facing the trail. "Follow," "reverse," or "cross" responses were then recorded as follows: a "follow" represented 3 cm (3-4 body lengths) movement upon the trail in the direction of the trail-laying snail; a "cross" was represented by a 3 cm movement off the trail after the snail had encountered the trail; and a "reverse" corresponded to a 3 cm movement upon the trail away from the trail-laying snail. Snails were also seen to sit or spin on the trail for long periods of time. These trail encounters were relatively rare and were not included in any analysis reported here. Snails were removed from the plate after one trail encounter. After each set of trail encounters the plate was cleaned with 50% ethanol, rinsed with distilled water, and dried.

Snails were sexed under a dissecting microscope after being anesthesized with magnesium chloride isotonic with sea water. Males were identified by their sexual organ found just behind the eye spot on the right tentacle.

Littorina TRAILS

Trail age (time course) studies were carried out on both misted and dry plates. Misted plates were prepared by three squeezes of a spray bottle filled with sea water. In order to keep track of trail age, a stopwatch was started and zero time marked when the trail-laying snail started to move. Each minute following, the underside of the glass plate was marked at the rear edge of the trail-laying snail's shell. With these guide marks, and under the low level lighting, the trails could be seen. Encountering snails were placed alongside the time-marked trail, and trail age was recorded at the point of each encounter.

Lastly, six trail alteration experiments were set up:

(1) & (2) Nytex screen, 100 micron pore size, was wetted with sea water and placed over a misted (1) or dry (2) trail.

(3) A trail was laid upon 100 micron pore size Nytex screen, flipped over, and placed upon a dry glass plate for testing.

(4) Smeared trails were constructed by dabbing an anesthesized snail along a glass plate.

(5) Sea water wetted milipore filters, 0.22 micron pore size, were placed over 5-minute-old trails.
(6) Four anesthesized snails were detentacled distal to the eye spot, and allowed to recover one day. Each of these snails were then used to contruct a detentacled snail-trail on a dry glass plate.

RESULTS

Field work studies of *Littorina planaxis* showed significantly more males than females in clusters, as compared to a 1:1 ratio for unclustered individuals (Figure 1). This finding suggested that a sexual preference for trail following might exist, yet no highly significant preferences are seen here for *L. planaxis* (Figure 2). All four male-female combinations show between 70 and 100 percent directionally correct following, excluding those snails crossing the trail.

The effects of trail aging on polarity recognition can be seen in Figures 3a and 4a. Once again, snails crossing the trail are excluded from the analysis. On both misted (Figure 3a) and dry trails (Figure 4a) the probability of correct following, indicative of polarity recognition, declines from greater than 0.9 at early times to less than 0.7 at later times. The effects of trail age on trail recognition can be seen in Figures 3b and 4b. Difficulty recognizing the trail increases as trail age increases, and no highly significant differences are seen between misted (Figure 3b) and dry trails (Figure 4b).

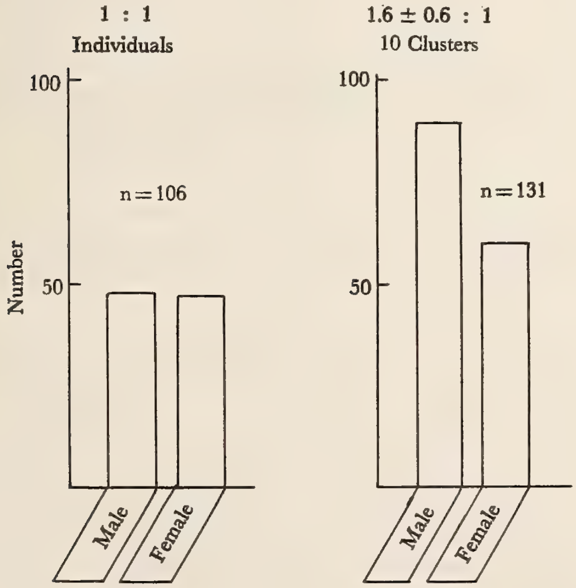

Figure 1

Field study of *Littorina planaxis* male-female distribution, isolated snails vs. clustered snails

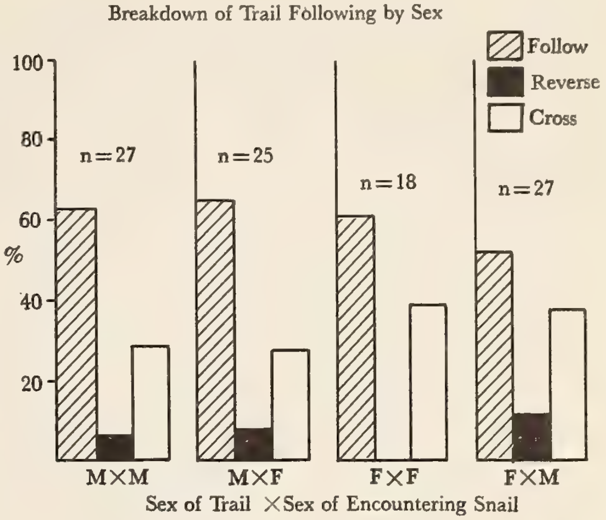

Figure 2

Sexual preference for trail following. Four combinations of sex of trail and sex of encountering snail were observed for preferential following. Percentage following in hash marks is equal to the number following divided by the total number of active encounters. Similarly, percent reversing, in black, and percent crossing, in white, are percentages of the total number (N)

Results of the trail alteration studies are summarized in Figure 5. Nytex screen (100 micron pore size) over misted trails showed essentially normal trail detection and polarity recognition. Nytex over dry trails shows far less trail detection. Trail polarity recognition is fairly ambiguous in this case because of the large number of snails crossing the path. Similarly, trail polarity data are difficult to assess for the flipped trail on Nytex and trail smear experiments. Millipore filters of 0.22 micron pore size show 100 percent crossing indicative of no trail detection whatsoever. Lastly, trails laid by snails that had been detentacled showed normal trail polarity information as exhibited by the large number of snails that did follow these "detentacled snail trails." The observed following (approx. 70%,excluding crosses) is at the normal level for dry trails 10-15 minutes old.

Although the tentacle action of the trail-laying snail does not play a significant part of trail polarity informa-

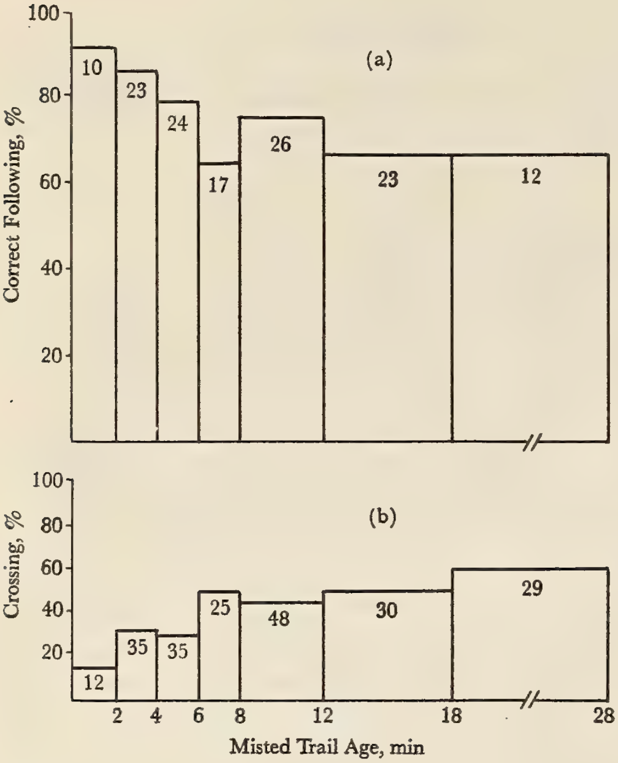

Figure 3

Misted trail time course of decline in ability to detect trail polarization as a function of trail age. Single trails were aged for the times indicated before the trail encounter occurred. a) Percent following, computed excluding snails crossing; *i.e.*, total N equals the number of snails following plus the number reversing. b) Percent crossing. Showing increasing difficulty to recognize the trail as the trail ages. All snails were included in this analysis. N equals the snails crossing plus following plus reversing

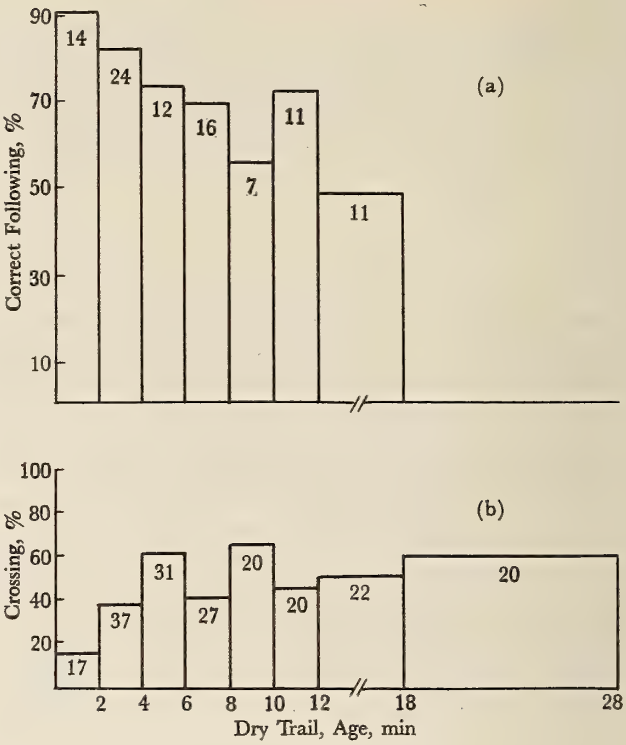

Figure 4

Dry trail time course. a) Percent following, computed excluding snails crossing. b) Percent crossing, showing increasing difficulty to recognize the trail as trail age increases

tion placement in the trail, the tentacle action of trail encountering snails has been shown to be essential for trail recognition and following (Peters, 1964). Tentacle action observed for misted trail encounters is either an alternating left-right touch of the tentacle pad near the tip, or a horizontal swaying motion of both tentacles together. On dry trail encounters, the tentacle action varied. Snails carrying a meniscus of water displayed the two above behaviors for misted trails. Snails without a meniscus of water displayed a very quick, alternating tip touching behavior. A unique tentacle action was seen in the encounters on Nytex screen over misted trails. The snail, upon encountering the trail, would arch its tentacles and alternately touch the tips to the screen over the trail. This behavior suggests the snails were sampling the trail through the Nytex screen.

DISCUSSION

Sexual preference studies suggest that a sexual preference for trail following might exist, yet no highly significant preferences are seen here for *Littorina planaxis* (Figure 2). This result agrees with those of *L. irrorata* (Hall, 1973) which also showed no highly significant sexual preference for trail detection or preferential following. For misted and dry trails, time course studies gave results similar to those shown for *L. littorea* (Gilly & Swensen, 1978). For *L. planaxis* misted and dry trails, the detectable level of the polarity information decays along a time course similar to that found for submerged *L. littorea* trails (Gilly & Swenson,

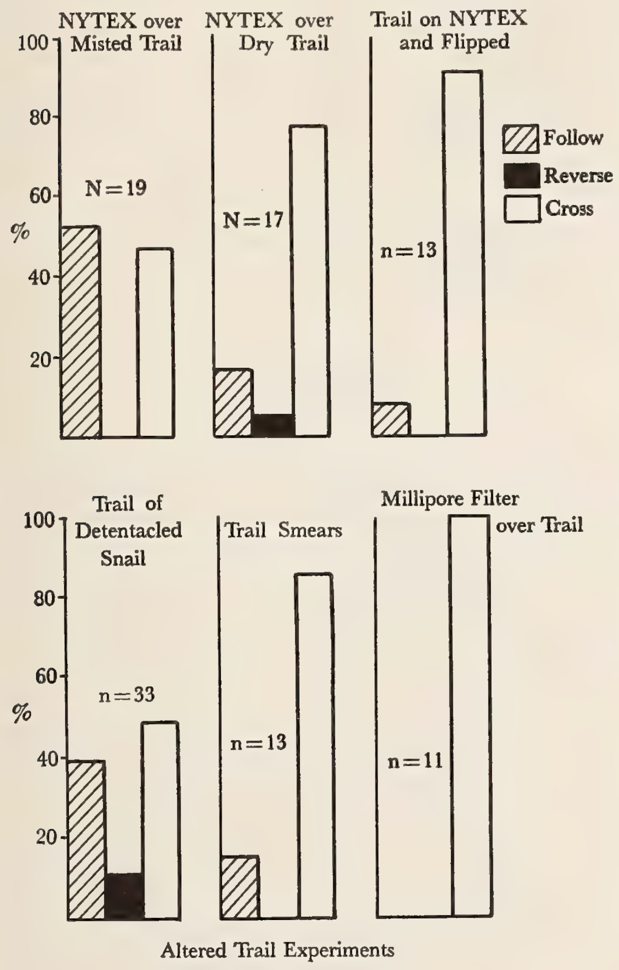

Figure 5

Trail alteration experiments. Percent following (hash marks), percent reversing (black), and percent crossing (white), represent percentages of the total number of encounters observed

1978). Assuming an exponential fit to their data, those authors cite a decay constant of seven minutes.

An early step of trail following is polarity recognition. One possibility is that directionality is detected as a concentration gradient of a sparingly water soluble chemical secreted by the foot of the snail. The similar time courses of information washout in misted and dry trails suggest that if a diffusible chemical establishes a chemical concentration gradient, then this chemical must diffuse into sea water, or a thin layer of sea water and air, at approximately the same rate. Another possibility is that this chemical reacts with some common component of air and water (*e.g.*, oxygen gas) upon release, thus establishing a chemical gradient. Other possibilities for polarity recognition should not be excluded.

The results with 100 micron pore size Nytex screen over misted trails, and the associated tentacle action in detection of those trails, suggests that sampling can occur through the screen. Experiments with *Littorina sitkana* using 35 micron pore size Nytex screen also support this result. Of the 5 snails that travelled along the trail, of 11 tested, all 5 followed correctly (unpublished data).

While chemical detection seems likely in polarity recognition, structural information is difficult to rule out. The Nytex experiments, though, place the constraint on the structural theory that the structural information be on a spatial scale of 1000 square microns (*e.g.*, 35 × 35 microns). This eliminates obvious cues such as pedal waves. Backwards trail following experiments on *Littorina sitkana* are also consistent with this constraint (Gilly & Cahalan, 1978).

Several treatments were found to interfere with detection and proper following. For the flipped trail on Nytex and the trail smear experiments, trail recognition is greatly reduced and more data are required to determine if preferential following occurs. The 0.22 micron pore size millipore filter placed over a trail completely prevents all trail recognition. Lastly, the results of detentacled trail-laying snails suggest that the cephalic tentacles distal to the eye spot do not play a significant role in establishing trail polarity.

The cephalic tentacles, shown to be essential for trail recognition (Peters, 1964), must carry the receptors for detecting trail polarity. These receptors are under a size constant in a structural theory of 1000 square microns. Electron micrographs by Levinson at Hopkins Marine Station on *Littorina planaxis* tentacle tips show bundles of villi approximately 3 microns in length. These villi bundles fall within the size constraint of a structural theory, and may play a role in the structural or chemical detection of trail polarity.

SUMMARY

1) Preferential trail following is observed for all sexual combinations of *Littorina planaxis* snails with trail, and no highly significant sexual preferences for trail following are observed.

2) Preferential trail following is observed for *Littorina planaxis* on both misted and dry trails. Trail polarity information decreases as the trail age increases. The detectable level of polarity information decays along a time course similar to that found for submerged *L. littorea* trails (Gilly & Swenson, 1978).

3) Trail polarity information can be detected through 100 micron pore size Nytex screen, but cannot be detected through 0.22 micron pore size millipore filters.

4) The cephalic tentacles of *Littorina planaxis* distal to the eye spot play no significant role in placing polarity information onto the trail.

ACKNOWLEDGMENTS

I wish to thank Professor William F. Gilly of Hopkins Marine Station for his advice and insights on behavioral analysis.

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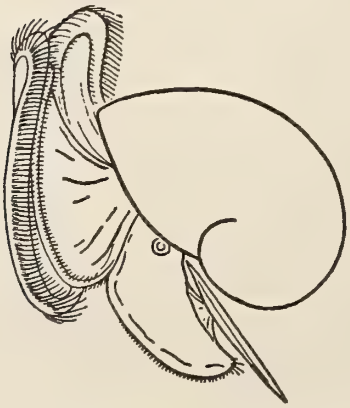

Range Extensions of Opisthobranchs in the Northeastern Pacific

BY

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(2 Text figures)

INTRODUCTION

The opisthobranch fauna varies little in species composition from northern California to Alaska. Most prominent are differences in abundance: some species being quite common in the northern end of their range and rare in the southern end, or vice versa. Towards the North, there are larger seasonal population fluctuations and decreases in species diversity. One cause of this apparent reduction in northern diversity is the occasional appearance of 'strays' from the rich opisthobranch fauna south of Point Conception into northern California. In addition, the opisthobranchs north of California have received comparatively little attention. One exception is the area around the marine station at Friday Harbor, San Juan Island, Washington. For a long time most reports of northeastern Pacific range limits for opisthobranchs came from just three areas: collections at Friday Harbor; reports by O'Donoghue (1921, 1922, 1924, 1927) who collected primarily around Nanaimo, Vancouver Island, British Columbia; and studies by Bergh (1879, 1880) of specimens from Alaska. More recently, ranges have been extended northward into British Columbia or Alaska by Robilliard (1971a, 1971b, 1974a, 1974b), Lambert (1976), Robilliard & Barr (1978) and Millen (1980). This paper reports extensions of known ranges for 16 species northward into British Columbia and Alaska, for 7 species within British Columbia and for 2 species southward from Alaska to British Columbia.

Species are listed in alphabetical order. Locations in southern British Columbia are on the map (Fig. 1) and all new locations are listed in Table 1. The new range extension is presented with an asterisk to mark the changed location. The old location follows in parenthesis with its reference.

Figure 1

A map of southern British Columbia showing the location of some of the collecting sites

Table 1

New distribution sites.

Location	Latitude N	Longitude W
Lisianski Inlet, Alaska	58°09′	136°27′
Hogan Is., Alaska	57°43′	136°15′
Louscoone Inlet, Moresby Is., B.C.	52°08′	131°17′
Port Hardy, Vancouver Is., B.C.	50°43′	127°29′
Stubbs Is. off Vancouver Is., B.C.	50°36′	126°49′
Nuchatlitz Is., Esperanza Inlet, Vancouver Is., B.C.	49°49′	126°58′
Earls Cove, Agamemnon Channel, B.C.	49°45′	124°01′
Pender Hbr., B.C.	49°38′	124°03′
Porlier Pass, Galiano Is., B.C.	49°01′	123°36′
White Rock, B.C.	49°01′	122°48′
Bamfield, Vancouver Is., B.C.	48°50′	125°08′
Saturna Is., B.C.	48°46′	123°10′
Botanical Beach, Pt. Renfrew, Vancouver Is., B.C.	48°33′	124°25′
Victoria, Vancouver Is., B.C.	48°26′	123°18′

RANGE EXTENSIONS

Adalaria pacifica Bergh, 1880 — Unalaska, Alaska to *Victoria, Vancouver Is., B.C. (Unalaska; Bergh, 1880). Note: This species may be synonymous with *A. proxima.*

Aldisa cooperi Robilliard & Baba, 1972—*Hogan Is., Alaska to Trinidad Head, Calif.; Japan. (Pearse Is.; LAMBERT, 1976).

Ancula pacifica MacFarland, 1905—*Bamfield, Vancouver Is., B.C. to San Diego, Calif. (San Juan Is.; ROBILLIARD, 1971a).

Cadlina modesta MacFarland, 1966—*Nuchatlitz Is., Esperanza Inlet, Vancouver Is., B.C. to La Jolla, Calif. (Muchatlat Inlet, Vancouver Is.; ROBILLIARD, 1971a).

Cargoa vancouverensis (O'Donoghue, 1921)—Rosespit, Graham Is., B.C. to *Saturna Is., B.C. (Rosespit; O'DONOGHUE, 1921).

Cumanotus beaumonti (Eliot, 1906)—*Saturna Is., B.C. to San Diego, Calif.; Sweden; Britain. (San Juan Is.; HURST, 1967).

Cuthona albocrusta (MacFarland, 1966)—*White Rock, B.C. to Palos Verdes, Calif. (San Juan Is.; HURST, 1967).

Cuthona concinna (Alder & Hancock, 1843)—*Lisianski Inlet, Alaska to *White Rock, B.C.; Nova Scotia to Maine; Norway; Sweden; Britain. (Brandon Is.; O'DONOGHUE, 1922).

Cuthona divae (Marcus, 1961)—*Botanical Beach, Port Renfrew, Vancouver Is., B.C. to Point Loma, Calif. (San Juan Is.; ROBILLIARD, 1971a).

Dendronotus subramosus MacFarland, 1966—*Bamfield, Vancouver Is., B.C. to Punta Cabras, Baja Calif., Mexico. (San Juan Is.; ROBILLIARD, 1970).

Doridella steinbergae (Lance, 1962)—*Bamfield, Vancouver Is., B.C. to Los Coronados Is., Baja Calif., Mexico. (Vancouver Is., no location; LANCE, 1962).

Doto amyra Marcus, 1961—*Port Hardy, Vancouver Is., B.C. to Ensenada, Baja Calif., Mexico. (Dillon Beach; MARCUS, 1961).

Doto columbiana O'Donoghue, 1921—*Louscoone Inlet, Moresby Is., B.C. to Duxbury Reef, Calif.; Guaymas, Mexico. (Pearse Is.; LAMBERT, 1976).

Doto kya Marcus, 1961—*Bamfield, Vancouver Is., B.C. to Punta Cabras, Mexico. (Palmer's Point; JAECKLE, 1981).

Eubranchus olivaceous (O'Donoghue, 1922)—*Nuchatlitz Is., Esperanza Inlet, Vancouver Is., B.C. to Baia de Los Angeles, Baja Calif., Mexico; northern New England. (Jesse Is. near Nanaimo; O'DONOGHUE, 1922).

Eubranchus rustyus (Marcus, 1961)—*Stubbs Is., near Telegraph Cove, Vancouver Is., B.C. to Punta Abreojos, Baja Calif., Mexico. (Bamfield, Vancouver Is.; ROBILLIARD, 1971a).

Eubranchus sanjuanensis Roller, 1971—*Porlier Pass, Galiano Is., B.C. to San Juan Is., Wash. (San Juan Is.; ROLLER, 1972).

Flabellina salmonacea (Couthouy, 1838)—Arctic Alaska to *Pender Harbor, B.C.; Greenland to Cape Cod, Maine; Iceland; Norway. (Arctic Alaska; KNIPOWITSCH, 1902).

Flabellina trilineata (O'Donoghue, 1921)—*Lisianski Inlet, Alaska to Los Coronados Is., Baja Calif., Mexico. (Procher Is.; LAMBERT, 1976).

Flabellina verrucosa (Sars, 1829)—*Hogan Is., Alaska to San Juan Is., Wash.; Japan; north boreo-Atlantic. (San Juan Is.; HURST, 1967). Note: This is the variety *rufibranchialis*. *Coryphella longicaudata* O'Donoghue, 1922 is probably synonymous, having the same reproductive system.

Hallaxa chani Gosliner & Williams, 1975—*Earl's Cove, Agamemnon Channel, B.C. to La Jolla, Calif. (Cape Argo; GODDARD, 1981).

Hermaea vancouverensis O'Donoghue, 1924—*Port Hardy, Vancouver Is., B.C. to Bodega Harbor, Calif. (Newcastle Is., near Nanaimo; O'DONOGHUE, 1924).

Onchidoris muricata (Müller, 1776)—*Port Hardy, Vancouver Is., B.C. to Lion Rock, Calif. (San Juan Is.; HURST, 1967).

Phyllaplysia taylori Dall, 1900—*Nuchatlitz Is., Esperanza Inlet, Vancouver Is., B.C. to San Diego, Calif. (Nanaimo, Vancouver Is.; DALL, 1900).

Triopha maculata MacFarland, 1905—*Bamfield, Vancouver Is., B.C. to Cabo San Quintin, Baja Calif., Mexico. (Palmer's Point; Jaeckel, 1981). Note: This is the yellow variety considered *T. occidentalis* (Fewkes, 1889) by McDONALD & NYBAKKEN, 1981.

DISCUSSION

I compared numbers of opisthobranch species found in north California, British Columbia and Alaska, taking into account the range extensions reported here. These three areas are all within the cold-temperate North-Pacific Province bounded at the south by Point Conception, California (VERMEIJ, 1978). The area from Point Conception to Puget Sound is considered a transitional zone. The Alaskan fauna has two components found, respectively, in a cold-temperate zone and an Arctic zone (Chukchi and Beaufort Seas).

Figure 2 presents the species composition of these three areas. Introduced species (from San Francisco Bay) have been omitted because they are not representative of the area. Undescribed species in BEHRENS (1980), McDONALD & NYBAKKEN (1981) and in my possession have been included. Relatively few opisthobranch species have been reported from more northerly regions. It is difficult to determine whether this is due to increased seasonality of organisms, fewer collections, actual decline in species numbers or a combination of these factors. The bullomorphs and dendronotaceans maintain their numbers best towards the north. The aplysiomorphs, pleurobranchomorphs and sacoglossans drop out altogether. This may well be a col-

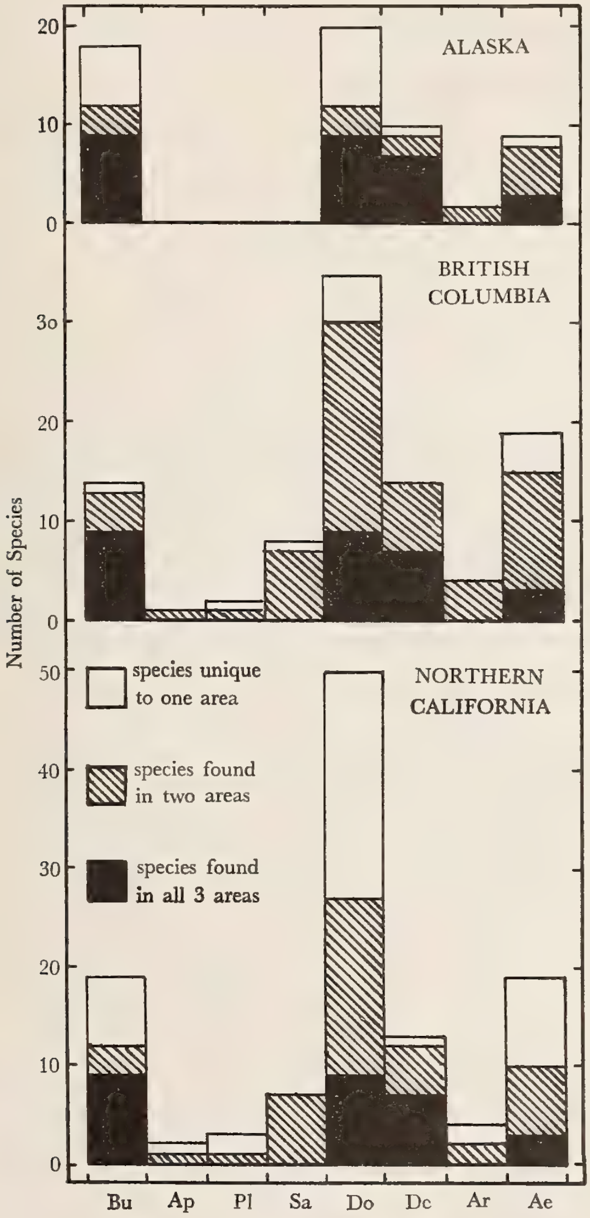

Figure 2

A graph comparing the number of species in the orders and suborders of opisthobranchs in northern California, British Columbia and Alaska. Order Bullomorpha (Bu); Order Aplysiomorpha (Ap); Order Pleurobranchomorpha (Pl); Order Sacoglossa (Sa); Order Nudibranchia, suborder Doridacea (Do), suborder Dendronotacea (De), suborder Arminacea (Ar), suborder Aeolidacea (Ae).

lection artifact because there are few species, and the largest group, the sacoglossans, are both small and seasonal. The largest number of unique animals are found in northern California. Many of these are spill-overs from south of Point Conception. Others are rare animals found thanks to intense collecting. Unique species found in British Columbia will probably be found to have Alaskan affinities in the future as more northern collections are made. The unique species in Alaska have Arctic affinities. Many of the Alaskan bullomorphs are poorly described and may represent synonymies. The unique dorid component is primarily found in the family Onchidorididae. The graph in Figure 2 represents one instant in a dynamic process. As species are found and described or synonymised, the numbers will change. I suggest that another comparison 10 years hence would give more species overall (especially in Alaska) and a larger number of cosmopolitan species in British Columbia.

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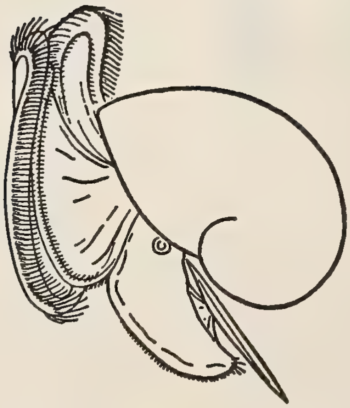

Distribution of Gastropod Genera over a Vertical Depth Gradient at Cape Maclear, Lake Malawi

BY

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(2 Text figures)

INTRODUCTION

LAKE MALAWI in the eastern rift valley of Africa holds a unique resource in its abundant and highly diverse fauna. For example, over 250 species of fishes have been described from this lake, most of them belonging to the family Cichlidae (*e.g.*, MARSH *et al.*, 1981). The gastropods, most of which are endemic to Lake Malawi, also present an ecologically and evolutionarily interesting array. The molluscs are abundant, relatively unknown, and the primary food source of an important subset of cichlids (JACKSON *et al.*, 1963, FRYER & ILES, 1972) including: *Cyrtocara ('Haplochromis') anaphyrmis, C. mola, C. placodon, C. sphaerodon,* and *Trematocranus microstoma* (McKaye and Louda, unpublished data). Information on snail composition, abundance, distribution, feeding, and life history cycles is, consequently, important both to an understanding of gastropod community dynamics in the African lakes and to the management of the sand bottom fish community in Lake Malawi.

This paper reports upon the distribution and relative abundance of the sand-dwelling gastropod genera along a vertical depth gradient in southern Lake Malawi. The data were collected at the west end of a 4km section of the sand beach at Cape Maclear (34°50′E; 14°5′S), 12km west of Monkey Bay. The two main questions underlying this study were: (1) what is the structure of the snail assemblage, a critical resource for the mollusc-feeding fishes, and (2) how does that structure vary along the water depth gradient? We quantified: vertical distribution, density, and population size structure of the gastropod genera present between 0-26m depths. These data are among the first direct observations of gastropod population parameters and community structure in the deep lakes of Africa.

THE GASTROPODS

Four genera of streptoneuran (prosobranch) gastropods and one genus of basommatophoran gastropod are part of the sand community. The basommatophoran genus is *Bulinus* Müller (Planorbidae); *Bulinus* is represented by one species in the open sand areas, *B. nyassanus* (Smith), and by another one, *B. succinoides* (Smith), on more heterogeneous substrates such as among aquatic macrophytes (WRIGHT, KLEIN & ECCLES, 1967; Louda & Gray, personal observation). The prosobranch genera include, in order of decreasing adult size: *Lanistes* Montfort (Ampullariidae), *Bellamya* Jousseaume (Viviparidae), *Melanoides* Olivier (Thiaridae), and *Gabbiella* Mandahl-Barth (Bithyniidae).

The "apple snails" of the Family Ampullariidae (Pilidae) are represented in our samples by three nominal species of the genus *Lanistes.* The largest snail at Cape Maclear is *L. nyassanus* Dohrn, which reaches 55mm total length and 42mm aperture length. *Lanistes solidus* Smith, another heavy-shelled species endemic to Lake Malawi, is smaller and with a higher spire (BROWN, 1980). Both of these species are reported dredged down to 30m (MANDAHL-BARTH, 1972). We have observed living specimens of *L. nyassanus* to 39m and of *L. solidus* down to 20m (LOUDA, McKAYE, KOCHER & STACKHOUSE, 1983). The third species, *L. ellipticus* Martens, is rare. *Lanistes ellipticus* is similar to *L. solidus;* however, *L. ellipticus* has an open umbilicus and straight columella, the axis around which the shell spirals, and a much lighter-weight shell. It is reported to be abundant in swamps along the shore of Lake Malawi but not to be found in the main lake (BROWN, 1980: 54). The two latter species may not, in fact, be distinct since *L. solidus* may be a heavier, lacustrine (lake) form of *L. ellipticus* (D. S. Brown, personal communication).

The genus *Bellamya* belongs to the family Viviparidae. Female snails of this family carry the developing young in the lower part of the oviduct. In *Bellamya* the young are released at the stage of about three whorls (BROWN, 1980). Three forms of *Bellamya* occur at Cape Maclear; *B. jeffreysi* (Frauenfeld) Mandahl-Barth, a medium-sized

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(40 × 30 mm) species whose shell is heavier than that of any other member of the genus (Brown, 1980), is the predominant form on our transect. *Bellamya robertsoni* (Frauenfeld) Mandahl-Barth and *B. capillata* (Frauenfeld) Germain also occur but are much less common. The second most common species, *B. robertsoni,* is a less heavy form that consistently has a higher spire but which may or may not be distinct from *B. jeffreysi* (Brown, 1980; Gray, unpublished data). Finally, *B. capillata* were found infrequently in our samples; this species occurs more typically in marshy habitats along the lake shore rather than over open sand in the lake. *Bellamya capillata,* which occurs in a variety of local forms, is hardly distinguishable from *B. unicolor,* a widespread northern species (Brown, 1980), except in having fewer and larger embryos (Mandahl-Barth, 1973). Crowley *et al.* (1964) consider all of the forms synonymous with *B. unicolor.*

The majority of the species in our samples belong to the genus *Melanoides* in the family Thiaridae (Melaniidae). Ten nominal species occur and nine of these are endemic (Smith, 1877; Crowley *et al.,* 1964; Mandahl-Barth, 1968a, 1972; Brown, 1980, and personal communication). These species are: *Melanoides tuberculata* (Müller), the cosmopolitan species; *M. pergracilis* (Smith), *M. nodicincta* (Dohrn), *M. nyassana* (Smith), *M. magnifica* (Bourguignat), *M. truncatelliformis* (Bourguignat), *M. polymorpha* (Smith); *M. pupiformis* (Smith); *M. turritispira* (Smith); and *M. simonsi* Smith. This interesting group is composed of small to medium-sized snails (10-47 mm total length for adults). They also represent the predominant portion of the molluscs in the stomach contents of the snail-feeding fishes examined at Cape Maclear (McKaye & Louda, unpublished data). Little, in particular, is known about the occurrence and biology of the majority of these Malawian species (Brown, 1980, and personal communication).

The last family, Bithyniidae, is represented by one species in Lake Malawi, *Gabbiella stanleyi* (Smith). This endemic species is small (5.3 × 3.3 mm) and distinctive. It is commonest in the littoral zone down to about 12 m (Brown, 1980) and is active at night on the surface of *Vallisneria* blades (Louda, personal observation). It also has been dredged from 95 m (Mandahl-Barth, 1968b). This small species also appears to be a major component of the fish diets (McKaye & Louda, unpublished data); this is contrary to the suggestion of Wright, Klein & Eccles (1967) who thought the heavier shell of *G. stanleyi,* compared to that of *Bulinus succinoides,* was a successful predator defense that allowed open grazing on the blades of *Vallisneria.*

MATERIALS AND METHODS

Samples were collected by aid of SCUBA during February-March 1981 to determine the density, distribution, and population size structure for the gastropod genera over the depth gradient at Cape Maclear. We recorded the number and size of all live gastropods found in 50 × 50 cm × 5 cm deep samples of substrate (N = 93), collected into individual sealable plastic bags by SCUBA divers. Pairs of samples were collected 25 m apart at 12 depths, from 0.25 to 25.5 m at 3 m increments (N = 8 per depth for 0.25-10.5 m and N = 4 per depth for 13.5-25.5 m). A major discontinuity in microhabitat occurs in 3.0-4.5 m depths where patches of aquatic vascular macrophytes occur (*Potamogeton* sp. and *Vallisneria* sp.). Consequently, separate samples were collected for comparison of density and snail size from two beds of the macrophytes at 3.0-3.75 m and 4.5 m in April 1981. Samples within the weed beds were placed in patches of high stem density and were compared to samples collected along the transect over open sand substrate at the same depths.

RESULTS

Depth Distribution: The center of distribution for all of the genera occurring at Cape Maclear was in the shallow portion of the depth gradient (Figure 1). The median depth for all gastropods collected (N = 514) was 3.0 m. These data particularly reflect the distribution of *Melanoides,* the most common gastropod genus in our collection (N = 458); 51.1% of all *Melanoides* found were in samples from the 3.0 m depth. The three other common genera appear to be displaced along the depth contour, one shallower and two deeper. The medians of these distributions from our samples are as follows: *Lanistes* 1.5-3.0 m, *Bulinus* 3.0-4.5 m, and *Bellamya* 4.5-6.0 m.

Density: Densities of all gastropods varied from 0.5 to 30.8 individuals per ¼ m^2 (2-123 snails/m^2) over the entire depth gradient sampled at Cape Maclear (Table 1). The highest concentration (123/m^2) was found in samples from 3.0 m depth. *Melanoides* species represent the predominant snails in our samples (89%) and the exceptionally high density at this depth reflected the density of *Melanoides* there (117/m^2). However, when this factor is partitioned out, the density of the other gastropod genera in our area was still highest from 3.0-4.5 m (Table 1). Among the other more common genera, *Lanistes* densities were highest at 3.0 m

Table 1

Density of gastropod genera over the depth contour at Cape Maclear, Lake Malawi (#/50 × 50cm).

Depth (m)	N	All gastropods $\bar{X}$	All gastropods SD	*Melanoides* $\bar{X}$	*Melanoides* SD	Non-*Melanoides* $\bar{X}$	Non-*Melanoides* SD	*Lanistes* $\bar{X}$	*Lanistes* SD	*Bulinus* $\bar{X}$	*Bulinus* SD	*Bellamya* $\bar{X}$	*Bellamya* SD
0.25	8	0.6	0.71	0.0	—	0.6	0.74	0.6	0.74	0.0	—	0.0	—
1.5	8	13.2	10.85	12.3	11.73	0.9	0.64	0.8	0.71	0.1	0.34	0.0	—
3.0	8	30.8	6.93	29.2	7.75	1.5	0.93	1.0	0.76	0.2	0.46	0.2	0.71
4.5	8	9.2	5.18	8.0	5.23	1.5	1.31	0.9	0.99	0.4	0.52	0.3	0.71
6.0	8	2.3	1.64	1.5	1.70	0.9	0.64	0.6	0.74	0.0	—	0.2	0.45
7.5	8	2.0	1.27	1.9	1.24	0.1	0.34	0.0	—	0.1	0.34	0.0	—
9.0	8	1.5	1.10	1.2	1.05	0.4	0.52	0.2	0.45	0.0	—	0.1	0.34
10.5	8	2.4	0.99	2.1	0.99	0.4	0.52	0.2	0.45	0.1	0.34	0.0	—
13.5	4	2.2	1.30	1.8	1.50	0.5	0.58	0.0	—	0.2	0.50	0.2	0.50
16.5	5	2.0	0.63	1.6	0.54	0.4	0.55	0.0	—	0.2	0.45	0.2	0.40
19.5	4	2.7	1.30	2.5	1.30	0.2	0.50	0.2	0.50	0.0	—	0.0	—
22.5	4	1.4	1.50	1.2	1.50	0.2	0.50	0.2	0.50	0.0	—	0.0	—
25.5	4	0.5	0.50	0.5	0.58	0.0	—	0.0	—	0.0	—	0.0	—

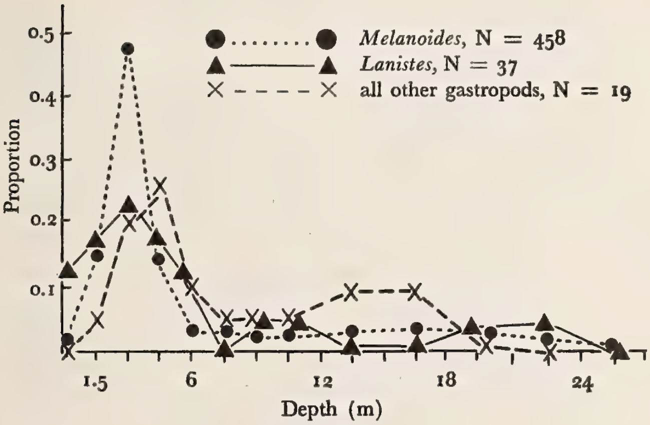

Figure 1

Relative distribution of each of the two main genera and of all other gastropods over the water depth gradient, Research Station site, Cape Maclear, February-March 1981

(4.0 snails/m²) while those of *Bulinus* (1.6 snails/m²) and *Bellamya* (0.9 snails/m²) appeared highest at 4.5m or relatively evenly spaced along the depth gradient.

Size with Depth: The large number of *Melanoides* collected (N = 458) allows us to examine if individual size varies with depth. Interestingly, there was a significant increase in mean snail size (total length) at the 6.0m depth along our transect (Figure 2). *Melanoides* size also increased in the protected, vascular macrophyte microhabitats. Average size for *Melanoides* was significantly greater in both of the weed beds than it was on the adjacent open sand at each of the two depths where weed beds occurred (Mann-Whitney U, $p < 0.05$; Table 2). Furthermore, the *Melanoides* in among stems of *Vallisneria* at 4.5m appeared to be larger than those among the stems of *Potamogeton* at 3.0-3.75m (Table 2).

DISCUSSION

At Cape Maclear the gastropod genera were concentrated in the shallow portions of the 0.25-25.5m depth gradient

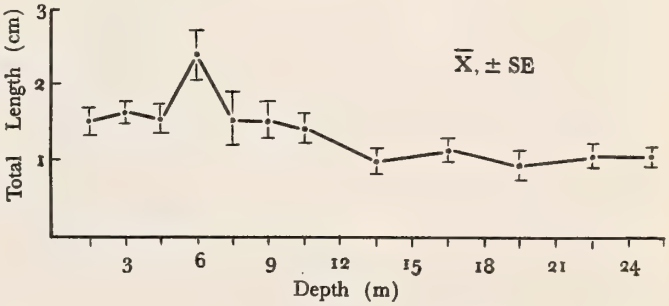

Figure 2

Size distribution of *Melanoides* individuals (Total Length, cm; N = 458) over the water depth gradient, in the sand microhabitat at the Research Station site, Cape Maclear, February-March 1981

Table 2.

Density and size of *Melanoides* in different microhabitats at 3.0-4.5 m on the depth contour.

	Density (#/50 × 50 cm)			Size (Total length, mm)		
Location	N	$\bar{X}$	SD	N	$\bar{X}$	SD
Open Sand						
3.0 m	8	29.2	7.76	8	16.3	1.90
4.5 m	8	8.0	5.23	7	15.7	2.46
Together	16	18.6	12.70	15	16.0	2.12
Weed beds						
Potamogeton, 3.4 m	4	11.5	11.73	4	21.0	4.48
Vallisneria, 4.5 m	4	13.5	5.07	4	29.6	4.96
Together	8	12.5	8.43	8	25.3	5.03
Mann-Whitney U test of Comparisons: p[1]						
For each microhabitat, by depth						
Open sand: 3.0 vs. 4.5 M		< 0.001			n.s.	
Potamogeton vs. *Vallisneria*		n.s.			0.058	
Comparison of microhabitats						
3.2 m: Sand vs. *Potamogeton*		0.072			0.042	
4.5 m: Sand vs. *Vallisneria*		0.048			< 0.006	

[1] Two-tailed, n.s. = $p > 0.10$

(Figure 1). This general result is consistent with information available on prosobranchs in benthic communities of other African lakes, such as Lake Chad (Lévêque, 1967, 1972, 1973; Dupont & Lévêque, 1969; Brown, 1974, 1980), Lake George (see Brown, 1980) and Lake Léré, about 350 km south of Lake Chad (Dejoux, Lauzanne & Lévêque, 1971). However, our study appears to be the first aimed specifically toward examining vertical distribution patterns of benthic snails in the deep African lakes; consequently, direct data for comparison are not available at present. Similar patterns have been found, though, for distribution of marine gastropods (Vermeij, 1972; Bertness, 1977, Louda, 1979). Furthermore, and quite interestingly, the data suggest there may be a replacement pattern occurring among genera along the depth contour in the shallow regions. The medians of distribution for the genera were ordered: *Lanistes, Melanoides, Bulinus,* and *Bellamya* between 1.5 and 6.0 m depth, suggesting some resource partitioning may occur among overlapping gastropod genera.

Two striking results were apparent in relation to gastropod density. As expected, density and dispersion varied along the gradient. Densities were highest at 3.0 m for gastropods overall. However, the extent of variation exhibited among samples within any one depth was striking. This was especially true in shallow portions of the gradient. Standard deviations were equal to the means (Table 1), suggesting that snail densities vary greatly between localities at the same depth (0.5-30.8 per 0.25/m^2).

Significant local variation in gastropod density is consistent with the results of Lévêque and his colleagues in Lake Chad (references above). However, estimates of maximum density and relative abundance for the two genera *(Melanoides, Bellamya)* which also occur in both Lake Chad and Lake Malawi, are approximately an order of magnitude higher in Lake Chad (Daget & Lévêque, 1969). Interestingly, each of these genera in Lake Chad is represented by only one species *(M. tuberculata* and *B. unicolor)* while in Lake Malawi at Cape Maclear each of these genera is represented by multiple forms. Interspecific competition may decrease the carrying capacity of sand bottom for *Melanoides;* alternately, however, other factors which differ between the benthic systems of the two lakes, such as fish species and density, may determine the lower densities of *Melanoides* in Lake Malawi.

The second striking result in relation to snail density was the variation observed at 3.0 and 4.5 m depths between snails occurring in weedy versus in open sand areas. The density of *Melanoides* was significantly greater at 3.0 m than at 4.5 m over open sand (Table 2). However, overall in open sand versus in a vascular macrophyte (weed) bed at 3.0-4.5 m no significant difference in density occurred. This result leads to two hypotheses. First, we suggest that the presence of sparse *Potamogeton* stands at 3.4 m led to decreased density of *Melanoides* at that depth compared to open sand by concentrating fish predators of snails in that area (Table 2). Second, increased *Melanoides* density was associated with the presence of the denser *Vallisneria* bed at 4.5 m, leading us to suggest that high density stands of this species provide a refuge for *Melanoides* from molluscivorous fishes (Table 2). The contributions of macrophyte species and density and of water depth to these patterns, however, cannot be separated definitively in our observations. Consequently, these hypotheses are being examined further.

The strongest pattern associated with the contrast between samples from the macrophyte beds and those from the adjacent open sand areas, however, was in average size of snails found. Mean total length for *Melanoides* observed was significantly greater in amongst the weeds, both among *Potamogeton* stems and among *Vallisneria* rosettes, than at similar depths over the open sand (Table 2). Since all samples were collected over the same period of time during the day (1000-1500 hrs), these apparent patterns are not explained by activity patterns related to diurnal cycles as some of other species *(Lanistes)* may be (Gray, 1980, Louda & McKaye, 1982). The two main mechanisms to explain these patterns are: (1) differential food availability leading to higher growth among the weeds, and (2) differential predation pressure leading to higher survivorship amongst the weeds. Our observations to date suggest that these are not mutually exclusive hypotheses and that they merit further research.

SUMMARY

Five genera of gastropod molluscs occur over the sand bottom at Cape Maclear, Lake Malawi *(Lanistes, Bellamya, Melanoides, Gabbiella, Bulinus)*. These snails are the primary food for at least six species of the sand-dwelling cichlids. Knowledge of the population dynamics of these gastropods should contribute to the understanding and management of fisheries in southern Lake Malawi. The distribution, densities, and relative abundances of the predominant gastropod genera were determined. Additionally, the size distributions in relation to depth and cover of vascular macrophytes were quantified for the most common genus, *Melanoides*. The results show that: (1) gastropods occurred at all depths sampled; (2) gastropod densities (to 123/m^2) were highest in shallow (1.5-4.5 m) water depths; (3) gastropod distributions were patchy; and (4) density of *Melanoides* was highest at 3.0 m but size of *Melanoides* was highest: at 6.0 m in open sand and at 3.0-4.5 m in vascular macrophyte microhabitats. Either differential availability of food or differential predation by fishes among alternative microhabitats, or both, could account for these patterns.

ACKNOWLEDGMENTS

We thank: D. S. Brown for taxonomic advice and stimulating discusssions and E. S. Chamveka, S. Bvalani and J. Smart for help in sorting samples. The Malawi Government gave permission to study the aquatic ecosystem at Cape Maclear and we appreciate it greatly. Support (for KRM) was provided by National Science Foundation grant DEB 79-12338.

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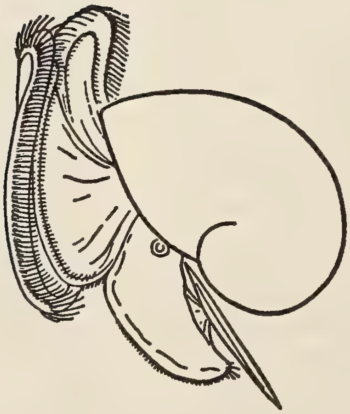

A New Species of Copepod Associated with *Pleurobranchaea californica*

(Gastropoda : Opisthobranchia)

with Discussion on *Anthessius* Associated with Notaspidean Sea Slugs

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(3 Text figures)

INTRODUCTION

Members of the copepod genus *Anthessius* (Poecilostomatoida : Myicolidae) are largely associated with marine pelecypods and gastropods. Currently 34 nominal species are known in this genus with five of them occurring on the west coast of North America. Four of these North American species are: *A. navanacis* (Wilson) found on *Navanax inermis* (Cooper) (Gastropoda : Aglajidae), *A. nortoni* Illg on *Diodora aspera* (Rathke) (Gastropoda : Fissurellidae) and *Megathura crenulata* (Sowerby) (Gastropoda : Fissurellidae), and *A. fitchi* Illg in *Chaceia ovoidea* (Gould) (Pelecypoda : Pholadidae) and *Zirfaea pilsbryi* Lowe (Pelecypoda : Pholadidae) (Illg, 1960; Humes, 1981). The fifth species, "*Anthessius* sp. A.," is so far known only from a single male specimen discovered accidentally in the gill cavity of a surfperch caught in the same trawl in which fifteen species of gastropods and three species of pelecypods were also found (Dojiri, 1977). The trawl was made off Huntington Beach in southern California.

Recently, Dr. F. G. Hochberg of Santa Barbara Museum of Natural History sent to me a collection of copepods containing five ovigerous females and one mature male of a species of copepod that were removed from a notaspidean sea slug, *Pleurobranchaea californica* MacFarland, that was trawled off the coast of Santa Barbara, California. A close examination of these copepods revealed that they are identifiable with Dojiri's (1977) *Anthessius* sp. With the discovery of ovigerous females and its natural host, a full description of this incompletely known species of *Anthessius* is now in order. In the course of studying this new species, certain characters in common were discovered in five species of *Anthessius* that are normally associated with sea slugs of the Order Notaspidea. Therefore, a discussion on this matter will be given following the description of the new species.

I wish to thank Dr. F. G. Hochberg for placing the copepod associates of *Pleurobranchaea californica* at my disposal. The holotype (USNM 189057), allotype (USNM 189058), and two paratypes (USNM 189059) have been deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Anthessius ***obtusispina*** Ho, spec. nov.

(Figures 1 through 3)

Female: The body (Figure 1A) measures 3.79 (3.63-3.90) mm long and 1.64 (1.57-1.71) mm wide. The fifth pedigerous somite (Figure 1B) is about as wide as long. The caudal ramus (Fig. 1C) is 3 times as long as wide. The egg sac (Figure 1A) is large, carrying numerous small eggs of about 60 μm in diameter.

The first antenna (Figure 1D) is 7-segmented; the armature on these segments is 4, 15 (7 + 8), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. The second antenna (Figure 1E) is 4-segmented, with the 2 distal segments indistinctly separated; the formula for the armature is 1, 1, 3, and 4 + III. The labrum (Figure 1F) is broad, with a large central incision on the posterior margin; each spherical posterolateral plate carries a blunt inner process. The mandible (Figure 1G) is typical of *Anthessius*, but a short dentate lamella is added between the apical lash and the long setiform element (Figure 1H). The first maxilla (Figure 1I) is bilobed distally; the inner lobe bears only 1 short, stubby element. The second maxilla (Figure 2A) has 11 or 12 teeth on its terminal process. The maxilliped (Figure 2B) is indistinctly 3-segmented and greatly reduced; the pointed distal segment bears a small subterminal seta.

Legs 1-4 (Figures 2C-H) are biramous, with each ramus being 3-segmented. The spine (Roman numerals) and setal

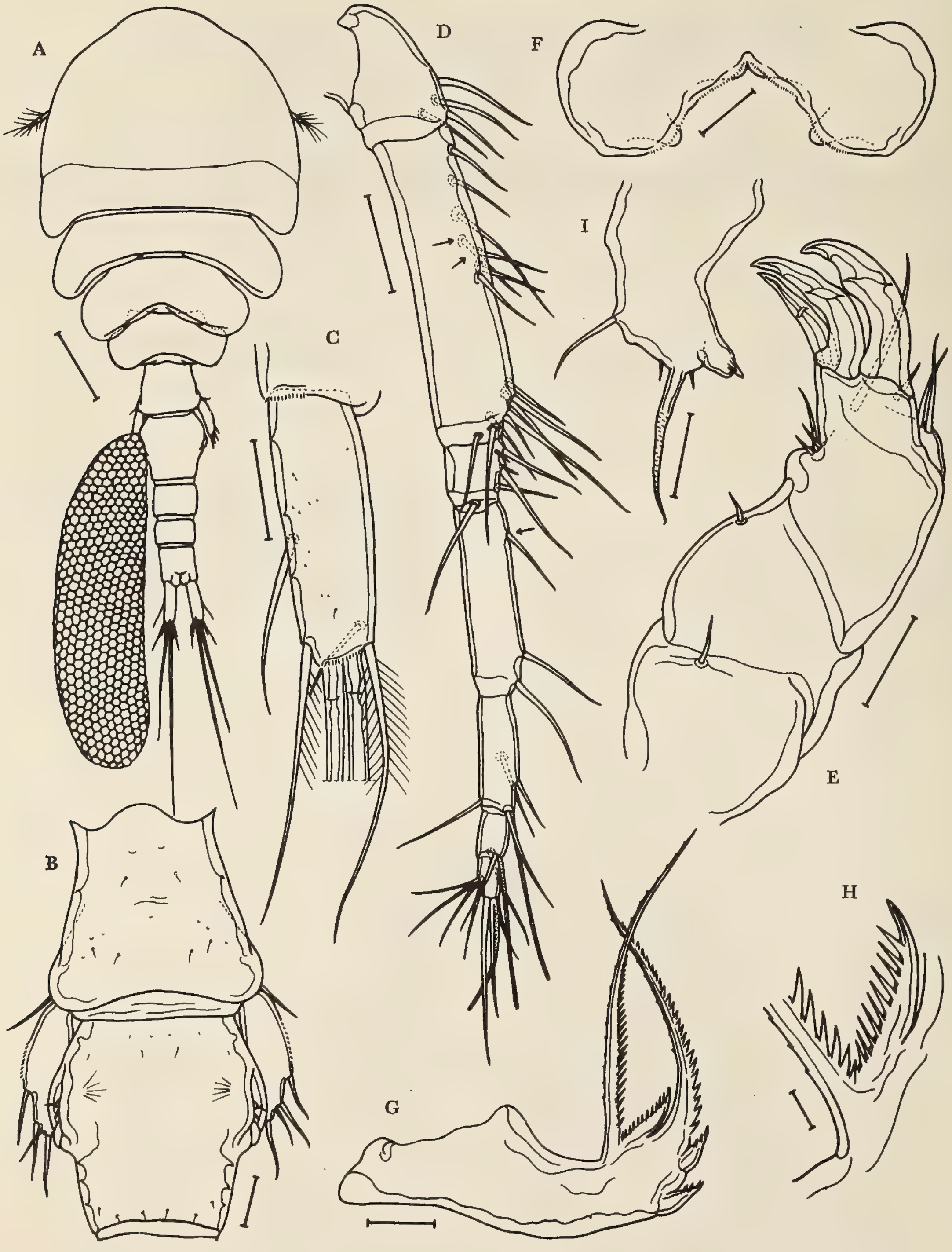

Figure 1

Anthessius ***obtusispina*** Ho, spec. nov. Female: A, habitus, dorsal; B, fifth pedigerous somite and genital somite, dorsal; C, caudal ramus, ventral; D, first antenna (arrows indicate positions of added aesthetes in the male); E, second antenna; F, labrum; G, mandible; H, dentate lamella on mandible; I, first maxilla Scale: 500 μm in A; 100 μm in B, C, D, E; 50 μm in F, G, I; 10 μm in H

Figure 2

Anthessius ***obtusispina*** Ho, spec. nov. Female: A, second maxilla; B, maxilliped; C, terminal segment of leg 1 exopod; D, leg 1 endopod; E, distal half of leg 2 endopod; F, distal half of leg 3 endopod; G, terminal segment of leg 4 exopod; H, distal half of leg 4 endopod; I, leg 5 Scale: 50μm in all drawings

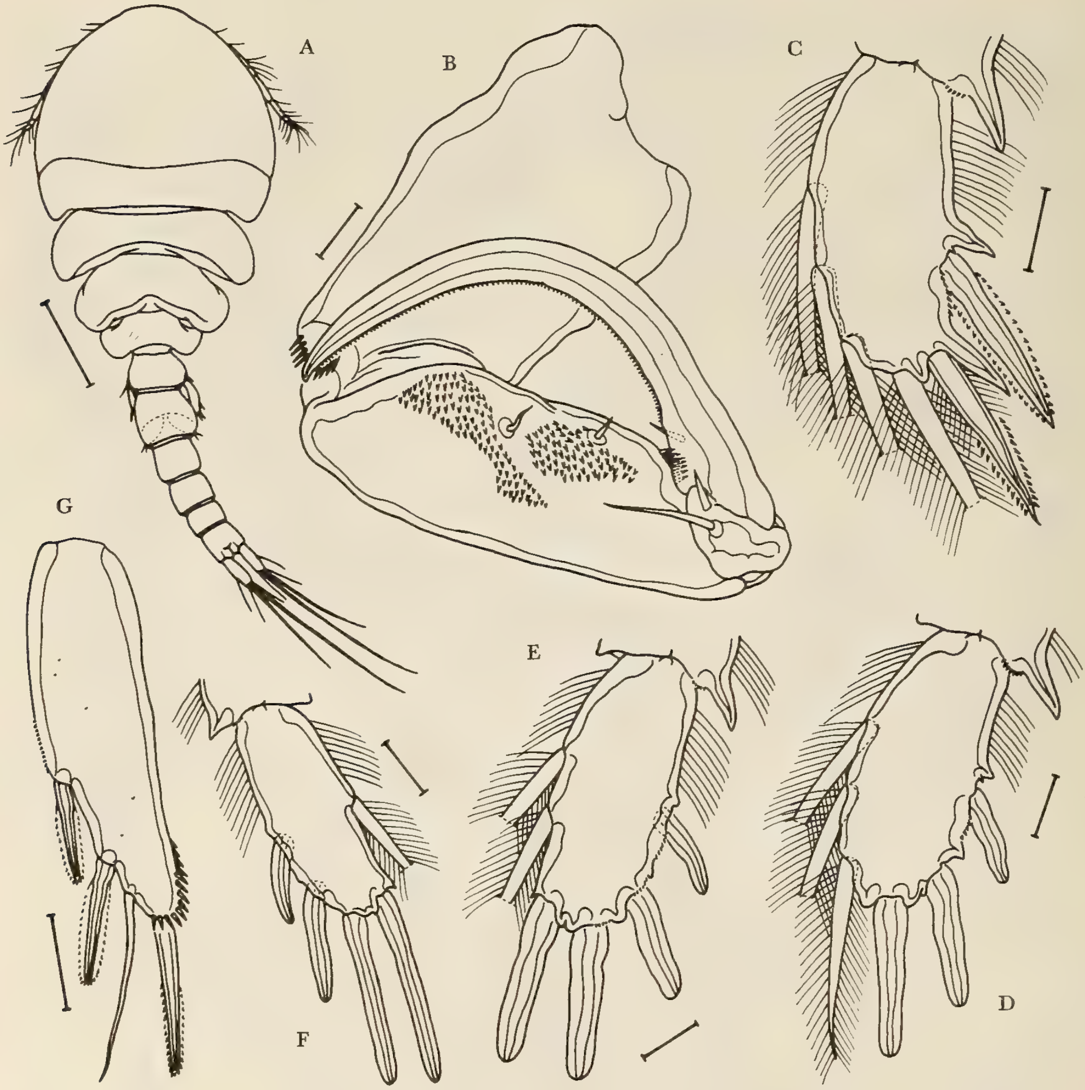

Figure 3

Anthessius obtusispina Ho, spec. nov. Male: A, habitus, dorsal; B, maxilliped; C, distal half of leg 1 endopod; D, distal half of leg 2 endopod; E, distal half of leg 3 endopod; F, distal half of leg 4 endopod; G, free segment of leg 5 Scale: 500μm in A; 50μm in B through G

(Arabic numerals) formulae on these rami are as follows:

	Exopod	Endopod
Leg 1	I-0; I-0; III,I,4	0-1; 0-1; I,5
Leg 2	I-0; I-0; III,I,5	0-1; 0-2; III,3
Leg 3	I-0; I-0; III,I,5	0-1; 0-2; IV,2
Leg 4	I-0; I-0; III,I,5	0-1; 0-2; IV,1

The free segment of leg 5 (Figure 2I) is about 2.9 times as long as wide; it is armed with 3 slender setiform spines and 1 simple seta. Leg 6 is represented by 2 small setae in the area of egg sac attachment on the genital somite.

Male: The body (Figure 3A) is only slightly smaller than the female, measuring 3.26mm long and 1.23mm wide.

The first antenna is armed slightly differently from that of the female in adding 2 aesthetes to the second segment and another aesthete to the fourth segment (indicated with an arrow in Figure 1D). The maxilliped (Figure 3B) is 4-segmented and armed as in many species of *Anthessius*. The endopod of leg 1 (Figure 3C) is armed in the terminal segment with 2 denticulate spines and 4 plumose setae. The spines on the terminal segment of the endopod of leg 2 (Figure 3D), leg 3 (Figure 3E), and leg 4 (Figure 3F) are characteristically smooth and obtuse. The spines on the free segment of leg 5 (Figure 3G) are different from those of the female in being strong and denticulate.

Etymology: The specific name ***obtusispina***, from Latin *obtusus* = blunt and *spina* = having spines, alludes to the characteristic obtuse spines on the endopod of leg 2 through leg 4 in the male.

Remarks: A close comparison with Dojiri's (1977) description of *Anthessius* sp. has led me to believe that the single male specimen found in the gill cavity of a surfperch off Huntington Beach is a member of *A.* ***obtusispina***. My belief is further supported by the fact that the natural opisthobranchiate host, *Pleurobranchaea californica* MacFarland, was on the list of gastropods that were captured in the same trawl with the surfperch that carried the copepod.

The present new species bears the closest resemblance to *Anthessius concinnus* (A. Scott), which was found in the plankton sample (2 females and 8 males) collected during the Siboga Expedition to the East Indies. When compared with A. Scott's (1909) description, the new species differs from *A. concinnus* mainly in the shape of the fifth pedigerous somite and the free segment of leg 5. Since the male of *A. concinnus* was hardly described in A. Scott's original work, it was reexamined and partially redescribed by Stock, Humes & Gooding (1963), when they reported *Anthessius* associates of West Indian invertebrates. Based on their redescription, the male of *A.* ***obtusispina*** is different from that of *A. concinnus* in the structure of leg 5.

Anthessius Associated with Notaspidea

The genus *Anthessius* was established by Della Valle (1880) based on two species of copepods that were found in Naples, Italy, in association with a pelecypod, *Solenocurtus strigillatus* (Linnaeus), and a gastropod, *Pleurobranchaea meckeli* (Blainville), respectively. He gave a rather detailed description for *A. solenocurti* but only one paragraph and three drawings for *A. pleurobrancheae*. However, he did point out that these two species were markedly different in the number of teeth on the second maxilla, while there were only four teeth in *A. solenocurti*, *A. pleurobrancheae* had more than ten.

There are now four species of *Anthessius* known to be associated with notaspidean sea slugs. In addition to the aforementioned Italian species and the above described Californian species, there are *A. hawaiiensis* (Wilson) found on *Pleurobranchus* sp. in Hawaii (Wilson, 1921; Illg, 1960) and *A. ovalipes* Stock, Humes & Gooding from *Pleurobranchus areolatus* Mitchell in the West Indies (Stock, Humes & Gooding, 1963). A comparison of the appendages of *Anthessius* has revealed that the notaspidean associates have five features in common that collectively distinguish them from the rest of the *Anthessius*. *A. concinnus* (A. Scott) should be included in this group although its host is still unknown.

The five common characteristics of these five species of *Anthessius* are: 1) a second antenna armed with three terminal spines, 2) a mandible bearing a short dentate lamella between the bases of the apical lash and the setiform element, 3) a second maxilla armed with a large number of teeth (at least ten) in the terminal process, 4) the last segment of leg 4 exopod having a formula of III,I,5 and 5) the endopods of legs 2 through 4 in the male bearing obtuse and smooth (instead of pointed and denticulate) spines. The property of mandible and the male endopods appear to be unique to these notaspidean associates. In view of the importance of the mandible in the modern taxonomy of the copepods associated with the marine invertebrates (Humes & Stock, 1973), I have thought of removing these five species from the genus *Anthessius*. However, since three of these five species are still incompletely known and the copepod associates of both *Pleurobranchaea* and *Pleurobranchus* from many parts of the world are yet to be discovered, it was concluded not to erect a new genus before more information is available for a better assessment of their character state.

It is interesting to note that two monotypic genera of Myicolidae, *Katanthessius* and *Neanthessius*, have the same kind of dentate lamella in their mandibles; *K. delamarei* Stock was found in association with *Marionia blainvillea* Risso (Nudibranchia: Tritoniidae) at Banyuls, France (Stock, 1960) and *N. renicolis* Izawa was reported from the renal sac of *Pleuroploca trapezium audouini* (Jonas) and of probably *Fusinus nigrirostratus* (Smith) (Prosobranchia: Fasciolariidae) at Seto, Japan (Izawa, 1976). However, both species are distinguishable from the notaspidean associates in the armature of the legs.

Two species of *Anthessius*, *A. pectinis* Tanaka and *A. pinctadae* Humes, are also worthy of mentioning. Both species were found in the mantle cavities of Pelecypoda (*Pecten laqueatus* Sowerby and *Pinctada margaritifera* Linnaeus, respectively) and they are, like the five species of notaspidean associates, armed with three terminal spines in the second antenna, carrying a high number of teeth (15 in *A. pectinis* and 8 in *A. pinctadae*) on the terminal process of the second maxilla, and bearing a formula of III,I,5 in the last segment of leg 4 exopod (Tanaka, 1961; Humes, 1973). Taking into consideration the fact that more than half of the known species of *Anthessius* are associated with Pelecypoda, it seems very likely that the modern myicolid copepods associated with the notaspidean sea slugs have evolved from the species of *Anthessius* or *Anthessius*-like copepods that was once associated with bivalves but succeeded in shifting its host preference to the Notaspidea. If this is really the case, then, the dentate lamella in the mandible and the transformation of spines in the male endopods are some apomorphic characters that were developed through the adaptation of life on the notaspidean sea slugs. Furthermore, *Katanthessius* and *Neanthessius* may represent two lines of further host-shifting among the copepod associates of the Notaspidea, with the former being adapted to live on the nudibranch and the latter, in the snail.

SUMMARY

A new species of poecilostomatoid copepod, ***Anthessius obtusispina,*** is described based on specimens recovered from a sea slug, *Pleurobranchaea californica* McFarland, caught at Santa Barbara, California. Five species of *Anthessius: A. concinnus* (A. Scott), *A. hawaiiensis* (Wilson), ***A. obtusispina*** Ho, *A. ovalipes* Stock, Humes & Gooding, and *A. pleurobrancheae* Della Valle, that have five characters in common, are discussed and speculated to have originated from those *Anthessius* or *Anthessius*-like copepods that were once associated with bivalves but had subsequently shifted to live on the gastropods of the Order Notaspidea.

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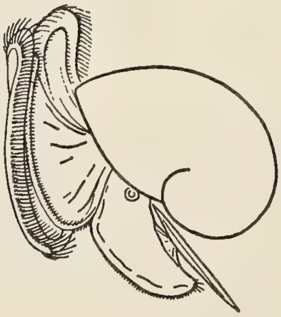

Notes on *Caledoniella montrouzieri* Souverbie, 1869 from Indonesia

(Gastropoda : Caledoniellidae)

BY

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THE MARINE GASTROPOD, *Caledoniella montrouzieri* Souverbie, 1869, which is found attached to the ventral surface of stomatopod Crustacea has been reported, *e.g.*, by PRESTON (1912 as *Epistethe gonodactyli*), HOLTHUIS (1941 as *Epistethe gonodactyli;* 1951), MANNING (1968; 1969), ROSEWATER (1969; 1975), MOOSA (1975), and REAKA (1978). The present study on this commensal gastropod is based on 13 specimens forwarded to and deposited in the Museum Zoologicum Bogoriense (MZB). One of the host specimens is deposited in MZB, while the rest are in the collection of National Institute of Oceanology (NIO). The stomatopods were collected from several localities in Indonesia by the second author.

The presence of gastropods on stomatopods is extremely rare. Table 1 shows the distribution of *Caledoniella montrouzieri* and its stomatopod host as well as their sexes and sizes. From the localities where gastropods were recorded, only 7 of 338 specimens of stomatopods are colonized. The stomatopods colonized are *Gonodactylus viridis*, *G. smithii*, *G. incipiens*, *G. mutatus*, and *G. glabrous.*

Table 1

Measurements and localities of the *Caledoniella montrouzieri* examined.

Gastropoda				Host				
Coll. No.	Height (mm)	Width (mm)	Sex	Coll. No.	Species	Length (mm)	Sex	Localities
					Gonodactylus			
MZB 7180 a	1.5	2.3	male	NIO 570-571	*mutatus*	38.36	female	Ayer Isl., Thousand Isls., off Jakarta
b	2.3	2.5	female					
MZB 7189 a	1.4	2.6	male	NIO 925	*smithii*	55.56	female	Tuhaha Bay, Saparua Isl., Moluccas
b	2.4	5.6	female					
c	1.2	1.9	male	NIO 926	*smithii*	55.74	male	
MZB 7190	1.4	2.9	male	NIO 082	*glabrous*	36.66	female	Untung Jawa Isl., Thousand Isls., off Jakarta
MZB 7192 a	0.1	1.6	male	NIO 1732-1733	*incipiens*	29.36	female	Said, Ambon Isl., Moluccas
b	1.3	3.7	female					
c	1.2	1.9	male	NIO 1734-1749	*viridis*	30.01	male	
d	1.4	3.5	female					
MZB 7395 a	1.2	2.5	male	MZB 891	*smithii*	31.23	unidentified, specimen damaged	Marsegu Isl., north of Ceram Isl., Moluccas
b	2.3	5.2	female					

MZB: Museum Zoologicum Bogoriense.
NIO: National Institute of Oceanology.

From Ayer Island, Thousand Islands, off Jakarta, only one specimen of *Gonodactylus mutatus* was found hosting two gastropods (1 male and 1 female). Stomatopods collected from this island are *Gonodactylus mutatus, G. ternatensis, G. chiragra, G. platysoma, G. smithii, Haptosquilla glytocercus, H. lenzi, Pseudosquilla ciliata, Anchisquilla fasciata,* and *Lysiosquilla maculata.* From Untung Jawa Island, Jakarta Bay, only one specimen of *G. glabrous* was found hosting one male gastropod. Stomatopods collected from this island are *G. glabrous, G. chiragra,* and *L. maculata.* From Tuhaha Bay, Saparua Island, Moluccas, two specimens of *G. smithii* were found hosting a male and a female gastropod. Stomatopods collected from this bay are *G. smithii, G. mutatus, G. platysoma, G. chiragra, G. viridis, Chirosquilla brooksii, H. glyptocercus, H. stoliura, H. hamifer, H. pulchella, Ps. ciliata,* and *Acanthosquilla multifasciata.* From off Kampong Said, Ambon Island, Moluccas, two specimens of stomatopods belonging to two species, *i.e. G. viridis* and *G. incipiens,* were found hosting male and female gastropods. Stomatopods collected from this locality are *G. viridis, G. incipiens, G. smithii, G. chiragra, G. mutatus, G. ternatensis, H. glyptocercus, C. brooksii, Ps. ciliata, Ps. megalophthalma, Ps. oxyrhyncha,* and *Parvisquilla multituberculata.* From Marsegu Island, north of Ceram, Moluccas, a specimen of *G. smithii* was found hosting a male and a female gastropod. Stomatopods collected from this locality are *G. chiragra, G. viridis, G. smithii, C. brooksii, Ps. ornata,* and *Mesacturoides spinosocarinatus.*

The male of this commensal gastropod is found attaching to the ventral part of the thoracic somites of the host, while the female is found on the ventral surface of the abdominal somites. This condition was also reported before. As was the case of Rosewater (1969), the search for radulae was unsuccessful.

All the above specimens agree with the description of *Caledoniella montrouzieri* made by previous authors, except for one abnormal female specimen (MZB-7180b). It has a sinistral shell with depressed spire, the first and second whorls are covered by the last whorl which narrows toward the base, and the aperture is ovate-elongate.

In this gastropod, the capsules containing egg masses are found attached to the pleopods of stomatopods. From the material examined, 20-57 capsules were found on one stomatopod each containing 55-79 eggs of nearly all stages of development.

It appears that *Caledoniella montrouzieri* is particularly attached to species of the *Gonodactylus chiragra*-group and *G. falcatus* group. So far only 7 species of stomatopods, all belonging to the genus *Gonodactylus,* are known to host *Caledoniella montrouzieri, i.e., Gonodactylus chiragra, G. platysoma, G. falcatus, G. smithii, G. viridis, G. mutatus,* and *G. paulus* (Preston, 1912; Holthuis, 1941, 1951; Manning, 1968, 1969; Moosa, 1975; Rosewater, 1975; Reaka, 1978). Manning (1968) revised the *Gonodactylus falcatus*-group; this suggests that the older identifications of species belonging to this group should be reviewed. In his revision, Manning (1968) stated that the distribution of *Gonodactylus falcatus* for certainty is the Red Sea. In re-examining his material the second author found that his material from Ayer Island belongs to *Gonodactylus mutatus* and *G. ternatensis* and that hosting the gastropod is *G. mutatus;* the material from Untung Jawa Island belongs to *G. glabrous.* The record of Holthuis (1941) also needs further confirmation, since at the time of his publication *Gonodactylus viridis* was not yet established. The present record added three new additional hosts of *Caledoniella montrouzieri, i.e., Gonodactylus mutatus, G. glabrous,* and *G. incipiens.* The first two species belong to the *Gonodactylus falcatus*-group and the third belongs to the *Gonodactylus chiragra*-group together with *G. smithii* and *G. platysoma.*

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NOTES & NEWS

First Record of *Littorina punctata* (Gmelin, 1791)

(Gastropoda: Prosobranchia)

on the Island of Mallorca (Spain)

BY

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(2 Text figures)

On August 5, 1978, during collecting 2700 specimens of littorines and the observation of many more *in situ* along the coast of the island of Mallorca (Western Mediterranean), where *Littorina neritoides* is very common, five living specimens of *L. punctata* were found in the Bay of Palma. This bay is between the Cala Gamba and the Cala Estancia. In a later collection at the same place (June 30, 1981), 11 additional specimens were found. Adjacent areas were thoroughly explored, without success. This indicates that the population of *L. punctata,* although very limited, is well established.

These animals showed the characteristic features of the species, separating them clearly from other littorine species.

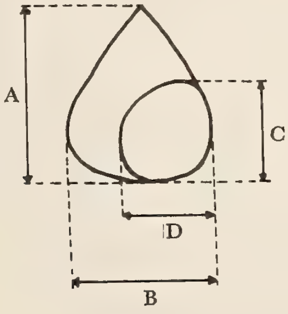

Figure 1

The four dimensions indicated in Figure 1, varied as follows:

Material of August 5, 1978 (N = 5)

A — 7.90mm to 10.30mm; mean 8.88mm
B — 5.55mm to 7.40mm; mean 6.33mm
C — 5.00mm to 6.35mm; mean 5.33mm
D — 3.90mm to 5.00mm; mean 4.19mm

Material of June 30, 1981 (N = 11)

A — 6.50mm to 11.25mm; mean 9.17mm
B — 4.55mm to 8.00mm; mean 6.57mm
C — 3.70mm to 6.60mm; mean 5.31mm
D — 3.05mm to 4.95mm; mean 4.10mm

If the size of these specimens is compared with that of the material of Palant & Fishelson (1968) it appears that the specimens from Mallorca are fully developed and sexually mature. Palant & Fishelson recognize three size groups: large (7.5 to 13mm); medium (5 to 7.5mm) and small (< 5mm). The present specimens belong in the first of these groups.

Distribution: This is a common species on the warmer coasts of the Mediterranean Sea, especially in Israel, North Africa and South Sicily. Rosewater (1970; 1981) states that the range of this species is quite extensive from the Mediterranean to South Africa via West Africa. Bandel (1974) reports this species from the W of Jandia Peninsula (Lanzarote Id., Canary Ilds.) and Nordsiek & Garcia-Talavera (1979) state that the forms from Lanzarote Id. are larger than those of the Mediterranean region.

Locality: The exact locality where the specimens reported on here were found is the center of the Bay of Palma, between Cala Gamba and Cala Estancia, between the places locally known as "Es Carnatge" and "La Pineda" (Figure 2). It is a rocky shore of calcareous Upper Quaternary marine littoral formation (Cuerda, 1975). The *Littorina punctata* specimens were found in pools about 2.5mm from the water's edge and about 0.7m above water level among many specimens of *L. neritoides.*

DISCUSSION

The distribution of *Littorina punctata* overlaps that of *L. neritoides;* the latter is always more abundant than the former. *Littorina punctata* is present in warmer areas while *L. neritoides* extends farther to the north.

Cuerda (1975) reports *Littorina punctata* as a fossil in the Upper Quaternary of the Balearic Islands with other

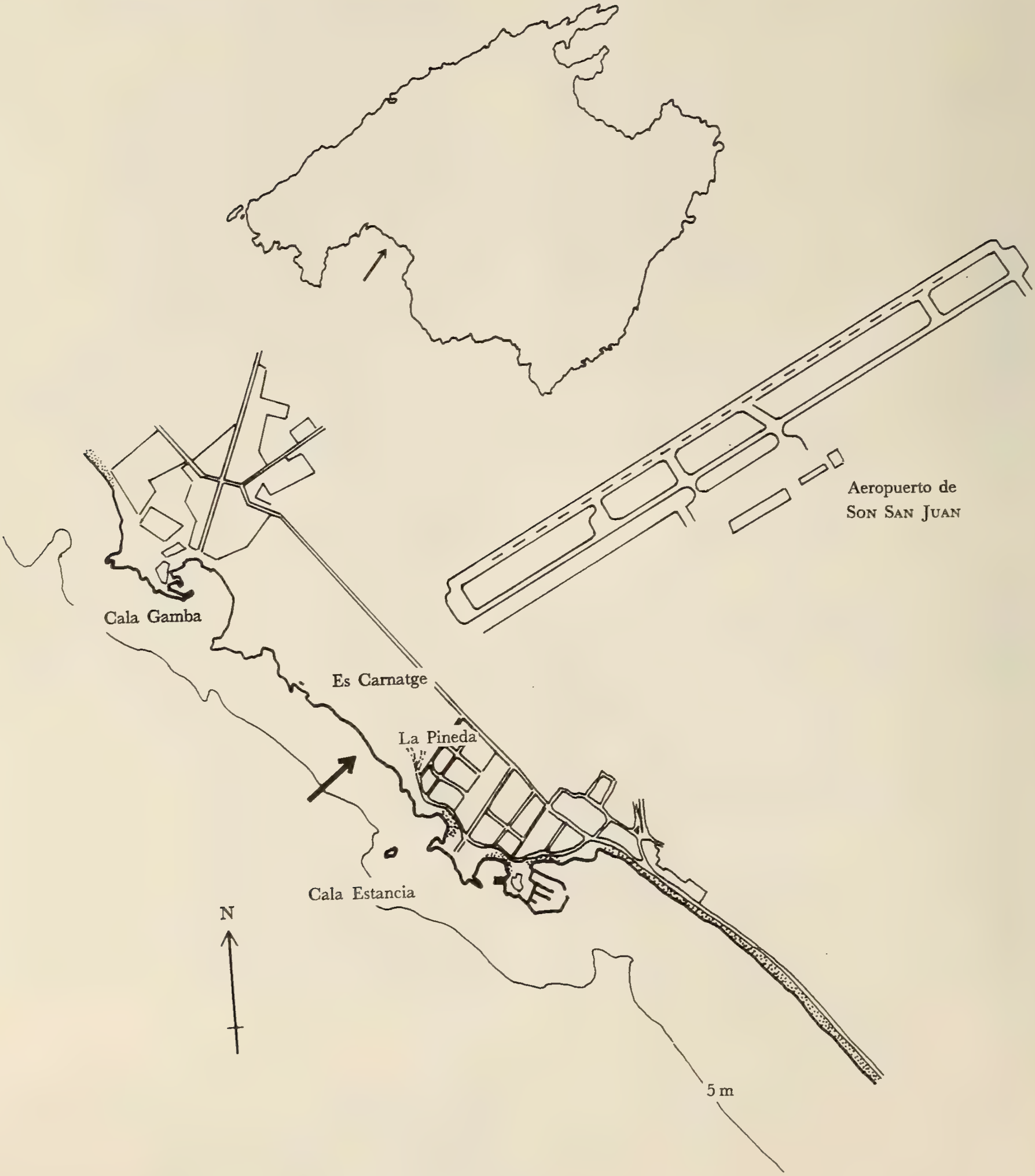
Aeropuerto de
Son San Juan
Cala Gamba
Es Carnatge
La Pineda
Cala Estancia
N
5 m

Figure 2

species of warmer waters than those in the present Mediterranean. It is assumed that *L. punctata* has undergone a biogeographical regression in the Mediterranean Sea with the Bay of Palma and Valencia in Spain being its northern limit.

SUMMARY

Sixteen specimens of *Littorina punctata* are recorded from the coast of Mallorca. The ranges of measurement are given; the locality where the specimens were found is described.

ACKNOWLEDGMENTS

The authors thank Dr. Joseph Rosewater of the U.S. National Museum of Natural History for valuable information and suggestions.

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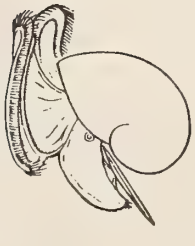

On the Sponge-Diet of *Archidoris pseudargus* (Rapp, 1827)

BY

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Archidoris pseudargus IS AN OFTEN MENTIONED example of a dorid sponge-eating nudibranch (Doridacea, Archidorididae), and several investigators have established the main diet to be the bread-crumb sponge, *Halichondria panicea* (Forrest, 1953; Miller, 1961; Swennen, 1961; Thompson, 1964; Carefoot, 1967; Todd, 1981). A number of other sponge species have, however, occasionally been reported to be eaten by *A. pseudargus* in certain localities, *viz. Grantia compressa, Tethya aurantia, Hymeniacidon perleve, Mycale aegagrophila,* and *Myxilla incrustans.*

Archidoris pseudargus and *Halichondria panicea* are intertidal to upper subtidal species, and all localities mentioned for the snail are within the very large geographical distribution area of the sponge. The former is quite often, however, found at greater depths, down to about 300m, while the latter is generally found no deeper than about 20m, the deepest certain record being about 110m.

To get an impression if *Archidoris pseudargus* changes to another main diet at depth, we dissected out the stomach-caecum from 20 specimens and investigated the contents for sponge spicules. The specimens, which were selected from the collections of the Zoological Museum, Copenhagen, originated from localities scattered from Iceland, the Faroes, Norway and southwards to Plymouth, and which covered a depth range from 20 to 280m.

Of the 20 specimens, 5 contained a little fine-grained unidentifiable matter, or they were empty. Of the other 15, 11 contained spicules from one species, 3 contained spicules from 2 species, and 1 contained spicules from 3 species of sponges. *Halichondria* spicules (which could not be identified to species) were found in 6 specimens. *Suberites ficus* or *S. luetkeni* were found in 5 specimens (the two are very closely related, but could be distinguished), while *Leucosolenia* sp., *Tethya aurantia, Corybas (Mycale) ovulum, Myxilla rosacea, Myxilla* sp., *Lissodendoryx* sp. (?), *Jophon piceus,* and *Hymedesmia* sp. (?) were found in one case each.

We got no clear answer to our initial question, but despite the smallness of the investigated material, two trends can be outlined. One is a further confirmation of the observation that *Archidoris pseudargus* at subtidal depths feeds on other sponge species than *Halichondria panicea;* this is underlined by the fact that the list of known food-species can be augmented from 6 to at least 15, and it should be added that the deep records of *Halichondria* were other species than *H. panicea,* and that scattered spicules belonging to species that could not be identified to more than order were found in some cases. With respect to feeding biology, *A. pseudargus* might thus be characterized as *Halichondria* "specialist" at intertidal and upper subtidal depths, and as sponge "opportunist" in the deeper subtidal. Another trend is that Bloom's results (1976,1981) seem to be corroborated. One of his conclusions is that dorid species with caecum and relatively weak radula feed on sponge-species with a rather loose skeleton. Most *Halichondria* species are characterized by such a skeleton, and so are the two *Suberites* species found, and the *Leucosolenia* sp.

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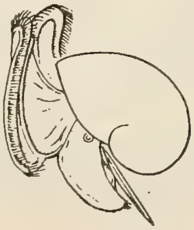

CORRECTION

The Veliger 25(2): 139-148

Lucina s.s. (Mollusca: Bivalvia) in the Western Atlantic:
A Reappraisal
by J. Gibson-Smith and W. Gibson-Smith.

In the text, the authors of the three new taxa ***Lucina (Lucina) caymanana*** (p. 143), ***L. (L.) roquesana*** (p. 143) and ***L. (L.) belizana*** (p. 144) are wrongly given as Gibson & Gibson, instead of Gibson-Smith & Gibson-Smith.

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per volume-year (July 1 to April 1). This means that the "dues" will increase a minimal 25¢ to $18.75. On the other hand, the Society is forced to increase the mailing charges for members and subscribers to $3.25 for all domestic address and to $6.00 for all foreign addresses (including Canada and Mexico). The initiation fee for new members remains at US$2.00; the reinstatement fee, due if membership renewals are not made to reach the Society on or before April 1 preceding the start of the new volume will also remain at US$1.00. Reinstatement is not possible if application is not made within 11 months after original renewal was due. A new application for membership and the payment of a new initiation fee will be required.

Similarly, the need to include a self-addressed, stamped envelope or (in the case of foreign members) the envelope and two International Postal Reply Coupons, was reaffirmed.

In view of the deplorable fact that the postal services throughout the world seem to become ever more expensive and also more unreliable, members are urged to lodge complaints for intolerable delays in deliveries of their journals with their local postmasters. Most likely, this will not result in better service, at least not immediately, but it may be hoped that in the long run it will lead to some improvement. Complaints to the Society cannot lead to any improvement, since we already do more than the requirements of the postal service in respect to second class mailings stipulate.

The NINE DIGIT ZIP code . . . .

is coming! And although the Postmaster General keeps asserting that its use is entirely voluntary, there are certain consequences to be anticipated if it is not used. One consequence which will affect us directly is the fact that "addressed pieces with the 9 digit code" will be entitled to a discount (this applies to bulk mailings, such as the quarterly dispatch of our journal). In other words, if the code is not used, we have to pay what really amounts to a penalty. Another consequence, which will undoubtedly apply to all mail, will be the fact that "properly coded mail" can be handled more expeditiously. The implication seems to be that those pieces that do not have the new zip code may be subject to delays in delivery.

For these reasons we earnestly ask all our subscribers and members to inform us as early as possible of their correct new zip. Since our mailing list is not on a scale as large as those of the various news weeklys, we cannot take advantage of the computer tapes that the Postal Service has prepared and will lend to the volume mailers. We will, of course, endeavor to obtain the correct codes; but we would prefer not to have to spend hours on the telephone obtaining the numbers in that way.

That the Postal Service leaves much to be desired, not only in the United States, but abroad as well, was brought home to us with the delivery of our January issue. Second class mailing requirements make it necessary for us to tie securely the various copies of a particular issue going to a particular country in a bundle with a label of the country of destination. Thus, for example, all copies going to Japan will be tied together (in the case of certain countries we have a sufficiently large number of copies to make several bundles and combine them into a "direct sack"). Yet some individuals in each of the "direct sack"-countries received their copies from several weeks to 2 months later than others. We have, of course and unfortunately, no control over these vagaries of the postal services. Our complaints have no effect whatever.

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